Oculomotor Unit Behavior in the Monkey

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PAST STUDIES of single-unit behavior in the motor nuclei of the extraocular muscles have been few in number and have used such preparations as the anesthetized cat (26) or rabbit (22), or the paralyzed guinea pig (16). None of these preparations make many spontaneous eye movements, which must therefore be evoked by some form of vestibular stimulation. To obtain information on oculomotor neuron behavior more pertinent to man and associated with visual rather than vestibular stimuli, we undertook to record from single units, believed to be motoneurons, in the oculomotor nucleus of the intact, alert monkey. The eye movements of monkeys are similar to those of man both in their temporal patterns (12) and in their range of excursion ($\pm$ 50 deg horizontally) so that it is likely that the relationship between eye movements and the discharge patterns of ocular motoneurons in man and monkey will also be similar. The use of an alert, intact animal results in a great variety of spontaneous and optically driven saccadic and smooth pursuit eye movements. In this study these movements were accurately recorded and a relation was sought between motoneuron discharge rate and eye position and motion.

Eye movements are quite stereotyped in nature (9, 20). This may come about because the extraocular muscles, unlike most skeletal muscles, deal with the same mechanical load throughout life. Since motoneuron discharge rate is translated into muscle force and then into eye movement in a fairly simple way, one might anticipate that the stereotyped nature of the movements would be reflected in similar patterns of discharge rate, and the results indicate that this is the case.

METHODS

Recordings were made from three 6- to 7-lb. rhesus monkeys. They were chronically prepared, under pentobarbital sodium anesthesia, with four implanted devices. *1*) A coil of wire was implanted on one globe. When used in conjunction with magnetic fields, this provides a method, previously described (13), of recording vertical and horizontal eye rotation with a sensitivity of 15 min of arc and a bandwidth of 2 kHz. *2*) Stimulating electrodes were stereotaxically implanted on the third nerves where they pass over the clinoid processes. *3*) A chamber was implanted on the skull through which tungsten microelectrodes could be advanced by an eccentric hydraulic drive system modified from the type used by Evarts (10). The dura was left intact and the electrode was passed through it within a guard tube. *4*) A metal crown was bolted to the skull so that the animal's head could be immobilized during recording sessions. The animals were supported postoperatively by chloramphenicol and penicillin.

After a 3- or 4-day postoperative recovery period the eye coil was calibrated by rotating the animal's implanted eye, by a suction contact lens, through known horizontal and vertical angles while the monkey was under sedation (phencyclidine hydrochloride). After calibration, whenever the animal's head was immobilized for single-unit recording, the exact angle of the animal's visual axis with respect to its head was known at all times. Fixation, saccades, and pursuit movements were spontaneous on the part of the monkey in looking about the laboratory or following objects held in the hand or seen reflected in a rotating mirror. It was unnecessary to train the animals to make eye movements since attracting their attention with or without a rotating mirror easily and quickly produced fixation (the interval between saccades when the visual axis is stationary) in all parts of the visual field, saccades of many sizes in many directions from many initial positions and pursuit movements of different

velocities and directions in different parts of the visual field. Horizontal and vertical eye position and single-unit discharges were displayed on a dual-beam oscilloscope and recorded on magnetic tape. For analysis the data were transferred to recorder paper by an ultraviolet galvanometer recorder to produce records similar to the samples shown in Fig. 1. The overall system bandwidth was 2 kHz. Of principal interest in this study was the mean discharge rate associated with an eye position or an estimate of instantaneous discharge rate associated with a movement. Discharge rate in impulses per second is designated dimensionally in the text and figures by reciprocal seconds (1/sec). The time intervals used to estimate the mean rate depended on the speed of the movement and are described with the results.

Electrolytic lesions were made at sacrifice so that electrode tip locations could be confirmed by histological examination. Two additional methods were used to establish that the electrode tip was in the third nucleus. The first utilized the fact that in the nucleus the background activity became intense and clearly related to eye movement. The presence of many units firing at very regular rates up to 300/sec during fixation and 600/sec during saccades, and whose number and rates were modulated with eye movements only in a certain direction, created on the audio monitor, a singing beehive sound, unique to this structure. This distinctive sound was unlike that in any nearby structures including such eye-related areas as the nucleus of Darkschewitsch, the interstitial nucleus of Cajal, and the medial longitudinal fasciculus. The second method was by antidromic stimulation. The antidromic volley reached the nucleus so highly synchronized that this method could not be used to identify individual motoneurons but the massed response could be used to map out the location of the nucleus. The two methods agreed and the audio-monitor method was used routinely in deciding which isolated units were considered to be intranuclear.

RESULTS

General

As the electrode moved down through the nucleus in a coronal plane, it encountered cell groups whose activity correlated first with movements down, then up, and finally to the left or right. These units are believed to have been motoneurons of the inferior recti, then of the inferior obliques and superior recti in adjacent groups and, most ventrally, of the medial recti. Within any group the activity of the background units all correlated with the same gaze direction. The boundary between muscle regions was usually fairly sharp (e.g., 200 μ). This result supports the conclusion that the motoneurons of the four extraocular muscles are for the most part unmixed and lie in rostral-caudal columns in the arrangement given by Warwick (25). The belief that the units studied were motoneurons rests partly on Warwick's finding, by a degeneration study (25), that there are few interneurons in the nucleus and partly on the fact that, as will be shown, the discharge patterns of the units were all similarly related to eye movements. During the experiments, hundreds of poorly isolated units or small groups of units in the nucleus were observed which, although unsuitable for analysis, gave additional indication that the units isolated behaved in a manner representative of the majority of neurons in the nucleus.

