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Abducens Internuclear Neurons Carry an Inappropriate Signal for Ocular Convergence

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SUMMARY AND CONCLUSIONS

1. Single-unit recording studies in alert Rhesus monkeys characterized the vergence signal carried by abducens internuclear neurons. These cells were identified by antidromic activation and the collision of spontaneous with antidromic action potentials. The behavior of abducens internuclear neurons during vergence was compared with that of horizontal burst-tonic fibers in the medial longitudinal fasciculus (MLF) and to that of a large sample of unidentified abducens cells (presumably both motoneurons and internuclear neurons).

2. The results indicate that abducens internuclear neurons and lateral rectus motoneurons behave similarly during vergence eye movements: the majority of both groups of cells decrease their firing rate for convergence eye movements; a minority show no change for vergence. This finding is strongly supported by recordings of horizontal burst-tonic fibers in the MLF, the majority of which decrease their activity significantly for convergence eye movements.

3. These findings indicate that a net inappropriate vergence signal is sent to medial rectus motoneurons via the abducens internuclear pathway. Because medial rectus motoneurons increase their activity appropriately during symmetrical convergence, this inappropriate MLF signal must be overcome by a more potent direct vergence input.

4. Overall, both abducens internuclear neurons and lateral rectus motoneurons decrease their activity for convergence less than would be expected based on their conjugate gain. This implies that some degree of co-contraction of the lateral and medial rectus muscles occurs during convergence eye movements.

5. Some horizontal burst-tonic MLF fibers decrease their activity more for convergence than any recorded abducens neuron. These fibers may arise from cells in the nucleus prepositus hypoglossi or vestibular nuclei.

INTRODUCTION

Electrophysiological and anatomical studies in the primate (Büttner-Ennever and Akert 1981; Fuchs et al. 1988; Langer et al. 1986; McCrea et al. 1986; Steiger and Büttner-Ennever 1979) and cat (Baker and Highstein 1975; Graybiel and Hartwieg 1974; Highstein and Baker 1978; Nakao and Sasaki 1980; Spencer and Sterling 1977; Steiger and Büttner-Ennever 1978) have shown that the abducens nucleus is composed predominantly of two populations of neurons: lateral rectus motoneurons and abducens internuclear neurons (AINs). During conjugate eye movements, AINs have firing patterns similar to those of lateral rectus motoneurons. However, AINs do not project to the lateral rectus muscle; instead, their axons cross the midline and ascend in the contralateral medial longitudinal fasciculus (MLF) to provide excitatory innervation of the medial rectus subdivision of the oculomotor nucleus (see Fig. 1). Clinical studies in humans [see Cogan (1970) for a review] and lesions in primates (Bender and Weinstein 1944; Carpenter and Strominger 1965; Evinger et al. 1977) have revealed that this pathway is essential for normal conjugate horizontal eye movements. Damage to the MLF results in the syndrome of internuclear ophthalmoplegia, which is characterized by a marked decrease in the ability to adduct the eye on the side of the lesion during attempted conjugate gaze shifts. Importantly, these studies have also shown that vergence eye movements are spared in this syndrome.

These findings indicate that the horizontal conjugate eye movement signal sent to lateral rectus motoneurons is also sent to contralateral medial rectus motoneurons by way of the AINs. Although this coupling is essential when the eyes move conjugately, it presents a problem during the disjunctive eye movements that are required to fixate targets at different distances. During these vergence movements, in which the two eyes move in opposite directions in the horizontal plane, if the activity of AINs were the same as abducens motoneurons it would be inconsistent with requirements of the contralateral medial rectus motoneurons.

These considerations suggest two possibilities for the activity of AINs during vergence eye movements. Abducens internuclear neurons may carry an appropriate conjugate signal but no vergence signal. During pure, or symmetrical vergence movements, the activity of these internuclear neurons would be unchanged. Alternatively, AINs may behave similarly to lateral rectus motoneurons for vergence as well as conjugate movements. In this case, during ocular convergence, AINs would decrease their firing rate. This would result in an inappropriate vergence signal (i.e., decreased activity) being sent to the medial rectus motoneurons. To date, studies of the activity of abducens cells during vergence eye movements have been inconclusive on this issue. The first studies, which were conducted before the existence of AINs was known (Keller et al. 1972, 1973), found that all recorded abducens neurons carried both vergence and versional eye movement signals and that these signals were closely matched in magnitude. The results of this investigation implied that all of the cells that were recorded would have decreased their activity for symmetrical convergence, although this was not tested directly. A later study (Mays and Porter 1984b) reinvestigated abdu-

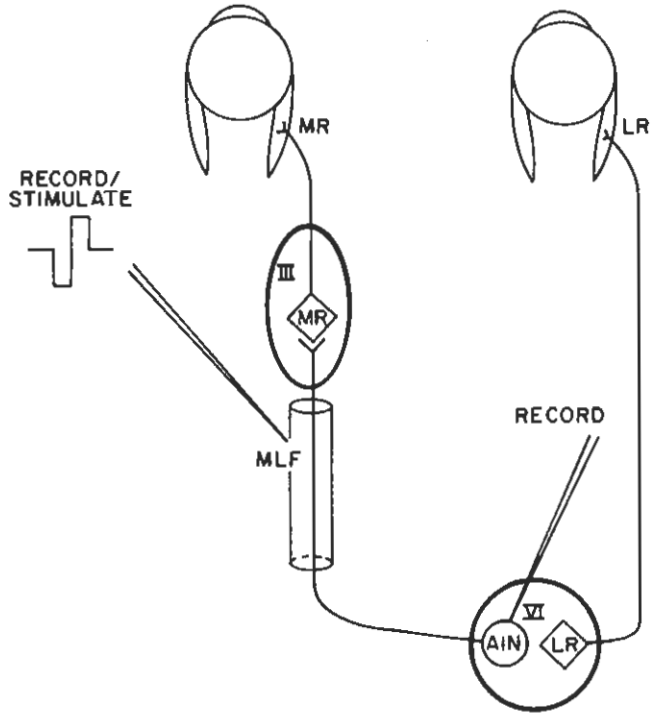

FIG. 1. Connections of abducens neurons and the electrode arrangement used to antidromically activate AINs. AIN, abducens internuclear neuron; LR, lateral rectus motoneuron; MLF, medial longitudinal fasciculus; MR, medial rectus motoneuron. See text for more details.

cens activity using improved behavioral techniques, symmetrical vergence movements, and a larger population of cells. It was intended to examine more closely the conjugate and vergence gains of individual neurons and to determine if a subset of the recorded abducens neurons did not change their activity during vergence eye movements. This investigation found that vergence and versional signals were not matched at the level of the individual neuron. Instead, there was a wide range in the ratio of vergence to conjugate gains. Furthermore, there was no evidence for two populations of abducens neurons based on the presence or absence of a vergence signal. However, the possibility was raised that the cells with the lowest vergence gains (averaging close to 0) might be AINs, whereas cells with higher vergence gains might be lateral rectus motoneurons. The hypothesis that AINs carry little or no vergence signal was strengthened by a more recent study in the cat, in which 75% of identified AINs were reported to show no change in activity during vergence eye movements (Delgado-Garcia et al. 1986).

The present study was designed to specifically characterize the vergence signal carried by *identified* AINs in the primate. By using long, stable fixation periods after symmetrical vergence movements and by studying a comparatively large sample of internuclear neurons, the issue of the vergence signal carried by these cells can be resolved. In addition, a group of horizontal burst-tonic fibers in the MLF were studied to examine their vergence signal and to compare it with that carried by AINs. Subsequently, these results were compared with the activities of a large sample of unidentified abducens cells (presumably both motoneurons and internuclear neurons).

Our results indicate that AINs and lateral rectus motoneurons behave similarly during vergence eye movements: most cells in both groups decrease their firing rate for convergence eye movements. This finding is strongly supported by recordings of horizontal burst-tonic fibers in the MLF, the majority of which decreased their activity significantly for convergence eye movements. Overall, these results indicate that an inappropriate vergence signal is sent to medial rectus motoneurons via the abducens internuclear pathway. Because medial rectus motoneurons increase their activity appropriately during symmetrical vergence (Mays and Porter 1984b), it appears that this inappropriate MLF signal is overcome by a more potent direct vergence input. A preliminary report of these results has previously been presented (Gamlin et al. 1988).

