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J Neurophysiol 69:74-94, 1993.

Journal of Neurophysiology publishes original articles on the function of the nervous system. It is published 12 times a year (monthly) by the American Physiological Society, 9650 Rockville Pike, Bethesda MD 20814-3991. ISSN: 0022-3077, ESSN: 1522-1598. Visit our website at http://www.the-aps.org/.

JOURNAL OF NEUROPHYSIOLOGY
Vol. 69, No. 1, January 1993. *Printed in U.S.A.*

Movement-Related Inputs to Intermediate Cerebellum of the Monkey

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SUMMARY AND CONCLUSIONS

1. The primary goal of this study was to characterize the information about single-joint forelimb movements supplied to intermediate cerebellar cortex by mossy fibers. Discharge of mossy fibers and Golgi cells was studied while monkeys operated six devices that required movements about specific joints. Additional control experiments in anesthetized cats and monkeys established criteria for identification of mossy fibers and Golgi cells.

2. The control experiments demonstrate that mossy fibers can be distinguished from Purkinje and Golgi cells by the waveshapes of their action potentials. Asynaptic activation from the inferior cerebellar peduncle, in combination with histological localization of recording sites in granular layer or subcortical white matter, verified that mossy fibers produce a variety of waveshapes that are characterized by brief initial phases and relatively small amplitudes. The same waveshapes were observed for the mossy fiber recordings from awake monkeys, and many identified mossy fibers had sensory properties similar to those found in the awake animals. From these combined criteria, we conclude that the recordings in the awake animals were from mossy fibers. Golgi cells, recorded exclusively in the granular layer of cerebellar cortex, were characterized by action potentials of longer duration and larger amplitude as compared with mossy fibers, and none were asynaptically activated from the inferior cerebellar peduncle.

3. Units were isolated while the monkeys made free-form and tracking movements. We studied movement-related discharge of 80 mossy fibers and 12 Golgi cells. Mossy fibers showed high modulations during use of at least one of the six manipulanda and had clear preferences for movement about a specific joint, although they often showed consistent but weaker firing during movement about a neighboring joint. Separation of movements by more than one joint produced a large reduction in discharge: shoulder units never fired well to movements of the finger, and finger units never fired well to movement of the shoulder.

4. The tracking task required maintenance of fixed limb positions (a static phase) as well as movements between these positions (a dynamic phase). Of 80 mossy fibers, 18% had purely tonic discharge patterns, 63% were phasic-tonic, and 20% were purely phasic. Discharge patterns were reciprocal (45%), bidirectional (42%), or unidirectional (13%).

5. Eighty percent of the mossy fibers exhibited tonic discharge that was significantly ($P < 0.01$) correlated with joint angle ($r = 0.65 \pm 0.19$, mean $\pm$ SD), and about one third had phasic components that were significantly correlated with movement velocity. Eleven mossy fibers were tested for correlations between the duration of the phasic discharge component and movement duration, and all revealed significant positive correlations. The onset time of mossy fiber discharge was distributed approximately equally about the onset time of movement. Thus discharge of about one fourth of 80 units significantly ($P < 0.05$) led movement onset and one third significantly lagged.

6. Twenty-nine movement-related mossy fibers were tested for sensory responsiveness by manipulation of joints and/or by mechanical disturbances of device position during static phases of the tracking task. In most (69%) cases, passive responses were of the same polarity as the modulations in discharge during comparable active movements; in 17% of the cases, they were of opposite polarity. Four units (14%) failed to respond to passive movement.

7. Recordings from 12 Golgi cells revealed properties strikingly different from mossy fibers. All showed phasic discharge without tonic components, and most cells showed bidirectional discharge patterns during both active and passive movements. Four of six cells showed modulations in discharge of equal magnitude during use of proximal and distal devices. These properties are consistent with extensive convergence of mossy fibers on individual Golgi cells.

8. It is clear from our results that mossy fibers provide intermediate cerebellum with position, velocity, and direction information about movement of individual forelimb joints. Several characteristics of the signals indicate that they may contain information derived from efference as well as afference.

9. A comparison of input information supplied by mossy fibers with output signals in the nucleus interpositus suggests that the intermediate cerebellum incorporates position and velocity information from individual joints, together with other inputs, into phasic signals relating to coordinated movements of the entire limb.

INTRODUCTION

This paper describes movement-related properties of mossy fiber inputs to the intermediate cerebellum in the awake monkey using the same behavioral techniques as used in the preceding report on interpositus neurons (Van Kan et al. 1993). The combined results of these studies represent a first step in attempting to understand the input-output transformations occurring in intermediate cerebellum.

Mossy fibers are known to arise from multiple sources, and it is generally assumed that fibers from different sources provide the cerebellum with different information (for reviews, see Bloedel and Courville 1981; Ito 1984; Llinas and Simpson 1981; Oscarsson 1973). Even if one focuses just on movement-related mossy fibers, considerable variety might be anticipated. Muscle, joint, and skin receptors could transmit different kinds of movement-related activity. Some of the spinocerebellar pathways are reported to carry specific information from a small number of muscles in a single limb, whereas others transmit highly convergent information from several limbs.

Mossy fibers also differ in the extent of their convergence from peripheral and central sources. For example, the cuneocerebellar tract and dorsal spinocerebellar tract (DSCT) are considered to transmit signals dominated by peripheral input, whereas the rostral spinocerebellar tract (RSCT) and

ventral spinocerebellar tract (VSCT) and the reticulocerebellar and pontocerebellar pathways receive appreciable input from central sources. The RSCT and VSCT are believed to transmit mainly efference copy signals (Arshavsky et al. 1986). [An efference copy signal is defined as an alteration in activity that is produced within the CNS and is closely correlated with a motor command from a motor center to an effector (see McCloskey 1981)].

The manner in which limb movement is encoded in the discharge of cerebellar afferents must depend on the fusimotor drive to the muscle spindles, the pattern of convergence of receptors, and the integration of ascending and descending signals along the pathways from receptors to cerebellar cortex. Fusimotor drive and possible integrative action at synaptic relays are clearly dependent on the experimental preparation and the animal's behavioral state. Therefore, the information received by the cerebellum may differ under active as compared with passive conditions. Only a few previous studies on discharge of mossy fibers to active or passive limb movements in awake, behaving animals have been reported (Bauswein et al. 1984; Cleland and Hoffer 1986; Horn et al. 1989; Matsunami 1987). The main goal of this study was to characterize movement relations of forelimb mossy fibers in the awake, behaving monkey.

The results allow us to compare mossy fiber input properties with the output properties of interpositus neurons described in the previous paper (Van Kan et al. 1993). We considered that this comparison would be particularly valuable if we used the same experimental protocols and the same animals. Therefore, single mossy fiber afferents and Golgi cells were studied while the animals operated the same tracking devices as were used in the study of interpositus neurons. The devices were designed to study discharge to movement about individual forelimb joints. In addition, we studied sensory responsiveness for many units.

Our results show that mossy fibers fire vigorously during free-form reaching and device use, display a relatively high degree of joint-specificity, are highly sensitive to joint position, and respond well to natural stimulation. These properties contrast strongly with those of interpositus neurons: interpositus neurons fire more strongly during reaching than during tracking, show relatively little joint specificity, and have no discharge related to joint position. On the basis of these results, we discuss information processing steps that are likely to occur within the intermediate cerebellum.

The mossy fibers and Golgi cells studied in this paper were recorded directly from the cerebellar cortex. Although this site was convenient for obtaining a representative sample of the relevant movement-related signals that enter the intermediate cerebellum, control experiments were needed to establish identification criteria. These controls were conducted in anesthetized cats and monkeys. Preliminary accounts of this work were reported in several abstracts (Van Kan et al. 1986, 1987a,b).

METHODS

The methods and results in this report are divided into two parts. The first part reports on control experiments in anesthetized animals that establish criteria for identifying mossy fibers and Golgi cells; the second part reports on movement-related discharge of mossy fibers and Golgi cells in behaving monkeys.

Part I: control experiments in anesthetized animals

Eleven cats and two monkeys (*Macaca arctoides*) were anesthetized with pentobarbital sodium (intravenous, to effect) and given supplementary doses as required. A craniotomy over the occipital lobe exposed the cerebral cortex overlying the cerebellum. In the cats, the occipital lobe was elevated and access to lobules IV–VI of intermediate cerebellar cortex was obtained through an opening in the tentorium. In the monkeys, microelectrode penetrations traversed the occipital lobe on their way into intermediate cerebellar cortex. Single units were recorded using methods similar to those used in the awake monkey experiments. However, only a few widely spaced electrode tracks were run in each animal, and marking lesions were placed at several recording sites along each track. These procedures facilitated histological reconstruction of electrode tracks and resulted in a highly reliable identification of the layer of intermediate cortex from which each unitary potential was recorded. This identification was used retrospectively to verify the accuracy of our identification of layer on the basis of physiological landmarks.

In the cats, a second craniotomy was made over the posterior lobe of the cerebellum to permit access to the inferior cerebellar peduncle; in the monkeys, the peduncle was accessed through the craniotomy overlying the occipital lobe. After the peduncle had been localized by recording with a single microelectrode, an array of three low-impedance (200 kΩ) stainless steel electrodes (tip spacing 0.3 mm) was inserted into the peduncle. The electrodes were arranged in parasagittal planes and pointed anteriorly at an angle of 45°. The array was used for both electrical stimulation and back-averaging unitary potentials.

For back-averaging, one of the electrodes in the peduncle was used for monophasic recording, and the amplified signal was delayed, sampled at 250 kHz, and averaged in response to a trigger derived from a unitary event in the granular layer. We judged the linkage between the peduncle and the unit to be asynaptic if we were able to show a short-duration peduncular potential that preceded the unitary event at a latency consistent with direct conduction from the peduncle. (Synaptic activation would have resulted in too much variability for the emergence of this averaged event.) At the conclusion of the experiment, the tip sites were marked by passing current, and their locations in the inferior cerebellar peduncle were confirmed histologically.

Somatosensory responsiveness of granular layer units was tested by touching and tapping the body surface, squeezing the appropriate body parts, and manipulation of joints and muscles as described for the awake animals in METHODS, *Part II*.

Part II: movement-related discharge of mossy fibers and Golgi cells in awake monkeys

Experiments were carried out on three male monkeys (*Macaca mulatta*). Two monkeys were also used in the study of nucleus interpositus reported in the preceding paper (Van Kan et al. 1993). The methods that were similar in both studies are described only briefly; sensory testing on a third monkey and some aspects of data analysis not included in the previous paper are presented in more detail.

The animals were trained to perform a visually cued tracking task that required operation of six forelimb manipulanda [see METHODS and Fig. 1 of preceding paper (Van Kan et al. 1993)]. Operation of three devices isolated movements about individual joints, the shoulder, elbow, and wrist. The finger device required simultaneous movement of the metacarpophalangeal joints. Two additional devices isolated supination/pronation of the forearm

and multijoint hand twisting that required the combined use of wrist and fingers.

After training, a recording chamber and head holder were implanted, and extracellular recordings of unitary discharge were made with tungsten microelectrodes. After a unit had been isolated and tested for reach-related discharge, we collected computer records of 15–100 trials while the animal operated the preferred device, which was defined as the device that elicited the largest modulation in discharge. In many cases, we subsequently switched to secondary tracking devices to collect additional trial data. Onset times of discriminated action potentials were collected as interspike intervals with 0.1-ms accuracy. Raw spikes were amplified with a half-amplitude bandwidth of 300–10,000 Hz and were recorded on analog magnetic tape. Manipulandum position was sampled at 250 Hz.

Toward the end of the recording period, small electrolytic lesions (−10 μA for 10 s) were made at selected sites along 10–15 penetrations. After recording was complete, larger lesions (+50 μA for 30 s) were made at corner positions of a rectangular volume of tissue that included all other penetrations. After formalin fixation, tissue was stained with either a cresyl violet Nissl stain or a luxol fast blue fiber stain counterstained with cresyl violet. Sections were enlarged and traced, and with the aid of stereotaxic coordinates, electrode paths, lesions, and recording sites were reconstructed.

SENSORY TESTING. One of the three monkeys (*BO*) was trained to relax and not to make active limb movements while the experimenter manipulated the animal's limb. This allowed for testing responses to somatosensory stimuli. Unitary receptive fields were determined by moving each joint of the limb through its normal range of motion while noting the general responsiveness of the unit. As each joint was manipulated, all other joints were immobilized manually. Receptive fields of units that appeared to be activated by rotation-induced stretch of muscles were then investigated in more detail with near-threshold natural stimulation, including gentle taps and light pressure to the appropriate muscle bellies. This made it possible to identify the general region of the receptive field and, in some cases, the specific muscle or muscle groups involved. Although these tests aided in distinguishing units with muscle receptor input from those receiving input from joint receptors, conclusive evidence for input from joint receptors was not obtained.

In addition to manual exploration of the limb by the experimenter, mechanical disturbances of device position were introduced with a servo-driven torque motor that was mounted on the rotation axis of the shoulder and elbow device. A torque transducer between the motor output shaft and the device arm provided force feedback to the servo-amplifier as well as a force record. The servomechanism enabled us to introduce pulse changes in mechanical load that generated sudden displacements of device position and that thus produced unexpected changes in angular position of the shoulder and elbow joints. Transient mechanical disturbances of the wrist and finger joints were introduced by a tap on the device by the experimenter.