The following analysis is based on 35 units isolated within the nucleus. Although the activity of the units correlated with different movement directions (12 up, 10 down, and 13 left or right) no difference other than direction was found in the way in which activity was related to eye movement. Consequently the data were pooled and the relationship between unit activity and eye movement in the direction of action of the muscle of which the unit was presumably a motoneuron was analyzed regardless of the direction involved. For simplicity, the direction of action of each muscle or motoneuron group (up, down, left, or right) was called the on-direction and the opposite direction, the off-direction. Figure 1 illustrates behavior typical of all units. The principal features, to be analyzed subsequently in greater detail, are as follows. For each position of gaze the discharge rate was fairly constant. As the eye assumed positions progressively farther in the on-direction (down in this case) the higher the discharge rate became. Conversely, the rate decreased as the eye position shifted in the off-direction. The discharge rate increased in a burst during saccades in the on-direction and the unit was inhibited during saccades in the opposite direction. The saccadic behavior of the discharge rate
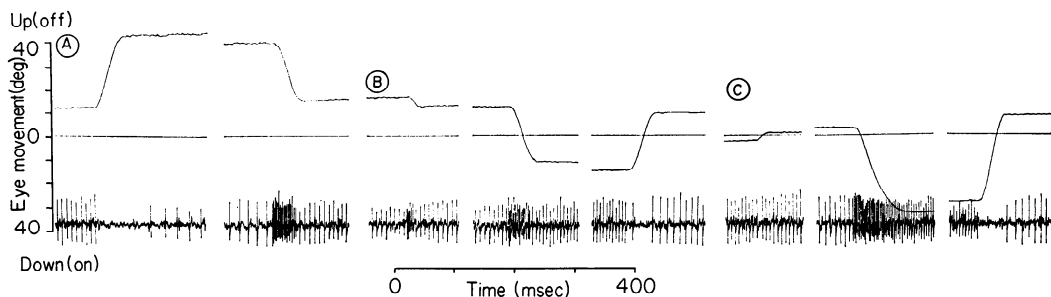
FIG. 1. Behavior typical of the discharge activity of single units (lower trace) in the oculomotor nucleus of the intact, alert monkey during fixation and saccadic eye movements (upper trace). The sections were selected from a continuous recording of the activity of a unit associated with downward movements and thought to be a motoneuron of the inferior rectus muscle.

was pronounced even for small 2- and 5-deg saccades, as shown in Fig. 1.

Several units were isolated dorsal to the nucleus whose activity was related to eye movements but was clearly not motor in character. Five additional units believed to be within the nucleus were isolated. One was uncorrelated with eye movements, two seemed involved in the near response, one was inhibited during saccades in all directions and another exhibited a burst of activity during saccades but the burst did not precede the movement. These discharge patterns did not seem to be motor in nature and the units were not included in the subsequent analysis.

Position behavior

When a monkey looked about the laboratory its eye movements consisted of rapid saccades followed by fixation intervals (Fig. 1) during which the eye was stationary (if the object being looked at was stationary). These intersaccadic fixation intervals were almost never shorter than 200 msec and 0.5–1.0 sec was usual. By placing interesting objects in the animal's visual field it was simple to rapidly obtain many samples of fixation angles over the whole range of possible eye positions. As Fig. 1 suggests, at each angle of fixation the discharge rate was fairly constant. Four interval histograms were constructed, each based on 50 successive interspike intervals; three for one unit for three different gaze angles, one for another unit. The standard deviations of the histograms, expressed as a percentage of the mean, were 6.0, 6.4, 6.5, and 13.2 %. This regularity of firing gave a distinct

tonal character to the activity heard on the audio monitor and was a characteristic feature of all the units. The mean discharge rate was measured for many different fixation angles (usually 20) spread as evenly as possible over the range of ocular motility in the on- and off-directions by counting the number of interspike intervals (including fractional intervals) in a 100-msec time bin. Since mean rates varied roughly between 50 and 300/sec the mean was estimated on from 5 to 30 intervals. This was considered adequate because of the regularity of firing. Lower rates were usually estimated from a 200-msec time bin to improve accuracy.

