Quantitative Analysis of Abducens Neuron Discharge Dynamics During Saccadic and Slow Eye Movements

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Sylvestre, Pierre A. and Kathleen E. Cullen. Quantitative analysis of abducens neuron discharge dynamics during saccadic and slow eye movements. J. Neurophysiol. 82: 2612–2632, 1999. The mechanics of the eyeball and its surrounding tissues, which together form the oculomotor plant, have been shown to be the same for smooth pursuit and saccadic eye movements. Hence it was postulated that similar signals would be carried by motoneurons during slow and rapid eye movements. In the present study, we directly addressed this proposal by determining which eye movement–based models best describe the discharge dynamics of primate abducens neurons during a variety of eye movement behaviors. We first characterized abducens neuron spike trains, as has been classically done, during fixation and sinusoidal smooth pursuit. We then systematically analyzed the discharge dynamics of abducens neurons during and following saccades, during step-ramp pursuit and during high velocity slow-phase vestibular nystagmus. We found that the commonly utilized first-order description of abducens neuron firing rates \( FR = b + kE + rE, \) where \( FR \) is firing rate, \( E \) and \( E^\prime \) are eye position and velocity, respectively, and \( b, k, \) and \( r \) are constants) provided an adequate model of neuronal activity during saccades, smooth pursuit, and slow phase vestibular nystagmus. However, the use of a second-order model, which included an exponentially decaying term or “slide” \( FR = b + kE + rE + uE + vE + wE - cFR \), not only improved our ability to describe neuronal activity when the eye was moving and also enabled us to model abducens neuron discharges during the postsaccadic interval. We also found that, for a given model, a single set of parameters could not be used to describe neuronal firing rates during both slow and rapid eye movements. Specifically, the eye velocity and position coefficients \( r \) and \( k \) in the above models, respectively) consistently decreased as a function of the mean (and peak) eye velocity that was generated. In contrast, the bias \( b \) (firing rate when looking straight ahead) invariably increased with eye velocity. Although these trends are likely to reflect, in part, nonlinearities that are intrinsic to the extraocular muscles, we propose that these results can also be explained by considering the time-varying resistance to movement that is generated by the antagonist muscle. We conclude that to create realistic and meaningful models of the neural control of horizontal eye movements, it is essential to consider the activation of the antagonist, as well as agonist motoneuron pools.

**INTRODUCTION**

To move the eye to a new position, the net force generated by the extraocular muscles must compensate for the passive restraining forces of the eyeball, extraocular muscles, and supporting orbital tissues (i.e., the “oculomotor plant”). Robinson (1964) characterized the oculomotor plant during saccadic eye movements and found that the mechanics are dominated by its viscoelastic properties. As a consequence of the viscous drag opposing eye rotation, the extraocular muscles must generate a burst of force (or “pulse”) to produce rapid saccadic eye movements. Furthermore, after a saccade, the muscles must generate a tonic force (or “step”) to counteract the elastic elements of the orbital tissues and hold the eyeball stationary in the orbit. Finally, during the transition from the pulse to the step, an exponential decay in force offsets the slow viscoelastic properties of the orbital tissues, thereby improving ocular stability.

Based on 1) his characterization of the oculomotor plant mechanics, and 2) a linear approximation of the relationship between motoneuron drive and resultant muscle force, Robinson (1964) proposed a model of the net neural drive \( (FR_{NET}) \) during saccades

\[
FR_{NET} = b + kE + rE + uE + vE + wE - cFR
\]

where \( FR_{NET} \) represents the difference between the firing rates of the agonist and antagonist motoneurons, \( b \) is the motoneuron’s activity when the eye is stationary in the center of the orbit, \( E, E', E^\prime, \) and \( E^\prime\prime \) are eye position, eye velocity, eye acceleration, and higher order derivatives of eye rotation, \( FR \) is the derivative of the net firing rate, and the parameters \( k, r, u, v, w, \) and \( c \) are constants. During saccades, the net neural drive \( (FR_{NET}) \) to the extraocular muscles is provided almost entirely by the agonist motoneuron pool, because most antagonist motoneurons cease firing or “pause” during saccadic eye movements (Fuchs and Luschei 1970; Robinson 1970; Schiller 1970). Therefore it follows that Eq. 1 should provide a good description of agonist motoneuron activity during saccades.

Robinson and colleagues showed that the “pulse-step” nature of oculomotor (Robinson 1970) and abducens (Robinson and Keller 1972) neuron discharges during saccades could be approximated using a first-order simplification of Eq. 1

\[
FR = b + kE + rE
\]

This model has since been commonly used to describe the saccade-related discharges of these neurons. To date, only a single study has attempted to develop a more complete description of abducens neuron discharges during saccades (Van Gisbergen et al. 1981). Using a graphic method, in which the acceleration term was determined by trial-and-error, Van Gisbergen and colleagues proposed that motoneuron discharges are dynamically related to both eye velocity and eye acceleration. They further proposed that a better description of the relationship between abducens neuron activity and eye movements might be obtained with

\[
FR = kE + f(E) + uE
\]
where $f(E)$ represents a nonlinear function of eye velocity. However, a limitation of this study was that the graphic analysis method did not lend itself to objectively determining the relative contribution of each of the linear and nonlinear terms in Eq. 3, because all terms were not simultaneously estimated. In addition, this study did not address the importance of the higher order eye movement derivatives and cFR terms in Eq. 1.

A first-order model (Eq. 2) has also been commonly used to describe neuronal discharges during slower eye movements including fixation, smooth pursuit, vergence, and slow-phase vestibular nystagmus (Henn and Cohen 1973; Keller and Robinson 1971; King et al. 1994; Robinson and Keller 1972; Skavenski and Robinson 1973). However, it has been suggested that some additional terms in Eq. 1 must be retained to describe the dynamics of abducens neuron discharges. Keller (1973) and Goldstein (1983) proposed adding an eye acceleration term, and a cFR term to Eq. 2, respectively. More recently, Fuchs et al. (1988) and Stahl and Simpson (1995) used Eq. 2 to calculate eye position ($k$) and eye velocity ($r$) sensitivities of abducens neuron discharges during sinusoidal eye movements at different frequencies. During such eye motion, the estimated eye position and eye velocity sensitivities are only “apparent” because, for example, they would also reflect neuronal sensitivities to acceleration and jerk, respectively. Indeed, Fuchs and colleagues proposed that a third-order simplification of Eq. 1 is required to describe the frequency dependence of their calculated $k$ and $r$ values. Stahl and Simpson (1995) obtained a similar frequency dependence in their analysis but argued that a second-order simplification of Eq. 1 is sufficient when the model’s time constants are properly selected. The conclusions of both studies were based on indirect estimates of the terms in Eq. 1 that were obtained by fitting the averaged $r$ and $k$ coefficients. To date, no direct evaluation of each term in Eq. 1 has been performed by fitting the discharges of individual neurons.

Although the discharge of abducens nucleus (ABN) neurons has been studied during rapid (e.g., saccadic) and slower (e.g., smooth pursuit and slow-phase vestibular nystagmus) eye movements, a unifying description of the agonist neuronal drive to the extraocular muscles has not yet been reported. However, Robinson (1965) demonstrated that the mechanics of the oculomotor plant are identical for saccades and smooth pursuit. Consequently, in this study, we sought to construct a mathematical model that best describes the input-output relationship between abducens neuron firing rates and eye movements during saccades as well as slower eye movements. We directly fitted neuronal discharges using an approach similar to that taken by Cullen and Guitton (1997), which allowed us to objectively evaluate the relative importance of each term in Eq. 1 during paradigms for which the dynamic profiles of eye position, velocity, and higher order derivatives differed.

Our results indicate that a second-order simplification of Eq. 1 provides an improved description of abducens neuron discharges when compared with that obtained with Eq. 2. However, the coefficients that were estimated for this higher order model varied as a function of both the mean and peak eye velocities generated during the different behavioral paradigms. Although these trends are likely to reflect, in part, nonlinearities that are intrinsic to the extraocular muscles (Barmack 1977; Close and Luff 1974; Collins 1971; Goldberg et al. 1998; Shall et al. 1996), we suggest that our results are also consistent with the relative change in active force that is generated by the antagonistic muscle during slow versus rapid eye movements. We conclude that to create realistic models of oculomotor control, future work should consider the activation of antagonist as well as agonist motoneuron pools.

**METHODS**

Two rhesus monkeys (macaca mulatta) were prepared for chronic extracellular recording using aseptic surgical techniques. All procedures were approved by the McGill University Animal Care Committee and were in compliance with the guidelines of the Canadian Council on Animal Care.

**Surgical procedures**

The animals were preanesthetized using ketamine hydrochloride (12–15 mg/kg im). In addition, atropine sulfate (0.04 mg/kg im) and valium (1 mg/kg im) were administered to reduce salivation and provide muscle relaxation, respectively. Surgical levels of anesthesia were then achieved using isoflurane gas (2–3%, initially) inhaled through an endotracheal tube, and maintained for the duration of the surgery (0.8–1.5%). Heart rate, blood pressure, respiratory rate, and body temperature were monitored for the duration of the procedure. To allow electrode access into the brain stem, craniotomies were performed on both animals. A dental acrylic implant was fastened to each animal’s skull using stainless steel screws. A stainless steel post, which was used to restrain the animal’s head during the experiment, and a stainless steel recording chamber, which was positioned to provide access to the abducens nucleus region (posterior angle of 30° and lateral angle of 30°), were cemented to the implant. In addition, an 18–19 mm diam eye coil (3 loops of teflon-coated stainless steel wire) was implanted in the right eye behind the conjunctiva (Fuchs and Robinson 1966). After the surgery, buprenorphine (0.01 mg/kg im) was utilized for postoperative analgesia, and the antibiotic trimethyl sulfate (TMS; 24%, 0.125 ml/kg im, for 5 days) was administered to prevent infection. Animals were given 2 wk to recover from the surgery before any experiments were performed.