DATA ANALYSIS. Averaged discharge was calculated from data files that contained a number of similar movements. For each trial, an interactive display program was used to align a cursor to movement onset. An averaging program then sorted the processed trials according to category, generated peristimulus time histograms aligned to movement onset, calculated the corresponding averages of analog records, and plotted discharge during individual trials in the form of raster displays. The binwidth of the histograms of average discharge rate was 12 ms.

The joint angle dependency of the unitary discharge was estimated by plotting tonic firing rate as a function of angular position of the preferred device. The mean tonic firing rate and angular position were calculated over 400-ms intervals during which the monkey was required to hold the limb steady. Data pairs for the three limb holding positions of the tracking task were collected during 15–100 individual trials, plotted on scatter diagrams, and evaluated by calculation of the Pearson product moment correlation (r).

Records of movement velocity were derived from the angular position records by a two-step procedure involving a numerical differentiation and a symmetrical smoothing. This process did not introduce phase shifts between the records. For a given sample of angular position, the differentiation algorithm determined the slope of the position record from samples immediately preceding and following the sample, and this procedure was repeated for all samples of the record. The resulting record was smoothed by an algorithm that calculated a weighted average on the basis of 10 samples preceding and following each sample.

Relations between discharge and movement velocity were assessed by calculating the mean firing rate and mean movement velocity over 100-ms intervals, centered around five angular positions that were equally spaced along the movement trajectory. Data pairs for both flexion and extension movements were plotted on scatter diagrams, and the correlation in a given direction was evaluated by linear regression analysis.

Onset and offset times and the duration of the movement and the movement-related discharge were determined from records of angular position and integrated spikes (a cumulative count of the number of action potentials vs. time) by using an interactive display program to align cursors to the appropriate inflection points in the records. Measurements of the duration of movement and movement-related discharge from single trials were plotted on scatter diagrams and evaluated by calculation of the Pearson product moment correlation (r).

The mean lead or lag time of a unit was determined by averaging single-trial measurements of the difference between the onset times of movement and movement-related discharge. t Statistics were used to determine whether the lead or lag time of a given unit differed from zero. The mean latency to the onset of perturbations during limb holding was determined by averaging single-trial measurements of the difference between the onset times of the perturbation and perturbation-related discharge.

RESULTS

In *Part I* of the RESULTS, we describe control experiments in anesthetized animals that were performed to verify the criteria for identification of mossy fibers and Golgi cells. In *Part II*, we describe movement-related properties of mossy fibers and Golgi cells recorded in awake monkeys.

Part I: control experiments in anesthetized animals

Initial recordings in trained monkeys suggested that mossy fibers might be identified on the basis of the waveshapes of their extracellular potentials, particularly if this information were to be combined with layering information. Waveshape criteria are well-established for the turtle cerebellum (Walsh et al. 1974), and there is evidence that similar criteria might apply to mammals (Bourbonnais et al. 1986; Taylor et al. 1987). Our strategy in these control experiments was to first establish reliable criteria for recognizing the different cerebellar cortical layers and then to demonstrate that certain waveshapes within the granular layer are reliably associated with mossy fiber activity.

IDENTIFICATION OF GRANULAR LAYER. The characteristic electrical activity of the Purkinje cell layer provided an an-

chor point for the identification of other layers of cerebellar cortex. Waveshapes and firing patterns of simple and complex spikes have been studied extensively and are commonly accepted as reliable identification criteria for Purkinje cells (Eccles et al. 1966a,b; Granit and Phillips 1956; Mano 1986; Thach 1967; Walsh et al. 1974). As the electrode moves away from a Purkinje layer, it must enter either a granular or molecular layer. The most useful criteria for differentiating granular and molecular layers result from the differing profiles of unitary electrical events.

The granular layer was distinguished by an agitated background of low-amplitude electrical activity and by a unique variety of isolated unitary potentials. Figure 1, *C1–C7* shows a sampling of the unitary potentials encountered as an electrode was advanced through two granular layers separated by a layer of white matter, and Figs. 1, *D1* and *D2*, show additional examples of confirmed granular layer potentials. In attempting to make sense of this great diversity of waveshapes, we have found it useful to first divide the potentials into fast and slow categories. The fast potentials are the most numerous. They share the following characteristics: *1*) durations <0.5 ms, *2*) modest amplitudes <0.5 mV (e.g., Fig. 1 *C2*), and *3*) short (usually <50 μm) tuning distances (i.e., the extent of microelectrode movement over which unitary recording can be maintained). The slow potentials have *1*) durations >1 ms, *2*) amplitudes that may attain a few millivolts (e.g., Fig. 1 *C1*), and *3*) tuning distances of $\geq$100 μm. The distributions of duration and amplitude of fast and slow potentials were largely nonoverlapping. Duration (from the foot of the action potential to the time of return to baseline) averaged 0.3 $\pm$ 0.1 (SD) ms for fast units and 1.4 $\pm$ 0.7 ms for slow units. Amplitude (peak to peak) averaged 0.25 $\pm$ 0.10 mV for fast units and 0.63 $\pm$ 0.38 mV for slow units.

The fast potentials discharged at rates that were frequently as high as 200 imp/s, and their interspike intervals were irregular and of short duration. Fast potentials had a variety of waveshapes. The most characteristic was a fast biphasic potential followed by a slower negative afterwave (NAW) (Fig. 1, *C4*, *C5*, and *D1*). These waveshapes have been attributed to pre- and postsynaptic events at mossy fiber glomeruli (Bourbonnais et al. 1986; Taylor et al. 1987; Walsh et al. 1972, 1974). The all-or-none biphasic spike, which can occur with or without a subsequent NAW, is thought to represent the invasion of a glomerulus by a presynaptic action potential, and the NAW, which is of vari-

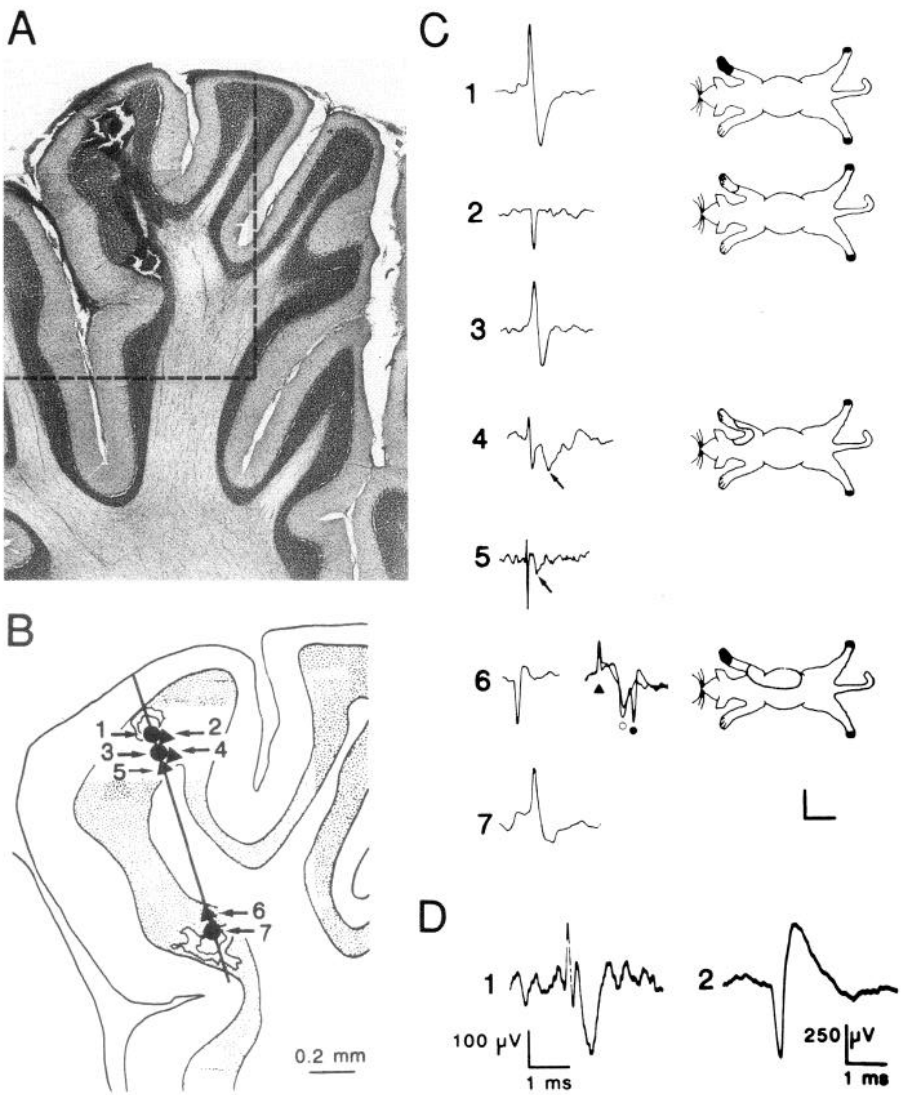

FIG. 1. Granular layer potentials in cat (*A–C*) and monkey (*D*). The photomicrograph (*A*) is a composite of adjacent sections through lobule Va of intermediate cerebellar cortex. Two electrolytic lesions were made in granular layer at the recording sites of 2 slow positive-negative potentials. The area marked by the broken lines is shown enlarged in (*B*). Numbers along the reconstruction of the penetration (*B*): recording sites of units whose waveshapes are shown in (*C*). The fast waveshapes shown in *C2*, *C4*, *C5*, and *C6* are attributed to mossy fibers. The biphasic potentials in *C4* and *C5* were followed by a negative afterwave (→). The unit in *C6* was identified as a mossy fiber by asynaptic activation from the inferior cerebellar peduncle, as illustrated by the records on the *right*. Two traces at threshold stimulation are shown superimposed. Note the all-or-none activation of the unit (●). Open circle: field potential. The activity patterns of the mossy fibers were briskly and tonically modulated by rotation of joints and/or tapping or squeezing the ipsilateral limb. Receptive fields are drawn on the cat figurines. Gray and black shading on cat figurines: excitatory and inhibitory subregions, respectively, of receptive fields. The units shown in *C3*, *C5*, and *C7* were not driven by peripheral input. The slow positive-negative waveshapes in *C1*, *C3*, and *C7* are attributed to Golgi cells. *D*: examples of a monkey fast positive-negative potential followed by a negative afterwave, attributed to a mossy fiber (*D1*), and a slow negative-positive potential attributed to a Golgi cell (*D2*). Calibration marks in *C* differ for different traces: *C1*, 300 μV, 1.3 ms; *C2*, 175 μV, 0.6 ms; *C3*, 165 μV, 0.6 ms; *C4*, 146 μV, 1.3 ms; *C5*, 160 μV, 0.6 ms; *C6*, 125 μV, 0.6 ms; *C7*, 280 μV, 0.6 ms.

