Discharge Patterns and Recruitment Order of Identified Motoneurones and Internuclear Neurones in the Monkey Abducens Nucleus

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SUMMARY AND CONCLUSIONS

1. Single neurones in the abducens nucleus were recorded extracellularly in alert rhesus macaques trained to make a variety of eye movements. An abducens neurone was identified as a motoneuron (MN) if its action potentials triggered an averaged EMG potential in the lateral rectus muscle. Abducens internuclear neurones (INNs) that project to the oculomotor nucleus were identified by collision block of spontaneous with antidromic action potentials evoked with a stimulating electrode placed in the medial rectus subdivision of the contralateral oculomotor nucleus.

2. All abducens MNs and INNs had qualitatively similar discharge patterns consisting of a burst of spikes for lateral saccades and a steady firing whose rate increased with lateral eye position in excess of a certain threshold.

3. For both MNs and INNs the firing rates associated with different, constant eye positions could be described accurately by a straight line with slope, \( K \) (the eye position sensitivity in spikes \( \cdot s^{-1} \cdot deg^{-1} \)), and intercept, \( T \) (the eye position threshold for steady firing). For different MNs, \( K \) increased as \( T \) varied from more medial to more lateral values. In contrast, the majority of INNs already were active for values of \( T \) more medial than 20° and showed little evidence of recruitment according to \( K \).

4. During horizontal sinusoidal smooth-pursuit eye movements, both MNs and INNs exhibited a sinusoidal modulation in firing rate whose peak preceded eye position. From these firing rate patterns, the component of firing rate related to eye velocity, \( R \) (the eye velocity sensitivity in spikes \( \cdot s^{-1} \cdot deg^{-1} \cdot s^{-1} \)), was determined. The \( R \) for INNs was, on average, 78% larger than that for MNs. Furthermore, \( R \) increased with \( T \) for MNs, whereas INNs showed no evidence of recruitment according to \( R \). If, as in the cat, the INNs of monkeys provide the major input to medial rectus MNs and if simian medial rectus MNs behave like abducens MNs, then recruitment order, which is absent in INNs, must be established at the MN pool itself.

5. Unexpectedly, the \( R \) of MNs decreased with the frequency of the smooth-pursuit movement. Furthermore, the eye position sensitivity, \( K \), obtained during steady fixations was usually less than that determined during smooth pursuit. Therefore, conclusions about the roles of MNs and premotor neurones based on how their \( R \) and \( K \) values differ must be viewed with caution if the data have been obtained under different tracking conditions.

6. Finally our attempts to model our data indicate that a first-order plant model using only position and velocity terms is woefully inadequate. Much better simulation was obtained with a modification of the original higher-order plant model proposed by Robinson (29).

INTRODUCTION

The discharge patterns of neurones in the sixth cranial nucleus of the monkey have been well documented in a number of laboratories (6, 12, 15, 19, 33). Early neuroanatomists assumed that all abducens neurones were motoneurones (MNs) innervating the
lateral rectus muscle, because sectioning the abducens nerve apparently produced chromatolytic changes in almost all abducens somata (40). More recently, however, investigators have discovered, in the cat abducens nucleus, a group of neurons whose axons do not exit in the sixth nerve but travel rostrally in the medial longitudinal fasciculus to innervate contralateral medial rectus MNs (14, 18, 37). Injections of horseradish peroxidase (HRP) into the oculomotor complex of the monkey label neurons in the contralateral abducens nucleus, suggesting that a similar internuclear pathway exists in primates (37). Furthermore, the abducens nucleus of the monkey contains at least one more interneuron, which is labeled by HRP injections into the flocculus (22). Hence, it is now clear that the abducens nucleus of both the primate and cat must be considered as more than a collection of MNs. Indeed, in contrast to the earlier retrograde degeneration study (40), HRP injection into the lateral rectus muscle of the rhesus macaque labels only ~40% (36) to 60% (27) of abducens neurons, suggesting that abducens interneurons are considerable in number.

Before the existence of abducens interneurons was known, there was a general consensus that all abducens neurons had qualitatively similar discharge patterns for all conjugate eye movements (6, 19, 20, 31). They exhibited a burst of spikes that began before every lateral saccade and ended just before the saccade landed. If a saccade moved the eye to a position that was more lateral than a certain threshold, \( T \), the abducens neuron fired at a steady tonic rate that was proportional to eye position. This firing pattern has come to be known as “burst tonic.”

Not only does the firing rate of abducens neurons vary with eye position \( (\theta) \), but it also varies with eye velocity \( (\dot{\theta}) \). The burst-tonic firing rate has been described by the equation (31)

\[
FR = K(\theta - T) + R\dot{\theta}
\]

where \( K \) is the position sensitivity \( (\text{spikes}\cdot s^{-1}\cdot\text{deg}^{-1}) \), \( T \) is the eye position threshold (degree) for steady firing, and \( R \) is the velocity sensitivity \( (\text{spikes}\cdot s^{-1}\cdot\text{deg}^{-1}\cdot\text{s}^{-1}) \). In 4 studies of almost 150 neurons, \( K \) averaged 4.3 (6, 12, 21, 35), whereas in 2 studies of 34 neurons, \( R \) averaged 0.72 (20, 35).

Although all abducens neurons exhibit qualitatively similar burst-tonic discharge patterns, Fuchs and Luschei (6) noticed that some had particularly high discharge rates of 800 spikes/s in a burst. Because identified MNs recorded in the trochlear nerve discharged at peak rates of only 400 spikes/s (7) and the lateral rectus muscle produced a fused tension when stimulated at rates in excess of 400 pulses/s (8), Fuchs and I uschei (7) suggested that those abducens neurons with high burst rates might be interneurons rather than MNs. Recently, this suggestion seems to have been confirmed for the cat, in which internuclear neurons (INNs) have burst-tonic discharges with both higher position and higher velocity sensitivities (5). Highstein et al. (17) have suggested that the “enhanced” discharges of INNs may compensate for the delay in transmission between the abducens and medial rectus subdivision of the oculomotor complex to permit horizontal gaze to be conjugate. Burst-tonic discharge patterns related to horizontal eye movements also constitute the majority of mossy fiber inputs to the flocculus (23-25), and it is very likely that some of these afferents also originate in the abducens nucleus (22).

These three identified targets for abducens neurons in the monkey (i.e., MNs innervating the lateral rectus, INNs, and granule cells in the flocculus) clearly are at different stages in the processing of signals for horizontal eye movements and, therefore, must play different roles in eye movement control. To evaluate whether the signals sent to two of these structures reflect those different roles, we contrast, in this paper, the behavior of identified INNs and MNs in the alert monkey.