When discharge rate is plotted against fixation angle, the points lie approximately on a straight line as shown by the data points and the line in Fig. 2A marked by an arrow. An analysis of two units for which 32 and 28 points were taken indicated that 80 % of the points fell within $\pm$ 7.5 impulses/sec from a straight line drawn by eye through the data. Since most units had a discharge rate in excess of 200/sec for fixation well in the on-direction, this variability amounted to less than 4 % of the full-scale fixation discharge rate. This degree of reproducibility between discharge rate and eye position made more precise methods of describing the relationship unnecessary. Figure 2A shows the discharge rate-position relationship of a sample of the 35 units analyzed in this way to illustrate the variety of slopes and intercepts found. The intercept, or eye position at which the unit was recruited into activity, was called the threshold. Some units never stopped firing even for extreme gaze in the off-
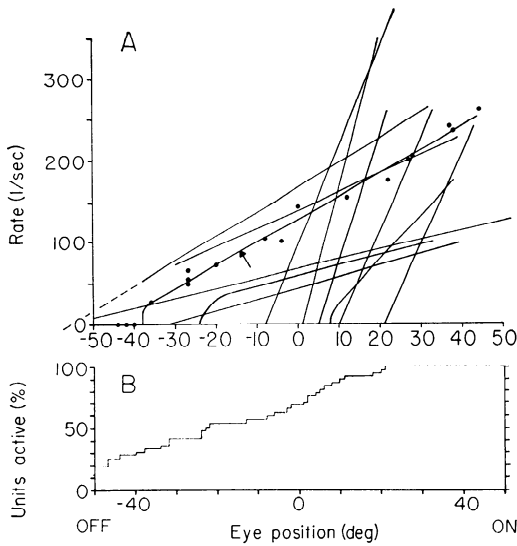
FIG. 2. *A:* relationship between discharge rate (ordinate) in impulses/sec (dimensions 1/sec) and eye position during steady fixation for a selection of units to show a variety of slopes and thresholds. Data points are shown for one curve marked by arrow to indicate the typical nature of the fit between the data and the straight-line approximation. *B:* percentage of units active out of the pooled population of 35 units during fixation at any angle of gaze. The on-direction could be either up, down, left, or right depending on which extraocular muscle was associated with the unit under study.

direction. Their thresholds were estimated by extrapolation as shown by the dashed line on the left in Fig. 2*A*. Thresholds ranged from −62 to +21 deg. Figure 2*B* shows the way in which the percentage of active units (the 35 units considered as a single population) would grow as the eye position moved in the on-direction. The distribution of thresholds appeared to be roughly uniform over the range. The absence of thresholds above 21 deg suggests that beyond this point muscle force must have increased by increasing discharge rate alone rather than further recruitment. A straight line approximation to the cumulative threshold distribution curve of Fig. 2*B* suggests that 11 % of the motoneuron population is recruited for each 10-deg change in eye position in the on-direction.

The slopes, *k*, of the discharge rate-position relationship (Fig. 2*A*) ranged from 1.25 to 27 (1/sec)/deg. There was a general trend, indicated in Fig. 2*A*, for low-threshold units to have lower slopes than high-

threshold units. Extraocular muscle motoneurons are known for their high discharge rates and, as shown in Fig. 2*A*, 200 to 300/sec was usual when the eye was well deviated in the on-direction.

Pursuit velocity behavior

All units participated in following movements by increasing or decreasing their discharge rates smoothly. For each eye position the discharge rate was greater or less than the fixation rate at that position by an amount proportional to the eye velocity in the on- or off-direction as illustrated in Fig. 3. The instantaneous discharge rate was estimated by finding the point in time when the eye passed through a certain position (always the same position for each rate-velocity analysis for any one unit) and measuring the mean rate based on the six interspike intervals which most closely sym-
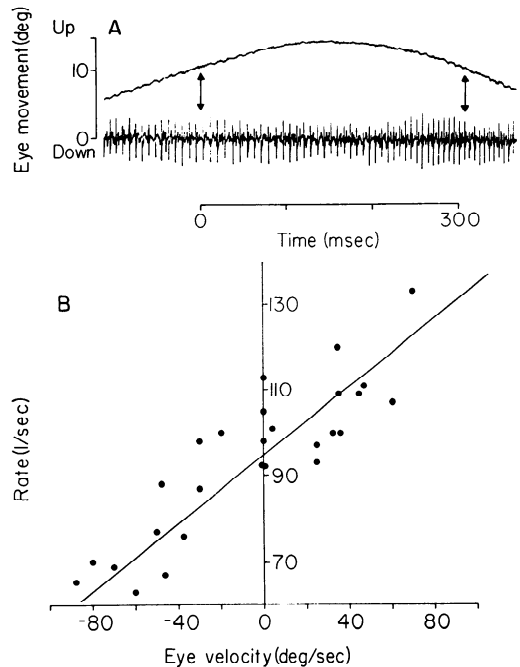

FIG. 3. Relationship between discharge rate and pursuit eye velocity. *A:* at each arrow the eye position was up 10 deg. The fixation discharge rate there was 130/sec but the rate was only 86/sec when the eye was traveling in the off-direction at 38 deg/sec (left) and was 167/sec when traveling in the opposite direction at 49 deg/sec (right). *B:* discharge rate of another unit plotted against pursuit velocity at instants when the eye passed through a given position going in the on-direction (+) or off-direction (−).

metrically bracketed that point in time. At a typical rate of 100/sec, the time bin involved would be 60 msec and smooth pursuit eye velocity departed little from the mean eye velocity, estimated by drawing a tangent to the eye position trace, in so small an interval. Position changes across the time bin cancelled since rate varied linearly with eye position so that short intervals on one side of the point in time of interest were compensated for by long intervals on the other side. The regularity with which the units discharged and the smooth modulation of discharge rate with changes in eye position illustrated in Fig. 3A make it likely that this method gives a reliable estimate of instantaneous discharge rate. Data points for such an analysis are shown in Fig. 3B. A straight-line approximation of the data was drawn by eye. The slope of the line was designated by r (impulses/sec)/ (deg/sec). Although all units showed discharge rate changes associated with pursuit eye velocity, sufficient data (pursuit movements near a common position) were available to determine r for only 10 units and the values of k and r determined for them are shown in Table 1.