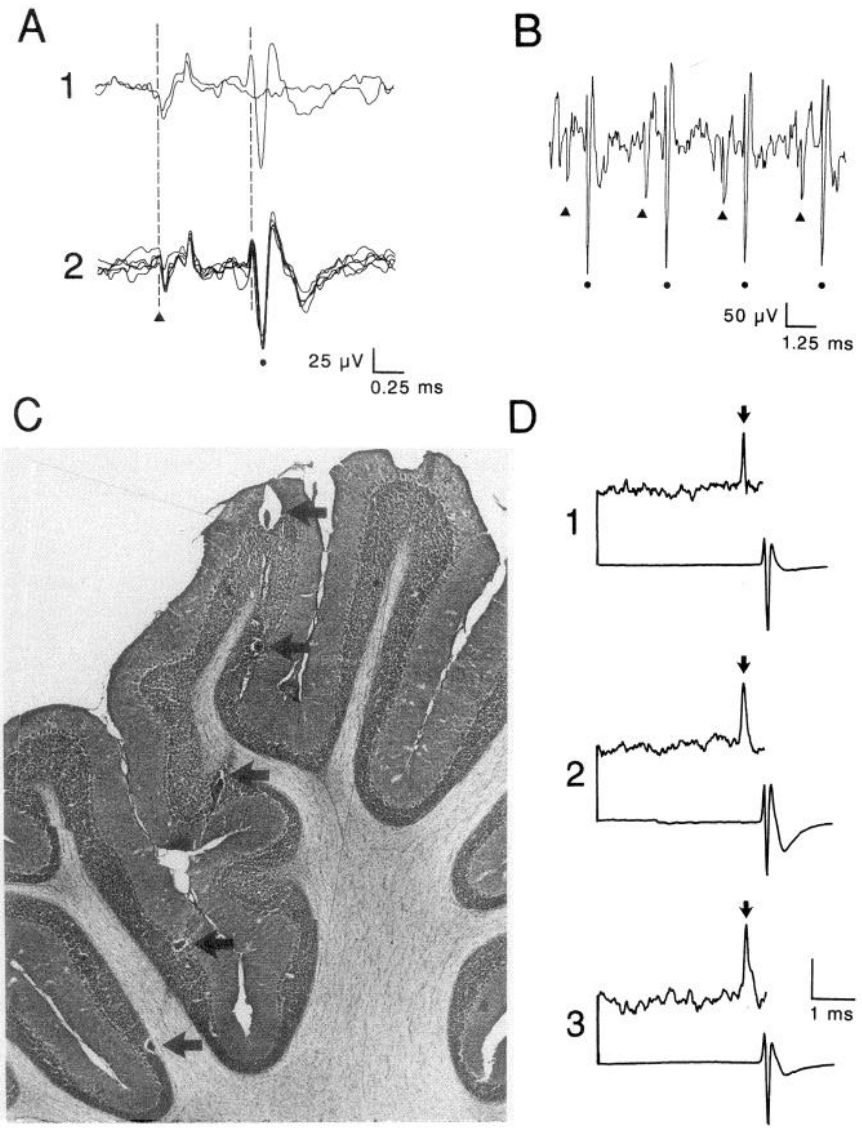

FIG. 2. Identification of mossy fibers by asynaptic activation after electrical stimulation of the inferior cerebellar peduncle (*A* and *B*) or by spike-triggered averaging of activity recorded from the inferior cerebellar peduncle (*D*). *A1*: trace just below threshold (5 μA) superimposed with a trace just above threshold. *A2*: 5 superimposed traces illustrating a fixed conduction latency characteristic of an asynaptic delay. Vertical lines: variation in conduction latency was <0.2 ms when the stimulus intensity was increased from threshold (*A1*) to supramaximal amplitude (*A2*). *B*: this unit was able to follow stimulation at frequency of 300 Hz with variation in conduction latency ≤0.2 ms. Triangle: stimulus onset. Dot: unit. *D*: activity recorded from the inferior cerebellar peduncle (*D1–D3, top* traces) was averaged over a 4.5-ms interval preceding the occurrence of successive action potentials recorded from single mossy fibers (*D1–D3, bottom* traces). Peduncular activity associated with the conducted action potentials of each of the units gave rise to potentials in the averaged records (*D1–D3*, ▼) that preceded the action potentials by ~0.65 ms. The photomicrograph (*C*) is a composite of 2 adjacent sections through lobule Va and IV of intermediate cerebellar cortex. Five lesions, indicated by arrows, verified the location of successively recorded Purkinje cell layers (1st, 2nd, and 4th lesions from the top) and transitions from white matter to granular layer (3rd and 5th lesions). The units whose records are shown in *A*, *B*, and *D* were recorded successively in the granular layer between the 1st and 2nd lesions. Vertical calibration mark in *D* differs for the different traces: *D1*, 8 μV (*top*), 160 μV (*bottom*), n = 5000; *D2*, 15 μV (*top*), 80 μV (*bottom*), n = 1157; *D3*, 6 μV (*top*), 60 μV (*bottom*), n = 4122.

able amplitude, may reflect excitatory postsynaptic current in granule cell dendrites. Good stability was required to record the NAW. The most frequently observed granular layer waveshape was a potential that was characterized mainly by a rapid negative phase (Fig. 1, *C2* and *C6*), which in most cases was preceded and/or followed by smaller positive phases (Fig. 2, *A*, *B*, and *D*). Potentials with these configurations are referred to as triphasic. A predominantly positive waveshape (Fig. 3 *A2*) is another category of fast potential that was occasionally recorded from the granular layer. This waveshape was more often recorded in subcortical white matter and in the inferior cerebellar peduncle and was attributed to myelinated fiber recordings (cf. Kiang 1965; Mountcastle et al. 1969; Thach 1967; Walsh et al. 1974).

The slow units were recorded exclusively from the granular layer and had either a negative-positive (Fig. 1 *D2*) or a positive-negative waveshape (Fig. 1, *C1, C3*, and *C7*). Frequently, the positive-negative potentials showed pronounced initial segment-Soma dendritic (IS-SD) breaks (Fig. 1, *C1, C3*, and *C7*). These units were encountered infrequently and, unlike Purkinje cells, were never recorded in groups. Discharge rates were low and regular: interspike intervals were never <10 ms and usually >20 ms.

Table 1*A* shows the frequency of occurrence of the different subcategories of fast and slow units. The locations of recording sites in the anesthetized cats and monkeys were confirmed to lie in the granular layer on the basis of detailed reconstructions of electrode tracks from histological sections. Table 1*A* also lists granular layer potentials of awake monkeys for which we were relatively confident of our histological reconstructions.

Two types of unitary events broke the relative silence of the molecular layer. Near the Purkinje cell layer, we encountered positive-negative potentials of intermediate amplitude that alternated between periods of repetitive firing at relatively high rates and periods of silence. These potentials may be produced by basket and stellate cells. Climbing fiber potentials were encountered throughout the molecular layer. Their characteristic complex waveshapes and low (<1 imp/s) and irregularly maintained discharge permitted recording sites in the molecular layer to be identified with confidence. When climbing fiber discharge was absent, the molecular layer could be confused with the white

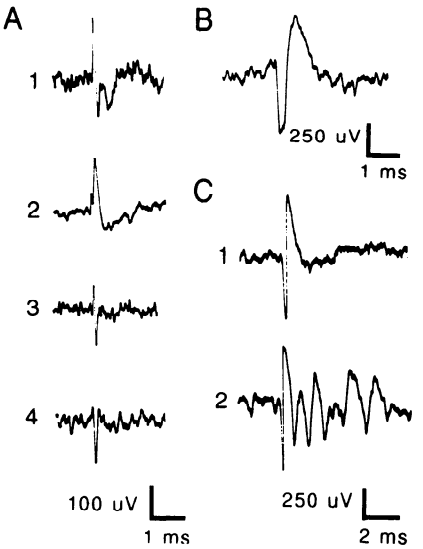

FIG. 3. Examples of action potential waveshapes recorded in awake monkeys. *A*: examples of fast potentials attributed to mossy fibers. *A1*: biphasic potential with a negative afterwave. *A2*: predominantly positive potential. *A3*: biphasic potential without a negative afterwave (NAW). *A4*: triphasic potential. *B*: example of a slow negative-positive potential attributed to a Golgi cell. *C*: simple (*C1*) and complex (*C2*) spikes recorded from a Purkinje cell.

matter, which is also relatively silent. In these cases, judgment of recording site had to be linked to the identification of adjacent layers. In general, this use of information about adjacent layers proved valuable for confirming a tentative identification of the layer on the basis of electrical activity.

When these various criteria were used in combination, we found that we could identify sequential recording sites with a high level of confidence, as verified by histological reconstructions of electrode tracks.

IDENTIFICATION OF GRANULAR LAYER POTENTIALS. Given that a recording site was in the granular layer, we then sought to identify the specific type of neuronal element responsible for the unitary potential. In the turtle cerebellum, most granular layer potentials derive from mossy fiber afferents (Walsh et al. 1974). By stimulating and recording from electrodes placed in the inferior cerebellar peduncle, we obtained strong evidence that mossy fiber afferents also produce triphasic, biphasic, and predominantly positive potentials in monkeys and cats. Because many mossy fibers enter the cerebellum through the inferior peduncle, we sought to demonstrate cases in which no synapse intervened between the peduncle and our unitary recording site in the granular layer.

Electrical stimulation through different pairs of an array electrode was used to test for asynaptic activation of granular layer units (see METHODS, *Part I*). On the basis of the assumption that synaptic linkages give rise to variability in transmission, the criteria used were: *1*) variation in latency of <0.2 ms when the stimulus was increased from threshold to above maximal intensity and *2*) an ability to follow high-frequency stimulation (100–300 Hz) with variation in latency <0.2 ms. Figure 2, *A* and *B* shows an example of a triphasic unit that passed these tests, and Table 1 *B* summarizes our data on 94 granular layer units. Nearly half of the fast units were asynaptically activated, indicating that they represented mossy fiber afferents, whereas none were synaptically activated. In contrast, none of the slow units were asynaptically activated, and two were synaptically activated, which is consistent with their identification as Golgi cells.

These results were remarkably clear, considering that a large fraction of units proved to be not testable. One technical problem is that electrical stimulation of the peduncle

TABLE 1. *Granular layer potentials*

A. Action Potential Waveshape

Unit	Waveshape	Anesthetized Cat	Anesthetized Monkey	Awake Monkey	All Cases
Fast	Biphasic with NAW	18	9	15	42
	Biphasic	6	9	2	17
	Triphasic	21	22	33	76
	Predominantly positive	7	5	8	20
	Subtotal	52	45	58	155
Slow	Negative-positive	4	6	8	18
	Positive-negative	7	1	4	12
	Subtotal	11	7	12	30
	Total	63	52	70	185

B. Electrical Activation

Unit	Asynaptic	Synaptic	Untestable	All cases
Fast	37	0	39	76
Slow	0	2	16	18
Total	37	2	55	94

C. Somatosensory Responsiveness

Unit	Modality	Cat	Monkey	All Cases	Percentage
Fast	Joint rotation	16	27	43	37
	Light cutaneous	12	7	19	16
	Squeeze	19	9	28	24
	Unresponsive	16	10	26	22
	Total	63	53	116	100
Slow	Squeeze	2	1	3	17
	Unresponsive	9	6	15	83
	Total	11	7	18	100

A: all units were localized in the granular layer of intermediate cerebellar cortex as verified by histological reconstructions. Fast units from awake monkeys localized in deep cerebellar white matter or with unverified recording sites or waveshapes are not included (n = 22). NAW, negative afterwave. *B*: all units were recorded in the granular layer of the intermediate cerebellar cortex of anesthetized animals as verified by histological reconstructions. Thirty asynaptic units were recorded in cats and 7 in monkeys. Waveshapes of asynaptic units were triphasic (18), biphasic with a NAW (10), biphasic without a NAW (4), and predominantly positive (5). The two synaptically activated slow units were recorded in cats and had negative-positive waveshapes. *C*: all units were recorded in the granular layer of intermediate cerebellar cortex of anesthetized animals as verified by histological reconstruction. The 90 fast units that responded to somatosensory stimulation had receptive fields in the forelimb (68), hindlimb (4), or face (13). The three responsive slow units had forelimb receptive fields. The response to joint rotation was dependent on rotation-induced muscle stretch. No evidence for input from joint receptors was obtained. Among the 37 fast units that were asynaptically activated from the inferior peduncle, 11 responded to rotation of joints, 6 to cutaneous stimuli, and 14 to squeezing muscles; the remaining 6 were unresponsive to peripheral stimulation.

often evoked large granular layer field potentials that obscured unitary responses. If the field potential was small at a stimulus intensity sufficient to evoke a unitary response, the unit could be distinguished superimposed on the field potential, as is the case for the example in Fig. 1*C6*. However, if the field potential (or the stimulus artifact) was large, it could obscure the unitary response, making it more difficult to identify mossy fibers with higher conduction velocities and higher thresholds of activation. As a consequence, a successful test required that the peduncle electrode be placed relatively close to those particular fibers that innervated the recording site in the granular layer. A second limitation is that many mossy fibers enter the cerebellum through the superior and middle cerebellar peduncles, and therefore would have remained unidentified by our procedures.

In some cases, spike-triggered backward averaging was used to test for asynaptic linkage. The discriminated action potentials of cerebellar cortical units were used to trigger the averaging of delayed peduncular activity (see METHODS, *Part I*). A unit was considered to be asynaptic if a short-duration peduncular potential preceded the unitary event at a latency consistent with direct conduction from the peduncle. Figure 2*D* shows three triphasic potentials that passed this test. The averaging procedure was successful in only nine cases, presumably because it depended on a favorable placement of the peduncular electrode. Four of the nine fast units identified as mossy fibers by this method were also shown to be asynaptic by peduncular stimulation.

SOMATOSENSORY RESPONSIVENESS OF GRANULAR LAYER UNITS. Table 1*C* summarizes our data on 134 granular layer units that were tested for somatosensory responses by rotation-induced muscle stretch, gentle taps on the underlying muscle bellies, light pressure on the skin, bending hairs, and squeezing the appropriate body part. Ninety (78%) of the 116 fast units showed prominent tonic responses that were maintained for the duration of the stimulus. Typically, these units also showed brisk phasic responses that accompanied joint rotation or occurred at the onset and/or offset of a tap or squeeze. Receptive fields were often small and had sharply defined borders. Forty-three (37%) fast units showed relations between tonic discharge and joint angle similar to those in the awake monkeys (see RESULTS, *Part II*). In contrast, 15 (83%) of 18 slow units were not influenced by peripheral somatosensory stimuli. Responsive slow units required higher intensity stimuli than fast units, and their responses were sluggish and not tonically maintained.

Part II: movement-related discharge of mossy fibers and Golgi cells in awake monkeys

A total of 80 mossy fibers and 12 Golgi cells from three monkeys were studied during forelimb reaching movements, during operation of a number of tracking devices, and during passive movements and perturbations. Two of the three monkeys were also used to study movement-related discharge of interpositus neurons, reported in the preceding paper (Van Kan et al. 1993).