METHODS

Many of the methods used in this study have been described previously in detail elsewhere (Mays et al. 1984a,b) and are only briefly described. Other methods, not previously used by us, are described more fully.

Animal preparation

A total of five juvenile Rhesus monkeys (*Macaca mulatta*) were used. Under pentobarbital sodium anesthesia, they underwent four aseptic surgical procedures and received postsurgical analgesics to minimize pain. Initially, animals were implanted with four stainless steel bolts in the skull. After ~6–10 wk a coil of fine wire

TABLE 1. *Identified abducens internuclear neurons*

Cell	R_0	k_c	k_v	k_c/k_v	T
AIN 1	35	3.1*	1.5*	0.48†	−11.5
AIN 2	−22	5.8*	1.3	0.23†	3.7
AIN 3	−15	4.8*	0.8	0.16†	3.1
AIN 4	21	4.2*	0.8	0.18†	−5.0
AIN 5	61	3.4*	−0.5	−0.16†	−17.9
AIN 6	114	6.1*	−0.7	−0.11†	−18.7
AIN 7	30	4.0*	−0.7	−0.18†	−7.5
AIN 8	39	4.2*	−0.7	−0.18†	−9.3
AIN 9	37	4.1*	−1.6*	−0.40†	−9.1
AIN 10	54	6.0*	−1.9*	−0.31†	−9.0
AIN 11	162	4.0*	−2.2*	−0.55†	−40.3
AIN 12	64	4.7*	−2.2*	−0.48†	−13.7
AIN 13	79	8.0*	−2.3*	−0.29†	−9.9
AIN 14	147	3.9*	−2.6*	−0.66†	−37.5
AIN 15	83	5.3*	−2.8*	−0.53†	−15.6
AIN 16	−40	6.0*	−2.9*	−0.48†	6.7
AIN 17	103	7.2*	−3.7*	−0.52†	−14.3
AIN 18	156	6.0*	−4.4*	−0.75	−26.2
AIN 19	109	7.6*	−4.7*	−0.61†	−14.3
AIN 20	130	4.3*	−4.7*	−1.09	−30.4
AIN 21	139	6.5*	−4.9*	−0.75†	−21.3
AIN 22	140	5.2*	−5.5*	−1.06	−27.2
AIN 23	140	5.3*	−5.6*	−1.05	−26.2
AIN 24	124	6.1*	−6.0*	−0.98	−20.3
AIN 25	166	7.3*	−6.4*	−0.88	−22.7
Mean	82	5.3	−2.5	−0.44	−15.8

R_0, firing rate at primary position; T, threshold; k_c, k_v, linear regression slopes; *AIN*, abducens internuclear neuron. *Slope is significantly different from zero ($P < 0.001$). †k_c/k_v ratio is significantly different from −1.

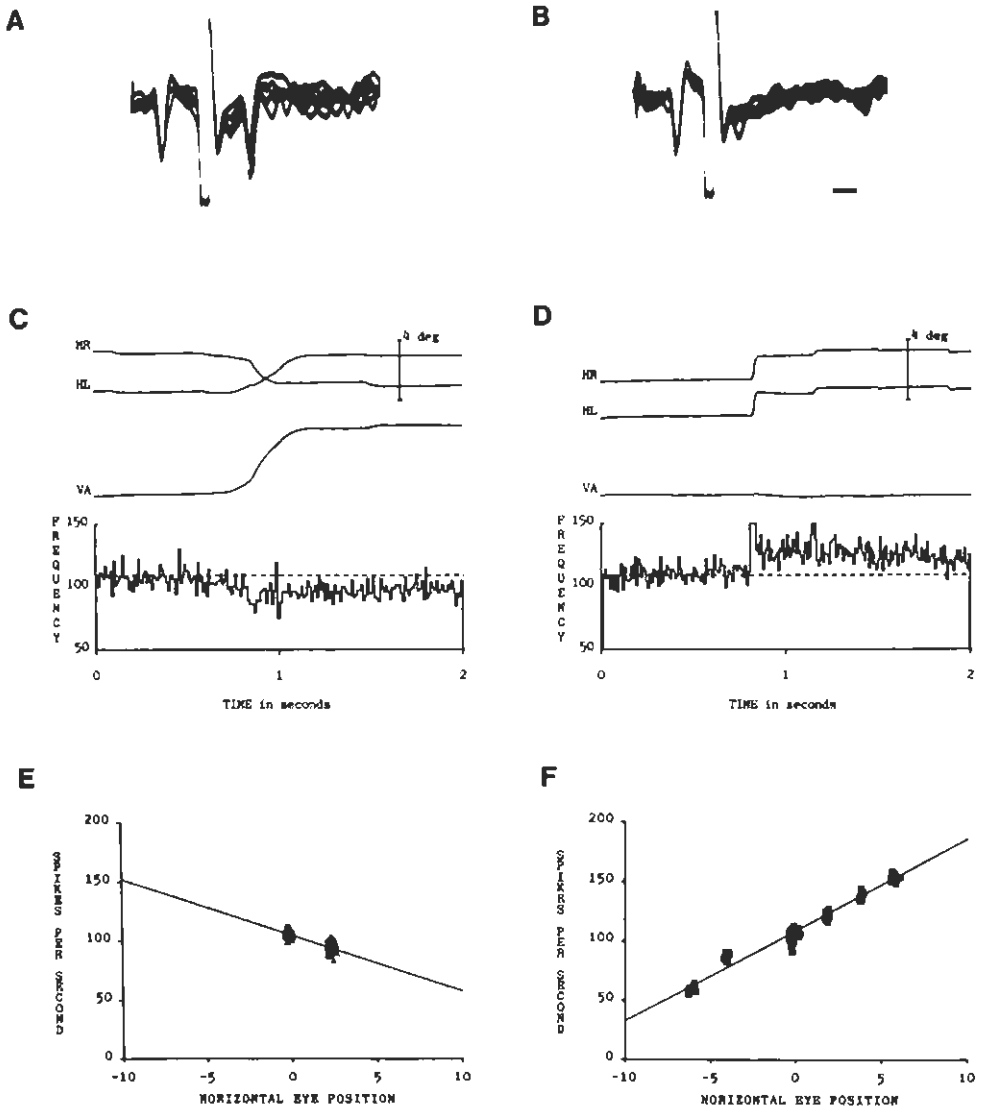

FIG. 2. *A*: 3 instances in which stimulation of the MLF produced an action potential in the recorded cell, *AIN 20*. Stimulation was triggered by the spontaneous action potential (*left*). The time between the spontaneous action potential and the stimulus was slightly longer than that required for collision. *B*: time between the spontaneous action potential and the stimulation has been shortened to 0.65 ms and 3 stimulation-induced action potentials now collide with 3 spontaneous action potentials. This demonstrates that the observed action potentials result from antidromic, and not orthodromic, activation. Scale bar = 0.5 ms. *C* shows that this cell decreases its activity for convergence while *D* shows that the cell has an appropriate conjugate gain. HL, horizontal left eye position, HR, horizontal right eye position, VA, vergence angle. *E*: firing rate/eye position sensitivity of this cell for vergence eye movements (k_v = −4.7 spikes·s^{-1}·deg^{-1}. *F*: firing rate/eye position sensitivity of this cell for conjugate eye movements (k_c = 4.3 spikes·s^{-1}·deg^{-1}).

was implanted under the conjunctiva of one eye, following a protocol similar to that of Judge et al. (1980). This allowed eye position to be measured using the search coil technique as described by Fuchs and Robinson (1966). Also, at that time, a lightweight aluminum headholder was attached to the bolts; this allowed the head to be immobilized during training and recording. Once animals reached a satisfactory level of training (see below), a second eye coil was implanted on the other eye. Finally, two recording chambers were implanted over 15-mm holes trephined in the skull. The two chambers, one on each side of the skull, were positioned stereotaxically over the midbrain at an 18° angle to the sagittal plane.

Behavioral training

Animals were trained to look at targets in an apparatus that had a mirror stereoscope and far- and near-target LEDs. The targets viewed through the stereoscope were small lighted crosses on a pair of computer-controlled TV monitors. The TVs and the far LED display were at a distance of 72.5 cm from the eyes. The near LED display was placed at a distance of 25 cm. Details of the visual display are provided elsewhere (Mays 1984a). Eye position signals for each eye were calibrated by requiring the monkeys to fixate targets on the far LED array. Any misalignment of the eyes could be seen by comparing eye positions under binocular and monocular viewing conditions. Based on these measures, no strabismus was apparent in any of the monkeys. Further details of the calibration procedures are described elsewhere (Mays 1984a). The positions of both the right and left eyes were sampled at either 333 or 500 Hz and stored on computer tape for analysis.