**Data acquisition procedures**

During each experiment, the monkey was comfortably seated in a primate chair that was mounted on a vestibular turntable. The monkey’s head was restrained for the duration of the experiment, and the room was dimly lit. Extracellular single-unit activity was recorded using enameled insulated tungsten microelectrodes (7–10 MΩ impedance, Frederick Haer) as has been described elsewhere (Cullen and Guitton 1997). The abducens nucleus was identified on the basis of an increase in background activity that occurred just below the fourth ventricle. The simultaneous activity of the neurons in this structure produced a characteristic “singing beehive” sound, which was clearly related to ipsilaterally directed eye motion, when the recorded activity was fed into an audio monitor (Fuchs and Luschei 1970; Robinson 1970). Only units for which this unique sound could be heard in the background were included in the present study. The location of each neuron was further confirmed using three-dimensional reconstructions of electrode tracts; units that were located in regions >0.5 mm from the estimated center of the abducens nucleus were not included in the present study.

The abducens nucleus contains three classes of neurons: 1) motoneurons (MNs) that project directly to the lateral rectus, 2) internuclear neurons (INNs) that project contralaterally to the medial rectus division of the oculomotor nucleus, and 3) neurons that project to the cerebellum. It has been shown that the signals carried by abducens MNs and INNs are qualitatively similar during all types of eye
movements (Delgado-Garcia et al. 1986a,b; Fuchs et al. 1988; Gamlin et al. 1989). Due to the invasiveness of implanting an electrode in the abducens nerve for antidromic activation (Delgado-Garcia et al. 1986a), and/or a recording electrode in the lateral rectus for spike-triggered averaging (Fuchs et al. 1988), we elected not to electrophysiologically identify MNs and INNs. Instead, we compared the discharge characteristics of the neurons in the present study with those of the identified MNs and INNs in the study of Fuchs et al. (1988), and estimated that our sample contained roughly equal numbers of MNs and INNs (see Fig. 11 in RESULTS). Floccular projecting neurons appear to constitute only a small percentage of abducens nucleus neurons and are primarily confined to the dorsal/rostral perimeter of the nucleus (Blanks et al. 1983; Langer et al. 1985; Rodella et al. 1996). Therefore we estimate that our sample contained only a small proportion, if any, of these units.

Unit activity, horizontal and vertical eye positions, target position, and table velocity were recorded on digital audio tape for later playback. The isolation of each unit was then carefully reevaluated off-line. An abducens neuron was only considered to be adequately isolated when discrete action potential waveforms could be clearly dissociated from the surrounding background activity during saccades (Fig. 1) as well as during fixation and smooth pursuit. During playback, action potentials were discriminated using a windowing circuit (BAK Electronics) following amplification and filtering of the recorded activity (Cullen and Guitton 1997). Eye position, target position, and table velocity signals were low-pass filtered at 250 Hz (analogue 8-pole Bessel filter) and sampled at 1 kHz. Subsequent analysis was performed using custom algorithms (Matlab, Mathworks).

**Behavioral paradigms**

Both monkeys were trained to follow a target light for a juice reward. The activity of abducens neurons was recorded during fixation, saccades, smooth pursuit, and whole-body rotations in the dark that elicited the vestibuloocular reflex (VOR). A target light (HeNe laser) was projected, via a system of two galvanometer controlled mirrors, onto an isovergence screen located 60 cm away from the monkey’s head. Target movements and on-line data displays were controlled using REX, a QNX-based real-time acquisition system (Hayes et al. 1982).

Ipsilaterally and contralaterally directed saccades were elicited by stepping the target between horizontal positions in blocked trials (predictable, ±5, 10, 15, 20, 25, and 30°) and unblocked trials (random, ±5, 10, 15, 20, 25 and 30°). In addition, saccades with different starting positions, amplitudes, and velocity profiles were obtained using the “barrier” paradigm in which a food target appeared unexpectedly on either side of an opaque screen facing the monkey (Cullen and Guitton 1997).

Smooth pursuit eye movements were elicited using two different types of target motion: 1) sinusoidal trajectories (40°/s peak velocity, 0.5 Hz) and 2) step-ramp trajectories (Rashbass 1961). A step-ramp trial began when the animal fixated a stationary target with its eye centered in the orbit (defined as “primary position”). After a random fixation period (750–1,500 ms) the target was stepped toward either the left or the right, and then began moving at a constant velocity (20, 40, or 60°/s) in the direction opposite to that of the step. When the step size was properly chosen, it was possible to obtain smooth eye movements that were not preceded by corrective saccades.
Neuronal activity was also recorded during slow-phase vestibular nystagmus. First, rapid manual rotations of the vestibular turntable were utilized while the monkey sat in complete darkness to elicit slow-phase velocities up to 200°/s (rapid VOR, VORk) (Roy and Cullen 1998). Second, a sinusoidal whole-body rotation paradigm in which the monkey maintained fixation on a target that moved with the vestibular turntable was used (VOR cancellation, VORc; 40°/s peak velocity, 0.5 Hz).

Analysis of abducens neuron discharges

Before analysis, recorded eye position signals were digitally filtered at 125 Hz and digitally differentiated to produce eye velocity profiles. A spike density function, in which a Gaussian function was convolved with the spike train (standard deviation of 5 ms for saccades and VORk, and 10 ms for fixation, VORc, step-ramp, and sinusoidal smooth pursuit), was employed to represent the neuronal discharges of abducens neurons (Cullen and Guitton 1997; Cullen et al. 1996).

Analysis during fixation. Only periods of steady fixation >100 ms in duration that did not include the 50-ms period following or preceding a saccade, and for which mean eye positions were within the linear range of the unit (Robinson 1970) were included in the analysis. A standard bivariate linear regression between mean firing rate and fixation position was used to obtain the horizontal eye position sensitivity (Kfix) and the resting discharge at primary position (碥) of each neuron.

Dynamic analysis during saccades. We utilized a system identification technique that has been previously developed for the analysis of horizontal inhibitory burst neurons (IBNs) located in the paramedian pontine reticular formation (Cullen et al. 1996; Cullen and Guitton 1997). This method allowed us to determine how well different models based on the dynamics of eye movement trajectories (models M1–M9; Table 1) predicted abducens neuron discharges during saccades. An advantage of using this approach was that each sampled data point could be utilized in the analysis. For example, a single saccade of 100 ms duration sampled at 1 kHz would have provided 100 data points to the optimization algorithm. A dynamic lead time value (tₐ) was determined for each abducens neuron (see results) and used in the optimization of the models shown in Table 1.

Saccade onsets and offsets were defined using a ±20°/s eye velocity criterion. For each unit, optimal model fits were obtained from an ensemble of ~40 ipsilaterally directed horizontal saccades of amplitudes ranging from 3–30° (Cullen and Guitton 1997). Special care was taken to include only saccades for which the initial eye position was ipsilateral to the neuron’s eye position threshold (Robinson 1970). Thus to characterize neuronal discharges during larger saccades (i.e., amplitudes up to 30°), only neurons for which the eye position threshold was contralateral to the primary position were included in the analysis.

To compare each model’s ability to estimate neuronal discharges, variance-accounted-for (VAF) coefficients were computed. The VAF was computed as (1 - [var (est - fr)/var (fr)]), where est represents the modeled firing rate and fr represents the actual firing rate. The VAF provided a normalized measure of each model’s goodness-of-fit that allowed comparisons across models and neurons. Note that a VAF of 0.50 indicates that 50% of the variability in a unit’s discharge is explained by the model, corresponding to a correlation coefficient (R) of 0.71 in a bivariate linear regression. Furthermore, because adding extra terms to a model invariably improves its goodness-of-fit, we also computed the Bayesian information criteria (BIC) (Caines 1988; Cullen et al. 1996). This value serves as a “cost index” that indicates whether increasing the complexity of the model can be justified by the accompanying increase in VAF (Schwartz 1978). A relative decrease in the BIC value indicates that an increase in model complexity is warranted.

Dynamic analysis during postsaccadic slide. Approximately 10 postsaccadic intervals were selected for each cell. Intervals were chosen that 1) were exempt of artifacts and 2) followed saccades of amplitudes between 5 and 15°. Each interval spanned the period from saccade onset until 200 ms after saccade offset (equivalent to Phase 5 as described by Goldstein 1983). Parameters were estimated for models M3 and M8 (Table 1). The same optimization techniques as described in the Dynamic Analysis during Saccades section were used to determine the best model fit. The initial conditions (ICs) for the exponentially decaying term of model M8 (cfR) were taken from the data (see Cullen et al. 1996), and the optimal lead time tₐ was taken from the saccadic analysis.