Since the rate of each unit depended linearly on both eye position, θ, and velocity, $d\theta/dt$, over a reasonable range,

TABLE 1. *Slope of discharge rate relationship to eye position, k, and eye velocity, r, for 10 oculomotor units arranged in increasing values of k**

Unit	$\dfrac{k}{(1/\text{sec})}{\text{deg}}$	$\dfrac{r}{(1/\text{sec})}{(\text{deg/sec})}$	$T = \dfrac{r}{k}$ (msec)	Threshold (deg)
1	2.56	0.35	136	−38
2	2.70	0.275	102	−32
3	2.75	0.90	327	−56
4	2.85	0.294	103	−40
5	3.00	0.40	133	−34
6	3.35	1.0	299	−3
7	3.65	0.52	142	−47
8	11.0	1.9	173	+10
9	13.5	4.0	370	+20
10	25.0	5.0	200	+11
Mean			198	
Range	10:1	18:1	3.6:1	

* Dimensions of these parameters are given in parentheses. Their ratio has the dimensions of time and is believed to be related to the time constant of the mechanical load.

then (except for a constant) a first-order approximation of the discharge rate D is

$$D = k\theta + r\, d\theta/dt \qquad (1)$$

The relationship between net muscle force F and globe rotation can be approximated by a similar differential equation,

$$F = K\theta + R\, d\theta/dt \qquad (2)$$

where K is an elastic and R a viscous coefficient whose ratio R/K is the time constant T of the mechanical load. With the supposition that changes in discharge rate, D, are the cause of changes in muscle force, F, equations 1 and 2 might be considered as restatements of each other. In this light, k reflects the muscle force requirements to overcome elastic forces, K, and r the force requirements to overcome viscous forces, R. Although the parameters k and r are numerically and dimensionally quite different from K and R and show great variability from one unit to another (Table 1), their ratio r/k is a time constant and one may expect that this ratio is determined by, and should be equal to, the mechanical time constant. Table 1 suggests that this is the case. Despite wide ranges in k and r, their ratio T varied over a range less than 4:1. The mean value for T, 198 msec, is in fair agreement with the time constant of the load determined mechanically (see DISCUSSION).

Saccadic behavior

All the units modulated their discharge rates not only for pursuit movements but for saccadic movements as well. If the discharge rate change was proportional to eye velocity as suggested by *equation 1*, then one might expect very large discharge rate changes during saccades when eye velocities reach very high values (typically 600 deg/sec for man, 1,000 deg/sec for monkey). That this was so is already indicated in Fig. 1. Figure 4 shows the instantaneous rate (reciprocal of interspike interval) during typical saccades in the on- and off-directions for two units with different thresholds. There was more variability in interspike interval during a saccade than during fixation but there seemed to be no consistent trend of interval length during the movement. Consequently the mean rate during the saccade was used
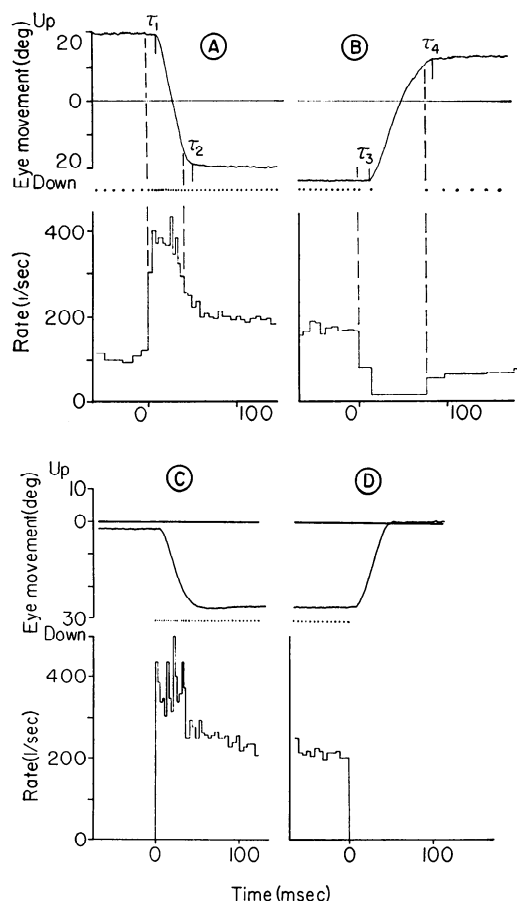
FIG. 4. The instantaneous rate or reciprocal of interspike interval (lower curves) of two units during saccades (upper traces) in the on-direction (*A*, *C*) and off-direction (*B*, *D*). One unit (*C*, *D*) had a high threshold and did not discharge near the primary position. The intervals τ in *A* and *B* indicate the times by which unit activity changes preceded the start and finish of eye movement for saccades in both directions.

as a measure of saccadic unit discharge rate behavior. This mean rate was based on the intervals that lay between the abrupt changes in rate associated with the beginning and end of each saccade. These changes are clearly seen in Fig. 4*C*, which was typical of most units. When there was any doubt about which intervals to include in the estimate, as is the case in Fig. 4*A*, especially at the end of the saccade, the intervals near the start and finish of the saccade were excluded. Since a common discharge rate during saccades in the on-direction was 400/sec and saccades had a typical duration of 30 msec, the mean rate

was usually based on the mean of 12 interspike intervals. The mean saccadic discharge rate was called the burst rate, for short.