Unit-recording procedures

Using a Kopf microdrive, a parylene-insulated tungsten microelectrode mounted in a 26-ga cannula was advanced through a 21-ga hypodermic needle puncturing the dura. Unit activity was sharply filtered above 5 kHz, and the occurrence of a spike was detected with a window discriminator and recorded digitally on computer tape to the nearest 0.1 ms. Initially, the oculomotor, trochlear, and abducens nuclei were located by noting their characteristic cellular activity and the eye movement elicited by their microstimulation. The location of the MLF was then identified based on its relationship to the oculomotor nuclei, on the presence of horizontal burst-tonic fibers, and fibers that were modulated for vertical eye movements but paused for saccades. Although these latter fibers were not tested for vestibular sensitivity,

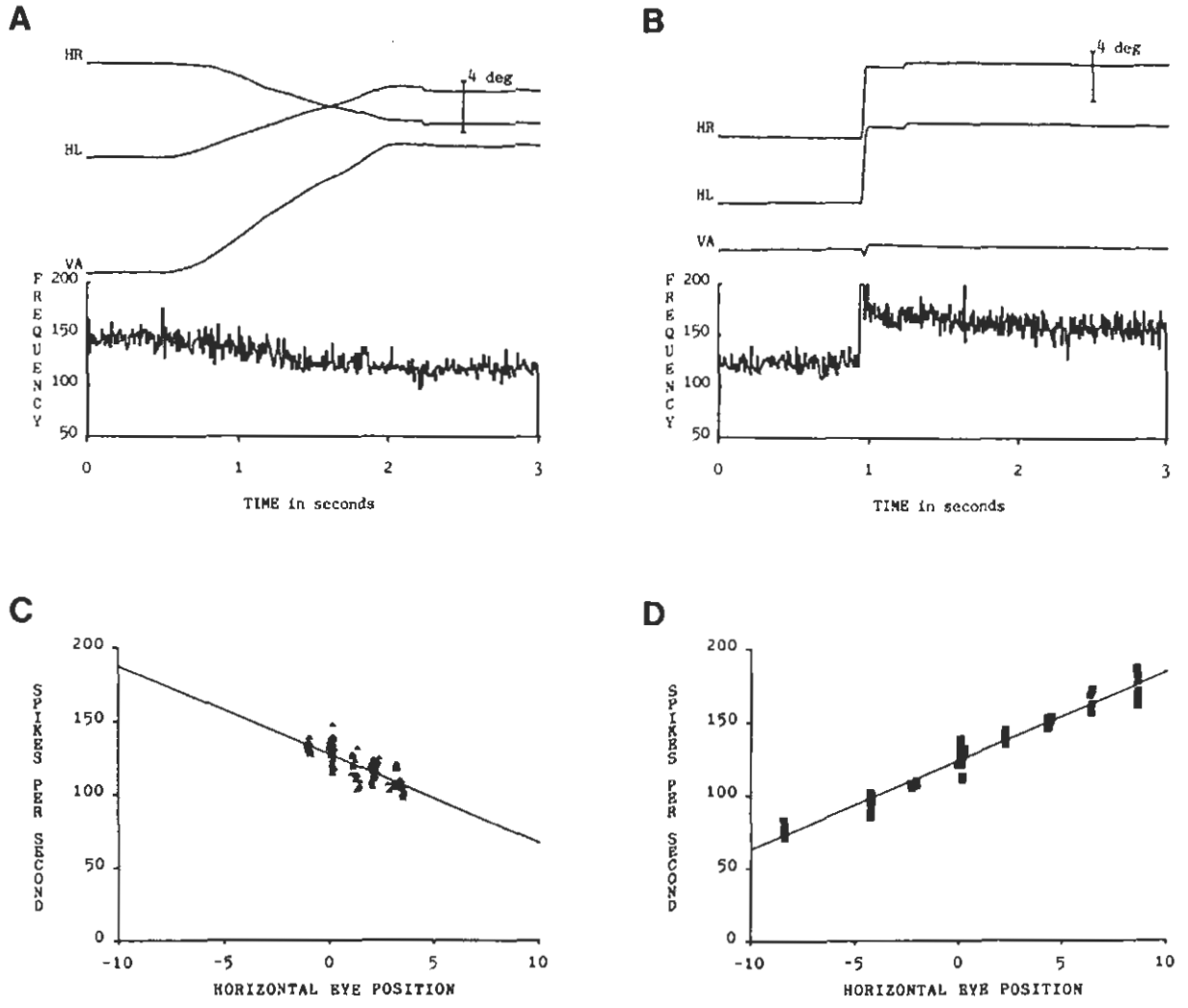

FIG. 3. *A*: behavior of an abducens internuclear neuron (*AIN 24*) during a 10° convergence eye movement. *B*: behavior of this cell during a 6° saccadic eye movement. *C*: firing rate/eye position sensitivity of this cell for vergence eye movements ($k_v = -6.0$ spikes·s^{-1}·deg^{-1}). *D*: firing rate/eye position sensitivity of this cell for conjugate eye movements ($k_c = 6.1$ spikes·s^{-1}·deg^{-1}).

they were probably tonic-vestibular-pause cells that have been reported in the MLF at this level (King et al. 1976; Pola and Robinson 1978). It was also noted that stimulation at these sites with low currents (<10 μA) produced a well-defined adduction of the ipsilateral eye. For antidromic activation of AINs, a low-impedance stimulating electrode (0.1–0.3 MΩ) was lowered to the MLF contralateral to the abducens recording site. A representation of the electrode arrangement used is shown in Fig. 1. Using the stimulating electrode, multiunit activity usually could be recorded, and the MLF could be identified based on its characteristic activity. To confirm that the electrodes were well placed, a single cathodal pulse of <100 μA (0.1 ms duration) had to produce a detectable, adductive twitch in the ipsilateral eye. By using the same coordinates with minor adjustments, the stimulating electrode could be quickly (usually <15 min) placed in a suitable location at the beginning of each recording session.

With the stimulating electrode in place, a recording electrode (0.5–1 MΩ) was lowered to the abducens nucleus. There were several criteria that were used during the recording sessions to ensure that the cells recorded were within the abducens nucleus. These included *1*) appropriate stereotaxic coordinates with respect to the oculomotor and trochlear nuclei; *2*) abrupt appearance of a succession of closely spaced cells, extending at least 1.0 mm, all showing only horizontal burst-tonic activity; *3*) a rapid, abductive twitch of the ipsilateral eye induced by electrical stimulation with <20 μA currents, with the contralateral eye displaying a smaller, rapid adduction.

Internuclear neurons were identified by antidromic activation and, in most cases, collision testing. Once an abducens neuron was well isolated, stimulation pulses were delivered to the contralateral MLF. The pulses were biphasic (cathodal-anodal), with each pulse 0.1 ms in duration. The cathodal stimulation intensity was gradually increased from 10 to 150 μA or until a spike was elicited. The intensity of the anodal pulse was adjusted to minimize the stimulation artifact at the recording electrode. Collision testing was done with suprathreshold cathodal stimulation (150 μA maximum). The occurrence of a spontaneous spike was detected by a window discriminator, which, in turn, triggered the electrical stimulator after a variable delay. The repetition rate for stimulation was limited to 1/s. The entire spike-stimulus-spike (or collision) sequence was captured by an oscilloscope for photography.