Dynamic analysis during smooth pursuit. We investigated the ability of different dynamic models to predict the activity of abducens neurons during sinusoidal smooth pursuit (model M3; Table 1) and step-ramp pursuit (models M1–M5, and M8; Table 1). Abducens neuron discharges were first characterized during five or more cycles of sinusoidal smooth pursuit that contained few saccades and for which pursuit gain was >0.8. Only segments that did not include the 50-ms period following or preceding a corrective saccade were included in the analysis (Cullen et al. 1993). Abducens neurons were also characterized during the initiation of step-ramp pursuit (initial 100–150 ms), where the eyes were still accelerating (Robinson 1965). The onset of the pursuit eye movement was determined using a double linear regression method (Carl and Gellman 1987; Wellenius 1999). Trials in which a corrective saccade was made were excluded from the analysis. Model fits were made to an ensemble of 5–10 trials of step-ramp pursuit. We studied the lead time of five neurons in detail and found that the effect of varying tₐ on ramps was extremely small when compared with saccades. Therefore we elected to offset the eye movement traces by the same tₐ that we had used in our analysis of saccadic eye movements (see results).

Dynamic analysis during VOR. We also investigated the ability of models M1–M5 and M8 (Table 1) to predict the activity of abducens neurons during slow-phase vestibular nystagmus. Segments of slow phase VOR were chosen in which the peak velocities ranged

### Table 1. Downstream models and mean VAF and BIC values estimated during saccades

<table>
<thead>
<tr>
<th>Model Number</th>
<th>Models</th>
<th>N</th>
<th>VAF</th>
<th>BIC</th>
<th>VAF re M3</th>
</tr>
</thead>
<tbody>
<tr>
<td>M1</td>
<td>$FR(t) = \tau\tilde{E}(t - t_0)$</td>
<td>1</td>
<td>-1.1</td>
<td>9.6</td>
<td>-1.7</td>
</tr>
<tr>
<td>M2</td>
<td>$FR(t) = b + \tau\tilde{E}(t - t_0)$</td>
<td>2</td>
<td>0.33</td>
<td>8.1</td>
<td>-0.26</td>
</tr>
<tr>
<td>M3</td>
<td>$FR(t) = b + \tau\tilde{E}(t - t_0) + \alpha\tilde{E}(t - t_0)$</td>
<td>3</td>
<td>0.59</td>
<td>7.6</td>
<td>0</td>
</tr>
<tr>
<td>M4</td>
<td>$FR(t) = b + \tau\tilde{E}(t - t_0) + \alpha\tilde{E}(t - t_0) + \beta\tilde{E}(t - t_0)$</td>
<td>4</td>
<td>0.60</td>
<td>7.6</td>
<td>0.01</td>
</tr>
<tr>
<td>M5</td>
<td>$FR(t) = b + \tau\tilde{E}(t - t_0) + \alpha\tilde{E}(t - t_0) + \gamma\tilde{E}(t - t_0)$</td>
<td>5</td>
<td>0.60</td>
<td>7.6</td>
<td>0.01</td>
</tr>
<tr>
<td>M6</td>
<td>$FR(t) = b + \tau\tilde{E}(t - t_0) + \alpha\tilde{E}(t - t_0) + \eta\tilde{E}(t - t_0)$</td>
<td>4</td>
<td>0.60</td>
<td>7.5</td>
<td>0.01</td>
</tr>
<tr>
<td>M7</td>
<td>$FR(t) = b + \tau\tilde{E}(t - t_0) + \alpha\tilde{E}(t - t_0) + \eta\tilde{E}(t - t_0) + \xi\tilde{E}(t - t_0) + \mu\tilde{E}(t - t_0)$</td>
<td>6</td>
<td>0.62</td>
<td>7.5</td>
<td>0.03</td>
</tr>
<tr>
<td>M8</td>
<td>$FR(t) = b + \tau\tilde{E}(t - t_0) + \alpha\tilde{E}(t - t_0) + \eta\tilde{E}(t - t_0) + \xi\tilde{E}(t - t_0) + \mu\tilde{E}(t - t_0) + \nu\tilde{E}(t - t_0)$</td>
<td>5</td>
<td>0.66</td>
<td>7.4</td>
<td>0.07</td>
</tr>
<tr>
<td>M9</td>
<td>$FR(t) = b_{ns} + k_{ns}\tilde{E}(t - t_0) + \tau\tilde{E}(t - t_0)$</td>
<td>3</td>
<td>0.38</td>
<td>8.1</td>
<td>-0.21</td>
</tr>
</tbody>
</table>

$N$ is number of model parameters. VAF, mean variance-accounted-for; BIC, mean Bayesian information criteria.
Segments of records spanning the interval 50 ms immediately preceding quick phases to 50 ms immediately following quick phases were excluded from the analysis. Each model fit was made to an ensemble of 20–40 VOR intervals. Eye movement traces for this analysis were offset by the optimal lead time \( t_d \) determined during saccades (see RESULTS).

RESULTS

Neuronal database

A total of 46 isolated ABN neurons were analyzed during steady fixation, during saccades, immediately following saccades (postsaccadic intervals), and during sinusoidal smooth pursuit. Recordings from 37 of these neurons were obtained from monkey B, whereas 9 were obtained from monkey C. In addition, the firing rates of 25% of these neurons were also analyzed during pursuit of step-ramp target motion and during VOR.

Figure 2 shows the firing rate of a typical ABN neuron, unit B76_2. During fixation, this unit’s tonic firing rate increased proportionally with ipsilateral eye position (Fig. 2A). It generated a burst of action potentials during ipsilaterally directed saccades (“on direction”) and ceased firing (paused) during contralaterally directed saccades (“off direction”; Fig. 2A, filled and open arrows, respectively). In addition, the modulation of this neuron’s firing rate led ipsilateral eye position during sinusoidal smooth pursuit (Fig. 2B). Finally, this unit was unresponsive to head movements; during sinusoidal VOR, paradigms, the residual modulation of this unit’s firing rate could be accurately predicted based on the neuron’s sensitivity to eye position and eye velocity (Fig. 2C).

In our sample, all neurons had an on direction response similar to unit B76_2 during saccades (Fig. 2A, filled arrows). Eighty-one percent of these neurons paused completely for off direction saccades of all amplitudes (\( \geq 3^\circ \)). Unit B76_2, which was in this category, paused completely during 5, 15, and 30° saccades (Fig. 3A). The remaining 19% of the neurons in our sample ceased firing only during large saccades. Figure 3B shows the response of the unit for which we found the least inhibition during off direction saccades (unit B11_1). This neuron paused completely only for saccades >15°.

Estimation of lead time

The time by which an ABN neuron’s burst led saccadic eye movements was calculated using two methods. In the first method, the dynamic lead time by which an ABN neuron’s firing rate preceded saccadic eye movement onset, \( t_d \), was estimated using a first-order model (model M3; Table 1) (Cullen et al. 1996; Cullen and Guitton 1997). Results are shown in Fig. 4A (B76_2, for example). The lead time that provided the largest VAF was defined as the optimal dynamic lead time, \( t_d \), and is shown by the thick arrow in Fig. 4A (in this example, \( t_d = 10 \text{ ms} \)). We also attempted to compute the value of \( t_d \) using a second-order model (model M4; Table 1).
Mark the onset and offset of saccades based on a 20°/s eye velocity criterion.

The onset of saccades was 13 ms (small thin arrow). The acceleration term is physiologically unrealistic, we reestimated that constant in model M4. Because a negative sign of the acceleration term estimated using “latency tuned” modeling (M4c) was inconsistent with a monosynaptic projection than is the 7.2 ms difference obtained using the first spike method.

Figure 4A clearly shows that model M3 was more sharply “latency tuned” than model M4. In addition, to our surprise, the sign of the acceleration term estimated using model M4 was always negative at the optimal lead time. Because a negative acceleration term is physiologically unrealistic, we reestimated \( t_d \) using a version of model M4 in which the sign of the acceleration term was constrained to be nonnegative (model M4c; not in tables). The results of this analysis are shown in Fig. 4B (thick line). We found that the value of the acceleration term in model M4c consistently converged to zero at \( t_d \). The \( t_d \) estimated using model M4c was always identical to the value determined using model M3. We also attempted to estimate the lead time with more complex models. However, it became increasingly difficult to compute a reliable estimate of lead time because the influence of this parameter was obscured by the other parameters that were simultaneously optimized (see Cullen et al. 1996). Accordingly, in the present study, we utilized model M3 for the determination of \( t_d \). When the eye movement trajectories were shifted by \( t_d \), the main portion of the ABN neuron burst was well aligned with the duration of the saccade.

Prior studies have estimated ABN neuron lead times by calculating the time interval between the occurrence of the first spike in the burst (as determined by visual inspection) and onset of saccadic eye movement. We also measured the lead times of our neurons using this method and found that the values obtained were significantly shorter than those provided by the dynamic analysis method (4.4 ± 1.2 versus 9.4 ± 1.9 ms, respectively; mean ± SE, Student t-test, \( P < 0.01 \)). Across our sample of neurons, we observed a weak but significant linear relationship (\( R = 0.37 \), \( P < 0.01 \)) between these two different estimates of lead time.

Figure 5 illustrates the distribution of lead times that were obtained using both methods (black bars). For comparison, the lead times obtained by Cullen and Guitton (1997) for short lead inhibitory burst neurons (IBNs located in the paramedian pontine reticular formation) are also shown (gray bars). A difference of 2.4 ms was found when comparing the mean \( t_d \) of short lead IBNs to that of ABN neurons (Fig. 5A). In contrast, the lead times estimated for short lead IBNs using the method of the first spike were on average 7.2 ms longer than those calculated using the same method for ABN neurons (Fig. 5B).