ACTION POTENTIAL WAVESHAPES AND RECORDING SITES. A total of 80 units were attributed to mossy fibers. Their waveshapes (Table 1*A*) were of brief duration (<0.5 ms), fast rise time (<0.1 ms), and relatively small amplitude (<0.5 mV). Most common were triphasic potentials (Fig. 3*A4*; 57%), biphasic potentials with (Fig. 3*A1*; 26%) or without a NAW (Fig. 3*A3*; 3%), and predominantly positive potentials (Fig. 3*A2*; 14%). As in our acute studies (see RESULTS,

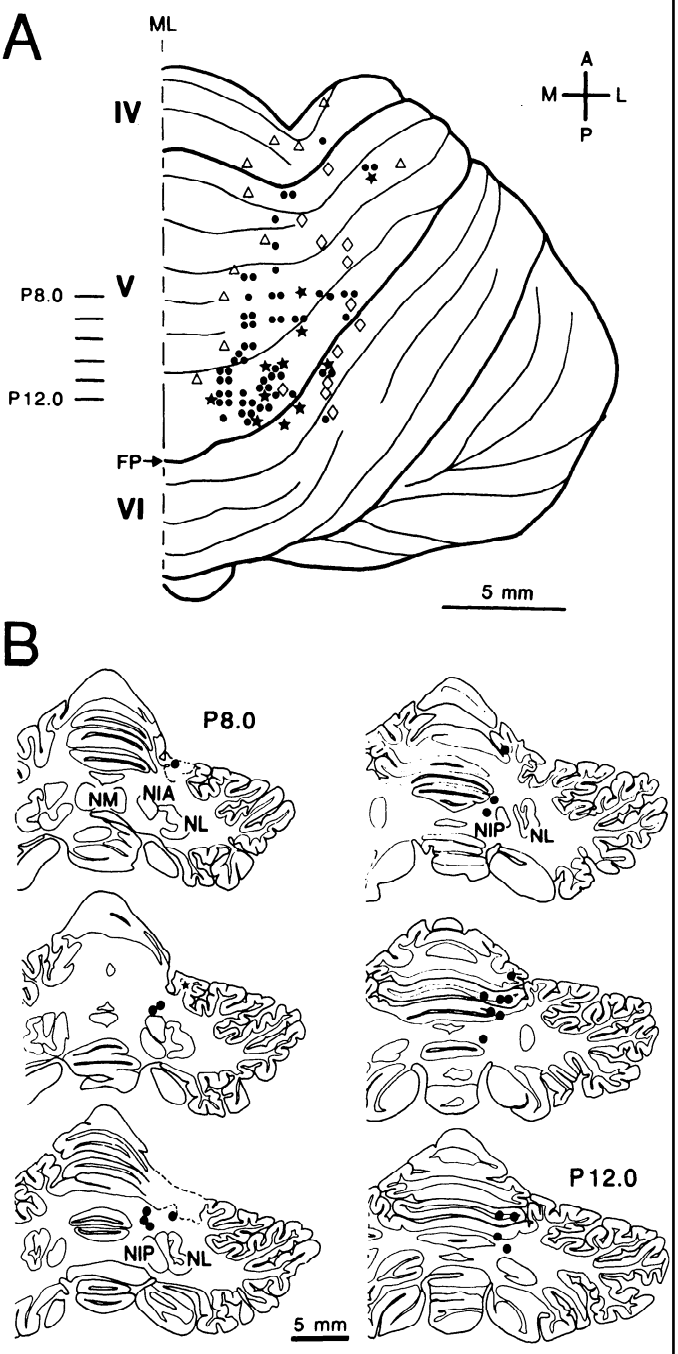

FIG. 4. Recording sites in awake monkeys of mossy fibers and Golgi cells. Recording sites of the 80 forelimb mossy fibers are located in intermediate cerebellar cortex and are indicated with filled circles on a dorsal view of the cerebellar surface (*A, monkey BO*), or on evenly spaced transverse sections through the cerebellum (*B, monkeys MAX* and *OSC*). Stars: recording sites of the 12 Golgi cells. Triangles and diamonds: sites where hindlimb- and face-related mossy fibers, respectively, were recorded. Horizontal lines in the *left* margin of *A*: approximate levels of the transverse sections shown in *B*. FP, primary fissure; ML, midline; IV, V, and VI, cerebellar cortical lobules.

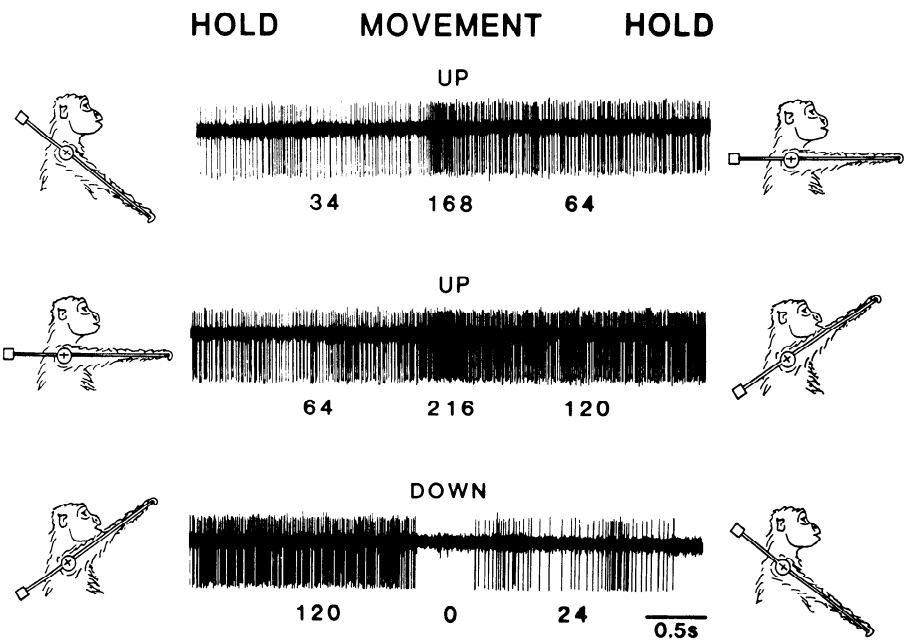

FIG. 5. Discharge pattern of a triphasic potential during operation of the shoulder device. The 3 traces represent a continuous interval of ~13 seconds, during which the animal moved between the 3 fixed limb positions of the tracking task. The maintained tonic rate during the steady limb holding phase was correlated to limb position, and the movement-related burst of activity was correlated to velocity of flexion. During extension, discharge was decreased. The unit (*MAX* 37-1) was classified as a phasic-tonic mossy fiber. The mean firing rate during movement and limb holding phases is indicated below the traces.

Part I), triphasic, biphasic, and glomerular potentials were the most frequently encountered unitary events in the granular layer; predominantly positive potentials were recorded mostly in subcortical white matter. Longer-duration potentials that met the criteria for Golgi cells were encountered more rarely. Of the 12 Golgi neurons studied, 8 had negative-positive waveshapes (Fig. 3*B*) and 4 had positive-negative waveshapes. For comparison, Fig. 3, *C1* and *C2*, shows waveforms of a simple and complex spike of a Purkinje cell, respectively.

In one monkey (*MAX*), we focused on the cerebellar nuclei [results reported in the preceding paper (Van Kan et al. 1993)] and obtained a few pilot recordings from mossy fibers as the microelectrode passed through intermediate cerebellar cortex and white matter. In a second monkey (*OSC*), we frequently studied units in intermediate cortex before proceeding to the cerebellar nuclei. Figure 4*B* shows the combined recording sites of 21 mossy fibers in the granular layer and white matter and one Golgi cell for *monkeys OSC* and *MAX*. In a third animal (*BO*), we focused on mossy fibers (59) and Golgi cells (11). The positions of the recording tracks in this animal are indicated in Fig. 4*A* on a dorsal view of the cerebellum; actual recording sites were reconstructed from parasagittal sections. Recording sites were either in the granular layer or in the white matter of intermediate cerebellar cortex, and these units were classified as mossy fibers or Golgi cells using the criteria described in RESULTS, *Part I*. Most white matter recordings were made in the subcortical white matter of intermediate cerebellar folia; nine mossy fibers were recorded deep in the cerebellar white matter (Fig. 4*B*) and may have terminated in regions other than intermediate cerebellar cortex.

DISCHARGE OF MOSSY FIBERS DURING MOVEMENT. Eighty forelimb mossy fibers were isolated while the monkeys reached for raisins held at different locations in space and were subsequently tested during tracking. Peak firing rates of 10 units were compared during both reaching and tracking, and the rates for the two tasks were approximately equal (182 ± 66 imp/s during reaching as compared with 190 ± 72 imp/s during tracking).

The tracking task required the monkeys to maintain a cursor in a target zone that pseudorandomly shifted to one of three angular positions on a CRT monitor. The corresponding limb positions required 30–40° of joint flexion or extension relative to a middle position. Static periods of maintained limb holding separated dynamic periods of active movement between positions. Figure 5 shows unitary discharge during several successive tracking trials on the shoulder device. Steady limb holding postures were associated with maintained tonic discharge at rates that increased with more flexed joint angles. Movement about the shoulder joint elicited a brisk phasic modulation: flexion resulted in an increase in firing and extension in a decrease. All task-related units modulated in relation to the tracking movements; none were specifically related to the tracking display or to the delivery of reward.

Device specificity. Mossy fiber discharge showed a strong device specificity. Devices that evoked the strongest discharge were the shoulder (18), elbow (36), supinator/pronator (2), wrist (10), twister (1), and finger (13) devices. Figure 6 shows computer records from the same unit as is illustrated in Fig. 5 during tracking on all six devices. The strongest modulation in discharge occurred during operation of the shoulder device (*A* and *B*), and a more modest modulation was observed during operation of the elbow device (*C* and *D*). The unit was not related to movements on the supination/pronation (*E*), wrist (*F*), twister (*G*), and finger devices (*H*).

Table 2 summarizes the movement-related discharge of 31 units that were tested on two or more devices. Units are arranged according to preferred device, from proximal (shoulder, elbow, supinator/pronator) to distal (wrist, twister, finger). Mossy fibers were related to movements involving either proximal or distal joints: units whose preferred device was proximal revealed little or no modulation

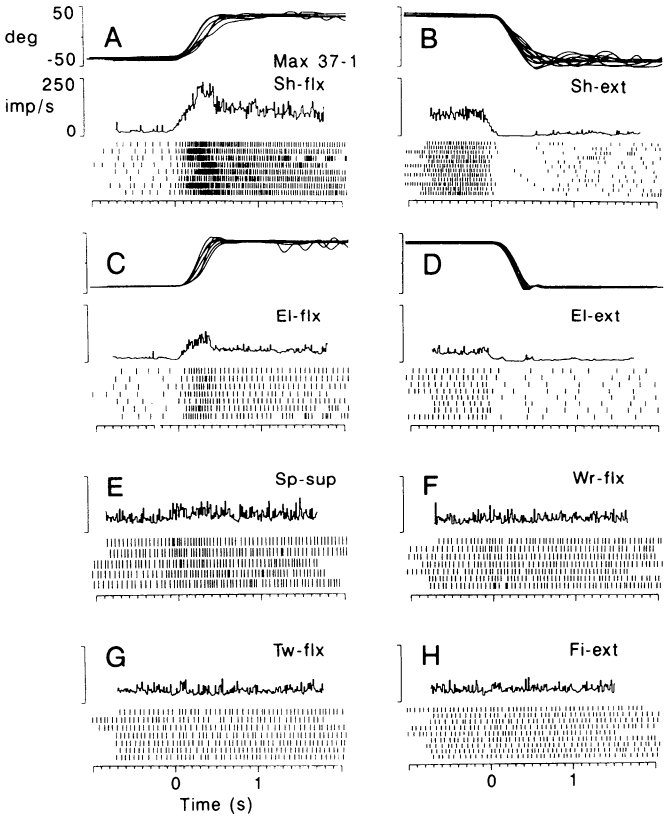

FIG. 6. Device specificity of mossy fibers. Discharge of the same unit during operation of 6 devices. This unit discharged strongest during operation of the shoulder device (*A* and *B*) and discharged to a lesser degree on the elbow device (*C* and *D*). The supination/pronation (*E*), wrist (*F*), twister (*G*), and finger device (*H*) were virtually ineffective in producing modulations in discharge. *A–D*: records of angular position (overplotted) and mean firing rate during flexion (*A* and *C*) and extension movements (*B* and *D*). In this and the following figures, records of angular position and spike frequency are from the trials displayed in the rasters, aligned on movement onset. Successive rows in the rasters represent individual trials illustrating repeatability of successive trials. For clarity, only every 3rd spike is plotted. *E–H*: average frequency records and rasters in the preferred direction only. The modulation in discharge during shoulder flexion followed movement onset by on average 104 ± 74 (SD) ms. flx, flexion; ext, extension; sup, supination; Sh, shoulder; El, elbow; Sp, supinator/pronator; Tw, twister; Fi, finger.

during operation of distal devices and vice versa. Most shoulder and elbow units modulated discharge on both devices, although modulation to one of the devices was clearly stronger. Finger units often modulated on the twister, and some modulated on the wrist device.