The ability to distinguish between MNs and INNs also allowed us to evaluate the accuracy of Eq. 1 in describing MN firing patterns. Equation 1 describes the oculomotor “plant” as a muscle, having no dynamics, that rotates the globe against a restoring force proportional to the deviation of the eye (like a spring) in parallel with another restoring force proportional to eye velocity (like a dashpot). According to this model, which we will call the “single-time-constant” or “first-order” model, the eye should respond to step changes in force with a movement having an exponential time course with a time constant of \( R/K \). In fact, the step response is composed
of the sum of at least two exponentials (29). Nevertheless, the single-time-constant model is universally used as an approximation of more accurate higher-order models (31, 32). The first-order model not only is inadequate to simulate the generation of the rapid saccadic eye movement (12, 13), but we show here that it also works poorly at the slow velocities of smooth pursuit or during the vestibuloocular reflex (VOR).

**METHODS**

Extracellular single-unit activity was recorded in the abducens nuclei of six rhesus macaques trained to make horizontal eye movements to follow a small moving target for a food reward. In some cases, the animal also was rotated horizontally about a vertical axis while fixating a target stationary in space so that we could test the discharge patterns during vestibular stimulation. Eye movements were measured using the search coil technique with a sensitivity of 15 min of arc from DC to 330 Hz (9). The animal was rewarded for accurate tracking and, after it was trained, we could determine eye position to within 0.5° of arc over a horizontal eye movement range of ±30°. Unit activity was recorded by tungsten microelectrodes that were insulated with Epoxylite. The microelectrodes were inserted into the brain through a chronically implanted recording chamber. Action potentials were preamplified by a local circuit near the animal's head, and the amplified unit activity and signals proportional to horizontal eye and target movement and vertical eye movement were stored on an FM tape recorder for later analysis. Further details of the eye movement transducer and the methods involved in unit recording are available elsewhere (6, 9).

**Identification of MNs**

Abducens neurons were identified as MNs if their action potentials triggered averages of electromyographic (EMG) activity recorded from indwelling electrodes in the lateral rectus muscle. The EMG electrodes were constructed from 13 strands of twisted #44 stainless-steel wire covered with Teflon. One millimeter of insulation was removed from the end of the wire so that individual strands splayed out like a grappling hook. A second, 4-mm collar of insulation was removed 2 mm from the end so that electrical activity from at least two areas of the muscle would be sampled. The electrode was inserted into a hypodermic needle with the grappling hook positioned just at its tip. In aseptic surgery with the animal under general anesthesia, the lateral rectus was retracted by cutting a hole in the lateral aspect of the bony orbit, and the eye was rotated nasally to expose as much of the body of the lateral rectus muscle as possible. The needle was inserted into the belly of the muscle, and an attempt was made to position the tip near the point of entry of the abducens nerve, where the EMG potential is likely to be monophasic. Then the needle was withdrawn and the electrode was left in position. Usually, two EMG electrodes were placed in slightly different locations in the muscle. The EMG leads were directed through the orbital defect, led under the skin, and soldered to a plug affixed to the skull. Finally, the temporalis muscle and the skin were closed over the defect.

The EMG activity was measured relative to an indifferent electrode placed near the orbit and processed by an amplifier with a band pass set usually between 10 Hz and 3 kHz. The EMG was not rectified because our early attempts with half-wave, full-wave, and direct recording showed that the best averages were always obtained with direct recordings. Initially, EMG activity was averaged by a computer of average transients (Nuclear Chicago model #1750) with a 75-μs sample width, but later an averaging program (sample width of 50 μs) written for a DEC 11/23 computer was used. Each sweep was 10 ms long and nonoverlapping.

**Identification of INNs**

In one monkey, abducens neurons were identified as INNs if they were activated antidromically by stimulating microelectrodes in the medial rectus subdivision of the contralateral oculomotor nucleus. Recording microelectrodes with large tips were driven into the third cranial nucleus through a second recording chamber, and medial rectus MNs were identified by their characteristic burst-tonic discharge pattern for medial saccades. When a track was located that contained medial rectus MNs over at least 0.5 mm of its dorsal-ventral extent, the recording electrode was fixed in position by a set screw, the microdrive was removed, and the electrode was used as a monopolar stimulating electrode. The efficacy of the stimulating electrode, as judged by the eye movements that stimulation evoked in the ipsilateral eye, remained relatively constant for ~5 days, after which the electrode was removed. The electrode in the medial rectus subdivision was replaced in four different 5-day sessions. It was usually located toward the caudal end of the oculomotor complex.

Once an abducens neuron was isolated, the animal was required to fixate at an eye position for which the unit fired at a very low rate. By controlling eye position, we were frequently able to find a direction of gaze where only one unit was firing. Single-shock stimuli (biphasic pulses of 200-μs duration) were delivered through the oculomotor nucleus electrode to attempt antidromic activation of the abducens neuron. To confirm that an activated...
cell was indeed the isolated cell, we used the action potential of the isolated cell to trigger the stimulus pulse after a short delay and gradually reduced the delay to test for collision between the orthodromic and antidromic action potentials. The maximum current used to test for antidromic activation was usually <400 μA; for some units, activation was obtained with currents of only 20 μA and, on average, 64 ± 62 μA (mean ± SD) were required. We believe these figures represent maximum currents, because the stimuli were delivered from a remote source through 15-ft leads in order not to disturb the behaving animal.

RESULTS

Identification of abducens neurons

When a group of burst-tonic neurons was encountered, weak current pulses were passed through the microelectrode to trigger an EMG average. If the electrode was indeed in the abducens nucleus, large (~250 μV) EMG averages would appear at monosynaptic latencies within 300 trials for stimulus currents of <30 μA. Once the abducens nucleus was located by this means, all eye-movement-related units in its immediate vicinity (+1 mm of its center) were tested for a spike-triggered EMG average.

Examples of representative single-neuron averages considered to be indicative of a direct connection between an abducens neuron and the lateral rectus muscle are shown in Fig. 1. About two-thirds of the averages were monophasic negative potentials, and most of the rest had biphasic positive-negative shapes. An average obtained from a particular EMG electrode often was similar from one MN to another, but the general shape of the average varied somewhat between electrodes in a single monkey (compare A and B in Fig. 1) and also between monkeys (Fig. 1, A and B vs. C). To determine the origin of the EMG potentials, averages produced by electrical stimulation in the abducens nucleus when the animal was alert and when it was paralyzed were compared in one animal. Just before the animal was sacrificed, it was anesthetized, given flaxedil, and placed on a respirator. When synaptic transmission was abolished by this procedure, 95% of the EMG potential produced by abducens stimulation also disappeared, leaving only an early, small positive deflection. This finding demonstrates that the averages were indeed due to muscle activity and not simply the incoming nerve volley.

