

# Apparent Dissociation Between Saccadic Eye Movements and the Firing Patterns of Premotor Neurons and Motoneurons

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**Ling, Leo, Albert F. Fuchs, James O. Phillips, and Edward G. Freedman.** Apparent dissociation between saccadic eye movements and the firing patterns of premotor neurons and motoneurons. *J. Neurophysiol.* 82: 2808–2811, 1999. Saccadic eye movements result from high-frequency bursts of activity in ocular motoneurons. This phasic activity originates in premotor burst neurons. When the head is restrained, the number of action potentials in the bursts of burst neurons and motoneurons increases linearly with eye movement amplitude. However, when the head is unrestrained, the number of action potentials now increase as a function of the change in the direction of the line of sight during eye movements of relatively similar amplitudes. These data suggest an apparent uncoupling of premotor neuron and motoneuron activity from the resultant eye movement.

## INTRODUCTION

One of the basic tenets of oculomotor research is that the activity of the motoneurons that innervate the eye muscles uniquely specifies the movement of the eye in the head under all circumstances (Robinson 1975). This has been demonstrated for abducens motoneurons, which drive the lateral rectus muscle to produce abduction of the eye (Fuchs and Luschei 1970). Furthermore, the discharge patterns of all abducens neurons are thought to be qualitatively similar (Keller and Robinson 1972); all reflect the passive constraints imposed by the globe and its connective tissue, known collectively as the oculomotor plant (Robinson 1975).

Most previous studies of eye-movement-related neurons in the brain stem were done with the subject's head restrained so that changes in the direction of the line of sight (gaze amplitude) were accomplished only with saccadic eye movements. During ipsiversive saccades, motoneurons exhibit a burst of action potentials, which overcomes the viscous drag of the oculomotor plant. During the stable fixations that precede and follow saccades, abducens neurons display a steady firing rate, which is proportional to the eccentricity of the eye in the orbit (Fuchs and Luschei 1970; Keller and Robinson 1972). This steady firing holds the eye in place against the elastic restoring forces of the plant.

Physiological data from several species indicate that the burst of motoneurons with ipsiversive saccades and their pause in activity with contraversive saccades is the result of direct inputs from medium-lead burst neurons (MLBs), which are part of a neuronal burst generator that resides in the brain stem reticular formation (Moshovakis et al. 1996). During saccades,

MLBs discharge a high-frequency burst, and saccade amplitude increases linearly with the number of action potentials. According to the Robinson (1975) model, MLBs transmit a saccade velocity command to motoneurons based on the eye motor error. This command also is integrated, in the mathematical sense, to provide the eye-position-related steady discharge of ocular motoneurons. The observed linear increase of saccade amplitude with the number of action potentials in MLBs is a corollary of this mathematical integration.

When the head is free to turn, gaze shifts can be achieved by a combination of eye saccades and rapid head movements (Freedman and Sparks 1997; Guitton and Volle 1987; Phillips et al. 1995). MLBs continue to discharge a vigorous burst for such head-unrestrained gaze shifts, and the number of action potentials in the burst of many such cells is better correlated with gaze amplitude than with eye amplitude (Cullen and Guitton 1997; Phillips 1993; Whittington et al. 1984). The fact that the number of action potentials in premotoneuron bursts does not predict the amplitude of eye movements suggests that premotor activity can be uncoupled from the resultant eye movement. However, the interpretation of the behavior of premotor brain stem neurons depends critically on how these neural signals are processed on the way to the eye muscles. Therefore it is important to know how ocular motoneurons behave when the head is unrestrained.

## METHODS

Extracellular action potentials were recorded from the brain stem of four monkeys trained to follow a small jumping light spot for an applesauce reward. Detailed descriptions of our target presentation and unit recording conditions have been published elsewhere (Phillips et al. 1999). Tracking of the jumping target was achieved either with the head unrestrained or held. Gaze shifts with the head unrestrained were collected before those with the head fixed; ~50% of the neurons were lost when the head was fixed. Activity was recorded from abducens neurons and MLBs. Although our abducens neurons were not identified by their projections, their discharge characteristics (thresholds and slopes of firing rate vs. eye position relations) were typical of the lateral rectus motoneurons or internuclear neurons, which project directly to medial rectus motoneurons, that we described previously (Fuchs et al. 1988). In contrast to burst-tonic neurons in the nearby nucleus prepositus hypoglossi, ours all paused for contraversive saccades. The MLBs considered here lay rostral to the ipsilateral abducens nucleus, i.e., were excitatory, and had latencies <10 ms; we will refer to them as excitatory burst neurons (EBNs). Each gaze shift and its associated instantaneous firing rate were displayed on a computer monitor, and locally developed programs identified the onset and end of the gaze shift and its eye- and

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head-movement components and counted the associated action potentials.