Burst rate varied with saccadic velocity. This was studied by selecting a group of saccades of various sizes in the on-direction, which crossed a given position about halfway through the movement, and by utilizing the fact that saccades of different sizes have different peak velocities (12). The results of such an analysis are shown for five units in Fig. 5*A*. Data points are shown for unit 5 (Table 1) to illustrate the considerable scatter. The curve through these points was drawn by eye. Data points for the other curves are omitted for clarity. Figure 5*A* also shows, for comparison, the discharge rate-velocity relationships for smooth pursuit velocities for the same five units determined at the same positions used in measuring saccadic velocities. Pursuit velocities seldom exceed 100 deg/sec and saccadic velocities are seldom less than 200 deg/sec so that the curves in Fig. 5*A* fall into regions, pursuit and saccadic, connected in the figure by dashed lines. Figure 5*A* shows that burst rate and saccadic velocity increased together but not in a simple way. Four of the five units showed a
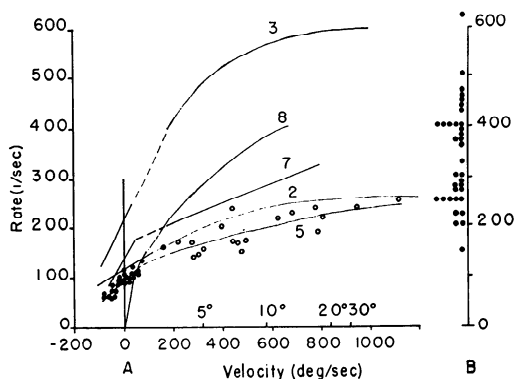

FIG. 5. *A*: relationship between unit discharge rate and eye velocity for five units listed in Table 1 over the entire range of pursuit (0–50 deg/sec) and saccadic (200–1,200 deg/sec) eye velocities in the on-direction. For each unit, discharge rates were always measured at a given eye position. For clarity, and to illustrate scatter typical of all five units, data points for pursuit (●) and saccadic (O) velocities are shown only for unit 5. Figures just above the abscissa indicate the sizes of saccades found to be associated with various eye velocities (12). *B*: distribution of maximum burst rates for all units studied.

trend toward saturation, i.e., a velocity region in which burst rate failed to increase further. There is some indication that units for which r was a large value also showed larger changes in discharge rate with changes in saccadic velocity than units with smaller r values. The discharge rate for low saccadic velocities was never lower than the highest observed rate for pursuit velocities but the slope of the curves in the pursuit region were always higher than the slope in the region of low saccadic velocities. Consequently, for some of the units the pursuit and saccadic portions of the curves appeared to be separate parts of a single smooth curve but for others, notably number 7, a sharp break appeared between the two regions suggesting that discharge rate and eye velocity bore different relationships, depending on whether the velocity came about in a pursuit movement or a saccade.

As an estimate of the maximum discharge rate of which the unit might be capable, each record was searched for very large saccades (e.g., 40–50 deg) in the on-direction and the largest burst rate found was recorded. The distribution of these maximum burst rates for all 35 units is shown in Fig. 5B. The mean of the distribution is 377/sec, the range is 150–620/sec. There was no apparent correlation between maximum burst rate and threshold.

Figure 6 shows the relationships between burst rate, starting position, and saccade size. A saccade is depicted here as a phase plane trajectory, starting and stopping on the rate-position curve (Fig. 2A) but passing through a high burst rate in transit. Figure 4 shows that a saccade is created by a pulse step of discharge rate, i.e., the combination of a pulse (or burst) and a step of discharge rate. The step of discharge rate, R_s, is the difference between the final and initial rates, and the pulse of discharge rate, R_p, is defined as the difference between the burst and final rates. They are indicated in Fig. 6B. Saccades 1, 2, and 3 for each unit in Fig. 6 show what was already demonstrated in Fig. 5, that for saccades near the same starting position the larger the saccade the larger the pulse of discharge rate, but that the amplitude of the pulse appears to saturate.

