Effects of Initial Eye Position on Saccade-Related Behavior of Abducens Nucleus Neurons in the Primate

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Ling L, Fuchs A, Siebold C, Dean P. Effects of initial eye position on saccade-related behavior of abducens nucleus neurons in the primate. J Neurophysiol 98: 3581–3599, 2007. First published October 3, 2007; doi:10.1152/jn.00992.2007. Previous work suggests that when the eye starts at different orbital initial positions (IPs), the saccade control system is faced with significant nonlinearities. Here we studied the effects of IP on saccade-related firing of monkey abducens neurons by either isolating saccade variables behaviorally or applying a multiple linear regression analysis. Over a 50° range of IPs, we could select 10° horizontal saccades with identical velocity profiles, which would require identical control signals in a linear system. The bursts accompanying ipsiversive saccades for IPs above the threshold for steady firing were quite similar. The excess burst rate for the saccade did not vary at all with eye position, the contributions of the agonist and antagonist might be different for centripetal and centrifugal saccades.

If the plant indeed presents a nonlinear load, it could affect saccades in different ways. In one scenario, the trajectories of similar saccades could depend on initial eye position, in which case the metrics of the saccades themselves—as such as velocity, duration, and amplitude—would reflect the effects of any plant nonlinearities. Alternatively, the metrics of the same saccades could be independent of eye position because the brain provides a nonlinear command to compensate for the nonlinear plant.

The effect of initial eye position on saccade generation has been addressed primarily by comparing the metrics of centrifugal and centripetal saccades. In humans (Abel et al. 1979; Frost and Pöppel 1976; Hyde 1959; Inchigolo et al. 1987; Jürgens et al. 1981; Rottach et al. 1998), centripetal saccades are faster than centrifugal saccades of the same size. This observation holds for both large (20–30°; Pélisson and Prablanc 1988) and smaller targeting saccades (10°; Abel et al. 1979). For scanning saccades of about 10° to stationary targets, one group reports no difference in centripetal and centrifugal saccades (Eggert et al. 1999) and another claims that centripetal saccades are faster (Collewijn et al. 1988). For scanning saccades of only 5°, there is no centripetal/centrifugal difference (Collewijn et al. 1988).

In monkeys with their heads fixed, centrifugal saccades of 10 to 30° in amplitude are slower than centripetal saccades of the same amplitude (Phillips et al. 1995). As with humans, the difference becomes greater for larger saccades. For saccades of 5°, although the peak saccadic velocity may vary significantly for movements launched from different initial positions, there is no consistent trend in the variations (Goldstein 1983; Goldstein and Robinson 1992). Consequently, the latter authors conclude that, at least for the 5° saccades that they tested, “peak saccadic eye velocity in the monkey does not depend on eye position over the range ±25°.”

The first place to look for a neuronal manifestation of the putative plant nonlinearity is in the discharge properties of oculomotor nuclei (MNs). It is well known that all neurons within the confines of the three oculomotor nuclei discharge at a steady rate that varies linearly with eye positions in excess of a certain threshold (Fuchs and Luschei 1970, 1971; Keller and Robinson 1971; Robinson 1970: Schiller 1970). In the case of abducens neurons, the steady rate increases for abducting

INTRODUCTION

Many authors have suggested that the peripheral oculomotor apparatus [the muscles, the globe, and its suspensory tissues and the other orbital contents, collectively referred to as the oculomotor plant (Robinson 1975a)] presents to the oculomotor control system a nonlinear load that varies with eye position in the orbit. Several sources of nonlinearities have been documented. First, both the length–tension (Collins et al. 1975; Miller and Robins 1992; Robinson 1975) and force–velocity (Goldstein and Robinson 1992; Koene and Erklen 2002) relations of the extraocular muscles are nonlinear. Second, motor units of the primate extraocular muscles appear to interact in a nonlinear way (e.g., Shall et al. 2003). Finally, because saccades are generated by the net force produced by a pair of antagonist muscles, a nonlinearity might be introduced by this push–pull arrangement. Even if the net force required...
(temporalward, on-direction) fixation positions (Fuchs and Luschei 1970; Fuchs et al. 1988; Goldstein 1983; Keller and Robinson 1971), and the slope of this rate—position relation generally becomes steeper for abducens neurons with thresholds more in the on-direction. The recruitment of neurons with increasing slopes represents a nonlinearity in the net steady firing pattern related to eye position.

Superimposed on the eye position–related firing there are phasic changes in activity associated with saccades, either a burst of spikes for on-direction saccades or a pause in discharge for off-direction saccades. Robinson (1975a) suggested that the phasic and steady firing arise from separate premotor inputs that add at the motoneuron membrane to produce the saccade and fixation components of motoneuron discharge, respectively. In this scheme, evaluation of the phasic activity in excess of the eye position–related firing would reflect the characteristics and metrics of the saccade generated through the plant and also provide an estimate of saccadic input signals to motoneurons.

To our knowledge, only one study has tested possible initial position effects on the burst of abducens neurons. In his thesis, Goldstein (1983) argued: “These effects were not small. Some important but unexplored nonlinear property must exist in the extracocular muscles to compensate the nonlinear position—dependency of the motoneuron signals.”

The dependence of motoneuron discharge on eye position must be documented to provide a basis on which to interpret the inputs to motoneurons and also to allow the construction of distributed models of the oculomotor final common pathway. Therefore we examine here the effect of eye position on burst characteristics by considering mostly 5 and 10° saccades where little behavioral effect of eye position is seen on saccade metrics, but also larger saccades where it is.

Part of this work was previously reported in an abstract (Siebold et al. 1992).

**METHODS**

**Surgical procedures**

We recorded single-unit activity in the abducens nuclei of five rhesus monkeys. To measure movements of the eye, we constructed a coil on one eye by threading three turns of a fine wire under the insertions of the four rectus muscles (Fuchs and Robinson 1966). Abducens activity was recorded both ipsi- and contraversive to the implanted eye. Animals in our laboratory performing saccades to implanted eye. Animals in our laboratory performing saccades to target locations every 5°. Finally, we rewarded the monkey for making a staircase of 5° horizontal saccades from initial positions located every 5°. Initially, we rewarded the monkey for making horizontal saccades of a variety of amplitudes (usually 5, 10, and 15° but occasionally as high as 30° or more) starting at one or more fixed initial positions.

**Recording and experimental conditions**

We used the standard electromagnetic method to measure eye movements with a sensitivity of 0.25° (Robinson 1963). At the start of each recording session, the eye movement signal was calibrated behaviorally against known positions of the target, which the monkey had been trained to fixate. All target locations were on the horizontal meridian, 5 to 25° from the primary direction of gaze. To compensate for the trigonometric nonlinearity of the eye movement transducer, we corrected the eye position on the basis of a cubic fit between the measured eye position and target position. The largest corrections, which were typically in the order of 1–2°, occurred at the extremes of the orbital range. The spread of initial eye positions that remained after the postcalibration was ±0.47° (mean SD) over ±25°. We used the corrected values of eye position to calculate saccade amplitude in all of the relations subsequently presented and peak velocities were determined digitally using a central difference scheme based on the corrected eye position samples.

Extracellular single-unit activity was recorded with homemade iron-plated tungsten microelectrodes (∼1 MΩ at 1 kHz) that were introduced into the brain stem by a hydraulic microdrive. We identified the abducens nucleus by its unique burst-tonic discharge patterns that had a definite musical quality when played over an audio monitor (Fuchs and Luschei 1970). Based on their anatomical projections, there are at least three different types of neurons within the confines of the abducens nucleus (Fuchs et al. 1988; Langer et al. 1985). Although we did not identify our neurons by spike-triggered averaging of muscle activity in the ipsilateral lateral rectus, most of our neurons had a threshold for steady firing within ±20° of the primary direction of gaze, a characteristic indicative of identified abducens motoneurons (Fuchs et al. 1988). Also, we feel confident that we were not recording from the nearby nucleus prepositus hypoglossi (NPH), whose neurons have qualitatively similar discharge patterns, because all of our neurons paused for nasalward saccades, whereas NPH neurons typically do not (McFarland and Fuchs 1992). Unit activity and horizontal and vertical eye position were recorded to tape (Vetter 4000A) to be digitized off-line.

To elicit horizontal saccades, we trained the monkeys to fixate small light-emitting diodes (LEDs) distributed at 5° intervals on a flat array located at a distance of 36 cm from the eye. The monkeys sat in a primate chair with their heads positioned so that the eye that carried the coil was at the center of horizontal and vertical magnetic fields. When an animal’s gaze remained within an adjustable reward window around the illuminated LED for 3 to 4 s, it earned a small dollop of applesauce. The reward window was disabled whenever the animal made a targeting saccade. Once a cell in the abducens nucleus was isolated, we asked the monkey to make a staircase of 10° horizontal saccades from IPs located every 10° along the horizontal meridian starting at ±25° from the primary direction of gaze. Next, we required the monkey to make a staircase of 5° horizontal saccades from initial positions located every 5°. Finally, we rewarded the monkey for making horizontal saccades of a variety of amplitudes (usually 5, 10, and 15° but occasionally as high as 30° or more) starting at one or more fixed initial positions.