Short lead IBNs are known to project monosynaptically to the abducens nucleus (Hikosaka et al. 1978; Strassman et al. 1986a,b). Because a monosynaptic connection is generally associated with <1.3 ms processing delays, the 2.4 ms difference observed between the dynamic latency estimates is more consistent with a monosynaptic projection than is the 7.2 ms difference obtained using the first spike method.

Metric analysis during fixation

Numerous studies have demonstrated that the mean firing rate of an ABN neuron is well related to eye position during periods of steady fixation. We verified this relationship for our sample of neurons. Figure 6A shows the results for unit B76_2. The inset illustrates two fixation intervals that complied with our criteria (see METHODS). Figure 6B shows the regression lines plotted for each neuron in our sample. During fixation, the mean firing rate was well correlated with eye position for all 46 neurons \( [b_{\text{FIX}} (y-intercept) = 97 \pm 67 \text{ spikes/s}, k_{\text{FIX}} (slope) = 5.2 \pm 2.7 \text{ (spikes/s)/deg, and } R = 0.80 \pm 0.14] \). In the present study, we made no attempt to control for hysteresis in ABN neuron firing rates (Goldstein and Robinson 1986). However, the strong correlations that we obtained in our analysis of fixation suggest that the relative contribution of hysteresis to the firing rate of ABN neurons was small.
were set to that provided by model M3.

provided a sharper estimate of the optimal lead time than did model M4.

component of their discharges. "burst"

inherent position sensitivity made it difficult to isolate the "burst" component of their discharges.

By using dynamic analysis techniques, we were able to obtain an objective estimate of each ABN neuron’s position sensitivity during saccades (see Dynamic analysis during saccades section below). We used model M3 (Table 1) to estimate the saccadic eye position sensitivity of each neuron (ksac; as a convention, the k refers to the model parameter, and the subscript SAC refers to the paradigm during which it was estimated). The neuronal firing rate was first corrected by subtracting the time-varying eye position contribution (ksacE), thus unmasking the remaining burst signal. An eye position–corrected NOS (NOSC) was then computed by multiplying the residual firing rate (during saccades only) by the saccade duration. As a control, we computed NOSc using a ksac value of 0 and found that NOSc estimates differed from the measured NOS on average by <1 spike (−0.6 ± 0.6 spike).

The NOSC was well correlated with saccade amplitude for our example neuron (Fig. 7A, unit B76_2). Figure 7B shows the regression lines for our sample of neurons (thin lines). The mean regression coefficient (R) for our sample was 0.89 ± 0.06. The averaged slope obtained for the NOSC versus saccade amplitude relationship was 0.96 ± 0.46 spikes/deg, with an intercept of 3.3 ± 2.3 spikes (thick line). Cullen and Guitton (1997) reported slightly lower correlation coefficients (R = 0.79), and similar slopes (1.0 ± 0.5 spikes/deg) in a comparable analysis of IBNs.

We also estimated the relationship between peak eye velocity and peak firing rate (corrected for eye position) during saccades. Figure 7C shows this relationship for our example neuron, unit B76_2. Although we observed lower correlations (R = 0.48 ± 0.19) than for the NOSC analysis, 85% of our units had significant relationships (P < 0.05) between their peak firing rate and peak velocity. The mean slope was 0.27 ± 0.22 (spikes/s)/(deg/s), with a mean intercept of 242 ± 116 spikes/s. Figure 7D shows the regression lines for the 39 ABN neurons for which this relationship was significant. Removing the seven units with nonsignificant correlations did not change the mean values significantly (P > 0.05). The mean correlation for this relationship was larger than that which has been reported previously for primate IBNs (mean R = 0.39) (Cullen and Guitton 1997). In addition, larger slopes were obtained for IBNs [0.40 ± 0.20 spikes/s/(deg/s)] (Cullen and Guitton 1997) than for the ABN neurons in the present study.

**Dynamic analysis during saccades**

We constructed a set of models that allowed us to systematically investigate which terms from Eq. 1 are required to predict ABN neuron discharges during saccades (models M1–M5 and M8–M9; Table 1). We also investigated other models that have been suggested by prior analyses of ABN neurons and IBNs (models M6–M7; Table 1). The mean VAF and BIC values obtained during saccades, for each model, are provided in Table 1. The improvement in the mean VAF value relative to model M3 is also shown for each model. We chose model M3 as our reference because it represents the first-order model that is often used in the oculomotor literature to describe ABN neuron discharges (Eq. 2). Table 2 provides the mean parameters that were estimated for each model during saccades (associated ranges are shown in parentheses).

Given that the saccadic burst of ABN neurons is thought to originate principally from EBNs that are known to carry an eye velocity signal, we determined the percentage of variance in an

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**Figure 4**. Example of the variance-accounted-for (VAF) provided by 1st- and 2nd-order models of ABN neuron discharges using different lead times. A: relationship between the VAF values and time by which a burst was shifted toward the saccade. This relationship was determined for B76_2 using models M3 (FR = b + kE + rE; ) and M4 (FR = b + kE + rE + aE; ). Model M3 provided a sharper estimate of the optimal lead time than did model M4 (t_a = 10 and 13 ms, respectively). B: acceleration term (α) estimated in model M4 was generally negative. Because a negative E term is physiologically unrealistic, we utilized a version of model M4 in which the acceleration term was constrained to take nonnegative values (M4c). The VAF values obtained with model M4c are illustrated as a function of lead time (thick line). Because the acceleration term in this model was invariably zero at t_a, the optimal lead times estimated using models M4c and M3 were identical. Dynamic lead times (t_a) were set to that provided by model M3 (and M4c) in the subsequent analysis.

**Metric analysis of saccades**

Excitatory and inhibitory premotor burst neurons in the paramedian pontine reticular formation (EBNs and IBNs, respectively) provide the primary drive to ABN neurons during saccades. Previous studies have demonstrated that the number of spikes (NOS) generated by EBNs and IBNs is well correlated to saccade amplitude (Cullen and Guitton 1997; Scudder 1988; Strassman et al. 1986a,b). A comparable analysis has never been performed on ABN neurons, presumably because their inherent position sensitivity made it difficult to isolate the “burst” component of their discharges.

By using dynamic analysis techniques, we were able to...
ABN neuron’s discharge that could be predicted by a model based solely on eye velocity (model M1; Table 1). The negative VAF obtained for model M1 (mean VAF = -1.1) indicates that the model fit was poor, and that in fact fitting a mean value through the firing rate profiles would have provided a better fit. The addition of a bias term (model M2; Table 1) resulted in a significant increase in VAF (mean VAF = 0.33). Including a position term (model M3; Table 1) further increased the VAF (mean VAF = 0.59), highlighting the need for such a term even when describing the “pulse” portion of the neuronal drive. Note that the BIC values decreased markedly as terms were sequentially added (compare models M1–M3), confirming the importance of the position and bias terms.

Model M3 is generally recognized as a good estimate of ABN neuron activity during fixation, smooth pursuit, and saccades (Fuchs and Luschei 1970; Keller 1973; Keller and Robinson 1972). The fit of model M3 to the firing rate of our example neuron during saccades is shown in the top panel of Fig. 8. The thicker line represents the model fit that is superimposed on the actual firing rate (shaded area). In addition, the average parameters and VAF estimated across all neurons are shown below the model fits.

The addition of an acceleration term to model M3 had little influence on our ability to predict ABN neuron discharges (model M4; Table 1). The mean VAF value of model M4 was increased by only 1%, and the BIC value was the same for both models (Table 1). Moreover, the value of the estimated acceleration term was most often (99%) negative and invariably very small (Table 2). The similarity between this model’s ability to fit the data and that of model M3 is illustrated in Fig. 8 (compare the 2nd and top panels). We also found that the addition of a jerk term to model M4 was not warranted, because
the mean VAF and BIC values obtained with model M5 were identical to those of model M4 (Table 1).

In the present study, we also investigated the usefulness of nonlinear models. The first nonlinear model (M6; Table 1) included an amplitude-dependent term (*r*). Prior analyses had demonstrated that such a term is important for describing IBN discharges during saccades (Cullen and Guitton 1997). We therefore postulated that an amplitude-dependent term might also be present on ABN neuron discharges. However, the addition of this term only marginally improved our ability to fit ABN neuron firing rates (VAF = 0.60 vs. 0.59, BIC = 7.5 vs. 7.6, M6 vs. M3, respectively).

A second nonlinear model was tested that included a second- and third-order nonlinearity (r1E2 and r2E3) in addition to the terms of model M4 (M7; Table 1). This model was included in our analysis to approximate the hypothesis of Van Gisbergen and colleagues (1981) that a nonlinear function of eye velocity as well as an eye acceleration term are necessary to accurately predict the firing rate of ABN neurons during saccades (Eq. 3).

Model M7 provided little improvement in the mean sample VAF when compared with model M3 (VAF = 0.62 vs. 0.59, BIC = 7.5 vs. 7.6, respectively). The small decrease in BIC for model M7 versus M3 implies that the addition of nonlinear terms was warranted. Nevertheless, the accompanying small increase in VAF indicates that these terms have a relatively small influence on neuronal discharge dynamics.