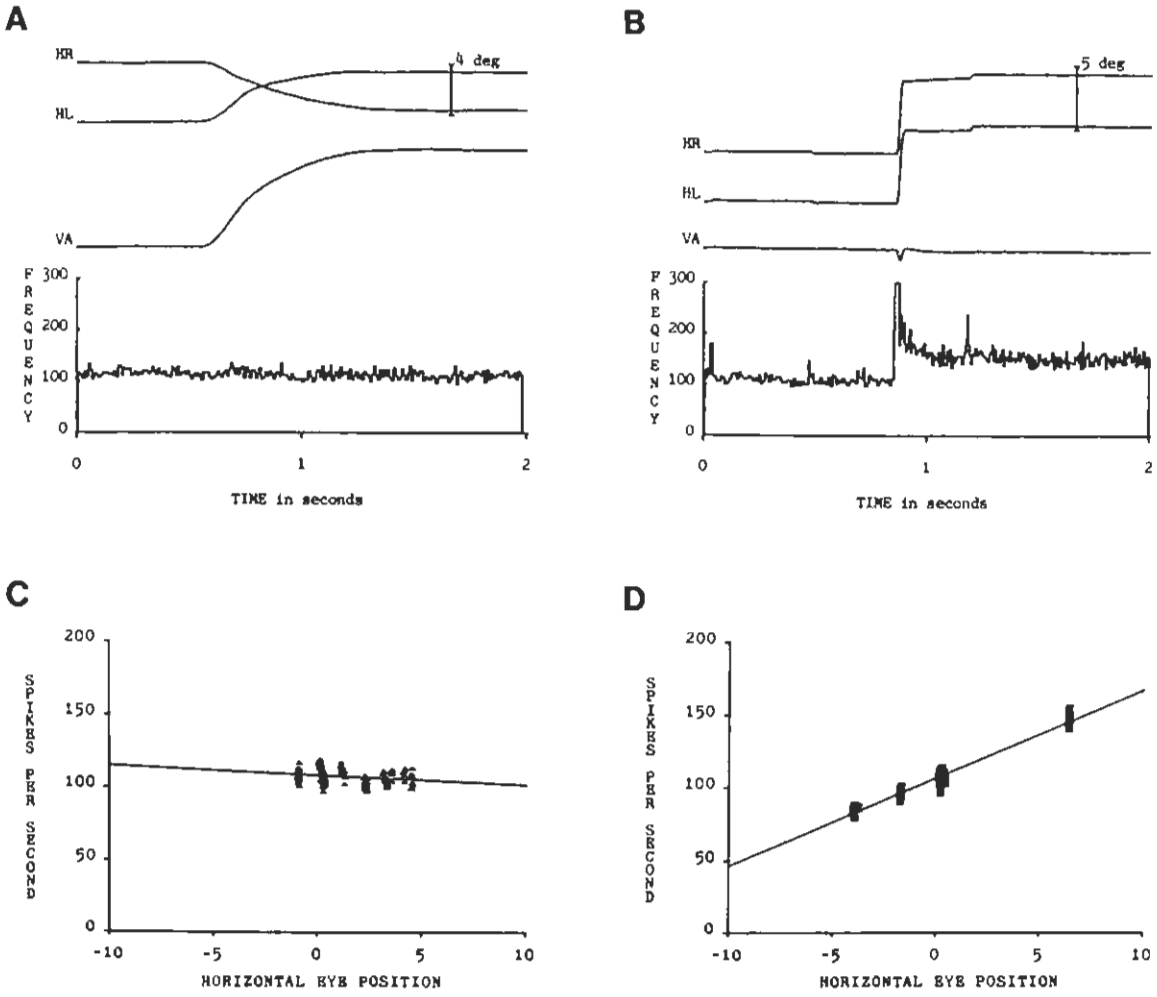

FIG. 4. *A*: behavior of an abducens internuclear neuron (*AIN 6*), which displays no significant change in activity for convergence. *B*: behavior of this cell during a 6° saccadic eye movement. *C*: firing rate/eye position sensitivity of this cell for vergence eye movements ($k_v = -0.7$ spikes·s^{-1}·deg^{-1}). *D*: firing rate/eye position sensitivity of this cell for conjugate eye movements ($k_c = 6.1$ spikes·s^{-1}·deg^{-1}).

Data analysis

The stored data were analyzed using a PDP-11/73 computer equipped with an interactive graphics display. Most of the analyses required the determination of firing rate/eye position slopes for changes in either conjugate or vergence eye positions. For the selected trials, eye position and unit data were displayed, and periods of steady fixation were manually delineated by a cursor. Averages of horizontal and vertical positions of the left and right eye and average unit firing rate were computed for successive 100-ms samples over this period. Even though cells and fibers were recorded from both sides of the brain, for simplicity data are presented as if all abducens recordings were in the right nucleus and the MLF-stimulating electrode was on the left side (as depicted in Fig. 1). MLF fiber recordings are also presented as if they were made on the left side. Within this scheme, horizontal eye position is always shown as the position of the left eye. Thus, in the scatterplots, the firing rates for all cells and fibers are referred to the position of the left eye, with rightward eye movement (adduction of the left eye) expressed as the positive direction. Clearly, this is appropriate for identified AINs, which if recorded in the right nucleus, provide their input to the left medial rectus motoneurons (refer to Fig. 1). This also seems appropriate for left MLF horizontal burst-tonic fibers, many of which are presumed to be axons of right AINs. Because there is no way to decide if an unidentified abducens neuron is an internuclear or lateral rectus motoneuron, for consistency the firing rate of unidentified right abducens neurons is also referred to the position of the left eye.

As a result of this convention for depicting the data, a positive correlation between firing rate and conjugate eye position would be expected for lateral rectus motoneurons, AINs, and MLF horizontal burst-tonic fibers. The relevant question for this study is the relationship between firing rate and changes in eye position caused by symmetrical convergence. Decreases in firing rate as a function of increases in convergence would be appropriate for right lateral rectus motoneurons, but would be inappropriate for neurons innervating left medial rectus motoneurons (AINs and horizontal burst-tonic MLF fibers).

Two scatterplots were plotted for each cell, and correlation coefficients and linear regression parameters were calculated. In one plot, vergence angle was held constant at 2.2°, and the firing rate of the cell was plotted as a function of conjugate eye position. This yielded a measure of the conjugate gain of the cell (k_c). Extrapolation of this slope to zero firing rate yielded the estimated threshold (T) for the cell. In the other plot, conjugate eye position was held constant, and the effect of symmetrical vergence angle

TABLE 2. *Horizontal burst-tonic MLF fibers*

Cell	R_0	k_c	k_v	k_c/k_v	T
MLF 1	50	5.7*	5.5*	0.96†	−8.7
MLF 2	9	4.1*	0.2	0.05†	−2.2
MLF 3	143	8.4*	0.0	−0.00†	−17.1
MLF 4	−25	3.9*	−1.0	−0.27†	6.4
MLF 5	42	2.0*	−1.2*	−0.60	−21.0
MLF 6	75	4.0*	−1.5*	−0.37†	−18.6
MLF 7	161	3.3*	−1.7	−0.50	−48.5
MLF 8	27	2.7*	−2.2*	−0.81	−9.9
MLF 9	120	6.5*	−3.2*	−0.48†	−18.4
MLF 10	51	2.9*	−3.3*	−1.14	−17.9
MLF 11	42	5.0*	−3.7*	−0.74†	−8.5
MLF 12	26	3.2*	−3.9*	−1.23†	−8.1
MLF 13	162	7.5*	−4.0*	−0.53†	−21.8
MLF 14	40	4.3*	−4.0*	−0.93	−9.3
MLF 15	57	2.7*	−4.5*	−1.68†	−21.3
MLF 16	128	3.3*	−4.5*	−1.38†	−39.4
MLF 17	133	4.9*	−5.4*	−1.10	−27.0
MLF 18	39	3.7*	−5.5*	−1.48†	−10.3
MLF 19	175	7.1*	−5.8*	−0.82	−24.6
MLF 20	217	7.2*	−6.6*	−0.92	−30.2
MLF 21	134	4.2*	−6.7*	−1.60†	−32.1
MLF 22	216	6.8*	−7.1*	−1.05	−31.8
MLF 23	169	4.3*	−7.3*	−1.73†	−39.8
MLF 24	43	4.7*	−8.0*	−1.73†	−9.1
MLF 25	122	3.4*	−8.1*	−2.42†	−36.3
Mean	94	4.6	−3.7	−0.90	−20.2

MLF, horizontal burst-tonic MLF fibers; R_0, firing rate at primary position; T, threshold; k_c, k_v, linear regression slopes. *Slope is significantly different from zero ($P < 0.001$). †k_c/k_v ratio is significantly different from −1.

changes on firing rate were plotted. This yielded a measure of the vergence gain of the cell (k_v). For all cells with thresholds <0°, the k_v was computed at primary position. For the remaining cells, the k_v was computed for symmetrical vergence movements about a conjugate position <8° beyond primary position. To determine if the k_c and k_v were significantly different from zero and from one another, t tests were performed. As noted above, the value for k_c was positive for all recorded cells, which would be appropriate for either right lateral rectus or left medial rectus motoneurons. For many cells the value for k_v was negative, which would be appropriate for right lateral rectus motoneurons but not for left medial rectus motoneurons.