**Data analysis**

**EXTRACTION OF BURST AND SACCADE PARAMETERS.** Off-line, we detected the occurrence of each action potential with 10-μs resolution and sampled the eye and target position signals at 1 kHz. One of the investigators acclimated the digitized data across a computer monitor. A customized computer program recognized saccades on the basis of an adjustable velocity criterion (usually ~30°/s) and automatically marked the salient times of the movement, such as saccade onset and end and the time to peak velocity, which were saved with their associated eye positions and velocity traces. If the program erred in any of these selections, the investigator could adjust them, although this seldom was necessary. The associated burst was marked as the interval between which the burst frequency exceeded the pre- or post-saccadic steady firing rate during steady fixation by 2SD. At the
end of all bursts, there was an initial rapid decrease in firing rate that gave way to a gradual increase in interspike interval over approximately 20–50 ms (a “slide” in firing rate) before the steady firing associated with the final fixation position was attained (Goldstein 1983). The end of the burst was taken as the end of the initial rapid decrease before onset of the slide. Although this initial decrease was clear to the experienced observer, it occasionally (~5–10% of trials) was missed by our automated analysis and therefore marked by hand.

The data generated by our marking program were imported into a second customized program that measured saccade parameters, such as amplitude and duration, and the associated parameters of the burst, such as burst duration, number of spikes, peak firing rate, and time to peak rate. These data were then exported to a commercial software package (Igor Pro, WaveMetrics, Lake Oswego, OR) for the correction of eye position nonlinearities (see earlier text).

RELATIONS OF BURST AND SACCADE PARAMETERS. Our analysis provided data for displays like those in Fig. 1, which shows the time course of five superimposed saccades and rasters of their associated spikes aligned on saccade onset. To construct an illustrative representation of the combined unit discharge for some figures (Figs. 1, 3, 6, and 7), we first determined the interspike intervals for each spike train and calculated the associated instantaneous firing rates, which were represented by vertical “sticks” of the appropriate height at the end of each interval (stickogram). All of the instantaneous firing rate sticks from all of the trials then were superimposed in a single display below the rasters.

As explained in the INTRODUCTION, a popular model for motoneuron discharge posits that the burst associated with an on-direction saccade is made up of a firing rate related to eye position, which we estimated to be the shaded region in the sample response in Fig. 1B and an additional or excess burst rate (EBR) associated with the high-velocity saccade (Robinson 1970). EBR is taken as the difference between peak firing (averaged over the shortest five spike intervals) and the steady rate during fixation for the IP at saccade onset, as calculated from the linear relationship between orbital eye position and firing rate during fixation. We chose the steady rate at saccade onset to measure EBR because the peak burst rate occurred near saccade onset for almost all movements studied. The excess number of spikes is taken as the total number of spikes in the burst minus the number of spikes represented by the shaded trapezoid, whose height is defined by the steady rates calculated from the eye positions at saccade onset and end (Fig. 1B). We used the peak firing and excess burst data sets in two different analyses.

SLICE ANALYSIS. In the slice analysis, we limited the variation of one or more of the saccade parameters and tested the parameters of the neural discharge with IP. We performed two manipulations. To examine the effects of initial eye position (IP) on burst parameters, we selected saccades that were very similar in amplitude across IPs (a constant-amplitude slice) and also showed minimal changes in peak velocity and duration with IP. A representative “slice” of data created a set of about 40 saccades whose amplitudes, durations, and peak velocities varied, respectively, by 0.007 deg/deg, 0.002 ms/deg, and 0.96 deg/s1/2 deg−1 over IPs ranging over ±35°. Therefore these 10° saccades with an average duration of 45 ms and an average peak velocity of 500°/s exhibited, on average, a change in amplitude, duration, and peak velocity of only 0.21° (2%), 0.25 ms (<1%), and 35°/s (7%), respectively, over the 35° range. The relations between burst parameters (frequency, number of spikes, duration) and IP were established for each slice of on-direction saccades and between pause duration and IP for each slice of off-direction saccades. We dealt separately with the relations for bursts that occurred above and below the threshold for steady firing (see RESULTS).

To examine the relations of burst parameters with saccade parameters, we considered saccades starting at a limited range of IPs. Such slices of IP were typically 2° wide. For these limited IP slices, we determined the relations either between saccade and burst parameters (frequency, number of spikes, duration) for ipsiversive saccades or between saccade and pause duration for contraversive saccades.

MULTIPLE REGRESSION ANALYSIS. For most neurons, there were insufficient data—i.e., not enough saccades with similar amplitudes and velocities, for a slice analysis. However, because the slice analysis
revealed that the excess number of spikes and also burst and pause duration varied linearly with IP, we were able to use a multiple linear regression analysis to expand our data set for those parameters. Specifically, we calculated the regressions of the excess number of spikes as a function of IP and saccade amplitude [number of spikes = (a × IP) + (b × Saccade amplitude) + c] and of burst and pause duration as a function of initial position and saccade duration [duration = (c × IP) + (d × Saccade duration) + e] using a commercial program (StatView, SAS Institute). Interaction nonlinearities were not significant. Note, however, as we subsequently show (e.g., Fig. 4), peak burst firing saturated with IP for some abducens neurons. In those cases, we could use only the slice analysis to study relations between peak and excess burst rate and IP.

We subjected the excess number of spikes and burst duration for ipsiversive saccades and pause duration for contraversive saccades from every unit to a multiple linear regression (MLR) analysis (except when the range of values in one variable was not sufficient, i.e., the pause analyses for five units). However, we used the results from the MLR analyses only for those units with insufficient data for a slice analysis. For <10% of all units, we needed to restrict the range of the independent variables to avoid correlations between the two independent variables. For instance, we excluded large-amplitude saccades if they were launched only from extreme starting positions.

Table 1 summarizes the burst and pause parameters that we considered, whether the data were generated with a slice or MLR analysis, and how many units were subjected to each analysis.

## RESULTS

### Saccade characteristics

As explained in the INTRODUCTION and METHODS, we collected unit activity for two behavioral conditions. In one condition, the monkey made saccades of fixed amplitudes from a variety of initial horizontal eye positions (e.g., Fig. 3). An example of such saccades for animal TM is shown in Fig. 2A for saccades of 5° (□) or 10° (■) from initial eye positions (IPs) ranging from −20 (in off-direction) to +10° (in on-direction). In the second condition, the monkey made variable-amplitude saccades from a fixed IP (e.g., Fig. 6A). Examples of such saccades ranging from 5 to 37° at an IP of 20° are also shown in Fig. 2A (+). The peak velocities for saccades made in the two conditions are shown in Fig. 2B. For this animal, centrifugal saccades (those starting at initial positions ≥0°) showed lower average peak velocities than did centripetal ones (those starting at <0°) for both 5 and 10° amplitudes (e.g., 10° saccades had an average centrifugal peak velocity of 320°/s and an average centripetal velocity of 510°/s). For monkey T (Fig. 2, C and D), IP had little influence on the peak velocities of 5 and 10° saccades but influenced the peak velocity of 20° saccades (X). Therefore as in previous studies (see INTRODUCTION), IP has its greatest influence on larger saccades.

Figure 2D also illustrates how we created a slice of (in this case 10°) saccades of very similar peak velocities to examine the effects of IP on neuronal firing. After saccade amplitude was limited to 9 to 11°, peak velocity still decreased at 1.9 deg·s⁻¹·deg⁻¹ (all squares). To eliminate this trend, we, in addition, produced a slice of similar peak velocities by restricting the peak velocities to a range of 60°/s, which reduced the remaining trend to −0.06 deg·s⁻¹·deg⁻¹ (■).

### Neuronal sample

We collected data from a total of 72 units. As previously documented (Fuchs and Luschei 1970; Fuchs et al. 1988; Keller and Robinson 1972; Schiller 1970), all of our abducens neurons discharged a burst of spikes for ipsiversive (on-direction) saccadic eye movements and exhibited an increase of steady firing for eye positions (fixations) in the on-direction (always indicated as positive). For saccades in the contraversive (off-) direction (off-direction always indicated as negative), all abducens neurons exhibited a pause in firing. A representative example of the effects of IP on firing in the on-direction is shown in Fig. 3. Like this neuron, 30 of 72 neurons fired steadily even for the largest contraversive (off-direction) IP (typically −25°) we tested. The threshold for steady firing (the x-intercept of the linear fit of steady firing rate vs. IP) for this neuron was −26.31°. Such low-threshold units supply only suprathreshold data. For other units, the threshold was more central in the oculomotor range but, once the threshold was exceeded, the steady firing rate also increased linearly with ipsiversive eye position. For such central-threshold units, we can characterize both sub- and suprathreshold responses. In addition to these low- and central-threshold units, there were occasional high-threshold neurons that exhibited a steady rate only at the most extreme ipsiversive IP we tested and provided only subthreshold data. The actual distribution of thresholds for all units is displayed in Fig. 10.