Discharge patterns. Mossy fibers were characterized by a great diversity of movement-related discharge patterns that ranged from purely tonic (Fig. 7, *A* and *B*) to purely phasic (Fig. 7, *G* and *H*), with various combinations of tonic and phasic discharge in between (Fig. 7, *C–F*). Although it seems convenient to classify units as tonic (n = 14, 18% of 80 units), phasic-tonic (n = 50, 63%), or phasic (n = 16, 20%), it should be emphasized that the discharge pattern of each unit was to some extent unique. The tonic discharge component of tonic and phasic-tonic units was significantly ($P < 0.01$) correlated to angular device position (see below). Discharge patterns of most units were reciprocal (n = 30, 45% of 66 units) or bidirectional (n = 28, 42%); eight (12%) units were unidirectional. A few units, included in the bidirectional category, increased discharge for movements in both directions but had different timing relations.

Figure 8 illustrates records collected from one unit during the six dynamic and the three static phases of the tracking task. Both the animal's behavior and the unit's phasic and tonic discharge were highly consistent from trial to trial, as is evident from the overplotted records of angular position and from the spike rasters for the individual trials. Records are aligned on movement onset. Discharge modulation to movements in opposite directions showed a strong reciprocity: elbow flexion was associated with an increase and a subsequent decrease in discharge, whereas the reverse was true for extension.

Tonic discharge. The most prominent feature of mossy fibers was tonic discharge dependent on joint angle. Sixty-four (80%) of 80 mossy fibers had discharge related to the angle of specific forelimb joints. Discharge was generally maintained for as long as the joint was held at a given position. When measurements of discharge taken immediately after a movement were compared with measurements taken ~4 s later (during the preperiod of the next trial), only 2 of 12 units revealed significant ($P < 0.01$) differences, and the differences were small (Fig. 12, *A* and *C*). Tonic discharge did not depend on the direction or velocity

TABLE 2. *Movement specificity of mossy fibers*

Unit	Shoulder	Elbow	Sup/Pro	Wrist	Twister	Finger
OSC 61-1	(++)	+			+/0	0
OSC 80-1	(++)	+			+/0	+/0
OSC 81-4	(++)	+			+/0	
OSC 83-4	(++)	+	+		+/0	+/0
OSC 92-1	(++)	+	+		0	+/0
MAX 32-1	(++)	+		0	0	0
MAX 37-1	(++)	+	0	0	0	0
BO 47-1	(++)	0				
BO 47-2	(++)	0			0	
OSC 71-1	+	(++)			0	0
OSC 78-2	+	(++)				
OSC 83-5	+	(++)				
OSC 96-2	+	(++)			0	0
OSC 96-5	+	(++)			0	
BO 6-3	0	(++)	0			
BO 21-1	+	(++)				
BO 23-2		(++)		0		0
BO 26-3	+/0	(++)	+/0	0		
BO 44-7	+/0	(++)				
BO 52-9	0	(++)				
BO 57-10	+	(++)				
BO 36-2		+/0	(++)			
BO 10-4		+/0		(++)		
BO 23-1	0	0	0	(++)	+	+
BO 53-5		+/0		(++)	0	
BO 27-2				0	+	(++)
BO 27-4				0	+	(++)
BO 36-4		0		+	+	(++)
BO 41-1	0	0	0	+	+	(++)
BO 50-2				+		(++)
BO 65-10	0	0				(++)

Modulation in discharge of 31 units during tracking on two or more devices. Units are arranged according to preferred device from proximal (*top*) to distal (*bottom*). Sup/Pro, supination/pronation; ++, strong modulation; +, clear modulation; +/0, weak or no modulation; 0, no modulation; no entry, not tested. Parentheses indicate device associated with strongest modulation.

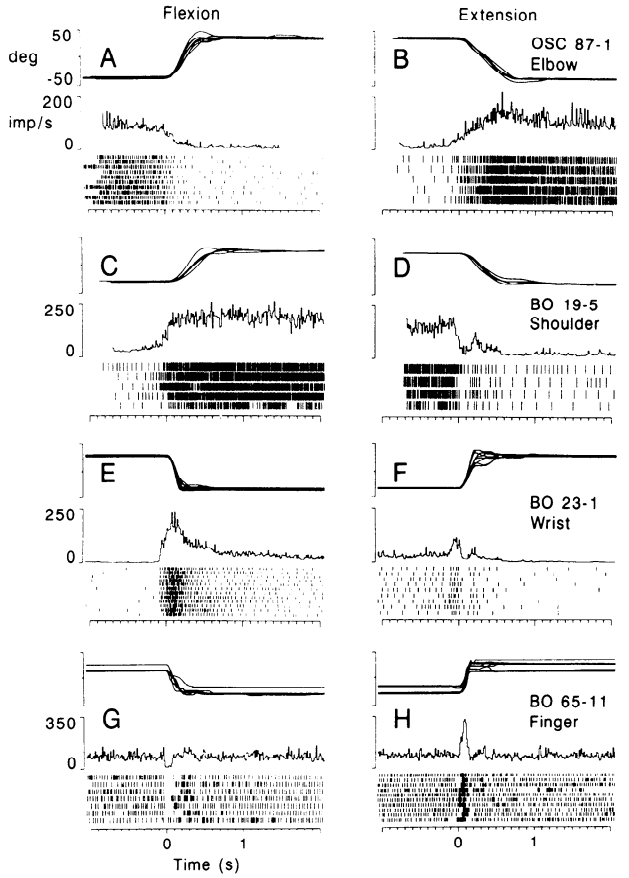

FIG. 7. Discharge patterns and timing relations of 4 mossy fibers during flexion (*A, C, E,* and *G*) and extension (*B, D, F,* and *H*) on the indicated devices. Units *OSC* 87-1 (*A* and *B*) and *BO* 19-5 (*C* and *D*) were classified as tonic, *BO* 23-1 (*E* and *F*) as phasic-tonic, and *BO* 65-11 (*G* and *H*) as phasic. Mean lead or lag times: *A*, −28 ± 31; *C*, 80 + 192 ms; *E*, 88 ± 20 ms; *H*, −19 ± 36 ms. Every 2nd spike is plotted in rasters for *OSC* 87-1 (*A* and *B*). For the other units, every 3rd spike is plotted.

of the movement that preceded or followed the holding position. Transitions between phasic and tonic components were usually sharp and coincided with movement termination.

The correlation between the tonic discharge and joint angle was estimated from scatter plots of rate versus angular position of the preferred device (Fig. 9). Sixty-four (80%) of 80 units showed significant ($P < 0.01$) correlations ($r = 0.65 \pm 0.19$). The slopes of the regression lines averaged 0.67 ± 0.55 imp $\cdot$ s^{-1} $\cdot$ deg^{-1}. Although rate/position relations for most units were well described by a linear regression, the data do not allow for a description of the precise function of the relation because most units were tested at only three positions. Rate/position relations for 8 of 10 units that were tested at five positions were well fitted by a straight line (correlations for the other 2 were not significant). A few units had clear nonlinear relations and modulated over a restricted range of positions (Fig. 9*D*). More units (42) increased discharge for more flexed than more extended (21) joint angles (1 unit for more supinated limb postures), but it is not clear whether this represents a real difference or a sampling bias.

Phasic discharge. Movement-related phasic discharge varied widely in time course, amplitude, and time of onset relative to movement onset. Phasic discharge of most units ($n = 62$, 94%) consisted of a single increase or decrease in discharge; four units had more complex discharge patterns that included biphasic or triphasic modulations. The amplitude of the phasic component was, for most units, larger than that of the tonic component, resulting in an overshoot that gradually decreased to the tonic level appropriate for the newly obtained limb position. The largest phasic components of phasic-tonic units were ~3 times as large as the tonic components. The phasic component of most units resembled the bell-shaped profile of movement velocity (Figs. 6*A*, 7*E*, 7*H*, and 12*A*), but phasic components of others (e.g., Fig. 12*E*) may also have been related to acceleration or the change in force.

Figure 10, *A–D* shows, for four units, scatter plots of discharge rate versus movement velocity. Twenty-five (31%) units showed significant ($P < 0.01$) rate/velocity relations on the shoulder (9), elbow (12), wrist (1), twister (1), and finger devices (2). The correlation coefficient averaged $r = 0.62 \pm 0.16$, and the average slope of the regression lines was 0.28 ± 0.18 imp/s per deg/s. Correlations for flexion and extension movements were of comparable strength. More units (19) showed correlations for flexion than extension (6) but, again, it is not clear whether the flexion bias represents a real difference or is due to uneven sampling.

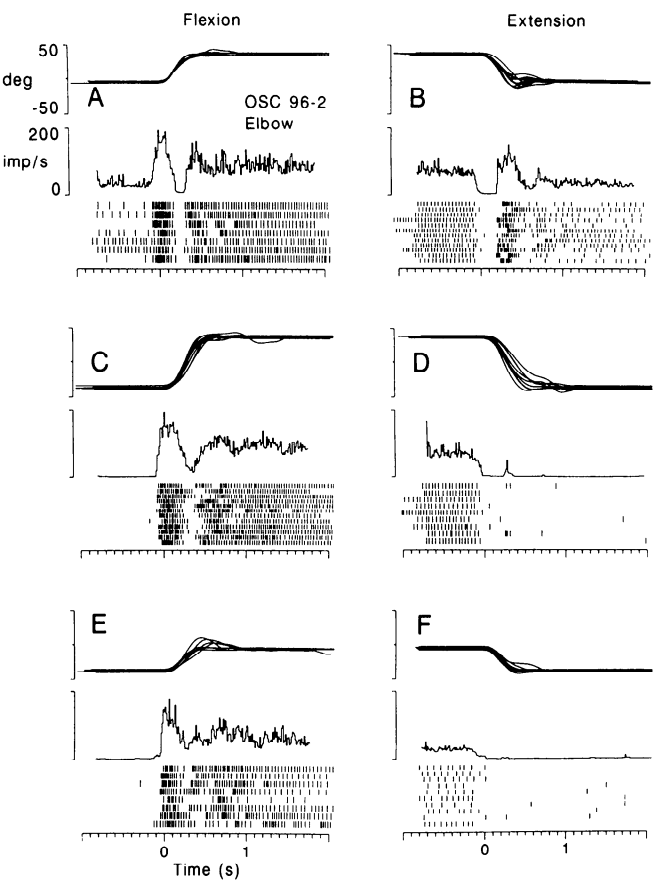

FIG. 8. Discharge of a phasic-tonic mossy fiber during elbow flexion (*A, C,* and *E*) and extension (*B, D,* and *F*). Flexion was associated with a triphasic modulation in discharge that was reciprocally related to that during extension. The discharge during flexion preceded movement onset by 92 ± 29 ms. Every 3rd spike is plotted in the rasters.

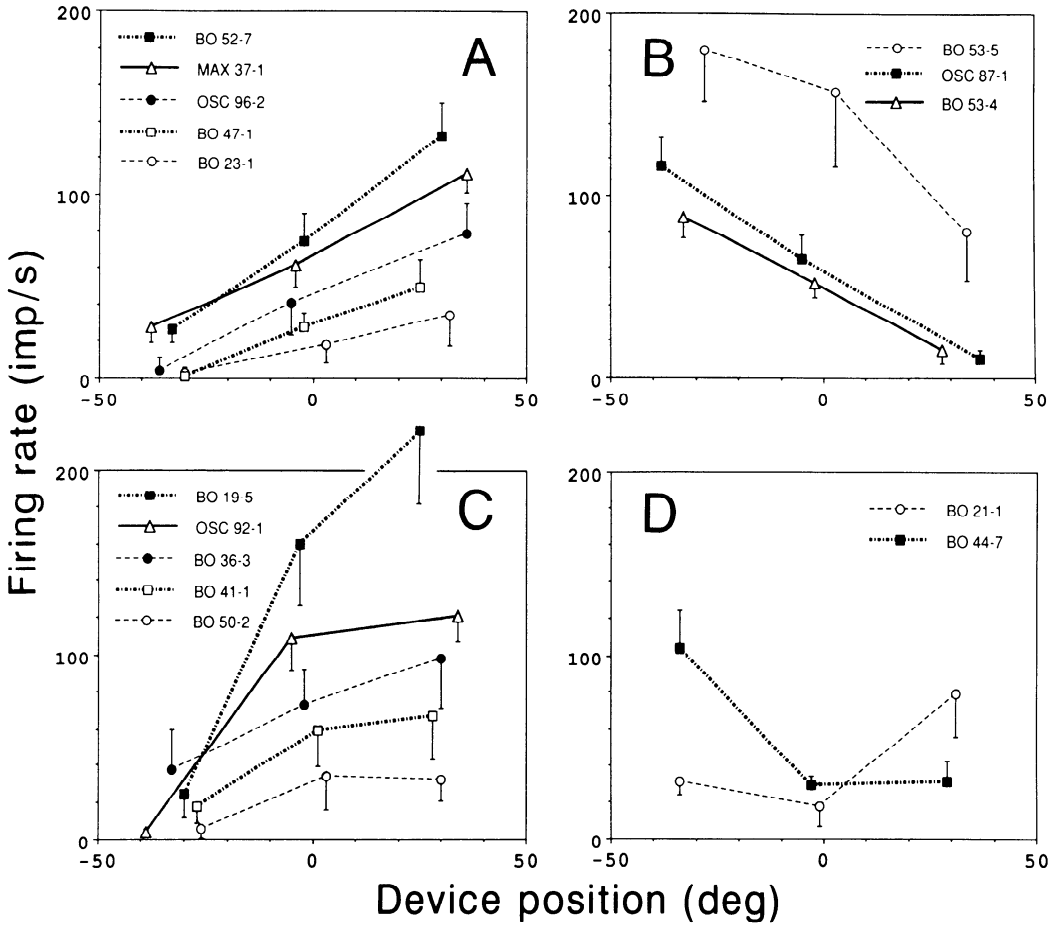

FIG. 9. Tonic discharge as a function of angular position of the preferred device for 15 mossy fibers. Relations for different units are plotted in 4 panels to minimize overlap between data points. Tonic discharge rates and angular device position were averaged over 400-ms intervals of steady limb holding. Each data point represents the average of 8–53 rate measurements. Error bars: 1 SDM. More flexed limb positions are plotted on the *right*. Correlations for the illustrated relations were statistically significant ($P < 0.01$), and the linear correlation coefficients ranged from 0.95 (*A*, *MAX* 37-1; *B*, *BO* 53-4) to 0.61 (*C*, *BO* 50-2).