Histology

Because each animal was used for several months, it was not possible to make marking lesions at all relevant sites. However, the location of familiar landmarks (e.g., oculomotor, trochlear, and abducens nuclei), the X-Y location of our micropositioner, and the electrode depth for cells of interest were noted. To verify the location of our recording electrodes, marking lesions were made during the last 2 wk of recording by passing 30 μA anodal current for 20 s. The locations of the stimulating electrodes were determined from electrolytic lesions and the slight gliosis associated with the stimulation sites. Animals were deeply anesthetized with pentobarbital sodium and then perfused through the aorta with saline, followed by a suitable fixative. The brain was sectioned at 40 μm, and a Nissl-stained series was prepared.

RESULTS

Abducens internuclear neurons

In three animals, a total of 25 cells recorded from the abducens nucleus were identified as AINs based on their short-latency, invariant response to stimulation of the contralateral MLF at the level of either the oculomotor or rostral trochlear nucleus. The latencies of the antidromically activated action potentials ranged from 0.5 to 1.2 ms. Twenty-three of these cells were further confirmed as internuclear neurons by collision testing. Although AINs did not appear to be localized to a specific region of the abducens nucleus, they showed some degree of clustering with respect to one another. Table 1 provides the summary statistics based on the linear regression analyses for all AINs. Figure 2 shows the results from a representative abducens internuclear neuron (*AIN 20*). This cell was activated by MLF stimulation (Fig. 2*A*) when a spontaneous spike preceded the stimulation by >0.65 ms. Collision of spontaneous orthodromic spikes and antidromically activated spikes occurred at shorter intervals (Fig. 2*B*). A decrease in firing rate for convergence can be seen on single trials (Fig. 2*C*). An increase in firing rate is shown in Fig. 2*D* for a similar amplitude rightward conjugate eye movement. The firing rate/eye position slopes of this cell for conjugate and vergence eye movements are shown in Fig. 2, *E* and *F*. Because the firing rate of this cell increased for rightward conjugate eye movements and decreased for convergence, it exhibited the behavior expected of a lateral rectus motoneuron, even though it was an AIN.

Six identified AINs displayed gains for conjugate and vergence eye movements that were not significantly different in magnitude. Figure 3 presents an example of one of these neurons (*AIN 24*). This cell significantly decreased its firing rate during convergence eye movements ($k_v = -6.0$ spikes · s^{-1} · deg^{-1}), whereas it increased its firing rate with a comparable gain ($k_c = 6.1$ spikes · s^{-1} · deg^{-1}) during conjugate eye movements. Overall, 17 of 25 neurons significantly decreased their firing rate for convergence eye movements. Seven internuclear neurons were not significantly modulated during vergence eye movements but behaved appropriately during conjugate eye movements. An example of one of these cells (*AIN 6*) is shown in Fig. 4.

Horizontal burst-tonic MLF fibers

Twenty-five horizontal burst-tonic fibers were recorded from the MLF of five animals; two of these animals were also used in the study of AINs. Because the MLF ventral to the trochlear nucleus forms a compact bundle, activity was recorded from this level. Table 2 provides the summary statistics based on the linear regression analyses for all horizontal burst-tonic fibers. Twenty fibers significantly decreased their firing rate for convergence. Overall, most of these fibers behaved similarly to identified AINs. However, some were characterized by comparatively lower conjugate gains and higher vergence gains; i.e., their activity decreased more for convergence than did that of AINs. An example of one of these cells is shown in Fig. 5. This cell (*MLF 25*) had a conjugate gain of 3.4 spikes · s^{-1} · deg^{-1}, whereas its vergence gain was −8.1 spikes · s^{-1} · deg^{-1}.

Unidentified abducens cells

In addition to the recordings from identified AINs, data were collected from 46 cells in the abducens nuclei of four

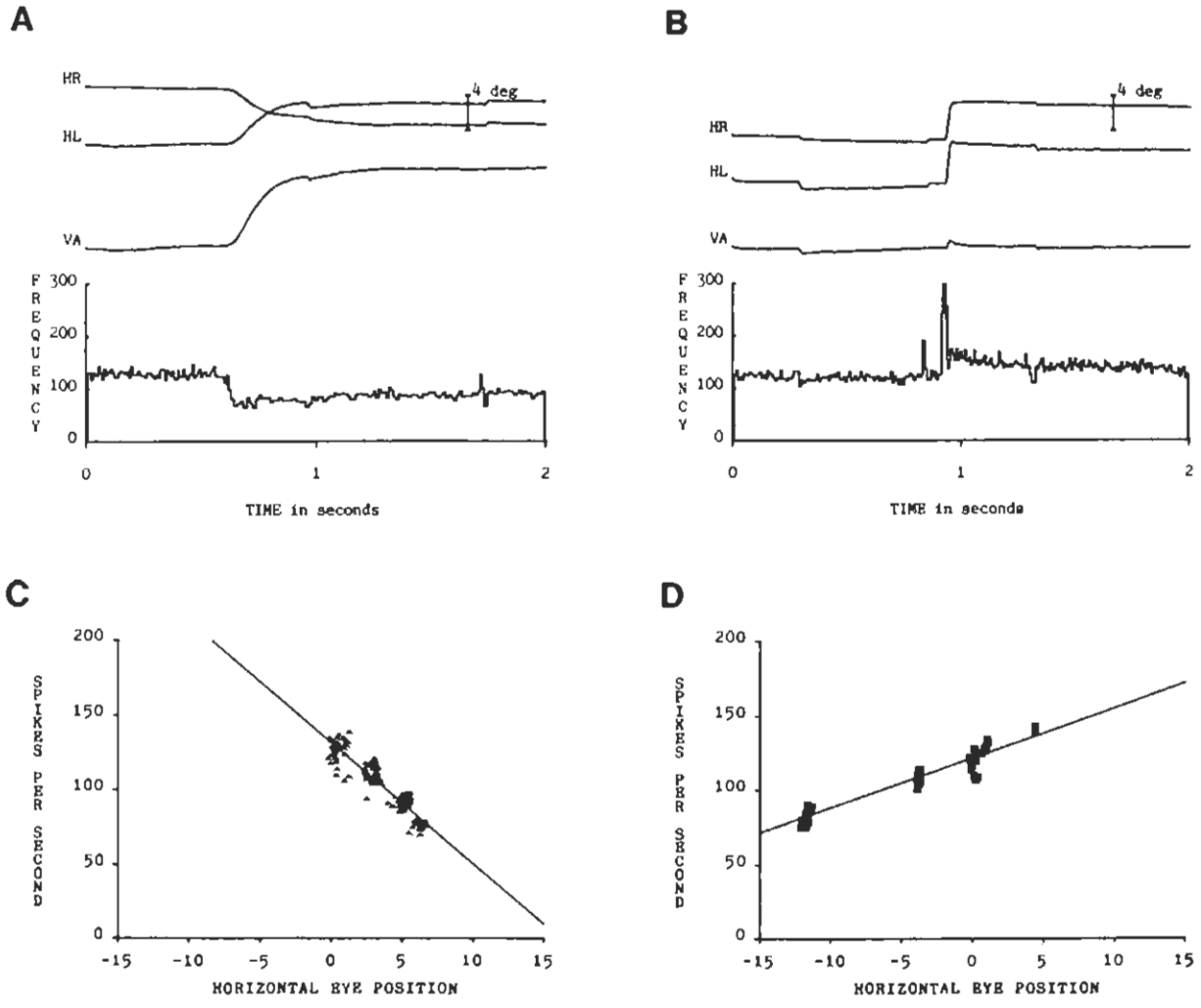

FIG. 5. *A*: behavior of a horizontal burst-tonic MLF fiber (*MLF 25*) during an 8° convergence eye movement. *B*: activity of this cell for a 4° saccadic eye movement. *C*: firing rate/eye position sensitivity of this cell for vergence eye movements ($k_v = -8.1$ spikes $\cdot s^{-1} \cdot deg^{-1}$). *D*: firing rate/eye position sensitivity of this cell for conjugate eye movements ($k_c = 3.4$ spikes $\cdot s^{-1} \cdot deg^{-1}$).

animals; three of these animals were subsequently used for the study of AINs. Table 3 provides the summary statistics based on the linear regression analyses for all these cells. The vergence gain (k_v), the conjugate gain (k_c), the ratio of these gains (k_v/k_c), the firing rate at primary position (R_0), and the estimated threshold (T) for these cells were compared with those for AINs and MLF fibers using the Mann-Whitney test.