To examine the effects of IP on burst discharge, we considered both the raw burst (i.e., the uncorrected saccade-related discharge) and the excess burst rate (EBR). For the 10° saccades shown in Fig. 3, the raw peak firing rate increased as IP shifted from the off-direction (−20) to about −5° in the on-direction. There was a small decrease of peak velocity with IP, as well, especially noticeable at the most extreme eccentric

**Table 1. Summary of the burst and pause parameters considered and how many units were subjected to a slice or MLR analysis for each parameter**

<table>
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<th>Slice</th>
<th>MLR Added</th>
<th>Total</th>
<th>Figure(s)</th>
</tr>
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<td>A. IP series</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Suprathreshold burst</td>
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<td></td>
<td></td>
</tr>
<tr>
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<td>0</td>
<td>22</td>
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<tr>
<td>EBR</td>
<td>22</td>
<td>0</td>
<td>22</td>
</tr>
<tr>
<td>Number of spikes</td>
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<td>49</td>
</tr>
<tr>
<td>Duration</td>
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<td>27</td>
<td>49</td>
</tr>
<tr>
<td>Subthreshold burst</td>
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<td></td>
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<tr>
<td>Peak rate</td>
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<td>0</td>
<td>9</td>
</tr>
<tr>
<td>EBR</td>
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<td>0</td>
</tr>
<tr>
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<tr>
<td>Duration</td>
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<tr>
<td>Both</td>
<td>22 + 4*</td>
<td>27 + 4b</td>
<td>57</td>
</tr>
<tr>
<td>Pause</td>
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<td></td>
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<tr>
<td>Duration</td>
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<tr>
<td>Duration</td>
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*The 22 suprathreshold units include 6 central-threshold units, which also contribute to the 10 subthreshold units. *The MLR was performed on 3 central-threshold units, which are counted in both the supr- and subthreshold columns.
positions. Therefore to determine the effect of IP on burst rate without the confounding changes in peak velocity, we further limited the saccades used for the slice analysis on the basis of peak velocity; i.e., we took a velocity slice as in Fig. 2.

Of the 57 units analyzed to study the influence of IP on the burst accompanying ipsiversive saccades, 26 had sufficient data to allow slices of both amplitudes and peak velocities. For the remaining 31, we applied the MLR analysis to supplement the slice data. To determine whether merging slice and MLR data is justified, we compared the data from the slice analysis with data generated by the MLR analysis for the 26 neurons. The slice and the MLR analyses produced very similar results. The mean difference between the excess number of spikes versus IP sensitivities calculated using the slice (measured as a slope) and MLR analysis (measured as a coefficient) was 0.003 spikes/deg, which amounted to a 6% error relative to the ideal.

**FIG. 2.** Saccade amplitude and peak velocity as functions of initial eye position for representative data sets from monkeys TM (A, B) and T (C, D). A: for the experiment with TM, we gathered saccades of 5 (○) and 10° (■) from a variety of initial positions (IPs) and also saccades of different amplitudes from a single IP of −20° (+). C: in the experiment with monkey T, we gathered saccades of 5 (○), 10 (■), and 20° (△) from a variety of IPs. B and D show that, for saccades of the same size, the peak velocities of centripetal saccades (those starting from negative IPs) tend to be greater, on average, than those of centrifugal saccades (those starting at positive IPs) for amplitudes ≥10°. D shows how we then further constrained the data to reduce the remaining trend in the peak velocity with IP from −1.9 (○) to −0.16 (■) deg·s⁻¹·deg⁻¹.

**FIG. 3.** Discharge characteristics of a representative abducens neuron (TM 138:2) for 10° saccades in the unit’s on-direction initiated from different IPs ranging from −20° (off-direction) to +10° (on-direction). From top to bottom: eye velocity, eye position, associated rasters indicating the occurrence of individual action potentials, and a summary stickogram for similar saccades. All traces aligned on saccade onset. Rate position relation for this neuron: firing rate FR = 5.6 E_h − 26.31 (r = 0.98).

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Neuronal firing characteristics

The relation of burst rate with IP ranged from that illustrated in Fig. 4A to that illustrated in Fig. 4B. For the unit in Fig. 4A, peak burst rate increased with IP, whereas the excess burst rate (EBR) remained nearly constant. If the peak burst rate showed a statistically significant increase with IP and the EBR showed no significant change, we say the unit exhibited a nonsaturating behavior. In contrast, the unit illustrated in Fig. 4B discharged at a nearly constant (i.e., saturated) peak burst rate, for all IPs but exhibited a declining EBR with IP. If the slope of the peak rate with IP did not differ significantly from zero and EBR decreased significantly with IP, we say the unit exhibited a saturating behavior.

Determining whether a unit exhibited a saturating or nonsaturating behavior was sometimes problematic. First, the relation of the burst behavior with IP could depend on saccade amplitude. For the unit illustrated in Fig. 4C, the raw peak rate increased over most of the IP range for 5° saccades (square symbol) but was constant with IP for 20° saccades (triangle symbol). The two data sets exhibit different maximum peak burst rates because 5° saccades reach lower peak velocities than do 20° saccades. Second, for the same size saccade, peak rate can behave differently for different ranges of IP. For 10° saccades (+), peak burst rate increased linearly to an IP of about −15° after which it remained nearly constant for IPs to +20°. The transition from nonsaturating to saturating behavior occurred near the unit’s threshold for steady firing, which in this case was −13.1°. Therefore for this and all other units with a central threshold for steady firing, we considered separately the relations between burst parameters and IP for data above and below threshold.

Most of the IP data were collected under conditions in which neurons were operating above their eye position thresholds for

![Figure 4](http://jn.physiology.org/)

**FIG. 4.** Relation between the burst rate and IP. **A**: data from a unit with a nonsaturating behavior (TM 140:1) whose peak burst rate (PBR) increases with IP (●) and whose excess burst rate (EBR) is roughly constant ([ ]). Regression lines: PBR = 4.2 IP + 270 (r = 0.89) and EBR = −0.78 IP + 132 (r = 0.34). **B**: data from a unit with a saturating behavior (To 20:3), whose mean peak burst rate (520 ± 40 spikes/s) is relatively constant with IP (●, slope, −1.0 spikes−1·deg−1) and whose EBR decreases sharply with IP ([ ], slope, −5.5 spikes−1·deg−1, r = 0.87). **C**: dependence of IP sensitivity on saccade amplitude demonstrated on a unit (To 20:1) with a central threshold for steady firing (FR = 3.5 E0 + 47). For 20° saccades (●), the raw peak burst rate always was saturated mean [840 ± 35 (SD) spikes/s]. For 5° saccades ([ ], peak burst rate increased monotonically to saturate at IP ≈ −5°. For 10° saccades (+), peak burst rate increased more rapidly before saturating. At the 3 saccade amplitudes, peak firing rate saturated at different levels appropriate to the different peak saccade velocities. **D**: slope of the EBR vs. IP relation as a function of the slope of the peak burst rate vs. IP relation for all units subjected to the slice analysis. Squares and circles are data from nonsaturating and saturating units, respectively. Filled and open symbols represent supra- and subthreshold data, respectively. Data within vertical shaded region have slopes of peak burst rate vs. IP that do not differ significantly from zero. Data within horizontal shaded region have slopes of EBR vs. IP that do not differ significantly from zero.
steady firing. We now deal with the suprathreshold behavior and then the subthreshold behavior associated with ipsiversive saccades.

**IP sensitivity of burst rate**

**SUPRATHRESHOLD BEHAVIOR.** The separation of units into those exhibiting saturating and nonsaturating behaviors is an accurate description for the suprathreshold behavior of all units, whether they have low or central thresholds. For this behavioral dichotomy to hold, peak burst rate should remain constant with IP for units with saturating behaviors but increase for units with nonsaturating behaviors, whereas EBR should decrease and remain constant for saturating and nonsaturating behaviors, respectively. Figure 4D compares the slopes of the linear fits of burst rate versus IP before (peak firing rate) and after (EBR) the adjustment for the rate–position relation. For the units with a saturating behavior (Fig. 4D, ○), the slopes of peak rate versus IP relation were distributed around zero (mean 0.31 ± 2.11 spikes·s⁻¹·deg⁻¹, n = 14), and the relations of EBR versus IP all had negative slopes (mean −4.50 ± 2.72 spikes·s⁻¹·deg⁻¹). The vertical shaded region identifies data with slopes of the peak burst rate/IP relation that did not differ significantly from zero. In contrast, for the units with nonsaturating behavior (Fig. 4D, □), the slopes of the linear regression of peak burst rate versus IP were significantly greater than zero (mean 4.54 ± 2.20 spikes·s⁻¹·deg⁻¹, n = 8), whereas the slope of the relation of EBR versus IP (mean 0.14 ± 1.37 spikes·s⁻¹·deg⁻¹) was not (both at P < 0.05). The horizontal shaded region identifies data with slopes of the EBR/IP relation that did not differ significantly from zero.

In summary, for units whose peak burst rate increases linearly with IP above threshold, the relatively constant EBR is appropriate to specify the associated peak saccadic velocity, which, for the slice data, also is roughly constant with IP. In contrast, for units whose peak burst rate saturates with IP, the decreasing EBR with IP does not reflect the actual constant peak eye velocities. We caution that our assignment of units to the nonsaturating or saturating category applies only for the 10° saccades we considered here. Recall that larger saccades are usually accompanied by saturating behavior and smaller saccades by more linear behavior (Fig. 4C).

**SUBTHRESHOLD BEHAVIOR.** Now we evaluate whether the nine neurons with central and high thresholds also exhibited saturating and nonsaturating subthreshold behaviors in the slice analysis. For six, the threshold was central in the oculomotor range (from contraversive −13° to ipsiversive +1°; mean = −7°). For three high-threshold units the threshold was ≥15° eccentric of primary gaze. Figure 5A shows the saccade-related discharge of a central-threshold neuron with a threshold between 0 and +5°. For IP's from −15 to −5°, 5° saccades were accompanied only by a burst, which exhibited a linear increase.