All the surgeries, training procedures, and recording conditions in this study were approved by the Animal Care and Use Committee at the University of Washington.

RESULTS

Figure 1 compares the behavior of an EBN with that of an abducens neuron during head-fixed gaze shifts. As reported elsewhere, saccade amplitude increases linearly with the number of spikes in the burst (Fig. 1*B*). For the 14 EBNs examined here, the slope was  $1.07 \pm 0.34^\circ/\text{action potential}$  (mean  $\pm$  SD;  $r = 0.94 \pm 0.05$ ). As expected from the direct connections of EBNs to motoneurons, saccade amplitude also increases linearly with the number of action potentials in the burst of an abducens neuron (Fig. 1*D*). For 14 abducens neurons recorded with the head restrained, the slope of the relation was  $0.96 \pm 0.36^\circ/\text{action potential}$  ( $r = 0.93 \pm 0.04$ ).

Figure 2 shows the behavior of the EBN in Fig. 1 when the head is free to turn. In Fig. 2*A*, gaze shifts of different sizes are produced by eye displacements of nearly equal size. Because burst duration is longer for the larger gaze shift but peak firing rates are roughly comparable, the same amplitude eye saccade

is associated with different numbers of action potentials. After eye-movement amplitude saturates during the largest gaze shifts, the number of action potentials continues to increase (Fig. 2*B*). Consequently, the number of spikes shows a linear relation with gaze amplitude but a nonlinear relation with eye amplitude.

During head-unrestrained gaze shifts, the relation between movement amplitude and the number of action potentials in the burst of abducens neurons resembles that observed in EBNs. For the abducens neuron of Fig. 1, the number of action potentials in the burst again was larger for the larger of the two illustrated gaze shifts, although the amplitudes of the two eye-movement components were roughly equal (Fig. 2*C*). Indeed, although the number of action potentials ranged from 30 to 60, the amplitude of the saccade changed little. In contrast, gaze amplitude continued to increase with the number of action potentials.

We observed a saturation of the relation between eye amplitude and number of action potentials in all 30 of our abducens units recorded with the head unrestrained. To compare data across neurons, we fit the number of action potentials versus eye- or gaze-amplitude relations with exponential functions. The relation between either eye or gaze amplitude and the number of action potentials ( $N$ ) was fit with exponentials of