The animal's limb, moving at a certain velocity, is also moving through a trajectory of an infinite number of positions. Given that units may carry both position and velocity signals, an accurate measure of the velocity component would require that the position component at a certain position be subtracted from the discharge rate as the limb passes through that position at different velocities. Figure 10*E* shows, for one unit, rate/velocity curves at different positions. Data pairs of discharge rate and movement velocity were taken at five joint angles equally spaced between the most extended and most flexed positions of the tracking task (see METHODS, *Part II*). Data pairs (Fig. 10*E*, crosses) obtained at two joint angles between the middle and most extended positions were pooled and subjected to regression analysis. The same was done for data pairs (Fig. 10*E*, diamonds) at two joint angles between the middle and most flexed positions of the tracking task. If the phasic and tonic components were independent features of the neuronal discharge pattern, the regression lines would be parallel to each other and the offset between them would reflect the difference in tonic firing at the different joint angles. This was found to be the case for 6 units tested; for the remaining 19, the number of data pairs was insufficient to establish additivity of phasic and tonic components.

The duration of the movement-related phasic component of all of 11 mossy fibers tested was significantly correlated ($P < 0.01$) with movement duration. The correlation coefficients averaged $r = 0.80 \pm 0.09$. The slopes of these relations were for most units close to unity, with an average value of 0.94 ± 0.26 and an average offset of 6 ± 93 ms, indicating that on average, the duration of the phasic component was approximately equal to the duration of the movement.

Timing of discharge and movement. There was considerable variability in the onset time of discharge modulation relative to the time of movement onset, both for successive trials of individual units and between units. Mean lead or lag times were calculated for each unit by averaging the difference of movement and discharge onset times for a number of similar movements on the preferred device in the direction that elicited the largest discharge modulation. Figure 11 shows that the distribution of the mean lead or lag time of the 80 units was symmetrical around zero (-8 ± 79 ms). Lead times for 21 (26%) units were statistically significant ($P < 0.05$) and averaged 80 ± 47 ms. Lag times were significant for 24 (30%) units and averaged -101 ± 47 ms. Significant cases are represented by the shaded areas of the histogram.

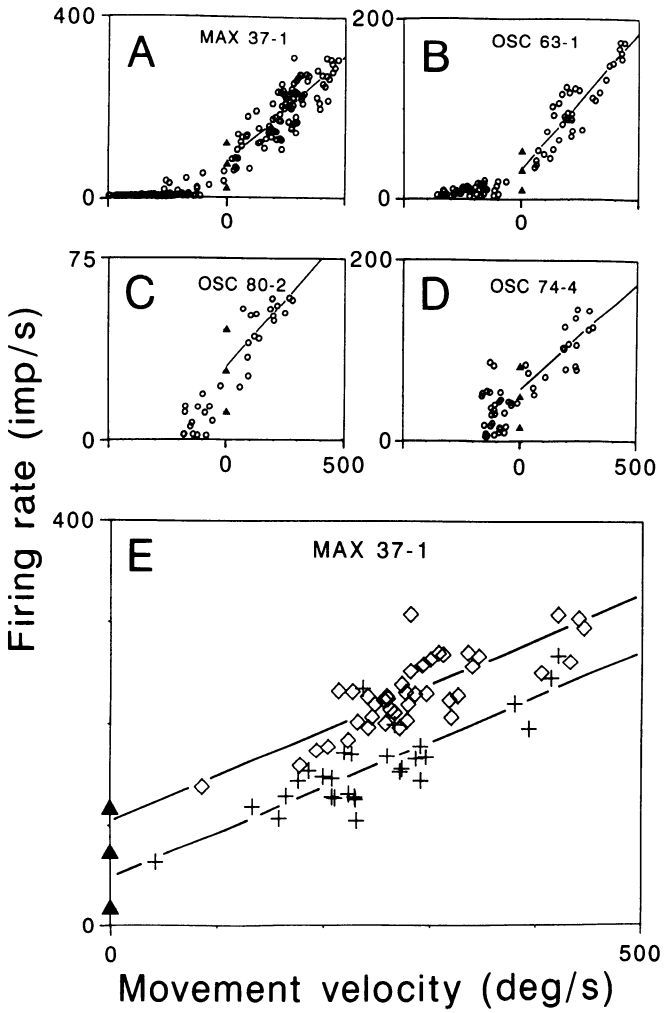

FIG. 10. Correlation between discharge and movement velocity. *A–D*: phasic discharge of 4 mossy fibers as a function of movement velocity. Each data point represents a pair of measurements obtained from an individual trial. Regression lines were calculated for movements in the on-direction only (positive movement velocities). Triangles (at 0 velocity): rates of tonic discharge for 3 limb holding positions. Correlations for the relations illustrated were statistically significant ($P < 0.01$), and the r values were 0.83 (*A*), 0.90 (*B*), 0.74 (*C*), and 0.70 (*D*). *E*: rate-velocity relations as a function of angular device position. The data illustrated were obtained from a single mossy fiber during operation of the shoulder device, and are a subset of those shown in *A*. Measurements obtained at the 2 positions between the most flexed and middle positions (see text) were pooled and are plotted as diamonds; measurements obtained between the middle and most extended positions were pooled and are plotted as crosses. Regression lines calculated for the 2 populations of data points are nearly parallel and are offset by approximately half the difference in tonic firing rates at the most flexed and most extended joint angles, indicating that tonic and phasic discharge components are relatively independent. Triangles on the y-axis: tonic firing rates at 3 limb holding positions. Linear correlation coefficients: 0.80 (diamonds) and 0.83 (crosses), both statistically significant ($P < 0.01$).

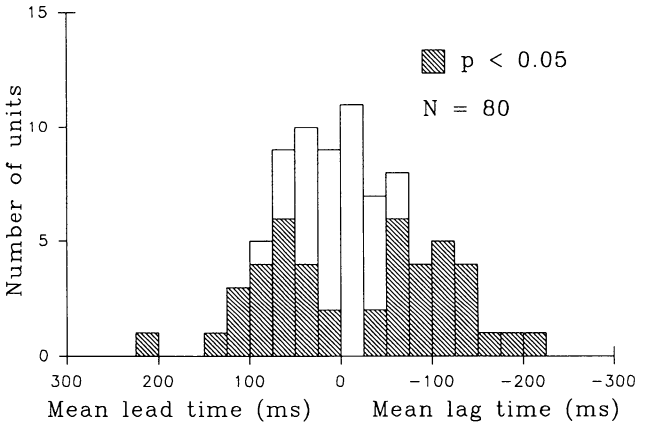

FIG. 11. Distribution of mean lead and lag times for 80 mossy fibers. Measurements of the difference between movement and discharge onset times were averaged for 3–14 movements on the preferred device in the direction that was associated with the largest discharge. Units with statistically significant ($P < 0.05$) lead and lag times are shaded.

MOSSY FIBER DISCHARGE RELATED TO PASSIVE MOVEMENT. Sensory responsiveness was evaluated for 29 of 80 movement-related mossy fibers. Sixteen units were studied by manually moving joints through their normal ranges of motion, and 24 units were studied by perturbing device position during limb holding phases of the tracking task (see METHODS, *Part II*).

Responses to manipulation of joints. All of 16 units tested revealed modulations in phasic and tonic discharge that were related to movement and holding positions of the elbow (5), wrist (5), or metacarpophalangeal joints (6). For a given unit, discharge modulation to active and passive movements involved the same joint. Units that responded to passive manipulation of joints usually responded to stimuli such as low pressure or gentle taps on the appropriate muscle bellies, thereby suggesting that they received input from muscle receptors. Receptive fields of some units were contained within individual muscles, such as biceps or triceps; receptive fields of others appeared to consist of groups of synergistic muscles.

The modulations in discharge of 12 (75%) of 16 units to active and passive movement in a given direction were of the same polarity, and they were of comparable amplitude. In one case, we found that a unit related to elbow movement responded to palpation of triceps, suggesting that the increase in discharge during active and passive flexion of the elbow was due to passive stretch of triceps muscle receptors. However, in another case, a unit that increased discharge during active and passive elbow flexion responded to palpation of biceps. Four (25%) units showed modulations in discharge that were of opposite polarity for comparable active and passive movements.

Although we did not routinely search for mossy fibers with cutaneous receptive fields, in two cases, cutaneous units were encountered and then tested for movement relations. One unit had a receptive field that was restricted to the dorsal surface of the thumb and responded phasically to touch and gentle taps. Operation of the finger device elicited phasic modulations that averaged ~50 imp/s for movements in either direction; however, inspection of individual trials revealed that bursts of discharge were produced by device contact. The other unit responded phasically to bending hairs of the ventral surface of the forearm and was only occasionally modulated during tracking or reaching movements.

Responses to perturbations. Twenty-four units were tested by perturbations of the angular position of the shoulder (5), elbow (10), wrist (3), and finger (6) devices. Twenty (83%) of these responded to perturbations. Response latency averaged 41 ± 27 ms. Seventeen (85%) of

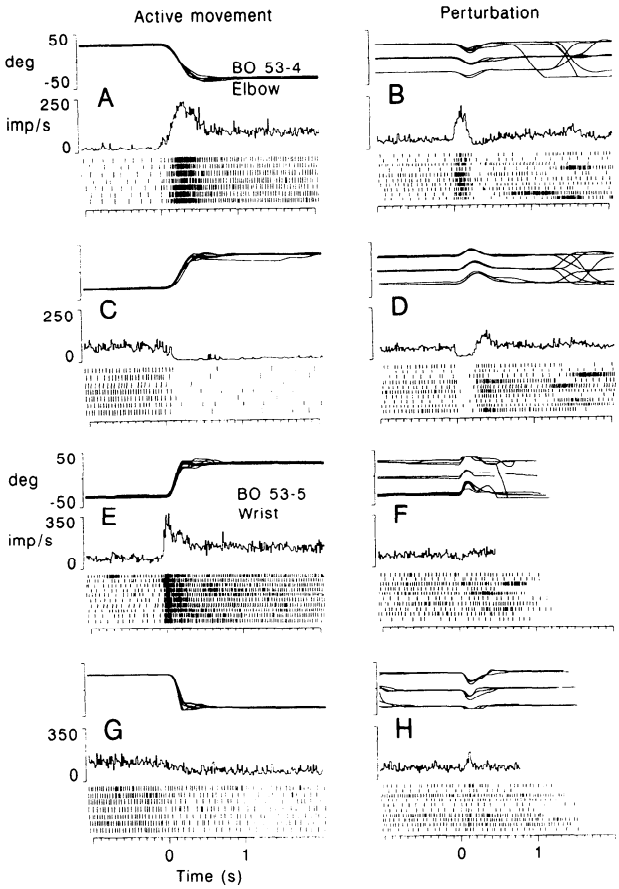

FIG. 12. Sensory responsiveness of mossy fibers. *A–D*: discharge of a single mossy fiber during active elbow extension (*A*) and flexion (*C*) is compared with discharge during perturbations in the extension (*B*) and flexion (*D*) directions. Perturbation responses during passive movement in a given direction were of the same polarity and were of similar amplitude as the modulations in discharge during active movement. Perturbations were produced by a torque motor mounted on the device arm, and perturbation onset corresponds to time 0. *Top* records: device position, overplotted for the trials included in the rasters. The changes in device position subsequent to the perturbations are due to active movement. Every 3rd spike is plotted in the rasters. *E–H*: discharge of a single mossy fiber during active finger extension (*E*) and flexion (*G*) is compared with discharge during perturbations in the extension (*F*) and flexion (*H*) directions. Perturbations were produced manually by the experimenter. For a given direction of movement, the perturbation responses and the modulations in discharge during active movements were of opposite polarity. The modulation in discharge. Modulation in discharge was bidirectional for operation of all 6 devices. In the rasters of this figure and Figs. 14 and 15, every spike is plotted.

the 20 responsive units responded to comparable active and passive movements with modulations in discharge that were of the same polarity; 3 showed modulations of opposite polarity.