**FIG. 5.** Relation of burst characteristics with IP for units with central rate–position thresholds. A: discharge patterns of a central threshold neuron during selected 5° saccades in the on-direction initiated from IPs ranging from −15° to +10°. Traces as in Fig. 3. B: regressions of peak burst rate vs. IP for the unit in A (open squares and blue line) and for the 5 other neurons with central thresholds (solid lines with symbols at ends) and the 3 units with thresholds so high that their presaccadic rates were always subthreshold (dashed lines with symbols at ends). C and D: number of spikes and burst duration vs. IP, respectively, for the same 9 neurons (data from neuron in A shown as open squares and blue regression line).
in peak rate with IP (Fig. 5B, open squares, thick regression line). Similar linear increases of peak burst rate with IPs below threshold occurred for the five other central threshold and the three high-threshold units (Fig. 5B, solid and dashed lines with symbols at end, respectively). The mean slope for all nine neurons was 6.82 spikes·s⁻¹·deg⁻¹ (±1.38 SE).

Excess discharge associated with the saccade. As we saw in Fig. 4D, almost all of the low- and central-threshold units had suprathreshold firing patterns that, for the same size saccade initiated from different IPs, could be accounted for by the linear addition of a constant burst to an underlying rate–position relation (nonsaturating units). We ask now whether such a model also can account for the subthreshold behavior of the central- and high-threshold units described in Fig. 5.

For suprathreshold behavior, the contribution of the rate–position relation to burst discharge can be evaluated with reasonable assumptions (cf. Fig. 1B). However, it is unclear whether and how one should take into account a possible contribution of the rate–position relation when saccade-related bursts occur for IPs below the threshold for steady firing. One possibility is that when saccades are launched at IPs below threshold, abducens neurons are in an inhibited state corresponding to an extrapolation of the rate–position relation into negative firing rates (Hazel et al. 2002). In this scenario, the correction for the rate–position relation adds, rather than subtracts, firing rates. If we apply this correction for subthreshold firing to determine the EBR for the unit in Fig. 5, A and B (thick line), the subthreshold relation of EBR with IP becomes flat, as is characteristic of a nonsaturating unit. When we apply this correction to the six central-threshold and three high-threshold units with enough data for the slice analysis, the average slope falls from 6.82 spikes·s⁻¹·deg⁻¹ for peak burst rate versus IP to 0.82 spikes·s⁻¹·deg⁻¹ for EBR versus IP. For eight of the nine units (Fig. 4D, open symbols), the slope after the correction was not significantly different from zero (i.e., it was within the horizontal shaded band).

In summary, the suprathreshold EBR is not sensitive to IP except for the neurons whose peak firing rate exhibits a saturation, which, as we subsequently discuss, could be a membrane property of those neurons. In contrast, the infrathreshold burst rates are strongly influenced by IP. We now consider the sensitivity of other aspects of the burst, such as number of spikes and burst duration to IP.

**IP sensitivity of the burst: other burst parameters**

**NUMBER OF SPIKES.** Suprathreshold, all of our abducens neurons showed a linear increase in the raw number of spikes in the burst with IP. Therefore for this analysis, unlike the previous burst rate analyses, these data also could be subjected to MLR analysis. Across all 49 units, 22 subjected to a slice and 27 to MLR analysis, the linear regression of number of spikes with IP had a median slope of 0.16 ± 0.11 spikes/deg; 73% (36/49) of the individual slopes were significantly greater than zero (P < 0.05). The slopes of the relation between number of spikes and IP were weakly correlated with the slopes of their rate–position relation (r = 0.72, P < 0.01).

In contrast, the excess number of spikes remained constant or decreased modestly. To eliminate the contribution of the rate–position relation, we implemented the trapezoid correction as illustrated in Fig. 1. After this correction, the slope of the excess number of spikes versus IP relation was zero or slightly negative (population mean: −0.05 ± 0.06 spikes/deg for most (41/49) units. None of the positive slopes was significantly different from zero, but about half (20/41) of the negative slopes were. The mean slopes calculated separately by the slice (−0.04 spikes/deg) and multiple regression (−0.06 spikes/deg) analyses were not significantly different (P > 0.20). The slopes of the relations of EBR and excess number of spikes with IP were not correlated. Thus units whose EBR exhibited a saturation with IP are not more likely to lose spikes in the burst with ipsiversive IPs.

Subthreshold, the number of spikes also increased linearly with IP (Fig. 5C) so again the MLR analysis was appropriate. For the 9 units evaluated with the slice analysis, the mean regression slope of the relation of the raw number of spikes with IP was 0.22 ± 0.04 spikes/deg. We also subjected 4 additional central-threshold and 4 additional high-threshold units to the MLR analysis. The mean subthreshold slope of raw number of spikes with IP for all 17 units was 0.28 ± 0.15. The slope for the excess number of spikes was 0.05 ± 0.21. However, for 8 of 17, the slopes of excess number spikes with IP was > +0.1 spikes/deg. Whereas the suprathreshold data of very few units showed increases in excess spikes with IP, half of the subthreshold data did.

**BURST DURATION.** Suprathreshold, burst duration changed little with IP. For all the neurons, the slopes of the burst duration versus IP relations obtained with either the slice or MLR analyses lay mostly between −0.4 and +0.6 ms/deg (mean 0.08 ± 0.34 ms/deg, n = 49). Thirty-one of 49 had positive slopes, which for 12 were significantly different from zero; none of the negative slopes was. Burst start latencies (time from burst onset to saccade onset) showed hardly any trend with IP. Therefore any modest relation between burst duration and IP was the result of the relations of burst end latencies (time from the end of the burst to the end of the saccade) with IP. Indeed, across our population of abducens neurons, the correlation between the slopes of the relation for burst end latency versus IP and the slopes of the relation for burst duration versus IP was quite robust (with a slope of 0.87, r = 0.93).

Subthreshold, in contrast, burst duration increased monotonically with IP. The mean regression slope of the burst duration versus IP relation was 0.67 ± 0.28 ms/deg for the 9 neurons subjected to the slice analysis (Fig. 5D). For all 17 neurons, the mean was 0.4 ± 0.77 ms/deg. This value is larger than that for the suprathreshold data.

In summary, several characteristics of the burst for very similar saccades differ above and below the threshold for steady firing. For the 6 central threshold units, peak burst rate showed a steady increase with IP below threshold (Fig. 5B), but was relatively constant across units [0.15 ± 1.01 (SE) spikes·s⁻¹·deg⁻¹] above threshold. Therefore EBR decreased with IPs above threshold, as was the case for units with saturating behavior. Also, the slopes of burst duration with IP tended to be statistically (P < 0.05) higher in the subthreshold than in the suprathreshold region (means of 0.39 vs. 0.08 ms/deg, respectively). For these neurons, some of the higher slopes were caused, in part, by the shorter lead times for bursts initiated from sub- and suprathreshold IPs (means of 1.1 and 5.0 ms, respectively). In contrast, the raw number of spikes of
all but one central threshold unit showed no clear discontinu- 
eties at the IP transition from sub- to suprathreshold regions, 
and all could be fit by single straight lines with positive slopes.

Relations of burst activity to saccade metrics

Our second goal was to document the relations of saccade-
related discharge with the metrics of the saccade. Earlier (Fig.
4), we described the effect of IP on burst rate in isolation by
deliberately limiting peak velocity to a narrow range (or slice).
Here we examine the effect of a varying peak velocity on burst 
rate in two different ways. First, we consider saccades of
different sizes and therefore different peak velocities initiated
from a constant IP. Second, we select saccades of the same size 
but use their natural variation in peak velocity (e.g., Fig. 2D, all 
squares).

PEAK RATE WITH PEAK VELOCITY: SACCADES OF DIFFERENT SIZES 
FROM THE SAME IP. The peak burst rate of abducens neurons 
depended on saccade velocity. For the representative neuron 
illustrated in Fig. 6A (same as that in Fig. 3), the peak rate 
increased for saccade amplitudes from 5 to 15°. For larger 
saccade amplitudes (25 and 35°) where peak velocity de-
creased, peak burst rate did as well.

Because all saccades were launched from the same IP, the 
peak and excess burst rates differed by a constant, i.e., the rate 
at saccade onset (Fig. 1B). In what follows, we will thus use 
EBR alone to allow a comparison with our previous data with 
variable IPs (e.g., Fig. 4D). For the neuron illustrated in Fig.
6A, EBR increased linearly with peak eye velocity and showed 
no evidence of firing rate saturation (Fig. 6B, ●); its eye-
velocity sensitivity was 0.249 ± 0.027 spikes/deg.

Eye-velocity sensitivity can depend on IP as illustrated by
another neuron that reached higher burst rates (Fig. 6B, To 
20:1). If IP was far in the off-direction (−25°, ◦), the slope of 
the linear fit was steeper than when IP was well into the 
on-direction (10°, □). Also, the correlation coefficient was 
greater for an IP more in the off-direction (0.98 vs. 0.90). For 
both IPs, the maximal burst rate was about 800 spikes/s.

These data suggest that to avoid nonlinear behavior due to 
the interaction of IP and saccade amplitude and the possible 
saturation imposed by a unit’s maximum firing rate, data must 
be taken from far in the off-direction. At such off-direction IPs,
the slope of the relation between EBR and peak velocity also 
will be steepest (Fig. 6B).