We also evaluated the importance of the cFR in Eq. 1 for describing ABN neuron discharges during saccades. Goldstein (1983) first quantified this term in the interval immediately following saccades. In our analysis, we investigated whether such a transient term was important during saccades. We first added this term to model M3 (FR = b + kE + rE – cFR; not in tables). This model yielded generally negative and invariably very small estimates for cSAC (mean = –0.0003 ± 0.0008 ms). Note that during saccades, the shapes of the firing rate and of the eye velocity profiles were very similar (Fig. 8), and consequently, FR(t) ≈ E(t – t0), approximately. Hence it follows that adding a cFR term to model M3 roughly simplifies to model M4. Furthermore, adding a cFR to model M3 resulted in a relative increase in BIC (7.7 vs. 7.6, respectively), which confirms that the simple addition of a FR(t) term to model M3 was not warranted.

We next tested a model that provided a second-order simplification of Eq. 1, model M8. This model contained an acceleration term in addition to a slide term. It provided a notable increase in mean VAF when compared with model M3 (mean VAF = 0.66 vs. 0.59, respectively), which was accompanied by a relative decrease in BIC (mean BIC = 7.4 vs. 7.6, respectively). As previously mentioned, FR(t) ≈ E(t – t0), approximately, during saccades. However, although the dynamic profiles of these two terms may be similar, it is clear that they are not identical; the resultant increase in VAF obtained with the addition of both acceleration and slide terms indicates that the dynamics of the two terms interact in a synergistic manner to fit neuronal discharges.

The parameter values (*b*, *k*, and *r*) obtained using model M8 did not differ significantly from those estimated using model M3. Importantly, this model was the only one for which the estimates of the acceleration term were in the ON direction of the unit (Table 2). The model fit to the firing rate of unit B76_2 using model M8 is illustrated in Fig. 8 (bottom panel) for the same three example saccades that were used to illustrate fits for models M3 and M4. Note that the parameter estimates for the term obtained in the present study (cSAC = 15 ± 16 ms) were comparable to those previously calculated for short lead IBNs using a similar model (cIBN = 19 ± 16 ms) (Cullen and Guitton 1997).

We also tested a variation of model M8 for which the ICs of the cFR term were estimated separately for each saccade rather
TABLE 2. Mean model parameters estimated during saccades, with associated ranges

<table>
<thead>
<tr>
<th>Model Number</th>
<th>Bias, $\hat{b}$</th>
<th>Position, $k$</th>
<th>Velocity, $r$</th>
<th>Acceleration, $\hat{a}$</th>
<th>Others, $\bar{v}$, $\bar{z}$, or $\bar{c}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$M1$</td>
<td>180 (54–401)</td>
<td>0.97 (0.39–2.8)</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>$M2$</td>
<td>156 (4–387)</td>
<td>0.32 (0.03–1.5)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$M3$</td>
<td>163 (5–389)</td>
<td>0.42 (0.12–1.5)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$M4$</td>
<td>156 (2–391)</td>
<td>0.41 (0.11–1.5)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$M5$</td>
<td>151 (4–395)</td>
<td>0.41 (0.11–1.5)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$M6$</td>
<td>134 (4–292)</td>
<td>0.41 (0.11–1.5)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$M7$</td>
<td>172 (–15–404)</td>
<td>0.42 (0–1.26)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$M8$</td>
<td>96 (2–247)</td>
<td>0.42 (0–1.26)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$M9$</td>
<td>156 (4–389)</td>
<td>0.42 (0.12–1.5)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$M10$</td>
<td>156 (4–387)</td>
<td>0.42 (0.12–1.5)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$M11$</td>
<td>156 (4–387)</td>
<td>0.42 (0.12–1.5)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$M12$</td>
<td>156 (4–387)</td>
<td>0.42 (0.12–1.5)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Values in parentheses are ranges.
The model often yielded highly nonphysiological values for estimated parameters. For example, large unrealistic values were generally estimated for the bias (mean bias = −346 spikes/s). Similar results were obtained in a prior analysis of IBN discharges (Cullen and Guitton 1997).

We conclude that model M3 provided a good description of ABN neuron discharges during saccades. Adding higher order derivatives of eye position or nonlinear terms to this simple first-order model only marginally improved our capacity to predict ABN neuron saccadic firing rates. Finally, a second-order model that included a cFR term (model M8) provided the most accurate description of ABN neuron discharges of the models that we tested.

A striking result of this analysis was that the dynamic eye position sensitivities of ABN neurons estimated using either model M3 or M8 during saccades were considerably smaller than the static values estimated during fixation (\(k_{SAC} < k_{FIX}\), \(P < 0.05\)). In addition, the biases estimated during saccades were notably larger than those estimated during fixation (\(b_{SAC} > b_{FIX}\), \(P < 0.01\)). To further emphasize this result, we tested a final model (model M9; Table 1). This model was similar to model M3, with the difference that its bias and position parameters were assigned the values estimated during fixation (i.e., \(b_{FIX}\) and \(k_{FIX}\)). The mean sample VAF provided by this model was very poor (Table 1); the value was comparable to those of our worst models (M1 and M2; Table 1).

Dynamic analysis of postsaccadic slide

We next analyzed the firing rate of ABN neurons during the 200-ms time interval that immediately follows the end of a saccade. During this interval, the eyes are immobile; however, the firing rate of ABN neurons decays exponentially. Theoretically, the cFR term of Eq. 1 would express itself as an exponentially decaying term with a time constant of \(\tau\). To evaluate the importance of a cFR term during the postsaccadic interval, and to characterize its time course, we estimated the parameters of two models: model M3, and model M8 (Table 1). Note, because \(\dot{E} = 0\) and \(\ddot{E} = 0\) during the postsaccadic interval, model M3 simplifies to \(FR = b + kE\), and model M8 simplifies to \(FR = b + kE - cFR\).

Figure 9 shows the fits obtained using these two models for our example neuron, unit B76.2. Comparison of the top and second rows of Fig. 9 (models M3 and M8, respectively) clearly shows that an exponentially decaying term is required to properly model the firing rate of ABN neurons during this post-saccadic interval (mean VAF: 0.49 vs. 0.92, M3 vs. M8). Figure 10 shows the distribution of time constants (\(c_{POST}\)) for the 46 neurons in the present sample (filled bars). The mean \(c_{POST}\) obtained for our sample was 26 ± 20 ms. This value did not differ significantly from the estimate obtained during saccades (\(c_{POST} \approx c_{SAC}\); \(P > 0.05\)). The \(c_{POST}\) values obtained by Goldstein (1983), who used a similar approach, are shown in Fig. 10 for comparison (\(c_{POST} = 72 ± 28\) ms, \(n = 14\)). Note that our estimated \(c_{POST}\) values were significantly smaller (\(P < 0.01\)) than those reported by Goldstein (1983). We consider this difference in the DISCUSSION.

200 sp/s
200 deg/s
20 deg
100 msec

FIG. 8. Examples of model fits to ABN neuron B76.2 burst activity during saccades. A simple 1st-order model, model M3 (\(FR = b + kE + \dot{E}\)), provided excellent predictions of ABN neuron discharges during saccades (top row). Furthermore, the addition of an acceleration term to model M3, to produce model M4 (\(FR = b + kE + \dot{E} + aE\)), was not very effective in decreasing model error (2nd row). However, the addition of a term that decayed exponentially with time (cFR) as well as an acceleration term to model M3 (M8: \(FR = b + kE + \dot{E} + aE - cFR\)) provided a significant improvement in our ability to fit ABN neuron discharges during saccades (mean sample VAF = 0.59, 0.60, and 0.66 for models M3, M4, and M8, respectively). The mean parameter values for the entire sample of neurons are provided below each model fit. The figure illustrates 3 example saccades for unit B76.2 where the shaded trajectories represent firing rates, and the superimposed curves represent the fits produced by each model. Bottom two rows: the accompanying eye velocity and eye position trajectories that have been shifted in time by the estimated optimal dynamic lead time \(t_d\).
DYNAMICS OF ABDUCENS NEURON DISCHARGES

The average eye position ($k_{SP}$) and eye velocity ($r_{SP}$) sensitivities for our sample of cells were $5.6 \pm 3.5$ (spikes/s)/deg and $1.3 \pm 0.9$ (spikes/s)/(deg/s), respectively (not in tables). The average bias ($b_{SP}$) was $108 \pm 76$ (spikes/s)/(deg/s). The position sensitivity values estimated during sinusoidal smooth pursuit using model M3 were on average slightly larger, although not significantly, than those estimated during fixation ($k_{SP} \approx k_{FIX}$). The same also applied to the bias values estimated during the two behaviors ($b_{SP} \approx b_{FIX}$). However, the eye position and eye velocity sensitivity values estimated during sinusoidal smooth pursuit were significantly larger than the values estimated during saccades ($k_{SP} > k_{SAC}, P < 0.05; r_{SP} > r_{SAC}, P < 0.01$). In contrast, the bias values estimated during sinusoidal smooth pursuit were significantly smaller than those estimated during saccades ($b_{SP} < b_{SAC}, P < 0.01$).

For each unit in our sample, its eye position sensitivity during fixation ($k_{FIX}$) and its eye velocity sensitivity during sinusoidal smooth pursuit ($r_{SP}$) were plotted as a function of eye position threshold (Fig. 11, A and B, respectively). Figure 11A shows the regression line that Fuchs and colleagues (1988) obtained for the relationship between eye position sensitivities during fixation ($k_{FIX}$) and eye position thresholds for identified abducens MNs. Many of the neurons in the present study were plotted in the vicinity of this line. We also plotted each neuron’s eye position threshold versus its eye velocity sensitivities during sinusoidal smooth pursuit ($r_{SP}$; Fig. 11B). The broken line in Fig. 11B is based on the data of Fuchs et al. (1988); neurons that were located above and below this line were, in general, INNs and MNs, respectively. We utilized this line to estimate the percentage of MNs versus INNs in our sample (an approach similar to that of Broussard et al. 1995), and concluded that our sample contained approximately 24 MNs and 22 INNs. We investigated whether the discharges of putative MNs were better described by dynamic models than the discharges of putative INNs. We found that regardless of the paradigm that was utilized, a given model described the discharges of both groups of neurons equally well.