The relationship between burst rate and starting position was quite different for the three units in Fig. 6. The burst rate varied little in A, more in B, and considerably in C. Figure 6C shows a high-threshold unit and suggests, by the dashed lines below zero rate, that subthreshold variations in excita-
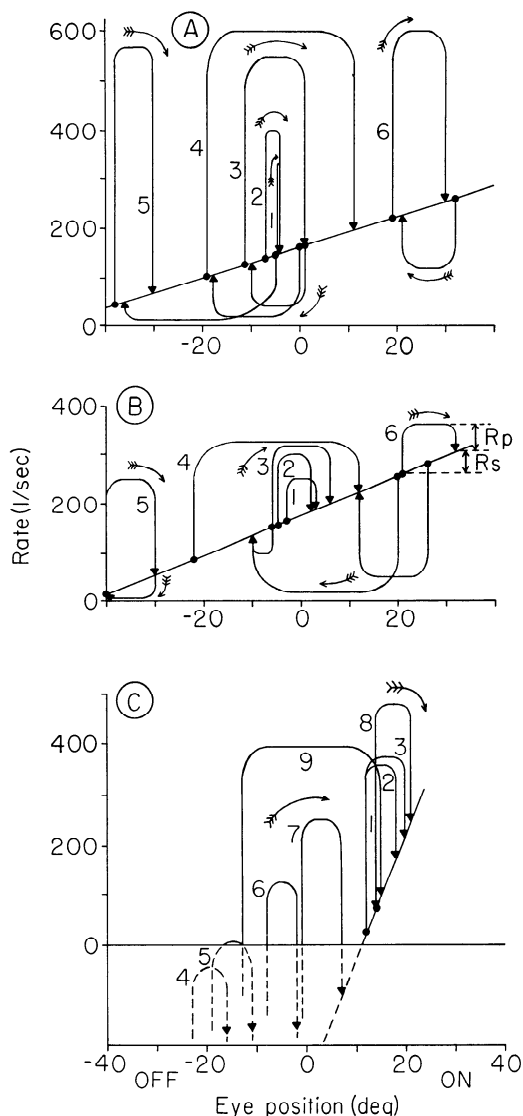

FIG. 6. Loci of discharge rate plotted against eye position for saccades of different amplitudes and initial positions. The phase plane trajectories (indicated by arrows) are schematic and indicate only initial and final eye position and initial and final discharge rates and burst rates. A and B show two low-threshold units with similar discharge rate-position relationships but markedly different relationships to changes in eye velocity. C is an example of a high-threshold unit.

tion were still going on during eye movements even though such activity was not expressed in discharge rate. This permits one to estimate the pulse steps of excitation although only portions of the trajectories project into positive rates. The differences in behavior are compatible with the hypothesis that saccades in the on-direction of a given size were the result of a pulse of excitation, perhaps from a separate prenuclear structure, that did not vary with starting position. If the discharge rate had not saturated, this would have produced a pulse of discharge rate that was also unrelated to starting position. However, since the rates did saturate, the excitation pulse could create a larger pulse of discharge rate from positions in the off-direction than in the on-direction. The unit in Fig. 6A (unit 3 in Table 1 and Fig. 5) showed marked discharge rate changes with velocity changes and had a sharp saturation curve. Consequently, discharge rate saturated during all 10-deg saccades (no. 5, 3, and 6) starting from any part of the visual field and the burst rate appeared unrelated to starting position. The more typical unit in Fig. 6B (unit 7 in Table 1 and Fig. 5) saturated much more slowly and here it was more apparent (saccades 5, 3, and 6) that the pulse of discharge rate, rather than the burst rate itself, was the more intrinsic measure of saccadic excitation. Because of saturation, however, the pulse of discharge rate decreased as the starting eye position moved farther in the on-direction. Saccades 4, 5, 6, 7, and 8 in Fig. 6C show the same variation in the pulse discharge rate with eye position, but more dramatically because of the high threshold and large slope, k, of the discharge rate-position relationship. For positions in the off-direction the unit was so inhibited that even saccades in the on-direction (no. 4) caused no discharges or perhaps a single spike (no. 5). Thus, the variability in the pulse of discharge rate associated with different starting positions may be due to differences in the shape of saturation of the discharge rate-velocity curves and not necessarily to changes in the pulse of excitation arriving at the nucleus from more central structures.

Burst rate also depended on saccade direction in such a way that only the velocity component in the on- or off-direction was important. All units behaved similarly; their rates did not change during saccades perpendicular to the on-direction and their burst rates correlated only with the velocity component in the on- or off-directions and did not correlate with velocity components perpendicular to the on-direction. The muscles thus appeared to act independently, and were concerned only with the component of a movement that lay in the direction of their mechanical action. There have been conflicting reports based on electromyography as to whether antagonist muscles cocontract during version movements (1). The present results give no indication that cocontraction occurs during eye movements in the monkey. Units were not observed to increase their discharge rates without a resulting movement of the eye in the direction of action of the appropriate muscle.