The eye-velocity sensitivity (slope of the steepest EBR vs.
peak velocity relation) increased with the peak burst rate for 
our sample of 24 abducens units with sufficient data (Fig. 6C).
For the vast majority of neurons, the peak burst rate was 
<500 spikes/s (median 340 spikes/s, range 150–970). The slope of 
the relation between EBR and peak velocity ranged from 0.13 
to 1.0 with a mean of 0.46

\[
\text{EBR (spikes/s)} = \text{peak velocity (°/s)} \\
\times \text{slope (spikes/°)}
\]

 Units with higher 
peak rates tended to have greater slopes. The steeper slopes

![Image](http://jn.physiology.org/)

**FIG. 6.** Relation of burst rate and peak saccadic velocity. A: firing patterns for unit TM 138:2 (Fig. 3) for saccades of 5 to 35° from the same IP (−20° in off-direction). Traces as in Fig. 3. B: relation of EBR vs. peak eye velocity for the unit in A (●) and for another unit (To 20:1), whose data were collected during 
saccades starting either in the off- (−25°, ◦) or on-direction (10°, □). C: slopes of the EBR vs. peak velocity relation, like those in B, as a function of peak burst 
rate for the 24 units subjected to the slice analysis. When the slice analysis was performed at different IPs, the data used in C were taken from the relation with 
the largest correlation coefficient, e.g., for unit To 20:1 in B, the data at IP = −25°. IPs for this population of neurons ranged from −25 to 0°. × symbols identify 
the 2 units in B.
peak saccade velocity on EBR. A: peak velocities of a series of 10° saccades decrease as a function of IP for a set of representative data (IPs have different symbols to identify the same data sets in B). B: for these same saccades, the associated EBR increases linearly with peak velocity with a slope of 0.33 spike·s⁻¹·deg⁻¹·s⁻¹). C: comparison of velocity sensitivities (V_{sens}) obtained in the IP (cf. B) and amplitude (cf. Fig. 6C) experiments for all 15 neurons with sufficient data. Like the neuron in A and B, the data from all 15 neurons exhibited a clear trend of peak velocity with IP (mean ~6.4 ± 3.5/s) and an extended range of peak velocities (150–500/s). Regressive line: V_{sens} (from IP) = 0.98 × V_{sens} (from AMP) + 0.05 (r = 0.74).

FIG. 8. Relation between number of spikes and saccade amplitude. A: raw number of spikes vs. amplitude for saccades starting at either −20° (○) or zero (×) for unit TM 140:2. Although linear relations nicely captured both sets of data (r = 0.98 for both), the data also were associated with higher correlation coefficients. The mean correlation coefficient was 0.75 (±0.16 SD) with a range from 0.45 to 0.98.

Peak saccade velocity also can vary with IP for 10° saccades (cf. Fig. 2). Figure 7A shows the [peak velocity vs IP] relation for the saccade data illustrated in Fig. 2. The slope of the linear regression for this unit is −6.2 deg·s⁻¹·deg⁻¹; the mean slope for all 15 neurons with sufficient data was −6.4 deg·s⁻¹·deg⁻¹. For this unit, EBR increased linearly with peak saccade velocity with a slope (the velocity sensitivity) of 0.33 spikes/deg (r = 0.86, Fig. 7B). In comparison, its velocity sensitivity obtained from the constant IP slice analysis with different saccade amplitudes was 0.25 spikes/deg (cf. Fig. 6C).

We compared these two measures of velocity sensitivity in 15 neurons with sufficient data. Like the neuron in A and B, the data from all 15 neurons exhibited a clear trend of peak velocity with IP (mean −6.4 ± 3.5/s) and an extended range of peak velocities (150–500/s). Regressive line: V_{sens} (from IP) = 0.98 × V_{sens} (from AMP) + 0.05 (r = 0.94).

Number of spikes with amplitude. The number of spikes in a burst increased with saccade amplitude. However, the relation between the number of spikes and amplitude also depended on IP. Figure 8A shows the number of spikes as a function of saccade amplitude for saccades starting at −20° (○) and straight ahead (×) for unit TM 140:2. Although linear relations

FIG. 7. Effect of peak saccade velocity on EBR. A: peak velocities of a series of 10° saccades decrease as a function of IP for a set of representative data (IPs have different symbols to identify the same data sets in B). B: for these same saccades, the associated EBR increases linearly with peak velocity with a slope of 0.33 spike·s⁻¹·deg⁻¹·s⁻¹). C: comparison of velocity sensitivities (V_{sens}) obtained in the IP (cf. B) and amplitude (cf. Fig. 6C) experiments for all 15 neurons with sufficient data. Like the neuron in A and B, the data from all 15 neurons exhibited a clear trend of peak velocity with IP (mean −6.4 ± 3.5/s) and an extended range of peak velocities (150–500/s). Regressive line: V_{sens} (from IP) = 0.98 × V_{sens} (from AMP) + 0.05 (r = 0.94).
for saccades launched from further in the on-direction (0°, X) have a steeper slope (1.4 vs. 0.87 spikes/deg). If we plot the excess rather than raw number of spikes, the difference disappears (Fig. 8B). In six of seven other neurons with sufficient data, the slope of the relation between number of spikes and saccade amplitude also was steeper when saccades were launched from IPs more in the unit’s on-direction. However, the unit illustrated in Fig. 8, A and B displayed the greatest difference in slopes.

Because the excess number of spikes versus amplitude relation explicitly estimates the strength of the transient activation associated with the saccade and is invariant with IP, we use the slope of that relation to compare data from all our neurons. For all but six units, these slopes (sensitivities) from the slice (Fig. 8C, solid bars) and MLR (hatched bars) analyses are <1.0; the median is 0.47 ± 0.38 spikes/deg. For 49 of 52 neurons, the relation between excess number of spikes and saccade amplitude was significant (P < 0.05). As shown in Fig. 8D, the velocity sensitivity of a unit (i.e., the slope of its EBR vs. peak velocity relation) increases with the slope of the excess number of spikes versus amplitude relation (r = 0.70).

BURST DURATION WITH SACCADE DURATION. The duration of the burst was well correlated with the duration of the saccade and the slope of the relation changed little when saccades started from different IPs. For the units analyzed with the slice (median correlation coefficient 0.92 ± 0.13) and MLR analysis, the slopes of 28/52 (54%) were clustered between 0.7 and 1.0 with a mean slope of 0.80 (±0.30). The relation between burst and saccade duration was significant for all but 4. For most units (42/52; 81%), the slopes were ≈1.0 because the slopes of the relation between burst end latency and saccade duration tended to be negative (mean slope = −0.16 ± 0.29). There was little variation in burst start latency with burst duration.

**IP sensitivity of the pause: suprathreshold behavior**

For contraversive saccades selected to have similar amplitudes and velocities in the slice analysis, pause duration decreased as IP increased in the ipsiversive direction. This is shown for the exemplar neuron illustrated in Fig. 9A where rasters are ordered from bottom to top according to increasing ipsiversive IPs. For this neuron, pause duration shortened from about 80 ms for 10° saccades beginning at −10° to about 40 ms for movements launched at +20° (Fig. 9B). Because pause start latency remains constant with IP (Fig. 9B, □), the pause must end ever later relative to the end of the saccade (pause end latency) as the saccade begins more in the off-direction (▲). Thus the end of the pause leads saccade end by about 25 ms at an IP of +20° but lags the end of the saccade by about 10 ms at an IP of −10° (Fig. 9B).

The sensitivity of the pause to IP was due to changes in pause end latency for all our units, as shown in Fig. 9C, which compares the slope of the pause end latency versus IP relation with the slope of the pause duration versus IP relation. Most data fall close to the line of slope 1.0 (actual slope = 1.02, r = 0.95). Also, the pause duration versus IP relation had a negative slope for 44/45 units, indicating that pause duration decreased with ipsiversive IP for virtually every neuron. The mean regression slope was −1.2 ms/deg, and the slopes of 39/45 relations were significant (P < 0.05). Furthermore, this negative relation was quite robust (r ≈ 0.7 for 23/28 units evaluated with the slice analysis where a correlation could be done).

When duration varied for different size saccades launched from the same IP, pause duration increased with the duration of the contraversive saccade. For all 41 neurons, the mean slope of pause versus saccade duration was 0.76 (±0.43 SD). For most units (34/41; 83%), the slope was <1.0. Pause start latency varied little with pause duration [mean slope was −0.12 ms/deg (±0.17 SD)]. On the other hand, pause end

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**FIG. 9.** Relation of pause duration with IP. A: activity of unit TM 141:1 associated with selected 10° saccades launched in the off-direction from different IPs. Saccades and their associated rasters are ordered from top to bottom according to IP from +20° to −10°. All records are aligned on saccade start time. B: pause duration (●), pause start latency (□), and pause end latency (▲) as functions of IP for all 10° saccades in the off-direction for unit TM 141:1. Linear regressions for pause duration (PD), pause start latency (PSL), and pause end latency (PEL) are PD = −1.31 IP +59.5 (r = 0.84), PSL = −0.16 IP +8.6 (r = 0.29), and PEL = −1.20 IP −3.1 (r = 0.86), respectively. C: slope of pause end latency vs. IP as a function of the slope of the pause duration vs. IP relation for 10° saccades. ▲ and △ represent data from the slice (n = 28) and multiple regression analyses (n = 17), respectively. Entire data set is fit by the regression: slope PEL/IP = 1.02 slope PD/IP +0.18 (r = 0.95).
latency did: the slope of the relation between pause end latency and saccade duration was tightly correlated with the slope of the relation between pause duration and saccade duration ($r = 0.93$, slope $= 0.83$). Therefore deviations from the ideal unity relation between pause and saccade duration were largely due to the relation between pause end latency and saccade duration.