The discharges of a subset of neurons in our sample ($n = 11$) were also analyzed during step-ramp pursuit. Step-ramp trajectories are well suited for this approach because they elicit smooth pursuit eye movements for which the eye acceleration profiles are distinguishable from the eye position profiles (Fig. 12). This contrasts with sinusoidal smooth pursuit, for which the eye position and eye acceleration profiles are exactly 180° out of phase.

During ipsilaterally directed step-ramp pursuit, the firing rate of ABN neurons increased continuously (Fig. 12, A and C, units B96_1 and B116_2, respectively). The neuronal firing rate likewise decreased during contralaterally directed pursuit (Fig. 12, B and D, units B96_1 and B116_2, respectively), and often (for 40% of the units in our sample) reached cutoff (when the unit stops firing action potentials) during the initial acceleration interval. On average, those cells that were driven into

![Figure 9](http://jn.physiology.org/...) Examples of model fits to ABN neuron activity (unit B76_2) immediately following saccades (postsaccadic interval). A simple 1st-order model, model M3 ($FR = b + \kappa E + \dot{E}$), provided poor predictions of ABN neuron discharges during the postsaccadic interval (top row). In contrast, the addition of an acceleration ($\ddot{E}$) and an exponentially decaying term ($cFR$) to model M3 (e.g., M8) greatly improved our ability to estimate ABN neuron postaccadic activity (mean sample VAF = 0.49 and 0.92 for models M3 and M8, respectively). The time constant of the exponential term for a typical neuron (unit B76_2) was long when compared with that of the sample mean ($t_{POST} = 65$ vs. 26 ms, respectively). Top 2 rows: shaded areas show the actual firing frequency profiles, and heavy solid lines show the estimated firing rates. Bottom 2 rows: the accompanying eye velocity and position trajectories that have been temporally shifted by the estimated optimal dynamic lead time $t_{o}$. Dynamic analysis during smooth pursuit

The firing rates of all 46 ABN neurons in our sample were modeled during 0.5 Hz, 40°/s peak velocity sinusoidal smooth pursuit eye movements using model M3. The average eye position ($k_{SP}$) and eye velocity ($r_{SP}$) sensitivities for our sample of cells were $5.6 \pm 3.5$ (spikes/s)/deg and $1.3 \pm 0.9$ (spikes/s)/(deg/s), respectively (not in tables). The average bias ($b_{SP}$) was $108 \pm 76$ (spikes/s)/(deg/s). The position sensitivity values estimated during sinusoidal smooth pursuit using model M3 were on average slightly larger, although not significantly, than those estimated during fixation ($k_{SP} \approx k_{FIX}$). The same also applied to the bias values estimated during the two behaviors ($b_{SP} \approx b_{FIX}$). However, the eye position and eye velocity sensitivity values estimated during sinusoidal smooth pursuit were significantly larger than the values estimated during saccades ($k_{SP} > k_{SAC}, P < 0.05; r_{SP} > r_{SAC}, P < 0.01$). In contrast, the bias values estimated during sinusoidal smooth pursuit were significantly smaller than those estimated during saccades ($b_{SP} < b_{SAC}, P < 0.01$). For each unit in our sample, its eye position sensitivity during fixation ($k_{FIX}$) and its eye velocity sensitivity during sinusoidal smooth pursuit ($r_{SP}$) was plotted as a function of eye position threshold (Fig. 11, A and B, respectively). Figure 11A shows the regression line that Fuchs and colleagues (1988) obtained for the relationship between eye position sensitivities during fixation ($k_{FIX}$) and eye position thresholds for identified abducens MNs. Many of the neurons in the present study were plotted in the vicinity of this line. We also plotted each neuron’s eye position threshold versus its eye velocity sensitivities during sinusoidal smooth pursuit ($r_{SP}$; Fig. 11B). The broken line in Fig. 11B is based on the data of Fuchs et al. (1988); neurons that were located above and below this line were, in general, INNs and MNs, respectively. We utilized this line to estimate the percentage of MNs versus INNs in our sample (an approach similar to that of Broussard et al. 1995), and concluded that our sample contained approximately 24 MNs and 22 INNs. We investigated whether the discharges of putative MNs were better described by dynamic models than the discharges of putative INNs. We found that regardless of the paradigm that was utilized, a given model described the discharges of both groups of neurons equally well.

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During ipsilaterally directed step-ramp pursuit, the firing rate of ABN neurons increased continuously (Fig. 12, A and C, units B96_1 and B116_2, respectively). The neuronal firing rate likewise decreased during contralaterally directed pursuit (Fig. 12, B and D, units B96_1 and B116_2, respectively), and often (for 40% of the units in our sample) reached cutoff (when the unit stops firing action potentials) during the initial acceleration interval. On average, those cells that were driven into
cutoff were silent for approximately \( \frac{1}{3} \), \( \frac{1}{2} \), and \( \frac{2}{3} \) of the acceleration interval duration for 20, 40 and 60°/s step-ramp trials, respectively. Figure 12D shows an example of a neuron (unit B116_2), which demonstrated cutoff during 40°/s OFF direction pursuit.

The VAF values provided by models M1–M5 and M8 are shown in Table 3 for each of the three ramp velocities tested. Several conclusions can be made from these results. First, model M3 is the simplest model to provide an accurate description of ON direction firing rates (Table 3; Fig. 12, A and C). Recall that negative VAF values mean that the model fit provided by a given model was worse than simply fitting the data with a mean value. Second, the BIC values suggest that adding an acceleration term is not warranted, but that adding both acceleration and jerk terms marginally improved the model fit (models M4 and M5, respectively; Table 3). None of the model parameters differed significantly (\( P > 0.05 \)) across the three step-ramp velocities tested (Table 4). We also tested the usefulness of model M8 during step-ramp pursuit. The improvements in VAF values obtained during step ramps using model M8 relative to M3 were similar to those observed during saccades (Table 3). The parameter values of \( b \), \( k \), and \( r \) estimated using model M8 did not differ significantly (\( P > 0.05 \)) from those estimated using model M3. Furthermore, the time constant estimates \( (c_{SR}) \) for the exponentially decaying term were smaller than those estimated during saccades (6 ± 20, 8 ± 17, and 8 ± 9 ms for 20, 40, and 60°/s velocity, respectively); however, these differences were not significant (\( P > 0.05 \)).

We also tested the ability of model M3 to predict OFF direction discharges during step-ramp pursuit. Example model fits are shown in Fig. 12B for unit B96_1. This neuron was typical of the majority of ABN neurons in our sample (60%) that did not reach cutoff during the initiation of OFF direction step-ramp pursuit. Its discharge could be modeled as a mirror image of its ON direction responses, because the parameter values obtained during ON and OFF direction pursuit were very similar (82 vs. 83 spikes/s, \( b_{ON} \) vs. \( b_{OFF} \); 3.0 vs. 4.2 (spikes/s)/deg, \( k_{ON} \) vs. \( k_{OFF} \); 0.40 vs. 0.37 (spikes/s)/(deg/s), \( r_{ON} \) vs. \( r_{OFF} \)). Figure 12D shows an example of an ABN neuron, unit...
B116_2, that reached cutoff during OFF direction pursuit. As for unit B90_3, the ON and OFF direction responses were nearly mirror images while the unit was firing (thick black line). However, when the parameter values estimated before cutoff were utilized to predict the neuron’s discharge after cutoff, unrealistic negative firing rates were obtained (thick gray line). Hence the OFF direction responses of 40% of the units in our sample could not be modeled as a mirror image of their ON direction responses for the duration of the acceleration interval.

We also compared the parameter values estimated during 40°/s step-ramp pursuit (using model M3) to the values estimated during other paradigms. Note that the saccadic data obtained for the subset of neurons that were analyzed during step-ramp pursuit were included in Tables 3 and 4 to facilitate comparison. The bias and the eye position sensitivity values estimated during step-ramp pursuit did not differ significantly from the equivalent values estimated during fixation (biX ≈ biSR; kiX ≈ kiSR). However, the values estimated during step-ramp pursuit for all three parameters of model M3 were found to differ significantly from the values estimated during saccades (biSAC > biSR; Pi < 0.01; kiSAC < kiSR; Pi < 0.01; riSAC < riSR; Pi < 0.01). In summary, we observed significant trends in the parameter values estimated during different behavioral paradigms (i.e., biSR, biFIX < biSAC; kiSAC < kiFIX < kiSR; riSAC < riSR). We will consider these differences in the DISCUSSION.

Dynamic analysis during rapid VOR

In the previous sections, we have reported the results of our analysis of ABN neuron spike trains during smooth pursuit and
In addition, all ABN neuron
eral whole-body rotations (ON direction responses; Fig. 13)
movements falling in a “velocity gap” (~100—300°/s) be-
tween these two different classes of eye movements. Here we
have analyzed the activity of ABN neurons during slow phases
of VOR elicited by rapid whole-body rotations (VORR). The
VORR responses generated during this paradigm were of par-
cular interest because nonsaccadic eye velocities up to 200°/s
could be achieved, thus effectively bridging the velocities
generated in smooth pursuit and saccadic eye movement par-
adigms.