A change in unit activity (excitation or inhibition) always preceded the start and stop of saccadic movements. The time of the change in activity was usually clear since the discharge rate changed abruptly, as in Fig. 4 B, C, and D. The change in rate was less sharp in Fig. 4A and τ_2 is shown in this figure for illustrative purposes only. The beginning and end of the saccades were determined by the points on the record where the eye velocity departed from or returned to zero. This transition was also abrupt and easily identified. The delays τ_1 and τ_3 (Fig. 4) were the same. Their mean was 7.5 msec with a range of 4–10 msec. Delays τ_2 and τ_4 were also the same with a mean of 10 msec and a range of −6 to +25 msec. The means and ranges did not differ between units and did not appear to depend on threshold. Evidence that antagonist inhibition preceded agonist excitation, i.e., that τ_3 was larger than τ_1, was not found. Inhibition during saccades in the off-direction was not always as abrupt and complete as in Figs. 1 and 4. Several units, whose discharge rate changed only little with changes in eye velocity, slowed their rates but continued firing during saccades in the off-direction. The spread in τ values also indicates that during a typical saccade in the

off-direction of 30 msec duration, some units resumed firing ($\tau_4 = 25$ msec) shortly after others finally stopped ($\tau_3 = 4$ msec) and, during the last half of the saccade, many antagonist motor units had resumed activity. Thus, it cannot be said that the antagonist muscle is wholly passive during a saccade, and this observed activity, in a lengthening muscle, must constitute a considerable viscous (15) control over eye velocity.

Figure 4 also shows that at the end of a saccade the discharge rate did not at once assume its new steady value but fell (or rose) to it slowly over about 100 msec. Most of the units (80 %) behaved similarly and it is felt that this behavior is a device to compensate for the slow stress relaxation of viscoelastic elements in the globe's suspensory tissues (21).

DISCUSSION

A distinctive feature of oculomotor units is their high discharge rates, not only during saccades but also during steady gaze. Low-threshold units commonly discharged at 100/sec in the primary position and they must discharge at this rate, on the average, during all the animal's waking hours. These motoneurons and their motor units must have a remarkable metabolic ability to maintain conduction, synaptic transmission, and contraction at these rates for such long periods without fatigue. The isometric contraction of extraocular muscle is said to fuse at 350/sec (7) and this rate is probably determined by the fast twitch-fiber content. The fact that the twitch contraction times of fast and slow twitch fibers is 6 and 24 msec, respectively (3), implies that the latter fuse at 88/sec. It is unlikely that all the units studied, especially low-threshold units, served fast twitch fibers. The high saccadic burst rates then appear to present a puzzle since it is difficult to see how slow or fast twitch fibers can distinguish between various discharge rates so far in excess of their fusion frequencies. However, it has been reported (4) that muscles develop a maximum rate of change of tension at stimulus rates far greater (5–6 times) than the rate at which the muscle is commonly said to be fused. Since the rapidity of tension develop-

ment is important in saccadic movements, this observation may form the basis for the high discharge rates observed during saccades.

There is no residue of the receptive-field organization found in visual physiology in the final common path of the oculomotor system. The "information" appears to be entirely coded in discharge rate. The results appear to support the simple hypothesis that motoneuron discharge rate is translated directly into muscle active-state tension with, on the average, an 8 msec delay, and that tension, in turn, creates an eye movement that may be governed approximately by *equation 2*. Since the load, specified by the parameters R and K, is constant, *equation 2* applies at all times and this leads to the observed rather reproducible machine-like relationship between discharge rate and eye position. There are complications in this scheme. Total muscle force is a function of the number of motoneurons firing as well as their rate, and an attempt at deriving muscle force from a population of motoneuron activity, which cannot be done with the small sample in this study, would show that the relationship between muscle force and the discharge rate of any one unit was nonlinear. Further, the relationship between muscle force and eye position is more correctly described by a differential equation of at least fourth order (18), with a small resonant peak (24) and several nonlinearities (6). Thus, *equations 1* and *2* are intended only as linearized first-order approximations of the actual situation and their value is to unify the data conceptually rather than offer an exact description.

For the human eye, the elastic coefficient K has been found to be 1.25 g/deg (5, 19) and the viscous coefficient R may be estimated from published data (19) to be 0.22 g/(deg/sec). The time constant R/K is thus 176 msec. The time constant may also be measured as the time taken to reach 63 % of final displacement when the eye is subjected to a sudden constant force (18). This method yields a value of 115 msec. The discrepancy lies in the simplifications made since the mechanics of the load is better described as a family of viscoelasticities with a spectrum of time constants. The

coefficients have not been measured for monkey but the time constant should be roughly the same since the movements are similar.

The idea that motoneuron discharge rate is translated directly into muscle force would predict that the position and velocity parameters, k and r, for the discharge rate equation must have the same ratio as the similar parameters, K and R, for the force equation, namely, the time constant, T, of the mechanical load. The fact that the mean time constant of 198 msec from Table 1 agrees fairly well with T measured mechanically suggests that the ratio r/k is a direct measurement, at the central end of the final common path, of the mechanical properties of the globe, muscles, and suspensory tissues.

All the units studied participated in fixation, pursuit, and saccadic movements. This does not support the theory that the different fiber types found in extraocular muscle serve different functions (2, 8). That theory cannot be wholly denied by the present results because vergence movements were not studied, and it was not conclusively shown that the few atypical units found were not motoneurons. It has been shown (25) that no motoneurons that send their axons into the third nerve are located outside the oculomotor nucleus so that a subset of motoneurons were not missed for this reason, but it is likely that the microelectrode preferentially isolated large cells and the existence of a subset of small cells whose behavior was differently related to eye movements remains a possibility. Thus the hypothesis that some cells participate only in certain types of eye movements cannot be denied but the converse, that some movements are effected only by certain motoneurons, can be denied by the present results for fixation, pursuit movements, and saccades.