Perturbation responses of 12 (60%) of 20 units were reciprocal: perturbations in one direction evoked an increase in discharge, and perturbations in the opposite direction evoked a decrease. Five (25%) units increased firing to perturbations in either direction, and three (15%) increased discharge to perturbations in only one direction with no response in the other. Figure 12 compares, for two units, discharge during active movements with perturbation responses. The unit illustrated in *A–D* discharged reciprocally to active movements and to perturbations about the elbow.

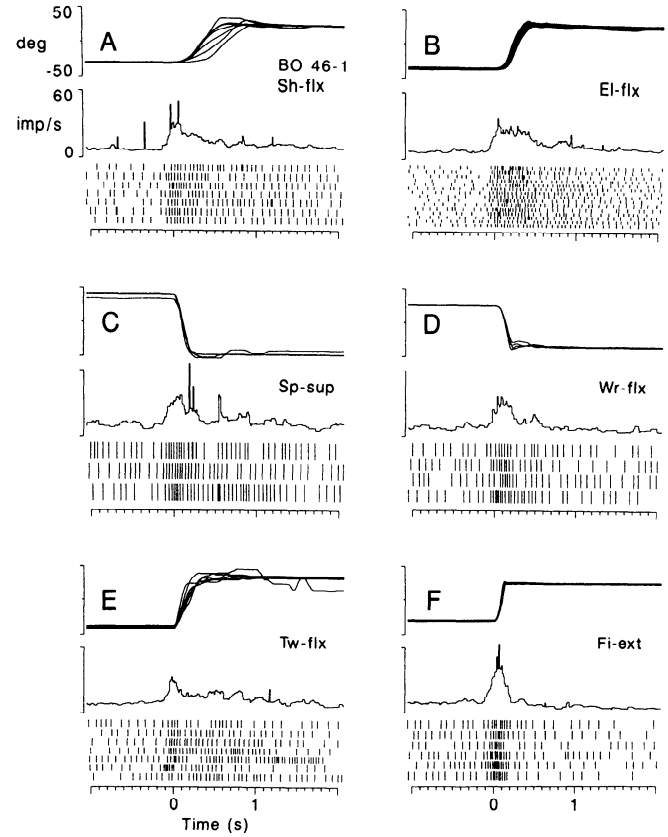

FIG. 13. Discharge of a Golgi cell during operation of 6 forelimb devices. The direction of movement shown was associated with the largest modulation in discharge. Modulation in discharge was bidirectional for operation of all 6 devices. In the rasters of this figure and figs. 14 and 15, every spike is plotted.

The modulations in discharge associated with perturbations (*B* and *D*) and active movements (*A* and *C*) in a given direction were of the same polarity and were of comparable magnitude. The unit illustrated in *E–H* showed a large increase in discharge with active extension of the metacarpophalangeal joints (*E*), but the perturbation response consisted of a small decrease in discharge (*F*). Active flexion (*G*) elicited little or no modulation, whereas perturbations resulted in a modest increase in discharge (*H*).

DISCHARGE OF GOLGI CELLS. We studied 12 Golgi cells related to forelimb movements. Their movement relations were qualitatively different from those of mossy fibers in

TABLE 3. *Movement specificity of Golgi cells*

Unit	Shoulder	Elbow	Sup/Pro	Wrist	Twister	Finger
BO 53-1	(++)	+				0
BO 49-6		(++)			+	++
MAX 13-5	++	(++)		0		0
BO 24-1	+			(++)		++
BO 22-1					++	(++)
BO 46-1	++	++	+	+	+	(++)
BO 47-4				0	+	(++)
BO 63-17		+		+		(++)

Modulation in discharge of 8 cells during tracking on two or more devices. Sup/Pro, supination/pronation; ++, strong modulation; +, clear modulation; +/0, weak or no modulation; 0, no modulation; no entry, not tested. Parentheses indicate device associated with strongest modulation.

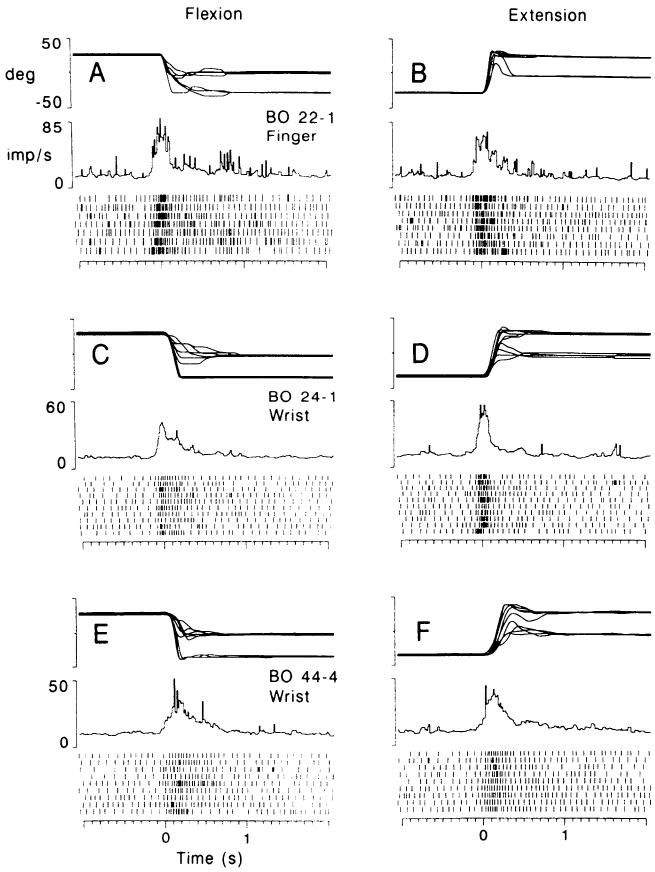

FIG. 14. Bidirectional discharge patterns and timing relations of 3 Golgi cells during flexion (*A, C*, and *E*) and extension (*B, D*, and *F*) movements on the indicated devices. Mean lead or lag times: *A*, 81 ± 36 ms; *B*, 61 ± 43 ms; *C*, 51 ± 26 ms; *D*, 78 ± 20 ms; *E*, −21 ± 22 ms; *F*, 5 ± 37 ms.

several respects: they did not show a tonic discharge that was dependent on joint angle, they lacked device specificity, and their average maintained discharge in the absence of movement was uniformly low (10 ± 4 imp/s) and regular. Golgi cells often discharged equally well during operation of more than one device (Fig. 13). Table 3 compares the movement-related discharge of eight cells during tracking on two or more devices. Cells are arranged according to preferred device, from proximal at the *top* of the table to distal at the *bottom*. Discharge of four of six cells tested on at least one proximal (shoulder, elbow, supinator/pronator) and one distal (wrist, twister, finger) device was modulated to both. Eight Golgi cells were bidirectional and four unidirectional. Figure 14 shows discharge patterns of three bidirectional units. Four cells had significant mean lead times (72 ± 15 ms) and none had significant mean lag times.

All of five Golgi cells tested responded phasically to manipulation of joints and to mechanical disturbances of device position (Fig. 15). Unitary discharge involved the same joints during active and passive movements, and in all cases, responses to passive movement and perturbations in a given movement direction were of the same polarity and amplitude as the modulation in discharge during active movement (i.e., responses to passive movement and perturbations were also bidirectional). The prominent responsiveness to passive movement in awake animals contrasted with its relative absence in anesthetized animals.

DISCUSSION

The results from two series of experiments are reported in this paper. The first series establishes criteria for identifying mossy fiber potentials; these criteria are then applied in a second series of experiments to study movement-related inputs to the intermediate cerebellar cortex of awake monkeys. Our findings indicate that mossy fibers transmit position and velocity information about specific joints and suggest that this information may derive from both sensory and efference copy signals. Golgi cells transmit relatively nonspecific movement-related information.

We begin with a brief discussion of the criteria for identifying units, which is then followed by a consideration of the possible origins of movement sensitivity in mossy fibers. Then we contrast the input properties reported in this paper with the output properties that were described in the previous paper (Van Kan et al. 1993). This comparison provides a basis for discussing information processing steps that are likely to occur within the intermediate cerebellum.

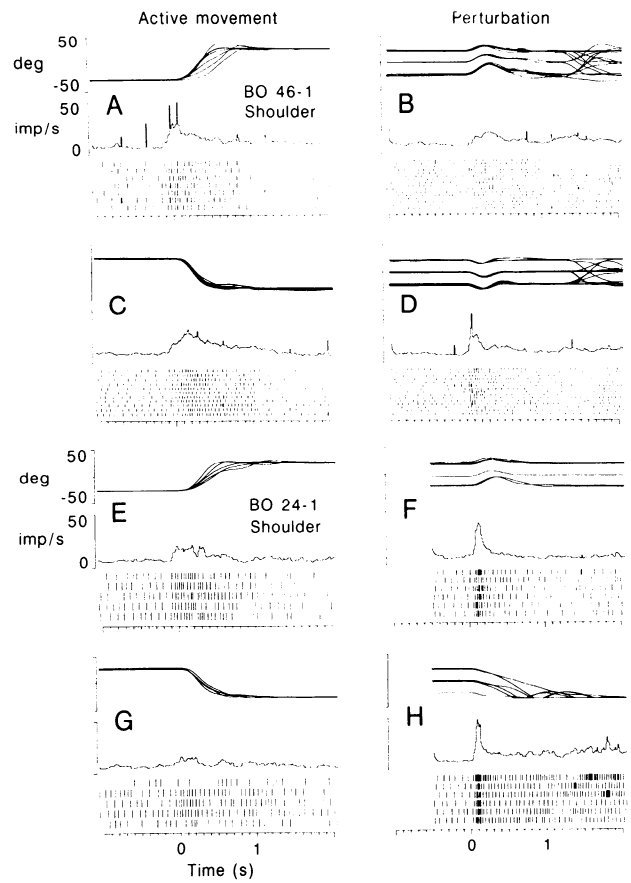

FIG. 15. Sensory responsiveness of Golgi cells. *A–D* and *E–F*: discharge of 2 cells during active shoulder flexion (*A* and *E*) and extension (*C* and *G*) is compared with discharge to perturbations in the flexion (*B* and *F*) and extension (*D* and *H*) directions. Perturbation responses for movements in a given direction were of the same polarity as the modulations during active movement. Perturbation responses of the cell shown in *A–D* were of similar amplitude as the modulations in discharge during active movement, and perturbation responses were larger for the cell shown in *E–H*.

Criteria for identification of granular layer neurons

The control studies in anesthetized cats and monkeys support the use of a two-step procedure for identifying granular layer potentials. The first step, an identification of the layer of the cerebellar cortex, utilizes a variety of criteria in addition to the usual reliance on complex spikes produced by climbing fiber inputs to Purkinje cells. Three additional criteria were found especially useful: *1*) a variety of waveshapes other than complex spikes, *2*) the degree of background activity, and *3*) constraints on the sequence of successively recorded layers imposed by the uniformity of the cerebellar cortex. Histological reconstruction of electrode tracks and marking lesions confirmed the validity of these criteria.

Once the granular layer is identified, the type of neuronal element responsible for a given potential can be determined by the waveshape of its unitary potential. Granular layer elements that might give rise to unitary potentials include granule cells, mossy fiber terminals, three categories of myelinated fibers (mossy and climbing fibers and Purkinje cell axons), and Golgi cells. Although granule cells are the most common anatomic elements of the granular layer, isolated granule cell potentials could not be demonstrated in earlier studies of the turtle cerebellum (Walsh et al. 1974). The currents generated by the small (0.2 μm) initial segments may be too small to generate isolated unitary potentials that can be recorded with tungsten microelectrodes. However, it would not be surprising for mossy fiber terminals to be recorded reliably because they are both numerous and of substantial size (Krieger et al. 1985; Mugnaini et al. 1974).

Asynaptic activation from the peduncle identifies a unit as either a mossy or climbing fiber, because Purkinje axons from intermediate cerebellar cortex do not pass beyond the cerebellar nuclei (Brodal 1981) [also, no asynaptic unit showed a pause in discharge resembling a Purkinje cell's pause in simple spikes after a complex spike (Thach 1968)]. Differentiation between mossy and climbing fibers is readily made on the basis of the unit's discharge pattern, because climbing fibers only fire at low rates (Thach 1968). Asynaptic activation verified that cat and monkey mossy fibers, like those of turtles (Walsh et al. 1974), produce four distinct waveshapes of extracellular potential: *1*) a triphasic potential, *2*) a biphasic potential, *3*) a biphasic potential followed by a NAW (also called a glomerular potential), and *4*) a predominantly positive potential. The observed variety in waveshape has been attributed to recording from different sites along the mossy fiber (Walsh et al. 1974), and compatible descriptions of mossy fiber potentials have been reported by others (Bourbonnais et al. 1986; Kase et al. 1980; Lisberger and Fuchs 1978; Miles et al. 1980; Taylor et al. 1987). Comparing sensory response properties of units in anesthetized and awake animals provides additional support for the identification of mossy fibers in awake animals, because many identified mossy fibers in the anesthetized preparations showed tonic discharge dependent on joint angle, as was found in the awake animals.