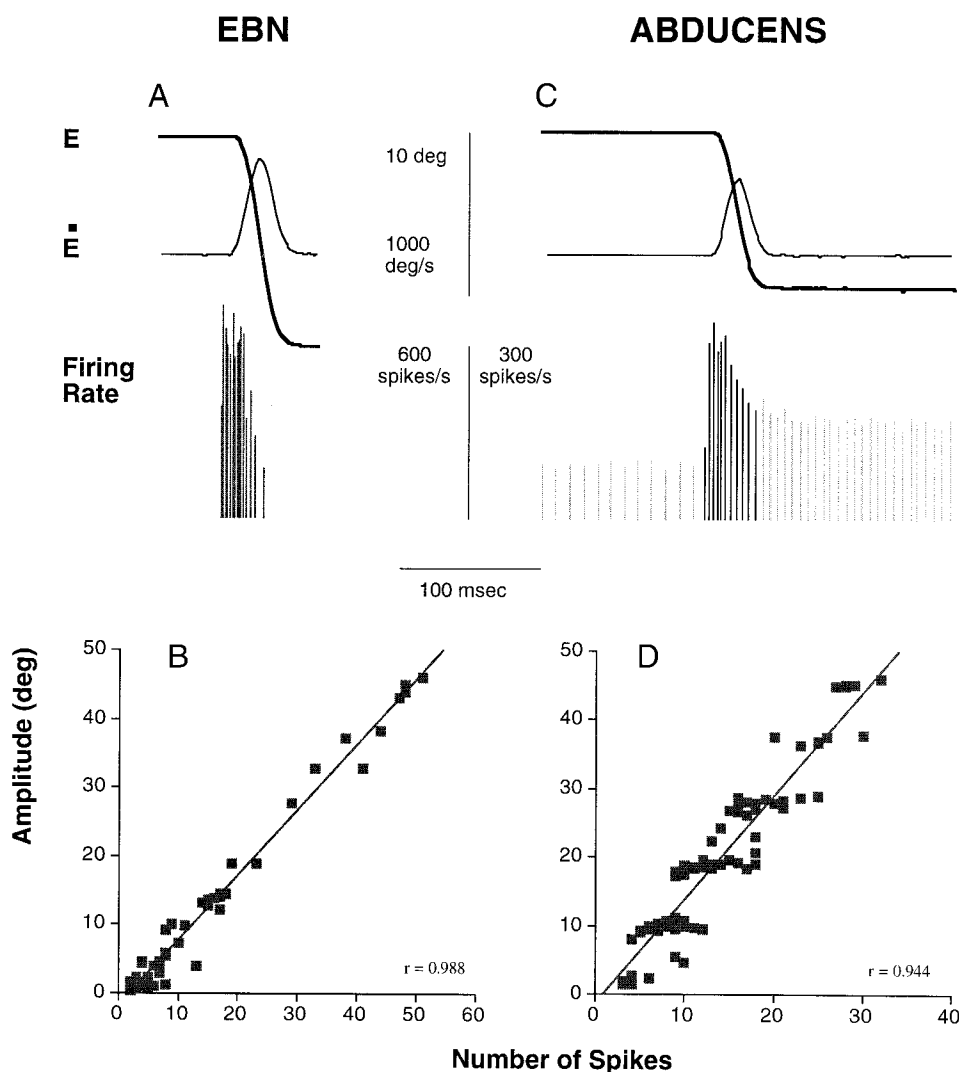


FIG. 1. Activity of an excitatory burst neuron (EBN) and an abducens neuron during a head-restrained horizontal saccade. *A* and *C*: firing rate and associated eye position (*E*) and velocity ( $\dot{E}$ ). Each action potential is represented by a bar whose height indicates the instantaneous firing rate based on the previous interspike interval. Darkened bars indicate the duration of the burst. *B* and *D*: relation between the amplitude of the saccade and the number of action potentials (or spikes) in the burst.