We analyzed the discharges of the same subset of neurons
that were previously characterized during step-ramp pursuit.
The ABN neuron firing rates increased during ipsilat-
eral whole-body rotations (ON direction responses; Fig. 13A).
In addition, all ABN neuron firing rates decreased, and most
reached cutoff, during contralaterally directed VORR eye
movements (Fig. 13B). The likelihood that a neuron would be
driven into cutoff was roughly half way between that observed
during 40°/s step-ramp pursuit (40%) and large saccades
(100%). Specifically, we found that within the first 100 ms of
VORR, 50% of the units were always driven into cutoff, 33%
of the units were driven into cutoff >60% of the time, and the
remaining 17% of the units were driven into cutoff <30% of
the time.

As was the case for saccades and step-ramp pursuit, model
M3 provided a good estimate of the neurons’ firing rate during
VORR (Table 3). The addition of acceleration or jerk terms did
not improve the VAF values markedly (models M4–M5, Table
3). We found that the average parameter estimates during
VORR tended to fall between those estimated during pursuit
and saccades (i.e., $b_{\text{FIX}}$, $b_{\text{VOR}}$, $b_{\text{SR}}$, $b_{\text{SAC}}$; $k_{\text{SAC}}$, $k_{\text{VOR}}$ < $k_{\text{FIX}}$
< $k_{\text{SR}}$; $r_{\text{SAC}}$ < $r_{\text{VOR}}$, $r_{\text{SR}}$). However, except for a significant

![Fig. 13](https://example.com/fig13)

**FIG. 13.** Examples of model fits to ABN neuron activity (unit B90.3) during VORR. Slow-phase segments with eye velocities up to 200°/s (vertical dotted lines) could be obtained using this paradigm. A: a 1st-order model (M3, FR = $b + kE$) provided good fits to this ABN neuron activity during ON direction VORR. B: this neuron was driven into cutoff during OFF direction VORR. The unrealistic firing rate values (i.e., less than zero) predicted by this model are shown as a gray extension of the model fits. **Top row:** shaded area shows actual firing frequency profiles, and the heavy solid line represents the estimated firing rates. **Bottom traces:** accompanying eye velocity, eye position, and head velocity trajectories.

<table>
<thead>
<tr>
<th>Paradigm</th>
<th>Model Number</th>
<th>Bias, $b$</th>
<th>Position, $k$</th>
<th>Velocity, $r$</th>
<th>Acceleration, $\dot{a}$</th>
<th>Slide, $\dot{c}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>SR 20°/s</td>
<td>M3</td>
<td>73 (28–172)</td>
<td>8.7 (2.1–18.0)</td>
<td>0.76 (0.15–1.5)</td>
<td>0.26 (0.05–1.8)</td>
<td>0.006 (0.0005–0.073)</td>
</tr>
<tr>
<td>SR 40°/s</td>
<td>M3</td>
<td>76 (8–173)</td>
<td>8.3 (0.95–16.7)</td>
<td>2.0 (0.13–8.0)</td>
<td>0.30 (0.17–1.2)</td>
<td>0.006 (0.0005–0.060)</td>
</tr>
<tr>
<td>SR 60°/s</td>
<td>M3</td>
<td>70 (30–169)</td>
<td>7.6 (2.2–15.9)</td>
<td>1.1 (0.14–2.0)</td>
<td>0.30 (0.17–1.2)</td>
<td>0.006 (0.0005–0.060)</td>
</tr>
<tr>
<td>VORR</td>
<td>M3</td>
<td>72 (34–170)</td>
<td>7.2 (2.7–13.0)</td>
<td>2.9 (0.26–9.9)</td>
<td>0.30 (0.17–1.2)</td>
<td>0.006 (0.0005–0.060)</td>
</tr>
<tr>
<td>Saccade</td>
<td>M3</td>
<td>77 (41–173)</td>
<td>6.0 (3.7–17.2)</td>
<td>1.0 (0.02–2.0)</td>
<td>0.30 (0.17–1.2)</td>
<td>0.006 (0.0005–0.060)</td>
</tr>
<tr>
<td></td>
<td>M8</td>
<td>95 (46–172)</td>
<td>7.4 (3.2–18.8)</td>
<td>3.0 (0.29–9.0)</td>
<td>0.54 (0.01–2.6)</td>
<td>0.006 (0.0005–0.060)</td>
</tr>
</tbody>
</table>

Table 4. Mean model parameters estimated during step-ramp pursuit, VORR, and saccades for a subset of units (N = 11)
difference between the position sensitivity values estimated during VOR\(_R\) and step-ramp pursuit (\(k_{\text{VOR}} < k_{SR}; \ P < 0.05\)), the values estimated during VOR\(_R\) did not differ significantly from those estimated during either step-ramp pursuit or saccades. Representative fits provided by model M3 for ON direction VOR\(_R\) are shown in Fig. 13A, for unit B90_3. Figure 13B shows that, in general, only a fraction of the OFF direction discharges could be accurately predicted using a model estimated during ON direction VOR\(_R\) (thick black line).

We also tested the usefulness of model M8 during VOR\(_R\). The results we obtained were consistent with those obtained during saccades and smooth pursuit: adding an eye acceleration and a slide term to model M3 improved our ability to fit ABN neuron discharges during VOR\(_R\) (model M8), and the parameter estimates of \(b, k,\) and \(r\) did not differ significantly from those obtained using model M3. Furthermore, the estimated time constants (\(c_{\text{VOR}} = 19 \pm 20\) ms, Table 4) were not significantly different from those estimated during saccades.

**Discussion**

The oculomotor system, because of its relative simplicity, is well suited to a modeling approach (see Robinson 1981a–c; Van Gisbergen and Van Opstal 1989). Here, we compared the ability of a series of linear and nonlinear eye movement–based models that have been postulated to describe MNs firing rates. The models that we tested were based on prior characterizations of 1) the oculomotor plant (Robinson 1964, 1965), 2) ABN neuron discharges (Fuchs et al. 1988; Goldstein 1983; Goldstein and Robinson 1986; Keller and Robinson 1972; Stahl and Simpson 1995; Van Gisbergen et al. 1981), and 3) the upstream drive to ABN neurons known to be carried by premotor burst neurons (Cullen and Guitton 1997).

**Comparison with previous studies**

In the present study, the dynamic lead time estimates were significantly longer than those determined using the onset of the first spike. Using the first spike method, we obtained a mean lead time of 4.4 ± 1.2 ms. While similar values were obtained by Keller and Robinson (1972) (5.4 ms), longer values have been obtained in other studies [7.0 ± 1.9 ms (Luschei and Fuchs 1972) and 8.8 ± 1.0 ms (Van Gisbergen et al. 1981)]. This interstudy variability suggests that it is difficult to objectively identify the first spike in the saccadic burst of tonically discharging neurons. Alternatively, our dynamic lead time method provided objective estimates that were consistent with the results of simian muscle activation studies. Following abducens nerve stimulation, twitch times of 6.2 and 7.0 ms have been reported (Fuchs and Luschei 1971 and Shull et al. 1996, respectively). Furthermore, Miller and Robbins (1992) have shown that eye movement lags the increase in agonist lateral rectus activity by 2.6 ms. Together, these results suggest a motoneuron lead time of ~9.2 ms, which is consistent with our dynamic lead time estimates (mean 9.4 ms).

The results of our analysis of primate ABN neuron activity during fixation and sinusoidal smooth pursuit were similar to those of previous studies (Fuchs and Luschei 1970; Fuchs et al. 1988; Robinson and Keller 1972). Moreover, during the interval immediately following saccades, we confirmed the importance of an exponentially decaying (or slide) term in modeling ABN neuron firing rates that was originally quantified by Goldstein (1983). This term was predicted by Robinson’s original characterization of the oculomotor plant and is now ubiquitous to many current models of oculomotor plant dynamics (for example, Fuchs et al. 1988; Optican and Miles 1985; Stahl and Simpson 1995). In the present study, our estimates of the time constant of this term were smaller than those of Goldstein (compare the black and gray bars in Fig. 10). The difference between the two studies could arise from a number of factors: first, to compute firing rates, Goldstein used a method based on interspike intervals that is inherently nonlinear, whereas we utilized a spike density function that rises linearly with increasing frequency (Cullen et al. 1996). Second, we used dynamic lead time estimates for our analysis, whereas Goldstein utilized shorter lead time estimates that were calculated via the first spike method. Finally, the amplitudes of the saccades that we analyzed were smaller than those included in Goldstein’s analysis (5–15 vs. 20° saccades, respectively). These methodological differences most likely explain the discrepancies in time constant measurements of the two studies.

**Dynamics of ABN neuron discharges during saccades**

Our results demonstrate that an adequate model of saccade-related ABN neuron discharges requires, in its most simple form, a bias term, an eye position term, and an eye velocity term (model M3; Table 1). We showed that simply adding higher order derivatives of eye movement (e.g., models M4 and M5; Table 1) to this first-order model only marginally improved its ability to predict neuronal discharges. In addition, we found that including nonlinear terms in our models resulted in little improvement in our ability to fit ABN discharges (models M6 and M7; Table 1). However, the addition of a slide term as well as an acceleration term to model M3 markedly improved our ability to fit saccadic discharges (model M8)

\[
FR = b + cE + \dot{E} + a\ddot{E} - cFR \tag{4}
\]

The fits obtained with model M8 for saccades provided a 12% increase in VAF relative to that of model M3. Furthermore, we found that 1) this model was the only one for which the estimates of the acceleration term were in the ON direction of the unit, and 2) the mean time constant of the decay term was not significantly different from that calculated for the same cells during the post-saccadic interval (\(c_{\text{SAC}} \approx c_{\text{POST}}\)). Hence we conclude that, of all the models we tested, model M8 (Eq. 4) best describes ABN neuron discharges during saccades.