FIG. 1. Representative examples of EMG averages from the lateral rectus muscle triggered on MN action potentials. A and B are from the same monkey, whereas C is from another. Vertical calibrations are 4.4 μV, each horizontal tic mark is 1 ms, and each record is the average of 3,000 sweeps.

Several criteria had to be met before we attributed an EMG average to a direct MN connection. First, a clear delay had to be present between the action potential trigger and the onset of the average. Latencies to the beginning of the potential typically ranged from 0.5 to 1.5 ms. As exemplified in the upper trace of Fig. 1C, averaged potentials sometimes began before the trigger signal, a situation that we think reflects the EMG activity produced by other abducens MNs firing in loose synchrony with the recorded neuron. Although the neuron of Fig. 1C produced a synchronous average in one electrode (lower trace), it produced a sharp potential in the other (upper trace), indicating that it was indeed a MN. Second, averages had to develop within 3,000 trials, indeed, many often devel-
opened within as few as 500 sweeps. Third, averages that were either small or slow to develop were calculated a second time, and both averages had to be very similar. The size of the averaged EMG potentials ranged from 0.5 to 48 μv; average values for the two monkeys with the most data were 5.2 μv (n = 52) and 8.8 μv (n = 15). An EMG potential meeting these criteria had to appear on only one of the muscle electrodes. Clear averages on both electrodes, such as those in Fig. 1A, occurred only infrequently.

In four monkeys, a large number of burst-tonic neurons (n = 337) were recorded within an area subsequently verified histologically to coincide with the abducens nucleus. The percentage of burst-tonic cells that triggered EMG averages was 27, 31, 37, and 44% in the four monkeys. Discharge properties were obtained from 81 MNs; most of these (n = 67) were obtained from two monkeys.

**Identification of abducens INNs**

An example of a representative collision test used to identify an abducens INN is shown in Fig. 2A. An action potential from a putative INN (open arrow) triggers, after a long delay, a stimulus pulse in the oculomotor nucleus (open circle), which evokes an antidromic action potential (closed arrow). As the delay is reduced (Fig. 2A2), collision block of the antidromically evoked action potential (open star) occurs for the stimulus pulse with the shortest latency (leftmost open

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**Fig. 2.** Collision block (A) and latency histogram (B) for abducens INNs. A: stimulation of oculomotor nucleus (open circles) triggered on spontaneously occurring INN action potentials (open arrows) evoked an antidromic spike (filled arrows) at long intervals (A1). At shorter intervals (A2), collision block of the antidromically evoked spike (stars) occurred, identifying the neuron as an INN. At short intervals (A3), the antidromic spike was consistently occluded. In A1–A3, there are 2, 3, and 2 superimposed traces, respectively. Time bar is 1 ms. B: latency histogram for INNs at 2 times threshold stimulating current measured from beginning of biphasic stimulating pulse to the foot of the action potential (stippled); latencies measured in other cells at different currents are shown as open bars.
circle in Fig. 2A2). At even shorter delays (Fig. 2A3), the antidromic spike was occluded consistently, but a small antidromic field (Fig. 2A3, stars) was still present. Twelve INNs were tested at 2 times threshold and their average activation time (stimulus delay for collision block minus twice the antidromic latency) was 0.25 ± 0.19 ms. For 21 INNs, the latency histogram (Fig. 2B, shaded) for antidromic activation at threshold, measured from the beginning of the biphasic stimulating pulse to the foot of the action potential, was unimodal with an average latency of 0.8 ± 0.2 ms. Other INNs identified by collision testing, but tested at greater than threshold currents, showed a similar latency distribution (Fig. 2B, open histogram). The average distance from the abducens nucleus to the caudal pole of the oculomotor complex was 10 mm as estimated from a marking lesion placed at the site of the stimulating electrode. Therefore, the conduction velocity of INN axons, taking activation time into account, was estimated at 12–40 m/s.

Of the 229 abducens neurons tested in one monkey, 17% were identified as INNs. Estimates in our lab (1. Langer, personal communication) indicate that ~420 neurons, or 29% of all simian abducens neurons, are INNs. Therefore, our antidromic stimulation activated almost 60% of all the available INNs. Discharge properties were obtained from 36 abducens INNs in one monkey. Of the eight identified INNs tested, none produced an EMG average in the lateral rectus. Similarly, none of the 18 identified MNs tested in that monkey were antidromically activated by electrical stimulation of the oculomotor complex.

**Firing patterns of abducens neurons**

**BEHAVIOR DURING FIXATION.** All of the abducens MNs and INNs in our sample had burst-tonic discharge patterns, examples of which are shown in Fig. 3. Both the representative MN (Fig. 3A) and INN (Fig. 3B) exhibited a burst of action potentials for lateral saccades and a steady firing rate that increased monotonically as the monkey fixated more lateral eye positions. All MNs and INNs had qualitatively similar discharge patterns, although the size of the burst and tonic components differed from unit to unit. The burst associated with the high-velocity saccade and the tonic rate associated with fixations indicate that the firing rates of both neuron types are related to both eye position and velocity.

The relation between tonic rate and horizontal eye position for MNs and INNs was obtained by requiring the monkeys to fixate successive horizontal target spots located every 5° from 25 or 30° medial to as far lateral as the unit’s isolation would allow and averaging the firing rate at each location over at least a 2-s interval. No attempt was made to study the hysteresis in firing rate reported by others.

The average firing rate as a function of eye position for the two units in Fig. 3 is plotted in Fig. 4. The data points for both units can be fit with straight lines with correlation coefficients of 0.99. Hence, these firing-rate/eye-position characteristics can be described by a slope, \( K (3.74 \text{ spikes/s} \cdot \text{deg}) \) for the INN and MN shown) and an “X”-intercept that reflects the threshold eye position, \( T \), at which the unit is recruited into steady firing (−33 and −1° for the INN and MN, respectively). All INNs and MNs had rate-position characteristics that could be fit accurately with straight lines (the worst correlation coefficient was 0.83 but the average correlation coefficient was 0.99).