**Timing of agonist and antagonist neurons**

Because horizontal saccades are generated by the net action of pools of agonist and antagonist motoneurons, it is important to know the relative timing of the agonist burst and antagonist pause. There are several differences in the characteristics of burst and pause duration. First, the correlation between pause and saccade duration is less robust. Sixteen of 31 units had linear regression coefficients $<0.8$ (average $0.75 \pm 0.20$), whereas only 5/24 relations of burst duration with saccade duration did.

Second, there were consistent differences in the variability and magnitude of the start latencies between the burst and pause for all units. The SDs of the burst and pause start latencies clustered around medians of 3.7 ± 1.5 and 6.4 ± 4.5 ms, respectively. The mean burst start latency was 5.0 ± 2.2 ms. The median of the average pause start latencies was essentially the same at 6.8 ± 4.8 ms.

Third, the end latencies for both the burst and pause were twice as variable as the start latencies. For the burst end latencies, the median SD was 8.7 ms. For the pause end latencies, the distribution of SDs was bimodal with a first peak at a mean of 12.1 ms ($\pm 4.1$ ms, $n = 30$) and an extended tail with a mean at 39.7 ms ($\pm 9.4$, $n = 21$). In previous sections, we often observed that the end latencies exhibited significant correlations with saccade duration or IP. However, those regressions did not account for the increased variability. Therefore the means of the end latencies are good representations of population behavior. The end of the burst preceded the end of the saccade by 15.6 ± 9.0 ms. The end of the pause preceded the end of the saccade by 11.0 ± 13.3 ms, with 45/51 preceding by $-30$ to $+10$ ms.

In conclusion, although the duration of the pause was well correlated with the duration of the contraversive saccade, the latencies both at the beginning and at the end of the pause were quite variable in comparison to those at the onset and end of the burst. Because the pause often started at the high rates associated with IPs in the on-direction, the variability in pause onset was not due to the variable intervals associated with low spike rates.

**Population/analysis summary**

Finally, the general behavior of our abducens neurons was similar to that described in the literature. Figure 10 shows the rate–position characteristics (slope $K$ and threshold for steady firing) for the data used to characterize the burst ($A$) and the pause ($B$) activity with the slice and MLR analyses (filled and open symbols, respectively, in both panels). For both data sets, the neurons with the lowest thresholds for steady firing also had the lowest slopes of the firing rate versus eye position relation (Fuchs et al. 1988). For the pause and burst analyses, we used the slice and MLR analyses equally often for the low- and high-threshold units.

**DISCUSSION**

To understand how the saccadic control system takes initial eye position (IP) into account, we recorded from abducens neurons in head-restrained primates during horizontal saccades initiated from different horizontal positions of the eye. Small (5–10°) saccades often had identical amplitude and velocity profiles over a wide range of IPs, yet the associated motoneuronal bursts or pauses varied with IP. Where tested, these same neurons showed the usual tight linkage between firing pattern and eye movement characteristics for saccades made from the same IP. Therefore our results indicate that one of the effects of IP is to disrupt this usual linkage, thus revealing a major nonlinearity in the saccadic signals sent to the extracocular muscles. A second effect of varying IP was to confirm the observations of other studies, which showed that centrifugal saccades, especially those $>10^\circ$, were slower and of longer

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**FIG. 10.** Summary of our unit population by plots of the slope of the rate–position slope $K$ against the threshold $T$ for steady firing. $A$: data from unit activity used to evaluate the burst. Filled symbols identify units with sufficient trials to perform an IP slice analysis; open symbols identify units subjected only to MLR analyses. A unit could furnish burst data about either suprathreshold IPs ($\triangle$ and $\Delta$) or subthreshold IPs ($\square$ and $\Box$), or both ($\diamond$ and $\bigtriangleup$). $B$: data from unit activity used to characterize the pause. Some units are the same as those in $A$. Symbols identify units subjected to a slice analysis for both amplitude and IP ($\blacktriangle$), to a slice analysis for amplitude or IP ($\blacktriangle$ and $\blacktriangleleft$, respectively) and to only a multiple regression analysis ($\bullet$).

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duration than were centripetal saccades. We show here how these effects of IP on saccade metrics are associated with changes in the burst behavior of abducens neurons.

Methodological considerations

Interpretation of the current data depends on which neurons we sampled and how we assessed the activity associated with the saccade. With regard to the former concern, the abducens nucleus contains at least three types of neurons with different targets: motoneurons that innervate the ipsilateral lateral rectus muscle (LR), immediate premotor interneurons that convey a very similar signal to contralateral medial rectus (MR) motoneurons, and neurons whose axons are destined for the flocculus (Langer et al. 1985). The precerebellar neurons are concentrated in the dorsal part of the nucleus, where—based on our experience—neurons tend to have higher thresholds for steady firing and reach lower rates. Our sample probably includes few of these because our recordings mostly were from neurons well within the nucleus.

It is more problematic to dissociate internuclear and motoneurons. In our earlier study, about 90% of identified internuclear neurons were recruited at thresholds < −15°, whereas only about 50% of identified motoneurons were (Fuchs et al. 1988). Of those neurons recruited at thresholds < −15°, internuclear neurons had substantially higher velocity sensitivities; 96% of internuclear neurons had velocity sensitivities > 1.0 spikes·s⁻¹·deg⁻¹·s⁻¹, whereas only 12% of motoneurons did. However, the velocity sensitivity in that study was determined during 0.5-Hz smooth pursuit movements rather than during the much more rapid saccade with its higher frequencies. If we assume that the velocity sensitivity at the highest frequency studied by Fuchs et al. (1988; their Fig. 7) approaches the sensitivities reported herein determined during the saccade, identified motoneurons in their study would have an average sensitivity of about 0.7 (74% lay between 0.4 and 1.0 spike·s⁻¹·deg⁻¹·s⁻¹). In our current study, of the 34 neurons with thresholds < −15°, 24 had relatively low velocity sensitivities between 0.1 and 0.5, which are more characteristic of motoneurons.

Therefore on the basis of their discharge characteristics, we conclude that many of our abducens neurons were motoneurons. Furthermore, our abducens neurons with linear and nonlinear behaviors were distributed throughout the threshold range (Fig. 10) so some of the neurons with either behavior were likely to have been motoneurons. Moreover, abducens interneurons provide the strongest conjugate input to the MR so, in a sense, their signal can be regarded to have an effect equivalent to that of a motoneuron. Therefore in what follows, we will consider all our neurons as a single population.

There are several reasons why we feel our results are not influenced by vergence. First, at our viewing distance, the maximal change in vergence angle amounts to < 2° of the usual 10° saccades we elicited. Second, the influence on firing of any modest vergence that might occur would be in opposite directions when, for example, the right eye moved centripedally (convergence) and when it moved centrifugally (divergence). Moreover, peak vergence velocities are at least an order of magnitude smaller than those of saccades and furthermore occur long after the saccades examined in our study would be over. Finally, our model accounts for the behavior of our neurons without having to resort to a vergence component.

Comparison with previous data

For saccades of differing amplitudes from the same IP, the excess burst rate (EBR) increased linearly with peak saccade velocity. The average velocity sensitivity was 0.46 spikes·s⁻¹·deg⁻¹·s⁻¹ (range 0.1 to 1.0) and was greater for units with greater peak burst rates (Fig. 6C). As mentioned earlier, identified motoneurons in our previous study (Fuchs et al. 1988) had an extrapolated average velocity sensitivity of 0.7. For their abducens neurons, Sylvester and Cullen (1999) reported a lower velocity sensitivity of 0.27 spikes·s⁻¹·deg⁻¹·s⁻¹, possibly because their saccades were initiated from a variety of orbital positions. The saccade velocity sensitivity of our abducens neurons was substantially less than that of EBNs (Strassman et al. 1986a; Ling et al. unpublished data) or IBNs (Cullen and Guitton 1997; Scudder et al. 1988; Strassman et al. 1986b).

The raw number of spikes increased with saccade amplitude but with different slopes for different IPs (Fig. 8). However, the excess number of spikes increased with saccade size at the same slope for all IPs. The average slope of that relation was 0.57 spikes/deg (0.1 to 1.9), a value slightly lower than the average reported by Sylvester and Cullen (1999; 0.96 spikes/deg; their Fig. 7).

Finally, as mentioned previously (Fuchs and Luschei 1970; Goldstein and Robinson 1992; Keller and Robinson 1971), the burst and pause durations of abducens neurons are strongly linked to the durations of on- and off-direction saccades, respectively. Both the burst and the pause began about the same time before the saccade. In both cases, the slopes of the burst or pause duration versus saccade duration relation tended to be < 1 (population means of 0.80 and 0.76, respectively), and the departure from a perfect match was related to the times that the burst and pause ended. Both the burst and pause ended before the end of the saccade, with the burst terminating on average slightly before the pause. We observed no rebound after the pause when the steady firing resumed. Thus it is the precise timing of the end of the burst and pause that brings the eye on target rather than some active braking pulse such as is used in the antagonist muscles in the somatomotor system (Hannaford and Stark 1985).

Similar saccades: a simple model of initial-position effects

Although these results appear complex, it is possible that a relatively simple pattern underlies the complexity. To test this possibility, we examined the behavior of a simple population model of the MN pool. The main assumptions of the model are as follows.

1) All motoneurons in a given pool receive identical burst (or pause) commands that do not vary with IP.

2) The burst (or pause) input during the saccade adds linearly to an eye position command, which is evident during the fixation between saccades. During the saccade, the eye position command exhibits a linear (i.e., ramplike) change from the pre- to the postsaccadic steady firing (as shown in Fig. 1B).
3) The fixation command can take negative values and is linearly related to static eye position over the entire oculomotor range.