**Dynamics of ABN neuron discharges during smooth pursuit and VOR\(_R\)**

The discharges of a subset of ABN neurons were also analyzed during slower eye movements. Our main conclusion is that the same models (i.e., M3 and M8) that are useful for predicting ABN neuron firing rates during saccades also provide excellent descriptions of ABN neuron firing rates during slower eye movements. Although model M3 provided a good representation of neuronal activity, model M8 provided a 7% increase in VAF values during sinusoidal pursuit, 26, 15, and 3% improvements in VAF values for 20, 40, and 60°/s step-ramp pursuit, respectively, and a 38% improvement in VAF values for VOR\(_R\). The acceleration terms provided by model
$M8$ were always in the ON direction of the unit, and the estimates of the time constant of the slide term ($c_{SP}$, $c_{SR}$, and $c_{VOR}$) were generally smaller, although not significantly, than those calculated during the postsaccadic interval (Table 4).

**Variability of parameter estimates across paradigms**

It is not possible to utilize the results from our analysis to generate a single linear transfer function relating agonist ABN neuron discharges to eye movement dynamics. Although the improvement in VAF provided by increasing model complexity relative to model $M3$ was comparable during saccades, smooth pursuit, and VORR, the coefficient values estimated during smooth pursuit and saccades differed significantly from each other, whereas the values estimated during VORR were located between the two. Figure 14 highlights the trends that we observed for parameters of model $M8$. The eye velocity ($r$) and eye position ($k$) coefficients decreased as peak and mean eye velocity increased (Fig. 14, A and B, respectively), whereas the biases ($b$) increased.

A similar relationship between model parameters and eye velocity has been observed by Fuchs and colleagues (1988). They reported that the values of the eye velocity coefficients estimated during sinusoidal smooth pursuit ($r_{SP}$) decreased as a function of increasing pursuit frequency. However, because the peak-to-peak amplitude of the target motion was kept constant in their experiments, an increase in target frequency was invariably accompanied by an increase in eye velocity. Once reanalyzed as a function of eye velocity, the trends that they reported are comparable to those described in the present study.

**Implications for modeling the control of eye movements**

Our results suggest that linear plant models are useful for describing the discharges of oculomotor motoneurons. However, we found that a single model equation could not be used to describe neuronal discharges across different oculomotor behaviors. This result implies that the model structure of $M8$ is not sufficient to generate a general description of the relationship between ABN neuron discharges and eye movements. To obtain an improved model, two approaches could be used. One obvious approach would be to include nonlinear terms in the model formulation. Prior analyses of extraocular motor-unit responses to nerve stimulation have revealed that the MN-to-muscle transformation is intrinsically nonlinear due to hysteresis, nonlinear summation, saturation of motor-unit force, and muscle mechanical properties (Barmack 1977; Close and Luff 1974; Collins 1971; Goldberg et al. 1998; Shall et al. 1996). However, many of these nonlinearities are not consistent with the trends illustrated in Fig. 14. For example, the inverse relationship between a neuron’s eye velocity coefficient ($r$) and peak/mean eye velocity is in the opposite direction from that which would be predicted based on saturation and nonlinear summation properties of extraocular muscles. Furthermore, it could be argued that attempts to formulate a general description of the relationship between ABN neuron discharges and eye motion are physiologically meaningless; such an analysis would invariably under model the control of eye movements, because it ignores the contribution of the antagonist MNs/muscle to the net force on the eye.

Based on these considerations, we suggest a second approach that includes the relative contributions of the antagonist as well as the agonist muscles to each type of eye motion. The possible role of the antagonist muscle in producing the trends

![Fig. 14. Eye position coefficients (k), eye velocity coefficients (r), and biases (b) varied as a function of the peak and mean eye velocity generated during different behavioral paradigms. Using model M8 (FR = b + kE + rE + uE = cFR), mean r, k, and b values were estimated for a subset of ABN neurons (n = 11). In each panel, the mean parameters that were estimated during 20, 40, and 60°/s step-ramp pursuit, VORR, and saccades are shown. A: values for both the velocity (r) and position (k) coefficients clearly decreased as the peak velocity generated during different paradigms increased. The opposite trend was observed for the bias (b) values. B: values for both the velocity (r) and position (k) coefficients clearly decreased as the mean velocity generated during different paradigms increased. Again, the opposite trend was observed for the bias (b) values.](http://jn.physiology.org/)

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shown in Fig. 14 can be best understood by using the oversimplified system described by model M1 as an example

$$FR^+ = rE$$  \hspace{1cm} (5)$$

where $FR^+$ represents the firing rate of an agonist ABN neuron, $r$ is its eye velocity sensitivity coefficient, and $E$ is the eye velocity. In this simple system, if $r$ is large, a greater change in $FR^+$ is required to generate a given eye movement than if the value of $r$ is small. Therefore because our analysis showed that $r_{SP} > r_{SAC}$ (see Fig. 14), we can conclude that agonist ABN neurons are more efficient at generating eye velocity during saccades than during smooth pursuit. [Note that previous studies on premotor burst neurons (Van Gisbergen et al. 1981) have reported comparable observations in their analysis of small versus large saccades.]

The mechanics of the oculomotor plant are determined by the viscoelastic properties of the agonist and antagonist muscles, as well as by the surrounding orbital tissues (Collins 1971; Robinson 1964, 1981a). During eye movements, the active (i.e., contractile) elements of the agonist muscle drive the rotation of the eye, whereas the inherent passive viscoelastic properties of the extraocular muscles and surrounding orbital tissues combine with the active viscoelastic properties of the antagonist muscle to oppose this movement.

Collins (1971) showed that the viscosity (the resistance to movement) related to stretching a dissected extraocular muscle (i.e., the antagonist muscle during an eye movement) varies nonlinearly as a function of that muscle’s stimulation frequency and stretch velocity (see Figs. 15B and 16B). He also demonstrated that the viscosity of the passive orbital tissues remains roughly constant, even at saccadic eye velocities. We propose that these observations can help explain the data in Fig. 14.

During saccadic eye movements, most antagonist extraocular MNs completely pause (Figs. 3 and 15A). It follows that shortly after saccade initiation, the viscosity of the antagonist muscle “jumps” from a high resting value to a much lower one (Fig. 15B, epochs 1 and 2). During the saccade, when the drive to the antagonist muscle is negligible and the eye velocity is large, the viscosity contributed by the antagonist muscle to opposing the eye movement is nearly equal to the passive viscosity of the muscle (Fig. 15B, epochs 2–4). At the end of the saccade, when the antagonist MNs resume firing, the viscosity of the antagonist muscle returns to a larger static value (Fig. 15B, epoch 5). Hence, during
saccades, the eye movement is driven by the rate of contraction of the agonist muscle, but is opposed, albeit minimally, by the combined passive viscous properties of the antagonist muscle and orbital tissues.

During pursuit eye movements, which generate slower eye velocities, the changes in viscosity for the antagonist muscle are considerably less dramatic. Figure 16B illustrates the temporal progression of viscosity for an example of 40°/s step ramp. We show unit B96.2 because like the majority of neurons in our sample (60%), it continued to fire throughout OFF direction pursuit initiation (Fig. 16A). Hence, in contrast to saccades, the firing rate of this antagonist MN during step-ramp pursuit does not rapidly reach zero, but rather it decreases smoothly, more or less as a mirror image of the firing rate of agonist MNs. The remaining 40% of the neurons in our sample reached cutoff approximately midway through the analysis interval. Figure 16 shows that the antagonist muscle viscosity is much larger during the initial acceleration phase of pursuit (epochs 1 and 2) than during saccades (compare with Fig. 15B). To summarize, during the initiation of slow pursuit eye movements, an additional active viscosity that results from the contractile properties of the antagonist muscle, and which is minimal during saccades, combines with the passive viscous properties of the antagonist muscle and orbital tissues to oppose the agonist drive.

The arguments presented above are consistent with our finding that r values were lower for faster eye movements given that saccadic eye movements encounter less viscous resistance than slower smooth pursuit eye movements. The changes in b and k values with increasing velocities are more difficult to explain because these parameters are generally related to static parameters. However, we suggest that similar principles that apply to the r coefficient (i.e., dynamic changes in antagonist muscle viscosity) may also apply to these parameters. For example, it is conceivable that the stiffness of a muscle, which is likely to affect the k coefficient, will vary with the strength of the neural drive to this muscle during eye movement, as it does during static conditions (Barmack 1976; Collins 1971; Goldberg et al. 1997; Shall and Goldberg 1992; Shall et al. 1996). Indeed, our current hypothesis is consistent with the recent findings of Miller and Robins (1992). These investigators directly measured the forces generated by the agonist and antagonist muscles in the alert monkey and demonstrated that the agonist/antagonist force ratio is greater for large than for small saccades. Nevertheless, future efforts aimed at describing the mechanical properties of the extraocular muscles and the time-varying contribution of the antagonist motor units during eye movements will be needed before a realistic model of oculomotor control can be fully elaborated.
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