In addition to determining the threshold by linear extrapolation of the firing rate vs. eye position characteristic, we also determined the threshold behaviorally by requiring the monkey to fixate more and more medial eye positions until the unit ceased firing. For MNs, the relation between the behavioral \( T_B \) and extrapolated \( T_E \) thresholds can be fit nicely by the straight line

\[ T_B = 0.85T_E + 2.9 \quad (r = 0.95, n = 72), \]

which suggests that the behavioral threshold is generally slightly more lateral than the extrapolated threshold. Indeed, when the fixating eye approaches the behavioral threshold from more medial eye positions, the firing rate does not increase gradually but jumps to some minimum steady rate of 10–20 spikes/s. The extreme medial recruitment thresholds for INNs (see below) usually made it impossible to obtain a behavioral threshold because the monkeys would not maintain extreme fixation positions. In what follows, therefore, all thresholds have been obtained by extrapolation.
Although the relations between steady firing rate and eye position are qualitatively similar for INNs and MNs, they exhibit important quantitative differences. The position sensitivity, $K$, of an MN depends on its threshold (Fig. 5). Those neurons that were recruited at eye positions in the medial direction tended to have lower values of $K$ than those recruited at eye positions far in the lateral direction. The relation between the position sensitivity and threshold was reasonably linear ($r = 0.81$). In contrast to the gradual recruitment of MNs, the majority of our INNs (86%) were already firing steadily for eye positions in excess of 20° medial. Furthermore, although position sensitivities for MNs varied from 1.0 to 17.8, $K$ values for 86% of the INNs were relatively constant at $<$5.1 (4.1 ± 0.8) and, with the single exception of the datum at the 10° lateral threshold, showed no tendency to increase with threshold (Fig. 5). Even when all the data are considered, the
correlation between $K$ and $T$ for INNs accounted for only 20% of the variance and the slope was four times more shallow than the slope of the regression relating $K$ and $T$ for MNs. One consequence of the early recruitment of INNs is that, on average, they had a higher discharge rate associated with the primary direction of gaze than did MNs (124.5 ± 65.6 spikes/s, $n = 36$ for INNs vs. 36.3 ± 71.7 spikes/s, $n = 81$ for MNs).

**BEHAVIOR DURING SMOOTH PURSUIT.** The relation between discharge rate and horizontal eye velocity was obtained by requiring the monkeys to track a spot moving sinusoidally through ±10° at a variety of frequencies. As shown in Fig. 6, such a target motion elicited a roughly sinusoidal smooth eye movement (interrupted by occasional saccades) that was preceded at a short-phase lead by a roughly sinusoidal modulation of instantaneous firing rate. These periodic data were analyzed on a DEC 11/73 computer programmed to display the digitized eye movement and instantaneous firing frequency (1/interspike interval) cycle by cycle. Using a joystick, a user manipulated $K'$ and $R'$ to obtain the best match by eye between a plot of the equation $FR = K'\theta + R'\theta$ and the instantaneous firing frequency data. $K'$ and $R'$ were averaged over 5–12 cycles to obtain their final values. With this method, the values of $K'$ and $R'$ determined by 2 different investigators (A.F.F. and C.A.S.) on 75 different averages of MN firing rates differed by only 0.5 + 7.1 and 2.5 + 10.4%, respectively. Because we will argue later that the first-order model of orbital dynamics fails to fit the data, it is important to realize that $K'$ and $R'$ provide as complete and adequate a description of these nearly sinusoidal data as do the usual parameters of gain and phase. We chose this method of analysis over one yielding gain and phase (e.g., a Fourier analysis) because it was better at fitting $I$ the piecewise sinusoidal firing rates that

![Image of graph showing relation between averaged firing rate and eye position for the MN (filled triangles) and INN (open circles) whose firing patterns are shown in Fig. 3. For both units individual data points are fit well by linear regression lines ($r = 0.99$) that can be described by a slope $K$ (3.74 and 7.44 for the INN and MN, respectively) and a threshold, $T$, for steady firing ($T_{\text{INN}} = -33^\circ$ and $T_{\text{MN}} = -1^\circ$).]
FIG. 5. Slope ($K$) of the rate-position relation as a function of the threshold ($T$) for MNs (filled triangles) and INNs (open circles). $K$ increases with $T$ for MNs as shown by the regression line ($K = 0.18T + 8.07, n = 81; r = 0.81$); the linear regression for the INNs (not shown) ($K = 0.050T + 6.03, n = 36$) accounts for only 20% of the variance in the data ($r = 0.45$).

accompanied those cycles of inadequate smooth pursuit requiring catch-up saccades and 2) the asymmetric firing rates that accompanied asymmetric pursuit in some monkeys (i.e., higher velocities often occurred for pursuit away from the recording site). Our matching method could also be used to analyze data from nonsinusoidal tracking such as those obtained during square-wave tracking and steady fixations (see below).

This analysis produced two unexpected results. First, the velocity sensitivity of MN firing decreased with frequency. As seen in Fig. 7A, this decrease, which occurred for all MNs tested, could be as much as 60% and averaged $45 \pm 11\%$ ($n = 14$) from 0.3 to 1.5 Hz. Second, most MNs showed little, if any, change in position sensitivity over frequencies from 0.3 to 2.0 Hz, although the average position sensitivity for all neurons was somewhat larger at 2.0 than at 0.3 Hz (heavy line, Fig.
FIG. 6. Discharge patterns of another MN and the INN of Fig. 3 during smooth pursuit of a target moving horizontally at 0.5 Hz. The instantaneous firing rate was very sinusoidal and was therefore fit by a sinusoidal function with adjustable gain and phase (see text). V and H are vertical and horizontal eye position; T is horizontal target position, which was displaced 5° upward for ease of comparison. Time bar represents 1.0 s.

7B). In contrast, >60% (14 of 22) had position sensitivities determined during smooth pursuit (the dynamic position sensitivity, $K_D$) that were larger than those determined while the eye fixated steady positions (the static position sensitivity, $K_S$, shown at zero frequency in Fig. 7B). The other eight showed either no significant difference ($n = 6$) or a decrease ($n = 2$). For all 22 units, $K_D$ at 0.5 Hz was $22 \pm 29\%$ greater, on average, than $K_S$ (the value at zero frequency). Although we had insufficient data to perform a complete frequency analysis on INNs, their $K_D$ values at 0.5 Hz were also greater than their $K_S$ values. Indeed, on average, $K_D$ was more than two times (115\%) greater than $K_S$. Possible
FIG. 7. Variation of $R$ (4) and $K$ (B) with the frequency of sinusoidal tracking for 23 abducens MNs. Thick lines are the averages for all cells.
reasons for the decrement in $R$ with frequency for MNs and the difference between $K_D$ and $K_S$ for both MNs and INNs will be considered in the DISCUSSION. A difference between the statically and dynamically determined values of $K$ has not been reported previously. To test whether the difference was an artifact of our new curve-fitting technique, we redigitized and reanalyzed the data obtained from 10 selected INNs during sinusoidal pursuit (0.5 Hz), square-wave tracking (0.5 Hz), and fixation so that the same procedures, including the curve-fitting program (see METHODS), were used throughout. The static $K$ determined during fixation by the fitting program was, on average, only 2% different from that determined by hand, showing that our curve-fitting method did not introduce an error. We also analyzed computer-generated firing rate data with a known phase shift, and the values of $R$ and $K$ thus determined successfully predicted the actual phase shift within 3%.