4) Motoneuron firing occurs only when the net input is positive.

We discuss the plausibility of these assumptions after we have shown their consequences for interpreting the current data.

**Behavior of single abducens neurons**

Figure 11A shows the output of the simple model for a single agonist motoneuron for 10° saccades from three IPs. The saccadic and eye-position–related inputs were added according to Eq. 1 in Hazel et al. (2002) with weights $w_j = 1$, intrinsic gain $G = 1$, and intrinsic threshold $B = 0$. The linear eye-position–related input for this neuron had an $x$-intercept (corresponding to eye-position threshold) of 0° and a slope (corresponding to eye-position sensitivity) of 8 spikes s$^{-1}$•deg$^{-1}$. The saccadic burst command has been given a Gaussian-shaped firing rate profile with a height of 300 spikes/s and a duration of about 50 ms. Even though we assume that the input profiles have identical shapes in each of the three panels, the output burst profiles do not remain identical for IPs below the motoneuron’s threshold. Thus for an IP of −30°, the motoneuron output for a 10° saccade has a peak rate of 100 spikes/s and a duration of 14 ms, whereas for an IP of −15° the corresponding values are 220 spikes/s and 26 ms. The simple model therefore reproduces the main qualitative features of the below-threshold firing we observed experimentally, i.e., an increase in peak frequency and burst duration (Fig. 5).

For IPs at or above the motoneuron’s threshold of 0° (e.g., Fig. 11A, rightmost panel), the output burst profiles do have a constant shape. Thus the extra firing associated with the burst (i.e., burst-related firing) remains constant at its input value (excess peak firing rate 300 spikes/s, duration 50 ms). Linear neurons exhibited similar burst characteristics above threshold (Fig. 4A). It should be noted that, as the shaded areas in Fig. 11A indicate, the term “burst-related firing” refers to the raw burst firing rates for saccades starting from IPs below threshold, and to excess burst firing rates for saccades starting from IPs above threshold. In both cases, the term refers to the motoneuronal output that is specifically related to the saccade and therefore represents the saccadic control signal that actually is sent to the lateral rectus muscle.

Figure 11B shows corresponding firing patterns for the pause command for a model antagonist neuron, here assumed to behave identically to its agonist equivalent apart from appropriate changes in sign. As IP moves in the antagonist’s off-direction (agonist’s on-direction), the duration of the pause increases (14 ms for an IP of −30°, 26 ms for an IP of −15°), becoming indefinitely long once the position threshold of the neuron is reached. This pattern of pausing corresponds to that we observed experimentally: when contraversive saccades were launched from IPs more in an abducens neuron’s on-direction, the associated pause decreased in duration for 44/45 neurons tested (e.g., Fig. 9A). The increase in pause duration was not simply the result of the lower steady rates associated with off-direction fixation landing sites because, as can be seen in Fig. 9A, the postsaccadic interspike intervals were usually less than half the pause duration.

**Behavior of the entire abducens population**

The saccadic command sent to an extraocular muscle is carried by a population of many motoneurons—for example, >2,000 in the case of the squirrel monkey lateral rectus muscle (McClung et al. 2001). Figure 12 illustrates the hypothetical qualitative pattern of IP-associated changes in the total saccadic command sent to the muscles from a model population of 61 motoneurons. Note that “saccadic command” here again refers to raw firing rates for below-threshold IPs and corrected firing rates for above-threshold IPs. For the 61 motoneurons, eye position thresholds (Θ) were spaced every 1° from −40 to +20° and eye position sensitivities (Κ) increased with thresh-

**FIG. 11.** Simulated motoneuron inputs and outputs for 10° saccades from different IPs. A: agonist motoneuron with an eye position threshold of 0° and an eye position sensitivity of 8 spikes s$^{-1}$•deg$^{-1}$. Its inputs were (i) a saccade burst command with a Gaussian-shaped profile of height corresponding to 300 spikes/s and duration 50 ms, and (ii) an eye position command that started at the value associated with saccade onset (allowing negative input commands; see main text) then increased linearly over 50 ms to the value associated with saccade end. Motoneuron input profile is the same in all 3 panels, but the above-threshold firing patterns vary appreciably as IP changes from −30° (left) to −15° (center) and 0° (right). Burst-related motoneuron output is shaded. B: antagonist motoneuron with position threshold of 0° and sensitivity of 8 spikes s$^{-1}$•deg$^{-1}$. Its inputs were (i) a saccade pause command, assumed to be the same as the burst command to the agonist motoneuron but with negative sign, and (ii) a position command that started at the value associated with saccade onset then decreased linearly over 50 ms to the value associated with saccade end. Motoneuron input profile is the same in all 3 panels but the above-threshold firing patterns vary appreciably as IP changes from −30° (left) to −15° (center) and 0° (right). Pause-related loss of firing is shaded.

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old \( (K = 8 + 0.1 \Theta) \). These recruitment characteristics of the neurons in the model were approximations to those observed experimentally (Fuchs et al. 1988; Fig. 5). The characteristics shown in Fig. 12, A and B appear robust with respect to the details of the modeling assumptions. For example, qualitatively similar patterns were observed when the relationship between motoneuron eye position sensitivity and threshold was changed from \( K = 8 + 0.1 \Theta \) to either \( K = 8 + 0.2 \Theta \) or even \( K = 8 \). Moreover, simulations that assumed an excess burst rate of 50 rather than 300 spikes/s for individual modeled motoneurons also produced results similar to those in Fig. 12. However, the simulation did depend on a distribution of recruitment thresholds.

All neurons received the same saccadic burst command, which we assumed did not vary with IP. Nonetheless, the population burst profiles varied substantially with IP (Fig. 12A), because of the variation in the number of motoneurons above threshold. Similarly large variations were seen in the pauses (Fig. 12B). Considering the two rows together, it can be seen that centripetal saccades starting at different (negative) IPs were associated with substantial changes in both agonist (A) and antagonist (B) commands, whereas centrifugal saccades (from positive IPs) were dominated by the agonist command (cf. Pelisson and Prablanc 1988).

This effect is shown more clearly in Fig. 13A, which shows how the peak excess burst rate produced by the agonist motoneuron pool (from Fig. 12A), and the peak firing rate pause summed over the antagonist motoneuron pool (from Fig. 12B), vary as a function of IP. For saccades starting from extreme centripetal positions (e.g., \(-40^\circ\)), the bulk of the saccade-related change in motoneuron firing is produced by the pause in the antagonist pool. As the IP moves toward the primary position, the relative contribution of the pause declines and becomes negligible as the IP moves centrifugally from the primary position where the burst of the agonist pool dominates. This pattern reflects the state of recruitment in the two horizontal motoneuron pools. For saccades starting from far centripetal IPs, few agonist motoneurons have been recruited, whereas almost all antagonist motoneurons are active before the saccades. The effects of the burst command are therefore small, but the effects of the pause command are large. In contrast, for far centrifugal saccades, almost all agonist and few antagonist motoneurons are active so that the effects of the burst command are large and the pause command small.

This simple model deals only with the commands sent by motoneurons to the muscle fibers in their motor units, and not the actual muscle force produced by those units. More detailed models of the forces produced by recruitment in extraocular muscle (Dean 1996; Dean et al. 1999) suggest that the actual muscle force can be explained only by assuming that motoneurons with high position thresholds tend to control stronger motor units in a manner related to the “size principle” (Henneman and Mendell 1981). If so, the differences between the two curves shown in Fig. 13A would be greater still for the forces generated as a result of those changes in firing rates. These agonist and antagonist forces are shown in Fig. 13B, although the amplification is rather modest. Figure 13B also shows that the net change in muscle force (black curve), obtained by adding the agonist and antagonist curves, varies relatively little with IP [maximum 9% deviation from the mean (4.55) across all IPs]. This modest variation in the net change in muscle force indicates that the globe and orbital tissues, on which the net muscle force acts, have mechanical properties that are scarcely affected by the position of the eye. Instead, the critical effect of IP is on the way in which the net change in muscle force is divided between agonist and antagonist muscles.

### Plausibility of assumptions

BURST/PAUSE INPUT TO MOTONEURONS IS INDEPENDENT OF IP. To our knowledge, there is only anecdotal evidence concerning the assumption that the burst commands sent to motoneurons from excitatory burst neurons (EBNs) are independent of IP. Keller (1974) says their “burst rate was not dependent on the initial eye position within a range of \( \pm 20^\circ \) from the primary position.” In the course of recording the abducens neurons for this study, we evaluated, with the slice analysis,
the IP sensitivity of two putative EBNs rostral of the abducens nucleus in monkey TM. For these two neurons, peak burst rate did not vary significantly with IP. Concerning the generation of pauses in abducens neurons, Scudder et al. (1988) concluded that “initial position (tested over a 30° range) had a weak effect on the number of spikes in inhibitory burst neurons (IBNs, the source of the pause in abducens motoneuron firing), having a slope of +0.13 spikes/° or ~10% of the slope of the number of spikes on size relation.” Unfortunately, that study did not examine the effect of IP on IBN burst duration, which we expect would account for the robust relation we found for pause duration with IP in abducens neurons (Fig. 9). Thus our assumption that the putative inputs that create both bursts and pauses are independent of IP requires further testing, although current evidence suggests that very large effects are unlikely.