VERGENCE GAINS. Most AINs, unidentified abducens cells, and horizontal burst-tonic MLF fibers decrease their activity during convergence eye movements. The distributions of the vergence gains (k_v) of these three groups of cells is shown in Fig. 6*A*. Although there is no statistical difference between these three distributions, the increased number of horizontal burst-tonic MLF fibers with k_v values in the -6 and -8 spikes $\cdot s^{-1} \cdot deg^{-1}$ bins should be noted. This is apparent in Table 2, which shows four cells with k_v values greater in magnitude than those seen for any abducens cell in the present study or in a previous study (Mays and Porter 1984b).

CONJUGATE GAINS. All the cells examined showed a burst of activity and an increase in tonic rate for horizontal saccades in the on-direction. They all also decreased their activity for saccades in the off-direction. The saccadic velocity sensitivity of these cells was not specifically examined; however, it varied from cell to cell, and whereas some AINs had comparatively high velocity sensitivities, others did not.

Figure 6*B* presents histograms showing the distribution of conjugate gains (k_c) for the three groups of cells. The conjugate gains of the unidentified abducens cells are not significantly different from that of the AINs, which is reflected in the similarities of the distributions of these two classes of cells. Also, there is no significant difference between the k_c values of the AINs and the MLF fibers. However, there is a significant difference between the k_c values of the MLF fibers and the unidentified abducens neurons ($P < 0.01$).

RATIO OF VERGENCE AND CONJUGATE GAINS. To examine the relative contribution that each cell made to conju-

TABLE 3. *Unidentified abducens neurons*

Cell	R_0	k_c	k_v	k_c/k_v	T
ABD 1	−39	6.8*	3.7*	0.55†	5.8
ABD 2	−4	7.8*	0.1	0.01†	0.4
ABD 3	−2	5.6*	−0.1	−0.01†	0.4
ABD 4	30	6.4*	−0.3	−0.05†	−4.6
ABD 5	33	3.4*	−0.9*	−0.25†	−9.7
ABD 6	10	9.6*	−0.9*	−0.09†	−1.1
ABD 7	77	6.7*	−1.3*	−0.19†	−11.5
ABD 8	38	5.4*	−1.5*	−0.28†	−7.0
ABD 9	65	6.5*	−1.7*	−0.27†	−10.1
ABD 10	65	7.3*	−2.0*	−0.27†	−8.9
ABD 11	24	8.2*	−2.2*	−0.27†	−2.9
ABD 12	2	3.3*	−2.3*	−0.70†	−0.6
ABD 13	65	8.9*	−2.4*	−0.27†	−7.3
ABD 14	81	4.4*	−2.5*	−0.57†	−18.6
ABD 15	98	8.1*	−2.5*	−0.31†	−12.2
ABD 16	56	3.7*	−2.6*	−0.70†	−14.9
ABD 17	135	3.0*	−2.6*	−0.88	−45.5
ABD 18	83	7.5*	−2.8*	−0.37†	−11.1
ABD 19	91	4.5*	−2.9*	−0.66	−20.3
ABD 20	117	4.6*	−3.2*	−0.68†	−25.2
ABD 21	122	3.1*	−3.2*	−1.04	−39.8
ABD 22	88	5.3*	−3.2*	−0.61†	−16.7
ABD 23	95	4.4*	−3.3*	−0.75	−21.8
ABD 24	39	7.3*	−3.3*	−0.46†	−5.4
ABD 25	−14	6.3*	−3.6*	−0.56†	2.2
ABD 26	99	4.5*	−3.6*	−0.80†	−22.1
ABD 27	104	4.1*	−3.6*	−0.89	−25.6
ABD 28	121	6.5*	−3.7*	−0.57†	−18.5
ABD 29	122	7.0*	−3.7*	−0.53†	−17.3
ABD 30	131	5.5*	−3.7*	−0.68†	−23.9
ABD 31	132	6.6*	−3.8*	−0.57†	−20.0
ABD 32	21	4.8*	−4.1*	−0.86	−4.3
ABD 33	94	6.0*	−4.4*	−0.73†	−15.6
ABD 34	−8	8.0*	−4.6*	−0.58†	1.0
ABD 35	70	7.5*	−4.7*	−0.62†	−9.4
ABD 36	51	6.1*	−4.8*	−0.79†	−8.4
ABD 37	89	4.1*	−5.0*	−1.20	−21.4
ABD 38	116	5.3*	−5.0*	−0.95	−22.1
ABD 39	117	5.8*	−5.0*	−0.86	−20.1
ABD 40	160	5.5*	−5.1*	−0.93	−29.1
ABD 41	106	4.4*	−5.2*	−1.17†	−24.1
ABD 42	128	5.9*	−5.4*	−0.92	−21.7
ABD 43	147	5.9*	−5.7*	−0.98	−25.0
ABD 44	149	6.9*	−5.9*	−0.86	−21.5
ABD 45	35	9.3*	−6.1*	−0.66†	−3.8
ABD 46	164	7.0*	−6.8*	−0.97	−23.5
Mean	76	6.0	−3.2	−0.58	−14.4

R_0, firing rate at primary position; T, threshold; k_c, k_v, linear regression slopes; *ABD*, unidentified abducens neuron. *Slope is significantly different from zero ($P < 0.001$). †k_c/k_v ratio is significantly different from −1.

gate and vergence eye movements, the ratio of the k_v to k_c was calculated. The distribution of these values for the three groups of cells is shown in Fig. 6*C*. The mean k_v/k_c ratios for AINs (−0.44) and unidentified abducens neurons (−0.58) are not statistically different. This is reflected in the similarities of their distributions. However, the k_v/k_c ratio of MLF fibers (−0.9) does differ significantly from that of AINs ($P < 0.01$) and unidentified abducens neurons ($P < 0.05$).

RELATIONSHIP BETWEEN THRESHOLD AND k_c, k_v. Previous reports have shown a clear trend for the k_c to increase as the threshold moves in the on-direction (e.g., Fuchs et al. 1988; Goldstein and Robinson 1986; Robinson 1970). However, the relationship between vergence gain and threshold has not previously been investigated. Figure 7, *A–C*, shows that, as determined by t tests, there is a significant regression of vergence gain on threshold, with k_v tending towards zero as threshold moves in the conjugate on-direction. For AINs, a linear regression of k_v on threshold gave a slope of 0.11 (t test for significance of slope; $P < 0.01$) with an

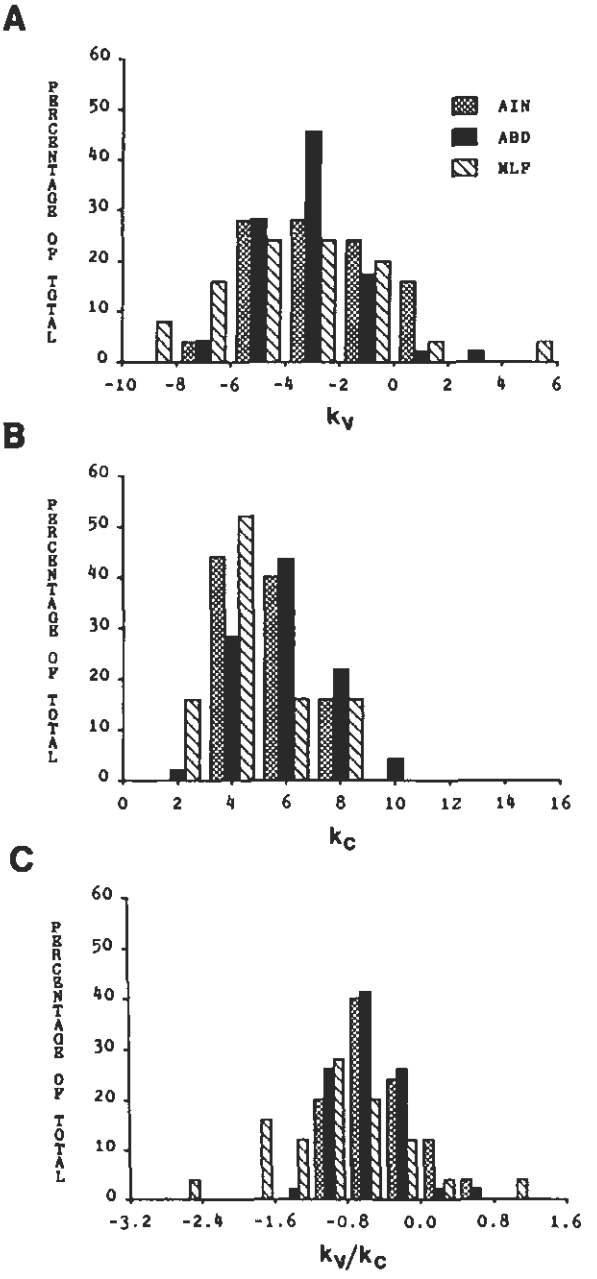

FIG. 6. *A–C*: respectively, the relative distribution of vergence gains, conjugate gains, and the ratio of vergence gain to conjugate gain for unidentified abducens neurons (ABD), AINs, and horizontal burst-tonic MLF fibers (MLF). The conjugate gain of the horizontal burst-tonic MLF fibers differs significantly from that of the unidentified abducens cells. Also, the ratio of vergence gain to conjugate gain (k_v/k_c) for the horizontal burst-tonic MLF fibers is significantly different from the other 2 groups of cells. There are no significant differences between AINs and unidentified abducens neurons (see text for more details).