We have already shown that $K_D$ during smooth pursuit of sine waves is higher than $K_S$. The application of the curve-fitting program to the firing rates of the 10 INNs during tracking of square-wave target displacements produced still another $K$ value, which lay between $K_S$ and $K_D$; it was higher than $K_S$ by
51%. This different value for $K$ during square-wave tracking is a consequence of the fact that the firing rate does not drop to its new steady level immediately following a saccade, but rather declines slowly through a series of exponential wave forms with increasing time constants (see also Ref. 12). Our program, which mimics first-order orbital dynamics, cannot fit this slow decline. Instead, we fit the firing rate $\sim 1$ s after the saccade and just before the next saccade. Because the $K$ value so obtained was higher than $K_S$, our data suggest that the decay in firing rate is not complete, even after 1 s. This overestimation of $K_S$ becomes progressively worse as saccades become more closely spaced, as in typical physiological experiments in which spontaneous saccades often occur every 0.5 s.

As demonstrated above for the position sensitivity $K$, the velocity sensitivities of INNs and MNs calculated at 0.5 Hz could be differentiated according to the threshold at which the neurons were recruited into steady firing. Because of their dependence on frequency, all $R$ values in Fig. 8 were calculated at the same frequency, 0.5 Hz. For MNs, those with low (i.e., medial) thresholds had lower velocity sensitivities than those with higher (i.e., lateral) thresholds; the relation between $K$ and threshold was reasonably linear ($r = 0.67$). On the other hand, for INNs, the velocity sensitivity had a much greater range of values (e.g., for thresholds between 30 and 45° medial, $R$ varied about threefold) and did not show a significant increase with threshold ($r = 0.26$). Furthermore, the average value of $R$ was significantly greater for INNs ($1.67 \pm 0.63, n = 26$) than for MNs ($0.94 \pm 0.39, n = 49; P < 0.01, t$ test for unequal populations).

![Figure 8](image-url)  
*Fig. 8.* Relation of the velocity coefficient, $R$, to the threshold for steady firing for MNs (*filled triangles*) and INNs (*open circles*). For MNs, $R$ increases with $T$ as shown by the linear regression ($R = 0.020T + 1.23, n = 49; r = 0.67$); the correlation for INNs ($R = 0.014T + 2.07; n = 26; r = 0.26$) was not significant.
The ratio of the velocity sensitivity to the position sensitivity provides a measure of the relative contributions of eye-velocity- and eye-position-related activity to the total discharge pattern. This ratio, $R/K$, which represents the time constant, $\tau$, of the solution of the first-order differential equation representation of firing rate (see Eq. 1), is plotted in Fig. 9 for both MNs and INNs at 0.5 Hz. Unlike the position and velocity sensitivities, their ratio was not related to threshold ($\tau = 0.000 T + 0.16, r = 0.09; n = 49$). For both MNs and INNs, most values of $\tau$ were tightly clustered between 0.1 and 0.22 s. The average value for $\tau$ was $0.16 \pm 0.03$ s and $0.14 \pm 0.19$ s for MNs and INNs, respectively.

In a previous abstract, we reported that the average time constant of INNs was almost twice that of MNs (10). In that abstract, the time constant was calculated by using $K_0$ which, as we have shown above, averages about three-quarters of $K_D$. When $K_D$ is used as in Fig. 9, the average values of $\tau$ for MNs and INNs are essentially identical.

**MN firing during vestibular stimulation**

For 19 MNs, the firing rate was recorded while the animal was rotating sinusoidally about a vertical axis and fixating a target that was stationary in space. Under these conditions, the eye movements and the MN firing rate modulation were even more nearly sinusoidal than during smooth pursuit because there were virtually no saccades. For 13 units, $R$ and $K_D$ were determined as a function of frequency. As during smooth pursuit, $R$ decreased by $44 \pm 4.8\%$ over the frequency range between 0.5 and 1.4 Hz. $K_D$ exhibited a small decrease ($7.2 \pm 7.2\%$) over the same frequency range, in contrast to its increase during smooth pursuit. For 10 units, the discharge patterns during both the stationary-in-space and smooth-pursuit conditions were tested. During stationary-in-space tracking,
both $K_0$ and $R$ were slightly less (by 8 and 9%, respectively) than those obtained during smooth pursuit. Because of the similarity of the data obtained in the 2 conditions, the time constants (measured at 0.5 Hz) obtained for 9 units only during stationary-in-space tracking have also been plotted in Fig. 9 (stippled bars).

Relation between averaged EMG potential and recruitment threshold

Recordings from various limb muscles have shown that as the muscle is required to generate increasing amounts of force, there is a gradual recruitment of ever larger and faster motor units (1). To determine whether a similar recruitment according to size could be demonstrated for the extraocular muscles, we plotted both the size and latency of individual spike-triggered EMG potentials as a function of unit threshold. We assumed that motor units generating more force would have larger EMG potentials and that the shortest latencies reflected the fastest conduction velocities and, thus, the largest neurons. These data were examined for the monkey with the greatest number of tested cells ($n = 50$); the behavioral threshold was used for these plots because the extrapolated threshold was not available for 15 units. The EMG amplitude showed a modest increase with threshold ($EMG = 0.06T + 4.57$), but the correlation coefficient was only 0.18. The latency to the beginning of the EMG response, a possible indicator of the conduction velocity of MN axons, showed a negative correlation with threshold ($r = -0.40$).

**Discussion**

Identification of subpopulations of neurons within the abducens nucleus

One finding of our study was that the technique of spike-triggered averaging can be used in the oculomotor system to identify MNs in alert animals. In 360 abducens cells sampled in 4 monkeys, an average of 35% produced discrete EMG potentials in the ipsilateral lateral rectus, thereby allowing us to identify them as MNs. Because anatomic estimates place the percentage of abducens MNs at 40–60% (27, 36; Langer, personal communication), our technique correctly identified, on average, 58–88% of the MNs. It is possible that a different electrode configuration (perhaps more exposed surface area) or a better placement in the muscle (perhaps closer to the nerve-root entry zone) might sample an even higher percentage of MNs. The technique can reveal not only monosynaptic connections between MNs and their muscle, but also some excitatory pathways that are 2 synapses distant from the muscle (34).

The percentage of abducens INNs that were identified also compared favorably with the percentage expected on the basis of anatomic studies. Antidromic activation and collision block testing in one monkey identified $\sim 60\%$ of the expected INNs.