BURST AND RAMP INPUTS TO MOTONEURONS ADD LINEARLY. The assumption that burst and ramp inputs add linearly is clearly consistent with the behavior of those motoneurons labeled nonsaturating in the present study. The discharge of abducens neurons during 10° saccades with similar metrics showed two different types of suprathreshold behavior. Slice analysis was used to generate such 10° saccade data sets for 26 units, 16 of which had thresholds lower than any IP in the range studied. For half of these very low threshold neurons, the raw burst rate increased linearly with IP and the slope of the relation of raw burst rate with IP was well related to the slope of the relation between steady rate and IP (slope = 1.2, r = 0.62). For units with such linear behavior, the EBR associated with similar saccades from different IPs was essentially constant (Fig. 4A). Moreover, the excess number of spikes and burst duration also was constant with IP, on average, across this population of neurons. The other half of the abducens neurons exhibited a saturation of raw peak burst rate with IP, but their excess number of spikes remained constant or decreased only slightly with IP. These saturating units would appear to be processing their inputs nonlinearly but this issue will subsequently be discussed further.

MOTONEURONS ARE ACTIVELY INHIBITED AT IPS BELOW THRESHOLD. Several observations suggest that this assumption is not unreasonable. First, the nuclei prepositus hypoglossi, which contain neurons whose discharge increases linearly with contralateral eye position, send inhibitory projections to the contralateral abducens nucleus (Escudero et al. 1992; McFarland and Fuchs 1992). If such an inhibitory eye position input varied in strength from motoneuron to motoneuron, its combination with a constant-strength excitatory eye-position input from position-vestibular-pause cells in the vestibular nuclei (Scudder and Fuchs 1992) could provide a simple mechanism for producing a correlation of population of motoneurons with the well-known positive correlation between eye-position threshold and eye-position sensitivity (Fuchs et al. 1988; Hazel et al. 2002). Second, when we applied the below-threshold inhibitory correction to abducens neurons recorded in the present study, excess burst rate became relatively constant with IP for some neurons and increased only slightly for others. This “correction” also “linearized” the behavior of the three remaining very high threshold abducens neurons for which we had only subthreshold burst data. After a subthreshold correction, which adds spikes to compensate for the putative subthreshold inhibition, the excess number of spikes remained approximately constant with IP for all subthreshold segments. These observations indicate that the assumption of active inhibition below threshold at least is reasonable and that its effects would serve to “linearize” the system. Finally, Robinson and colleagues (Goldstein and Robinson 1992; Robinson 1970) also proposed an active inhibition below the threshold for steady firing by opining that the “further below threshold the eye position, the more deeply the cell is inhibited” (Goldstein and Robinson 1992).

FIG. 13. Magnitude of changes in simulated agonist (burst) and antagonist (pause) motoneuron firing and muscle force associated with saccades from different IPs. A: for each IP, solid gray line shows the peak of the population firing rate profile produced by the burst command in the agonist as shown in Fig. 12A, and the dashed gray line the peak “loss” in firing rate produced by the pause command produced by the antagonist as shown in Fig. 12B. B: for each IP, the amount of extra force produced by the agonist (Fig. 12A), or “lost” by the antagonist (Fig. 12B), was calculated using the assumption that the strength of a motor unit varied with its threshold, from an arbitrary value of 1 (lowest threshold unit) to 50 (highest threshold unit). This 50-fold ratio of motor unit force is approximately that observed for the squirrel monkey (Goldberg et al. 1998). Curve at top (“total”) shows the net force produced by the pull of the agonist and push of the antagonist (see text).
Evidence for model results

Evidence that the antagonist muscle makes a substantial contribution to centripetal saccades but not to centrifugal saccades comes from both lesion and recording studies. In patients with sixth nerve palsies, 10° centrifugal saccades from the primary position of gaze were slower and of longer duration than normal, whereas 10° centripetal saccades to the primary position had normal velocity profiles (Wong et al. 2006). The authors suggest that these findings arise because in centripetal saccades “most of the change in force is contributed by relaxation of the normal antagonist, that is the medial rectus. When the movement begins from an orbital mid-position, however, the change in force comes mainly from contraction of the agonist, that is the paretic lateral rectus.” In monkeys, when transection of the medial longitudinal fasciculus eliminates both the ramp and burst input to medial rectus motoneurons from internuclear neurons in the contralateral abducens, the opposite happens: centrifugal abluding saccades are relatively normal, whereas centripetal abluding saccades are slowed (Evinger et al. 1977).

The suggestion that the antagonist muscle makes a substantial contribution to centripetal saccades but not to centrifugal saccades is supported by data from recordings of extraocular muscle activity with a multiple electrode needle array (Collins 1975). The changes in agonist muscle activity that accompanied 10° saccades were much greater if the saccades were centrifugal than if they were centripetal (Collins 1975; Fig. 9). Isometric tension in the extraocular muscles of strabismus patients also indicates that the change in agonist force associated with a 10° saccade is smaller when the saccade is centripetal rather than centrifugal (Lennerstrand et al. 2006; Fig. 2).

Effects of initial position on saccade metrics

Our simple model may also offer a clue as to why large centrifugal saccades are slower than centripetal ones. Centrifugal saccades are driven mainly by the pull of the agonist muscle (Fig. 13). As IP moves further into the on-direction, the agonist muscle force required just to hold the eye in position approaches the maximum force that the muscle can produce (Collins 1975), i.e., when all motor units are recruited and firing maximally. Therefore because centrifugal saccades start at more eccentric positions, there eventually will not be enough extra force available to produce a saccade of normal (main sequence) peak velocity.

Although the data that led to the model in Fig. 13 were generated for identical saccades selected to have no difference in their centripetal and centrifugal velocities (the slice analysis), some of our other data were obtained under conditions where peak velocity was not constrained. When velocity was allowed to vary for saccade amplitudes of 10°, peak velocity was greater for centripetal (Fig. 7A, negative IPs) than for centrifugal (positive IPs) saccades. Moreover, the change in peak velocity was tightly linked to the change in excess burst rate (Fig. 7B), indicating that peak burst rate varied with IP. This observation implies that, under natural conditions where the centripetal–centrifugal velocity differences are associated with changes in firing rate with IP, the rate of burst inputs to the abducens pool depends on IP. It is well known that the burst of pontine burst neurons, which provide excitatory inputs to abducens neurons, is related to saccade velocity when velocities change in association with saccades of different amplitudes (Van Gisbergen et al. 1981). Here we show that the velocity sensitivity of abducens neurons is the same whether varying IP or saccade amplitude causes the velocity changes (Fig. 7C). Consequently, it is reasonable to suggest that all of the input signals that contribute to saccade velocity are the result of a common sensitivity of the premotor burst neurons to different eye velocities, irrespective of the circumstances in which they are generated. In this situation, the difference between centrifugal and centripetal saccades is of central origin. Therefore it again seems desirable to examine the IP sensitivity of all aspects of the burst generator discharge, especially peak burst rate.

Behavior of saturating units

Some abducens neurons display a saturated peak burst rate and a consequent reduction in excess burst rate as saccades become more centrifugal, even in the situation (our slice analysis) where the velocity of the movements is maintained (Fig. 4B). In this situation, the relation between excess burst rate and peak eye velocity breaks down. Presumably, recruitment of additional motoneurons is effective in overcoming the decreasing excess burst rate of saturating units. However, in the extremes of centrifugal gaze, saccade velocity decreases, apparently due to a concomitant decrease in the net EBR (e., Fig. 3: +10°; Fig. 7B). This observation indicates that recruitment cannot continue to mobilize sufficient extra motor units to keep saccade velocity from decreasing in extreme IPs and suggests that the saturation of the agonist burst results in the IP-related velocity changes.

Some of our data bear on the nature of the saturation. It is possible that saturating behavior is caused, at least in some neurons, by changes in the input signal rather than mechanisms intrinsic to the motoneuron. This interpretation is consistent with the data illustrated in Fig. 4C, which shows a neuron that is capable of firing at about 800 spikes/s during 20° saccades, but exhibits saturation at only about 550 spikes/s for centrifugal 5° saccades. However, if the data illustrated in Fig. 4C indeed reflect a sensitivity of saccade inputs to IP, the burst generator would be providing different signals to abducens neurons with nonsaturating and saturating behaviors. It would provide a peak burst rate signal that did not vary with IP to units with nonsaturating responses and a peak rate signal that did vary with IP to units with saturating behavior. Furthermore, as pointed out earlier, the similarity of saccade velocity sensitivities in abducens neurons determined by causing velocity to vary with IP or saccade amplitude suggests a central origin for the IP-related changes. This possibility would be a further reason to examine the sensitivity of the EBN burst to IP.

Two points serve to summarize this report.

1) For 5–10° saccades at central orbital positions, IP has little or no effect on saccade velocity or duration, but does alter motoneuron firing rates. These alterations can be simply explained by assuming a burst (and pause) input command that is independent of IP. This command is distributed to all members of the motoneuron pool and is summed linearly with static eye-position–related commands that vary
from motoneuron to motoneuron (recruitment). The net effect is that centripetal saccades are driven by both agonist and antagonist muscles, whereas centrifugal saccades rely heavily on the agonist.

2) For larger saccades and smaller saccades at extreme orbital positions, centrifugal movements are typically slower than centripetal ones. This difference probably arises because the shortened agonist muscle on its own becomes incapable of delivering the required excess force for fast saccades as an increasing number of motor units reach saturation and few neurons remain to be recruited. In these circumstances, it appears that the burst command is lengthened to ensure a sufficient saccadic drive.

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REFERENCES