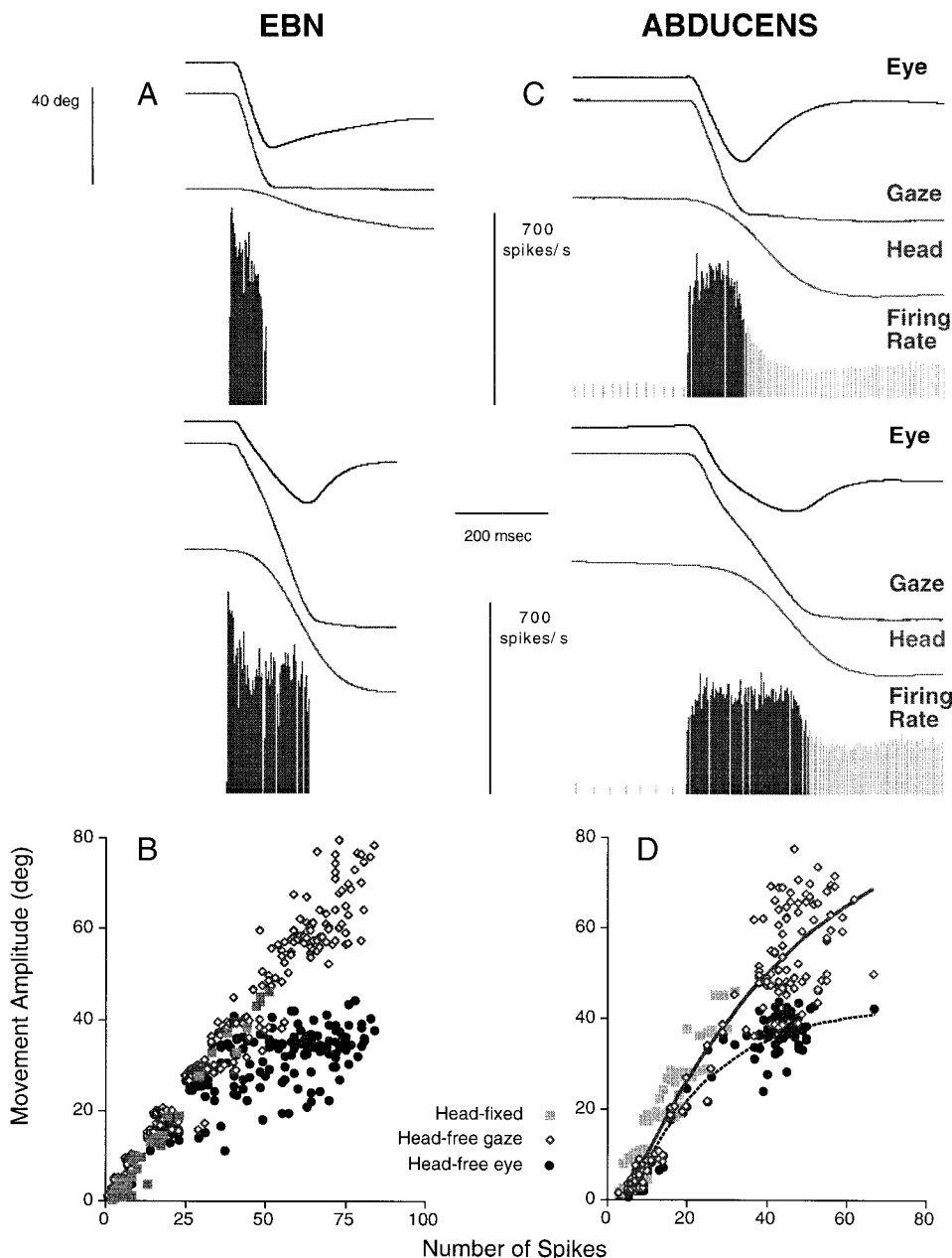


FIG. 2. Discharge characteristics of the EBN and abducens neuron illustrated in Fig. 1 when the head is unrestrained. *A* and *C*: firing rates associated with 2 different size gaze shifts with equal amplitude eye movements. *B* and *D*: relation between movement amplitude and the number of action potentials (spikes) in the burst. For comparison, the data for head-restrained saccades are also included (gray squares). Exponential fits to the head-unrestrained data are shown for the abducens neuron.

the following form:  $a_1 + a_2 * \exp(-a_3 * N)$ . For the example in Fig. 2D,  $r^2$  was 0.95 for gaze movement and 0.94 for eye movement. As can be seen in Fig. 3, the best fit with eye amplitude always appears to saturate, whereas that for gaze amplitude usually continues to increase.

It seems unlikely that the saturation is due to active braking by the antagonist because we saw no evidence of a burst of firing at the end of saccades in the contraversive direction. Also, correcting for the position component of the unit's discharge did not change the fundamental differences between the gaze and eye relations.

#### DISCUSSION

With the head unrestrained, the number of action potentials in a motoneuron burst no longer accurately predicts the amplitude of an eye movement as it did with the head restrained.

This is not to imply that when the head is unrestrained the dynamics of the oculomotor plant are different. Rather, when the head contributes to gaze shifts, the wide variety of movement kinematics exposes complexities of the plant that first-order approximations neglect (Fuchs et al. 1988). Dissociations between motoneuron discharge and eye movements also appear during monocular eye movements (Zhou and King 1998).

Because EBNs and motoneurons show similar relations between the number of action potentials and either eye- or gaze-movement amplitude, both must encode the same variable. If this variable were gaze, then we are left with the illogical conclusion that eye motoneurons encode eye-position-in-space. This clearly is incorrect because abducens motoneurons are deeply modulated if an animal stabilizes its gaze during the vestibuloocular reflex (Skavenski and Robinson 1973).

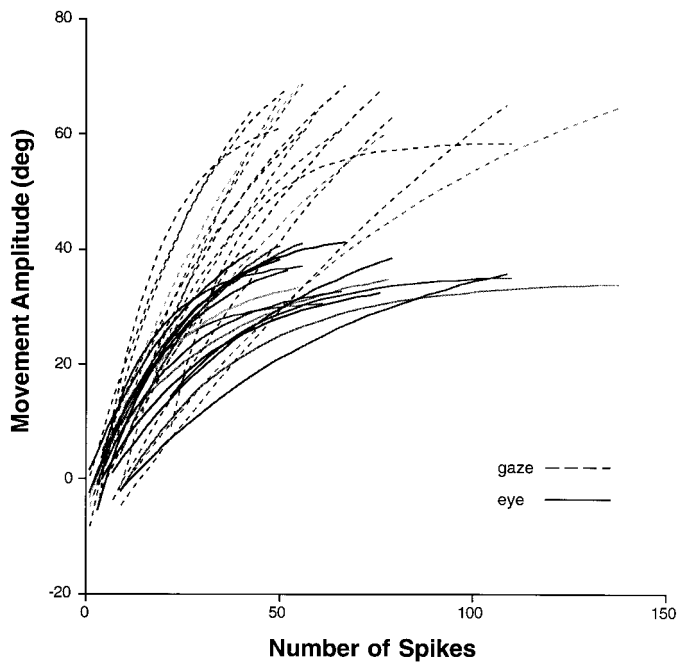


FIG. 3. Amplitude of a gaze shift and its eye component as a function of the number of action potentials (spikes) in the burst of an abducens neuron during a head-unrestrained gaze shift. Data from each of 16 neurons from *monkey HM* have been fit with exponential functions. Average  $r^2$  was  $0.95 \pm 0.03$  for eye movement and  $0.81 \pm 0.12$  for gaze movement. Similar fits were obtained for 14 additional abducens neurons in the 3 other monkeys.

The burst of motoneurons commands an eye saccade and nothing more. Because premotor elements behave in the same way as motoneurons, their discharge must be a “smart” eye movement command rather than a signal that encodes gaze amplitude, as previously suggested (Cullen and Guitton 1997; Pélisson et al. 1988; Tomlinson 1990; Whittington et al. 1984).

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