Qualitative properties of discharge patterns of identified abducens MNs

Every abducens neuron identified as either an MN or an INN exhibited a burst of firing for lateral saccades and a tonic discharge when the eye looked further lateral than the threshold for steady firing. Henn and Cohen (15, 16) claimed that, in addition to the burst-tonic units described here, there are MNs that exhibit only a burst of spikes with saccades or only a steady firing with fixation. There may be several reasons why our results disagree with those of Henn and Cohen. First, we identified all of our MNs directly, whereas they relied on the anatomic reconstruction of recording sites, the antidromic identification of “several” neurons, and their apparent finding of both burst and tonic units in the oculomotor nerve. Second, Henn and Cohen (15) suggested that some but not all of their burst neurons might be burst-tonic units with high thresholds for steady firing. We found that all of our apparent burst MNs did have tonic firing rates when our trained monkeys were required to look far enough eccentrically. Third, our criterion for identifying a unit as burst-tonic rather than tonic might have differed from theirs because neurons that they identified as predominantly tonic (e.g., Fig. 3C in Ref. 15) exhibited clear bursts during saccades.

Although all of our units had burst-tonic discharge patterns, it is possible that our electrodes did not record from all types of abducens MNs. Two observations suggest that sampling by our recording microelectrode
was not a problem. First, in our study, MNs with low (medial) thresholds were often recorded. If ocular MNs are similar to spinal MNs, those with low thresholds would be the smallest neurons (however, see below). Second, abducens MNs in the monkey are not so small that they should be missed; the smallest diameter is about 12 μm (Langer, personal communication). The range of sizes of lateral rectus MNs apparently is not as great as that of medial rectus MNs, some of which are quite small (i.e., those in group C) and preferentially innervate the outer muscle layer believed to contain lower-threshold, “tonic” muscle fibers (2). Although we believe that we sampled all types of abducens MNs, it is possible that the EMG technique did not detect potentials from small or nonspiking muscle fibers.

Quantitative differences in MN and INN discharge patterns

Although MNs and INNs have qualitatively similar burst-tonic discharge patterns, they differ in several important quantitative respects. MNs are recruited according to their sensitivities to both position and velocity whereas INNs show almost no evidence of an orderly recruitment dependent on those parameters (Figs. 5 and 7). Instead, the vast majority of our INNs had already been recruited at eye positions in excess of 20° medial, and those few recruited at more lateral positions, with one exception, did not have higher position sensitivities. On average, INNs had position sensitivities that were less than those of MNs but velocity sensitivities that were greater. A detailed comparison of MN and INN discharge properties is presented in Table 1.

IMPLICATIONS FOR RECRUITMENT ORDER.

Because INNs and MNs represent different stages in the processing of neural signals leading to horizontal eye movement, a comparison of their discharge properties may provide some insight into where recruitment order is established in the oculomotor system. INNs are known to provide a major excitatory input to medial rectus MNs (18). If, like abducens MNs, medial rectus MNs are recruited into steady firing according to their position and/or velocity sensitivities, then their recruitment order must be established at the MN pool itself because the INNs show little evidence of recruitment within the normal oculomotor range (±20°). It is possible, of course, that recruitment order is imposed by some other input. For example, in the cat, the ascending tract of Deiters (ATD) provides medial rectus MNs with an eye position, head velocity, and, possibly, a saccadic signal (28). The synaptic efficacy of the ATD input has been estimated to be about two-thirds that of the internuclear pathway (18). The rate-position characteristics of feline ATD cells are quite variable, however, and it is not known whether ATD neurons exhibit an orderly recruitment.

In spinal MNs, recruitment order is strongly correlated with MN size for many, but apparently not all, inputs (1). Unfortunately, we saw no evidence of recruitment by size in the relation between threshold and either averaged EMG amplitude (a possible measure of motor unit size) or latency (a measure of conduction velocity and thus cell

| Table 1. Comparison of MN and INN discharge properties (means ± SD)* |
|---------------------------------|----------------|----------------|
| Discharge Property              | Motoneurons    | Internuclear Neurons |
| 1. $K_s$ (spikes·s⁻¹·deg⁻¹)     | 6.2 ± 3.0      | 4.6 ± 1.5        |
| 2. Rate at straight-ahead gaze (spikes/s) | 36.3 ± 71.7 | 124.5 ± 65.6    |
| 3. Average T (deg)              | 10.7 ± 13.7    | 28.9 ± 13.1      |
| 4. Relation between $K_s$ and T | $K_s = 0.18T + 0.07$ | $K_s = 0.05T + 0.03$ |
| 5. $R$ (spikes·s⁻¹·deg⁻¹·s⁻¹) at 0.5 Hz | 0.94 ± 0.39 | 1.07 ± 0.63 |
| 6. Relation between $R$ and T   | $R = 0.02T + 1.23$ | not significant |
| 7. Dynamic time constant ($R/K_s$ s) | 0.16 ± 0.03 | 0.14 ± 0.19 |

* For motoneurons, $n = 81$ for properties 1–4, and $n = 49$ for properties 5–7; for internuclear neurons, $n = 36$ for properties 1–4, and $n = 26$ for properties 5–7.
size). These negative findings, however, are far from conclusive. The use of EMG amplitude as a measure of motor-unit size is suspect because the size of the EMG potential clearly depends on the proximity of the recording electrode to the motor unit studied. Likewise, the latency is undoubtedly a complicated function of a very short axonal conduction time, a longer and more variable delay associated with the synaptic latency, and the conduction time from the synapse to the EMG recording site. We measured the latency more precisely for seven MNs in one monkey by stimulating the abducens nerve intracranially via an indwelling bipolar stimulating electrode. As Delgado-Garcia et al. (4) found in the cat, there was a weak relation between the latency and $K_S$ and between $K_S$ and threshold (cf. Fig. 5). The critical relation between threshold and latency, which they did not plot, was not significant for our seven MNs ($r = 0.24$ for the linear regression). Although Delgado-Garcia et al. (4) interpreted their findings as supporting a "size principle" for recruitment of MNs in the cat, the question remains open in the monkey. They also interpreted similar data for INNs as supporting a size principle in premotor elements (5); however, our data for an equivalent number of monkey INNs show no relation between threshold and latency, even though we also found significant linear correlations between latency and $K_S$ and between $K_S$ and threshold.