Yet it is unreasonable that the motoneurons of different fiber types should not show some differences. One possibility is that high-threshold units serve fast twitch fibers. Since a primate whose head is free to turn seldom maintains a gaze deviation beyond 10 or 15 deg for very long, high-threshold units are normally active only during saccades in the on-direction. Con-

sequently, they participate in brief ballistic movements rather than movements requiring continuous and finely graded activity, and thus share some characteristics of fast twitch skeletal motoneurons (14). If this were the case then low-threshold units would presumably serve slow twitch fibers, but there appears to be no sharp subdivisions of thresholds or types of behavior. No consistent differences between low- and high-threshold units could be found in such parameters as time constant, maximum burst rate, steadiness of firing or latency between activity and movement. The terms tonic and phasic have been avoided since all units participated in tonic behavior (fixation) and phasic behavior (saccades).

There are suggestions in the present results that different prenuclear structures are involved in different types of eye movements. The 3.6:1 variation in T in Table 1 indicates that units whose position parameters k are the same can have quite different velocity parameters r. Units 2 and 3 in Table 1 and the units in Fig. 6, A and B are examples. A simple hypothesis to explain these parameter differences is that one prenuclear structure generates commands concerned with fixation (position) and another is concerned with pursuit (velocity). With this hypothesis, a certain amount of randomness in the synaptic connections between these proposed structures and the motoneurons would lead to the observed differences in parameters. The argument that the presynaptic fibers themselves might carry discharge rates that are variously related to eye position and eye velocity only transfers the argument by one synapse, since the question then arises of whether the cells from which the presynaptic fibers arise are differently influenced by two central structures, one concerned with position and the other with velocity. There are alternate hypotheses, e.g., that rapidly adapting stretch afferents synapse on the motoneurons creating a variability in discharge rate related to eye velocity, and other hypotheses which involve models of the entire organization of optomotor commands.

The suggested hypothesis has the advantage of a simplicity which may be more apparent than real because it proposes indirectly that there may be a neurological

system involved in steady fixation that is separate from another involved in pursuit. From a variety of experimental results (11, 17, 19, 23) it is generally held that pursuit and saccadic movements are also organized in different neurological pathways. This idea, based on good evidence, is not very apparent in the present results since only the lack of a smooth transition from the pursuit to the saccadic range in a few of the curves in Fig. 5 indicates any possible dissociation between pursuit and saccadic movements. However, the idea of a separate fixation system has not been previously considered in oculomotor physiology and apparently no experiments in the past have suggested it. This may be because the emphasis has always been placed on the movements themselves and the act of fixation without movement has perhaps been taken for granted. The present results show that fixation is just as much of an active process as movement and, in fact, displays a greater degree of fine motor control than do the movements. Thus it is not unreasonable to suspect a separate neural control for fixation, and the present results, though only suggestive, indicate the desirability of future experiments aimed more directly at revealing such a possibility.

SUMMARY

The discharge rates of 35 single units, believed to be motoneurons, were recorded during fixation, smooth pursuit, and saccadic eye movements in the oculomotor nucleus of the alert, intact monkey. As the eyes moved in the on-direction (the direction of action of the muscle involved), more units became active and those already active increased their discharge rates. The thresholds, or angles at which units became active, varied from 21 deg in the on-direction to 62 deg in the opposite direction (off-direction). For each 10 deg change in the on-direction, about 11 % of the population was recruited into activity. The discharge rate was quite constant for each angle of fixation and increased linearly with eye position in the on-direction. Discharge rates, when the eye was deviated in the on-direction, were commonly 200–300/sec. The discharge rate also increased or decreased with eye velocity in the on- or off-direction during pursuit movements. The slope of the discharge rate-position relationship of the units ranged from 1.25 to 27 (1/sec)/deg and the slope of the discharge rate-velocity relationship ranged from 0.28 to 5.0 (1/sec)/(deg/sec) but their ratio, which is thought to be a reflection in the motoneuron of the time constant of the mechanical load, varied only over a 3.6:1 range. The mean time constant was 198 msec, which is in good agreement with the time constant measured mechanically for the human eye. High discharge rates (burst rates) accompanied high saccadic eye velocities in the on-direction but the discharge rate-velocity curve showed saturation. Saturation burst rates ranged from 150 to 620/sec with a mean of 377/sec. Units were inhibited during saccades in the off-direction. The change in neural activity started 7.5 msec before the start of the saccade and ended 10 msec before the end. Discharge rates did not change during saccades perpendicular to the on-direction. All units participated in fixation, pursuit movements, and saccades indicating that each of these activities was not the exclusive product of one type of muscle fiber. The data were compatible with the idea that changes in motoneuron discharge rate are translated directly into changes in muscle tension since the relationship between eye position and discharge rate and eye position and muscle force are described by similar differential equations. Since the mechanical load is constant, the equation approximately describes the entire relationship between motoneuron discharge rate and eye position, which creates a rather machine-like quality in the discharge rate behavior. There was evidence suggesting that separate prenuclear structures were involved in controlling fixation and pursuit movements.

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