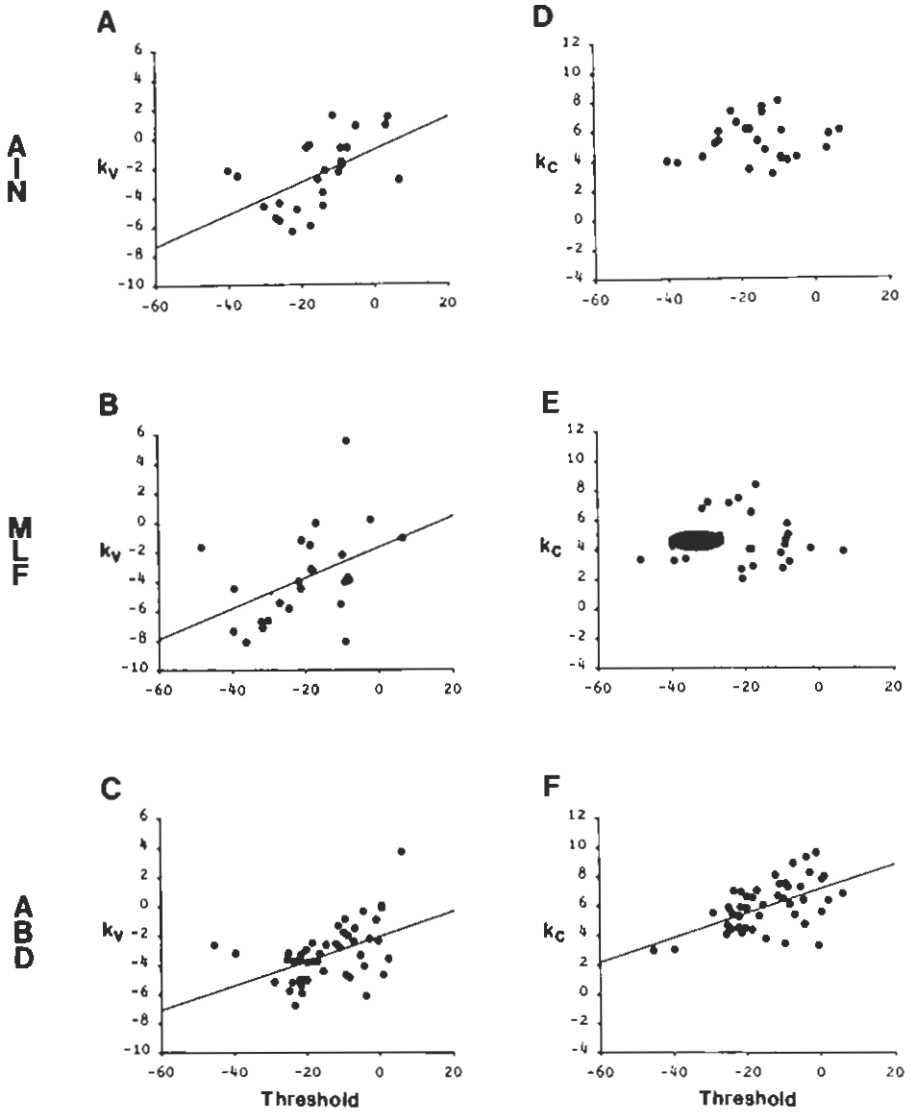

FIG. 7. *A–C*: relationship between threshold and vergence gain for the 3 groups of cells studied. In all 3 groups, the vergence gain tends towards 0 as threshold moves in the on-direction (AIN, $r = 0.56$; MLF, $r = 0.44$; ABD, $r = 0.48$). *D–F*: relationship between estimated threshold and conjugate gain for the 3 groups of cells in this study. The conjugate gain of the unidentified abducens neurons increases as threshold moves in the on-direction ($r = 0.55$). The slope of k_c vs. threshold is not significantly different from 0 for AINs or MLF fibers.

intercept of −0.77. For horizontal burst-tonic MLF fibers, it yielded a slope of 0.10 ($P < 0.05$) with an intercept of −1.65, and for unidentified abducens neurons, it yielded a slope of 0.08 ($P < 0.001$) with an intercept of −1.99.

To compare our results concerning conjugate movements with those of previous studies, the relationship between k_c and threshold was also examined in the three groups of cells (Fig. 7, *D–F*). As can be seen in Fig. 7*F*, there was a positive correlation between k_c and threshold in our sample of unidentified abducens neurons, and a linear regression of k_c on threshold gave a slope of 0.08 ($P < 0.001$) with an intercept of 7.16. No significant correlation between k_c and threshold was obtained for either the identified AINs or the MLF fibers.

DISCUSSION

Abducens internuclear neurons send an inappropriate vergence signal to medial rectus motoneurons

The major finding from the present study of identified abducens internuclear neurons is that the abducens internuclear pathway is carrying a net vergence signal that is inappropriate for the medial rectus motoneurons that it innervates. Further evidence supporting this conclusion comes from our single-unit recordings of horizontal burst-tonic fibers in the MLF. Many of these MLF fibers arise from abducens internuclear neurons (e.g., Büttner-Ennever and Akert 1981; Langer et al. 1986; Steiger and Büttner-Ennever 1979), and nearly all significantly decrease their discharge for convergence. Indeed, recordings from these fibers suggest that, overall, horizontal burst-tonic MLF fibers decrease their activity more for convergence than would be expected, based on data from AINs.

Additional evidence for an inappropriate MLF vergence signal is presented in the accompanying study of lidocaine-induced, unilateral internuclear ophthalmoplegia (Gamlin et al. 1989). Briefly, the rationale behind the experiment is the following: if the MLF carries an inappropriate vergence signal to medial rectus motoneurons, then an appropriate signal of higher gain, arising from elsewhere, must overcome it at these motoneurons. Unilateral blockade of the MLF, which obstructs this inappropriate signal and per-

mits only the appropriate, higher gain vergence signal to reach medial rectus motoneurons, should result in an increased vergence gain in the eye on the blockaded side. As demonstrated in the following paper, results obtained during reversible internuclear ophthalmoplegia were consistent with just such an increased vergence gain.

If the MLF carries an inappropriate vergence signal to medial rectus motoneurons, this has implications for the vergence-related, midbrain neurons that are believed to provide an appropriate vergence signal to these motoneurons (Judge and Cumming 1986; Mays et al. 1984a, 1986). Because medial rectus motoneurons increase their firing rate appropriately for convergence (Mays and Porter 1984), the inappropriate vergence signal from the MLF must be nulled out at the level of these motoneurons. Thus vergence-related, midbrain cells should be the source of a vergence signal that not only provides a suitable input to medial rectus motoneurons but that also overcomes the inappropriate vergence signal from the internuclear pathway. If this were the case, there might be differences between the vergence signals carried by the vergence-related, midbrain neurons and medial rectus motoneurons, and indeed, studies have shown that these cells differ from motoneurons in having higher gains for vergence (Judge and Cumming 1986; Mays 1984a) and different time constants (Judge and Cumming 1986).