**Interpretation of $K$ and $R$**

Three features of our data do not fit the single-time-constant model of MN firing. First, the rate-position constant, $K$, is not, in fact, constant. For most MNs and all INNs, the $K$ measured during movement was higher than that measured during static fixation. Second, the rate-velocity constant, $R$, also is not constant, but decreases significantly with increasing frequencies of sinusoidal pursuit (Fig. 7A). Accordingly, $R/K$, which has the dimensions of a time constant, also decreases with increasing frequency. Finally, following a saccade, the firing rate continues to decline slowly even though the eye is stationary. These data and other observations from the literature, including modeling, support the view that Eq. 1 (the first-order model) is not an accurate description of the relation between MN firing rate and eye position.

For the last 15 yr, the first-order description of MN behavior has served as a framework for interpreting neuronal signals not only to MNs but to other eye movement neurons as well. Our data suggest that some of these interpretations must be reevaluated. Two examples will illustrate this point. Delgado-Garcia et al. (5) noted that the time constant of their INNs calculated as $R/K$, in which $K$ was measured during fixation and $R$ was determined during the slow phase of the VOR, was considerably larger than that computed from the phase shift between firing rate and eye position during sinusoidal rotations in the light. Because the difference between these time constants was much smaller for MNs, they suggested that INNs must receive more "velocity input" via vestibular pathways than do MNs. On the basis of our findings, however, an alternative explanation is that the use of $K_S$ overestimates the actual dynamic time constant because $K_S < K_D$. Because the difference between $K_S$ and $K_P$ is greater for INNs, the overestimation of the time constant for INNs will be even more severe. Delgado-Garcia et al. (4, 5) also noted that $R$, measured as peak burst firing rate divided by peak saccadic velocity, differed from the $R$ measured during the VOR in the light. This finding also is not surprising because $R$ is strongly dependent on frequency (Fig. 7A). The dependence of the "constants" $K$ and $R$ on frequency and on the behavioral situations under which they are obtained requires that the discharge patterns of neural structures be compared under the same conditions.

Other subtle differences in the tracking during two behavioral conditions may also produce apparent differences in $K$ or $R$. For example, in pursuit of sinusoidal targets, saccades occur in the same direction as the smooth pursuit velocity. The effect of the slow decay (or "slide") of neural firing after the saccade is to increase a rising firing rate and decrease a falling one; thus, poor tracking, which requires more saccades, produces an apparent small-phase lead in firing rate when compared with ideal tracking. Indeed, our data show a slight tendency for MNs to have more phase lead during smooth pursuit
than during head rotations with a target fixed in space (when there are fewer saccades). Similarly, during the VOR in the dark, where saccades are opposite to the slow compensatory eye movements, the slide induces a small phase lag. The different values of $R$ in abducens MNs measured during smooth pursuit and during the VOR (35) may, in part, reflect this fact rather than a true difference in velocity inputs during the different behaviors.

Although differences in $K$ or $R$ for different behaviors should be viewed with caution, we believe these parameters are still useful descriptors, like gain and phase, with the understanding that their values are context-dependent. However, they should be considered only as summaries of the data and not as indicators of how the oculomotor system actually functions. For example, it is not valid to view the two terms of Eq 1 as corresponding to identifiable position and velocity input signals to MNs. The dependence of $K$ and $R$ on frequency in our data shows that $K$ reflects not only the effect of eye position on firing rate, but also reflects contributions of higher-order terms; similarly, $R$ reflects the effect of more than just velocity.

In an attempt to account for higher-order dynamics yet preserve the original meaning of $K$ and $R$, Keller (20) and van Gisbergen et al. (38) proposed that an acceleration-dependent term be added to Eq 1. The resulting equation better modeled the vergence (20) and saccadic (38) eye movements they studied, but was equivalent to multiplying the actual inertia of the globe by a factor of at least 25 and predicted unphysiological motoneuron firing rates and muscle forces (see below). In contrast, to explain the adaptation of the ocular slide produced by post-saccadic dysmetria, Optican and Miles (26) suggested a different, more sophisticated description. Their formulation, which is equivalent to the model proposed by Goldstein and Robinson (13) to explain the exponential decay of MN firing following a saccade, can be written as

$$ FR - K\dot{\theta} + R\dot{\theta} + u\dot{\theta} - T_{3}\dot{FR} $$

(2)

where $\theta$, $\dot{\theta}$, and FR are as before, $\ddot{\theta}$ is eye acceleration, $u$ is a constant, and $T_{3}$ is the time constant of the post-saccadic slide in MN firing rate. While not perfect, Eq 2 accounts for more of the available data than Eq 1. The last two terms not only produce the postsaccadic slide in MN firing, but also give rise to components of MN firing that are in phase with position and velocity and thus contribute to $K$ and $R$ during sinusoidal tracking.

It is not known whether the terms of Eq 2 can be attributed to specific MN inputs, as seemed to be possible for Eq 1. Translated into neural terms, the theoretical suggestion that MNs have position, velocity, and filtered velocity inputs (26) still implies that each signal (e.g., slide) may be supplied by a different type of oculomotor neuron. However, in at least one premotor nucleus, the medial vestibular nucleus, the discharge of many neurons already reflects an integrated combination of position, velocity, and filtered velocity signals. For example, most medial vestibular neurons that have eye-position sensitivity (i.e., burst-tonic and tonic-vestibular-pause neurons) also exhibit a slide in firing following saccades in both the on- and off-directions (Scudder and Fuchs, in preparation).

Indeed, because for all neurons membrane adaptation is likely to generate at least a rudimentary slide in neuronal firing rate following a change in input, and because every position change must be accompanied by the appropriate dynamic input, it is possible that position, velocity and filtered velocity signals are not separate anywhere in the oculomotor system.

Simulations of orbital dynamics

To quantitatively compare the ability of the various models to fit data reported here and elsewhere, we implemented the models (see APPENDIX) digitally, and used them to simulate MN firing rates for different types of eye movement. The second-order model of Goldstein and Robinson (13), which was derived for monkey saccades, provided a large improvement over the model responses produced by Eq 1. Unfortunately, the second-order model predicted that the phase shift between firing rate and eye position would have an inflection (between 0.5 and 1 Hz) that is present in neither our data nor those of others. To eliminate the inflection, we borrowed a term from Robinson (29) to approximate the dynamics of extraocular muscle activation. The resulting third-order model resem-
the third-order model, but are nicely fit by the third-order model. Goldberg (11) also found that the phase shift of cat MN firing as a function of frequency had a lower slope than that predicted by the single-time-constant model. The third-order model also correctly predicts that \( R \) should decrease with increasing frequency (Fig. 10B), although it underestimates the rate of decrease. Finally, the third-order model correctly predicts that \( K_3 \) should be larger than \( K_s \), and that, on average, it should exhibit a modest, albeit too rapid, increase between 0.3 and 2.0 Hz (Fig. 10C).