Activity of abducens motoneurons during vergence: evidence for co-contraction and a possible evolutionary compromise

The results indicate that the vergence signal carried by AINs is not significantly different from that carried by the general population of abducens neurons. Also, the k_v/k_c ratio for AINs is not significantly different from that of abducens neurons in general and is ~0.5. Because this ratio is considerably less than unity for both groups of cells, it implies that the k_v/k_c ratio for abducens motoneurons is also considerably less than unity. Thus when the eye moves to a given horizontal position as the result of convergence, the innervation to the lateral rectus muscle does not decrease as much as if the same position had been reached by a conjugate eye movement. This suggests that during convergence there may be some degree of co-contraction of lateral and medial rectus muscles. Interestingly, co-contraction of the lateral and medial rectus muscles during convergence has been reported previously in one electromyography study (Tamler et al. 1958), but not in others (Blodi and Van Allen 1957; Breinin 1957).

The results imply that AINs and abducens motoneurons carry the same vergence signal and that this signal is approximately one-half of the conjugate signal. We suggest that this observation reflects an evolutionary compromise. If it were not possible to send different vergence signals to AINs and lateral rectus motoneurons within the abducens nucleus, then the observed signals could represent a compromise, with lateral rectus motoneurons carrying only 50% of an *appropriate* vergence signal and internuclear neurons carrying only 50% of an *inappropriate* vergence signal. The net result would be a situation that required overcoming only a modest inappropriate signal at the medial rectus motoneurons at the cost of some degree of co-contraction caused by inadequate relaxation of the lateral rectus muscles. Thus it can be suggested that because of evolutionary constraints, not all neural pathways may carry the signals expected of them.

Other examples of this principle exist and are discussed by Dumont and Robertson (1986). For example, the escape response of certain crayfish involves a tailflip in which the anterior three abdominal segments are flexed, and the posterior three abdominal segments remain extended. However, all six segments receive excitatory inputs during the escape response, and the inappropriate excitatory signal to the posterior three segments is nulled out by an inhibitory input. The crayfish has evolved from more primitive crustacea in which all the abdominal segments receive excitatory inputs. It has, therefore, been suggested that evolution of the tailflip escape response came about not by removing, but by inhibiting, the excitatory input to the posterior three segments (Dumont and Robinson 1986).

The primate oculomotor system provides another example of the existence of inappropriate signals that arise from evolutionary accretion. During cancellation of the vestibular ocular reflex, an inappropriate vestibular signal is present on vestibular neurons (Buettner and Büttner 1979). This signal must be nulled out by an appropriate signal before, or at, the level of the oculomotor nuclei.

Atypical vergence signals on MLF fibers

Four MLF fibers decreased more for convergence than any abducens cell recorded in this study or previously (Mays and Porter 1984b), yet had low or average conjugate gains (*MLF 22–MLF 25*). These fibers may represent a population of MLF fibers that does not arise from abducens internuclear neurons and hence was not sampled in our abducens recordings. The origin of such a population is not clear. It is possible that some horizontal burst-tonic vestibular fibers course in the MLF (Carpenter and Carleton 1983), although they are generally reported to run in the ascending tract of Deiter's, ~0.5–2 mm lateral to the MLF (McCrea et al. 1987). Fibers that course in the MLF have also been reported to arise from the nucleus prepositus hypoglossi, which contains cells that have horizontal eye position sensitivities and burst for saccadic eye movements (Baker et al. 1976; McFarland and Fuchs 1987). The existence of a vergence signal on these cells has not been investigated. It appears unlikely that the MLF fibers represent the axons of oculomotor internuclear neurons, because the vast majority of cells recorded in, and around, the oculomotor nucleus that carry a horizontal conjugate eye position signal increase their firing rate for convergence (Judge and Cumming 1986; Keller 1973; Mays et al. 1984a,b).

Comparisons to previous studies

This study was primarily concerned with the vergence signal carried by AINs; it was not designed to investigate

differences between AINs and motoneurons. Therefore, identification of abducens motoneurons was not attempted. However, because few of the many previous studies of abducens neurons distinguished between AINs and abducens motoneurons, a number of comparisons can be made between the results of this study and those of previous studies.

CONJUGATE EYE MOVEMENTS. The findings on the conjugate sensitivities of unidentified abducens neurons agree reasonably well with those of previous studies. The value for the k_c of 5.96 spikes $\cdot s^{-1} \cdot deg^{-1}$ obtained in the present study is slightly higher than that obtained in some previous studies, e.g., 4.6 spikes $\cdot s^{-1} \cdot deg^{-1}$ (Mays and Porter 1984b), 5.1 spikes $\cdot s^{-1} \cdot deg^{-1}$ (Goldstein and Robinson 1986). This difference might result from k_c values being obtained using a range of 20° as opposed to the larger movements used in other studies. However, a recent study in the rhesus monkey (Fuchs et al. 1988) has also reported a higher k_c value (6.2 spikes $\cdot s^{-1} \cdot deg^{-1}$) for identified abducens motoneurons than had previously been reported.

The mean threshold for recruitment for our sample of 46 unidentified abducens neurons was −14.4°, which is somewhat closer to primary position than the value of −24.7 and −24.4° calculated from earlier studies (Goldstein and Robinson 1986; Mays and Porter 1984b, respectively). However, for experimental reasons, these previous studies were limited to cells that were active at primary position. The finding of a positive correlation ($r = 0.55$) between k_c and recruitment threshold for the general population of abducens neurons is also consistent with previous studies. Goldstein and Robinson (1986) found a correlation between k_c and threshold of 0.78. Also, published data on abducens neurons from an earlier study in this laboratory (Mays and Porter 1984b) yielded a positive correlation between k_c and threshold of 0.68.

There has been only one other study of the characteristics of identified AINs in macaques. Fuchs and colleagues (1988) found a mean k_c value of 4.6 spikes $\cdot s^{-1} \cdot deg^{-1}$ and an average threshold of −28.9° for their sample of 36 AINs. The mean k_c for AINs in the present study was similar, at 5.32 spikes $\cdot s^{-1} \cdot deg^{-1}$, although the mean threshold for recruitment was somewhat lower at −15.8°. In agreement with this other report, we were unable to find a significant positive correlation between k_c and recruitment threshold for AINs. This is in contrast to the positive correlation between these variables seen both for identified lateral rectus motoneurons (Fuchs et al. 1988) and the general population of abducens neurons (e.g., Goldstein and Robinson 1986; Mays and Porter 1984b; Robinson 1970).

In the course of this study, a number of horizontal burst-tonic MLF fibers were recorded. Previous studies of these horizontal burst-tonic fibers in the MLF have reported conjugate gains of 3.0 spikes $\cdot s^{-1} \cdot deg^{-1}$ (King et al. 1976) and 4.1 spikes $\cdot s^{-1} \cdot deg^{-1}$ (Pola and Robinson 1978). The value of 4.6 spikes $\cdot s^{-1} \cdot deg^{-1}$ reported in the present study is comparable to that seen in these previous studies.

VERGENCE EYE MOVEMENTS. In the present study, the vergence gain obtained for a group of unidentified abducens cells was −3.20 spikes $\cdot s^{-1} \cdot deg^{-1}$. This figure is close to the value of −2.6 spikes $\cdot s^{-1} \cdot deg^{-1}$ obtained from 28 abducens neurons in a previous study (Mays and Porter 1984b). Furthermore, as shown in Table 3, the correlation between k_c and k_v for this population of cells is not significantly different from zero ($r = 0.01$). This confirms the previous report of Mays and Porter (1984b) that conjugate and vergence gains of individual abducens neurons are not well matched.

This is the first study in the primate of the vergence signal carried by identified AINs. The only other available data on AINs are from a study in the cat, which indicated that 75% of identified AINs did not change their firing rate for vergence eye movements (Delgado-Garcia et al. 1986). However, the sensitivity with which changes in firing rate could have been detected in this study are not specified, and it is clear that the use of untrained cats made it impossible to generate large numbers of stable, reproducible vergence movements or to avoid contamination by conjugate gaze shifts. These factors would decrease the likelihood of detecting changes in firing rates associated with vergence and would inflate the number of AINs showing no change in rate. Nonetheless, this study did show that the firing rate of several AINs decreased substantially during convergence.

Based on their observations that only a few AINs were modulated for vergence and that these decreased in activity for convergence, Delgado-Garcia and colleagues concluded that the internuclear pathway could play no meaningful role in vergence eye movements. However, it is clear from the results of the present study that consideration of *any* vergence signal carried by AINs, whether it is appropriate or inappropriate, is central to our understanding of the control of vergence eye movements.

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