The third-order model is even worse at simulating the behavior of INNs. Even if longer time constants are used, the third-order model accounts for, at most, 35% of the 115% difference between \( K_s \) and \( K_3 \).

Figure 11 shows the predicted time course of MN discharge rate and muscle force that would be required to generate a saccadic eye movement with either the third-order model of orbital dynamics (solid lines) or the modifications of the first-order model (dotted lines) proposed by van Gisbergen et al. (38). These simulations confirm the conclusions of Goldstein and Robinson (13) that only high-

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**Fig. 10.** Comparison of our data (solid dots) with the parameters predicted by the simple first-order model of Eq. 1 (dashed lines) and our third-order model (solid lines). A-C show the relation of the phase shift (\( \phi \)) of unit firing relative to eye position, the position coefficient (\( K \)), and the velocity coefficient (\( R \)) as a function of the tracking frequency. \( K_s \) for both models was set equal to the \( K_s \) from the data; the time constants for both models were set equal to that of the data at 0.5 Hz. See APPENDIX for further details.

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**Fig. 11.** Simulated motoneuron firing rate and net muscle force required to generate the 10° saccade simulated in the bottom trace. Predictions were based on the third-order model detailed in the APPENDIX (solid lines), and the van Gisbergen et al. (38) modification of the first-order model (dotted lines). The latter model generates more force for a given discharge rate because it neglects the force-velocity relation of muscle. The eye velocity and position traces were generated from equations contained in the APPENDIX.
er-order models can generate saccades using physiologically reasonable muscle forces and MN discharges. For example, to generate a 10° monkey saccade, first-order orbital dynamics requires a peak force of about 100 g, about twice the maximum force that the monkey lateral rectus is able to generate (8) and about five times the force recorded during a similar human saccade (3). Although the peak motoneuron discharge rate of 560 spikes/s is only modestly excessive, the model ignores the decrement in active state muscle tension produced by the force-velocity relation. If this decrement is included, MNs would need to reach unrealistic peak discharges of about 900 spikes/s. Van Opstal et al. (39) revealed another difficulty with the modified first-order model, namely, that a huge braking force is required to shorten the duration of small saccades to realistic values. We have confirmed the existence of this problem and have also seen that the addition of muscle dynamics to the modified first-order model requires the antagonist MNs to discharge at a peak rate almost as high as the earlier agonist burst to stop a 2° saccade in time. In contrast, our third-order model (Fig. 11) generates a 10° saccade with a realistic 24 g of force, a peak discharge of 300 spikes/s, and requires no braking pulse. Also, the slow decline in MN firing rate following the saccade is an automatic consequence of the third-order model (13, 26, 29).

In conclusion, we believe that these analyses of pursuit and saccadic data argue compellingly that the single-time-constant model is a poor approximation of orbital dynamics under all circumstances and should be abandoned for a more realistic, higher-order description.

APPENDIX

Our model is Robinson’s (29) linear fourth-order plant with some parameters, $T_3$ and $T_m$ (see below), modified to describe monkey, rather than human, eye movements, and with the inertia of the globe ignored, thereby reducing it to a third-order model. We reduced the time constant of the muscle ($T_m$) from 20 to 10 ms to resemble the monkey’s rapid-twitch tension times. Assuming a peak force of 50 g, these parameters give a reasonable fit to the tetanic stimulation data of Fuchs and Luschei (8) for shock rates > 100 Hz.

The resistive forces surrounding the globe are modeled by two Voigt elements (each a spring and dashpot in parallel) that are connected in series. Using Laplace notation, the resulting relation between eye position $\theta(S)$ and muscle force $F_m(S)$ is given by

$$\frac{\theta(S)}{F_m(S)} = \frac{1}{K_1 + R_1S} + \frac{1}{K_2 + R_2S}$$  \hspace{1cm} (A1)

where $K_i$ is the spring constant and $R_i$ is the dashpot force-velocity coefficient for the $i$th Voigt element. Rearranging and substituting

$$\frac{\theta(S)}{F_m(S)} = \frac{1}{K_T(1 + T_1S)(1 + T_2S)}$$  \hspace{1cm} (A2)

where $T_1 = R_1/K_1 = 0.012$ s, $T_2 = R_2/K_2 = 0.760$ s, and $K_T = 1/(1/K_1 + 1/K_2) - 1.0$ g/deg are all taken from Goldstein and Robinson (1984) for the monkey and $T_3 = (K_1 + R_2)/(K_1 + K_2) = 0.140$ s was manipulated to fit smooth pursuit data at 0.5 Hz.

Our approach was to assume an eye movement, compute its derivatives, and integrate the differential equations for orbital dynamics to obtain the relation of muscle force with time. From Eq. A2

$$F_m - \frac{K_T}{T_3}(\theta + (T_1 + T_2)\dot{\theta} + T_1T_2\ddot{\theta}) = \frac{1}{T_3}F_m$$ \hspace{1cm} (A3)

We then used a differential equation for muscle dynamics to obtain the active state force, $F_0$. From Robinson (29)

$$F_0 = F_m + T_m\dot{F}_m + R_m\dot{\theta}$$ \hspace{1cm} (A4)

where $R_m = 0.04$ g·deg·s$^{-1}$, the damping due to the muscle force-velocity relation, $T_m = R_m/K_m = 0.01$ s, the time constant of the muscle, and $K_m = 4$ g/deg, the spring constant of the series elastic component.

Finally, motoneuron firing rate ($FR$) was obtained from active state tension according to

$$FR = \frac{K_S}{K_T}F_0$$ \hspace{1cm} (A5)

For pursuit, the eye movement was assumed to be sinusoidal ($\pm 10^\circ$). Calculation of the phase shift ($\phi$) during pursuit included a 4-ms delay owing to conduction time in the abducens nerve and muscle activation time (8, 30). $K_T$ was computed as (firing rate·cos $\phi$)/10$^3$, and $R_m$ was computed as (firing rate·sin $\phi$)/(10$^3$·2$\pi$f), where $f$ is the frequency. For saccades, we assumed a velocity ($V$) given by

$$V = V_0\left(\frac{\pi t}{D} + 0.2 \sin \frac{2\pi t}{D} + 0.04 \sin \frac{3\pi t}{D}\right)^{1/4}$$ \hspace{1cm} (A5)

where $0 < t < D$, $D = 30$-ms saccade duration, and $V_0 = 640^\circ$/s for a monkey 10° saccade. This arbitrary formula is simply one of many that gives a reasonable “eyeball” approximation of saccadic...
velocity but also allows the manipulation of skew (conveyed by the second harmonic) and saturation (conveyed by the third harmonic). Velocity was integrated to obtain eye position and differentiates to obtain acceleration.

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