The identification of Golgi cells is based on multiple criteria. The extracellular potentials that we attributed to Golgi cells were encountered much less frequently than mossy fibers and never occurred in groups, which is consistent with their sparse distribution in the granular layer. They were never activated asynaptically from the peduncle, and their broad negative-positive or positive-negative waveshapes and greater tuning distances contrasted with the brief potentials and short tuning distances of mossy fibers. Moreover, their low and regular firing rates differed from the higher and more irregular mossy fiber discharge. These criteria are similar to those used by others (Edgley and Lidierth 1987; Marple-Horvat and Stein 1987; Miles et al. 1980; Schulman and Bloom 1981; Walsh et al. 1974), and they do not rule out the possibility that some neurons may have been intermediate Lugaro cells or other medium-to-large neurons in the granular layer, although these are much less common than Golgi cells (Fox 1959).

Movement-related mossy fibers

Four fifths of the movement-related units discharged tonically at rates that were correlated with limb position, and phasic components were superimposed on most of these. The remaining units were entirely phasic. In this section, we first consider evidence that phasic and tonic discharge components may derive from a combination of sensory and efference copy origins, and then we review the pathways via which these signals may reach the cerebellar cortex.

MOSSY FIBER PROPERTIES. Sensory responses were demonstrated in 26 (90%) of 29 units tested. Responses to joint rotation typically showed both phasic and tonic components. Perturbations of device position during periods of limb holding produced prominent phasic responses that in some cases equaled the phasic discharge component during active movement. Sensory responses could have their origins in muscle, joint, or skin receptors. However, among the units that were consistently related to tracking movements, none responded to low-threshold cutaneous stimulation. Units with cutaneous input were not specifically sought, and when occasionally encountered, they showed more variable relations to the tracking movements. The units tested for sensory responses also failed to respond to pressure applied directly to joints and did not respond selectively to extreme flexion or extension, arguing against input from joint receptors (Clark et al. 1989). In contrast, many units that were activated strongly and tonically by passive joint rotation also showed responses to gentle pressure and light taps on muscle bellies in the absence of joint movement. These characteristics suggest that their main sensory input derived from muscle receptors (Campbell et al. 1974).

The observed correlations between tonic discharge and joint angle resemble those reported for mossy fibers during passive wrist movement in awake monkeys (Bauswein et al. 1984) and decerebrate cats (Kolb et al. 1987b). The generally consistent relations between tonic discharge and absolute limb position are likely to derive mainly from tonic sensory inputs, although some may derive from tonic efference copy signals. Tonic efference copy signals might originate from central sensorimotor neurons (Cheney and Fetz 1980; Fetz et al. 1980; Soso and Fetz 1980), or they may be obtained by mathematically integrating phasic efference copy signals. If the latter is the case, it is probably only true

for a small number of units, because most units fired in a similar fashion to both active and passive movement, which would not be expected if tonic discharge resulted from integration of efference copy.

Some features of the discharge did appear to derive from efference copy input, or they may reflect combinations of efference copy and sensory signals. Although this is to be expected from what is known about the various mossy fiber pathways (reviewed later), the actual evidence for efference copy in the present data is mainly indirect. The strongest evidence is the finding that a few units fired at high rates during active movement and failed to respond at all to passive movement or showed modulations in discharge of the same polarity to active and passive movement in opposite directions. Efference copy signals alone or in combination with sensory signals are likely explanations for these properties. Given a sufficient strength of fusimotor coactivation, muscle spindles could also discharge during active contraction and passive stretch of their muscle (Vallbo 1971), although this too would be a form of efference copy.

A second line of evidence for efference copy is based on the timing of the movement-related discharge. Although the timing varied considerably, both between trials for individual units and between units, about one fourth of units showed significant lead times (Fig. 11*B*). The distributions of the onset times of interpositus (Fig. 5*C* in Van Kan et al. 1993) and magnocellular red nucleus discharge (Fig. 7 in Gibson et al. 1985a) in the same task may be used to estimate the relative timing of efference copy signals. Interpositus sends a powerful input to both the rubrospinal and corticospinal pathways, and it is likely that both pathways provide efference copy inputs to pontine and reticular sources of mossy fibers. The distributions of lead times of interpositus and magnocellular red nucleus neurons are largely overlapping, and the peak of the distributions occurs ~100 ms before the peak of the distribution of mossy fiber onset times. This is clearly early enough for most interpositus and red nucleus neurons to influence the onset time of most mossy fibers. Interpretation of discharge modulations that precede movement as reflecting central influences must be done cautiously, however, because electromyographic (EMG) activity of some muscles may lead movement onset by as much as 200 ms (Fortier et al. 1989), and many dorsal root ganglion units are activated before their target muscles (Flament et al. 1992, but see Vallbo 1971). Also, some units may receive input from synergistic muscles that are not directly involved in movement of a particular joint but may be activated well before movement onset. For example, certain axial or distal muscles could be coactivated with the flexor and extensor muscles involved in movement about the elbow for the purpose of stabilizing the limb.

The mossy fibers that lagged movement probably represent sensory feedback, although some of the lag times are considerably longer than the delays anticipated in sensory pathways. The short lags could represent delayed spindle receptor responses (and short leads could be explained by Golgi tendon organ input) because muscle activation is estimated to precede movement by ~80 ms in the tracking tasks used here (Gibson et al. 1985a).

The temporal features of the movement-related discharge also suggest that some units receive efference copy. Some phasic-tonic units showed biphasic or triphasic fluctuations (e.g., Fig. 8), which are atypical of published receptor responses and better resemble the discharge patterns of central sensorimotor neurons (Fig. 12*A* in Kalaska et al. 1989; Figs. 3 and 6 in Soso and Fetz 1980; Fetz et al. 1989) and muscles (Fig. 1*C* in Fortier et al. 1989). On the other hand, efference signals recorded from magnocellular red nucleus and interpositus neurons are either entirely phasic (Gibson et al. 1985a,b; Van Kan et al. 1993) or are dominated by phasic components (Cheney et al. 1988), and many magnocellular red nucleus and interpositus neurons that showed consistent discharge during device use showed strong correlations between discharge rate and movement velocity (Gibson et al. 1985b; Van Kan et al. 1993). These signals could be the origin of the purely phasic discharge or of the phasic components of phasic-tonic units and may account for the velocity sensitivity found for about one third of mossy fibers. If this is the case, the signals would provide predictive information about intended movements.

MOSSY FIBER PATHWAYS. The experimental evidence suggests that movement-related mossy fibers carry both sensory and efference copy signals. Several studies indicate that different pathways may be specialized for supplying the cerebellum with this information. The most direct pathway providing sensory input from the forelimb is the cuneocerebellar tract, which originates from the external cuneate nucleus (ECN) and terminates in forelimb areas of cerebellar cortex (Cooke et al. 1971a,b; Gerrits et al. 1985; Grant 1962; Jasmin and Courville 1987a,b). ECN neurons, like their hindlimb equivalents, the neurons of the DSCT, receive input from muscle receptors (Abrahams and Swett 1986; Jasmin et al. 1985; Nyberg and Blomqvist 1984) and resemble mossy fibers in sensory responsiveness (Bourbonnais et al. 1986; Campbell et al. 1974; Horn et al. 1989; Jansen and Rudjord 1965; Johnson et al. 1968; Wei et al. 1984). The joint angle and velocity correlations of mossy fibers directly relate to the correlations between tonic response and amplitude of muscle stretch and between phasic response and stretch velocity that have been reported for ECN and DSCT neurons (Bourbonnais et al. 1986; Jansen and Rudjord 1965; Jansen et al. 1966).

The RSCT, which originates from cell groups in the cervical enlargement of the spinal cord (Hirai et al. 1976; Matsushita and Ikeda 1987; Oscarsson and Uddenberg 1964; Wiksten 1985; Wiksten and Grant 1986), is another potential input pathway. However, these afferents terminate predominantly in medial rather than intermediate cerebellar cortex (Matsushita and Ikeda 1987), show phasic rather than tonic responses to muscle stretch (MacKay and Murphy 1974), and receive extensive convergence from both distal and proximal muscle groups and flexor reflex afferents (Hirai et al. 1976; Oscarsson 1965). Therefore, it seems unlikely that many of the mossy fibers included in this study derived from the RSCT.

Movement-related mossy fibers might also arise from the lateral reticular nucleus (LRN) which may relay efference copy signals or mixtures of sensory and efference copy signals. LRN neurons receive input from the red nucleus (Courville 1966; Edwards 1972; Robinson et al. 1987) and

motor cortex (Brodal et al. 1967; Wiesendanger and Wiesendanger 1987), perhaps via rubrospinal and corticospinal collaterals (Zangger and Wiesendanger 1973, but see Alstermark and Lundberg 1982). LRN neurons also receive from *C3–C4* propriospinal neurons, which would convey efference copy signals (Alstermark et al. 1981a; Illert and Lundberg 1978). Direct evidence for efference copy in the discharge of LRN neurons has been reported by Arshavsky et al. (1978), who showed that during fictive scratching, when there is no afferent inflow from limb receptors, discharge is related to rhythmic activity in motoneurons. On the other hand, responses to muscle stretch (MacKay and Murphy 1974) and passive joint rotation (Marini and Wiesendanger 1987) may reflect sensory input to LRN neurons via cuneocerebellar collaterals (Burton et al. 1971, but see Ekerot and Oscarrson 1976).

Similar properties are to be expected of pontine sources of mossy fibers. Pontine neurons receive inputs from sensorimotor cortex (Brodal 1978; Glickstein et al. 1985) and show tonic and phasic-tonic discharge patterns and a range of onset latencies (Matsunami 1987) similar to those of mossy fibers. Cerebral cortical neurons receive substantial input from muscle afferents (Wiesendanger 1973; Wise and Tanji 1981) and resemble the mossy fibers of our sample in movement specificity (Kwan et al. 1978) and discharge patterns (Fetz et al. 1980; Hoffman and Luschei 1980; Kalaska et al. 1989; Lemon et al. 1976; Soso and Fetz 1980). Thus pontine mossy fibers might convey signals with both sensory and efference copy components.

Another potential source of movement-related mossy fibers is the nucleocortical projection (Tolbert et al. 1977, 1978). Some mossy fibers might be collaterals of interpositus efferents; however, our results provide no evidence for this because we did not encounter units with the same movement-related properties as interpositus neurons (Van Kan et al. 1993).

In summary, it seems likely that the observed properties of movement-related mossy fibers derive from multiple sensory and efference copy sources, which provide information about both intended and actual movements.

Information processing within the intermediate cerebellum

Comparison of signals that enter and leave the intermediate cerebellum should help to specify the information processing steps that take place within this structure. The present paper describes movement-related features of mossy fiber inputs to the intermediate cerebellum, and the previous paper (Van Kan et al. 1993) describes these features for the outputs via the interpositus nucleus. The combined data are particularly valuable for comparative analysis because the results were obtained using the same behavioral apparatus and very similar protocols and, in many cases, mossy fibers and interpositus neurons were recorded in the same animals, sometimes along the same microelectrode penetrations. In Table 4 we list the most striking differences in movement-related properties of mossy fibers and interpositus neurons.

TABLE 4. *Comparison of mossy fibers and interpositus neurons*

	Mossy Fibers	Interpositus Neurons
Joint specificity	High	Low
Discharge pattern	Tonic (Position)	Phasic (Velocity)
Reach versus device	Reach = Device	Reach ≫ Device
Sensory responsiveness	Often	Rare

GENERATION OF VELOCITY COMMANDS. The strong limb position signals, which are the dominant feature of the movement-related cerebellar inputs, differ remarkably from the phasic signals of cerebellar outputs: none of our interpositus neurons showed tonic discharge that was dependent on position, which is in general agreement with the results of others (Chapman et al. 1986; Harvey et al. 1979; MacKay 1988a,b; Thach 1978). Purkinje cells also lack position-dependent tonic discharge (Armstrong et al. 1973; Bauswein et al. 1983; Frysinger et al. 1984; Kolb et al. 1987a; Mano and Yamamoto 1980; Marple-Horvat and Stein 1987; Thach 1970). Only a few exceptions are reported by Marple-Horvat and Stein (1987) and by Frysinger and colleagues (1984), but in all cases the differences in tonic discharge for the different positions were small and averaging of many trials was required to reveal the effect. Instead, Purkinje cells modulate phasically during forelimb movement and appear to signal movement velocity (Frysinger et al. 1984; Harvey et al. 1977; Mano and Yamamoto 1980; Marple-Horvat and Stein 1987). At least some interpositus and magnocellular red nucleus neurons showed strong correlations between discharge rate and movement velocity. The neurons are relatively insensitive to sensory input (Gibson et al. 1985a; Harvey et al. 1979), frequently commence firing before onset of EMG activity or movement, and predict the velocity, duration, and direction of specific movements (Gibson et al. 1985b; Van Kan et al. 1993). Together these properties suggest that the output of intermediate cerebellum is a velocity motor command. It is likely that a system generating velocity commands would require information about current limb position to adjust the duration of the motor signal that is required to generate a movement of the correct amplitude. Movement-related mossy fibers may well provide such information.

Because movement amplitude can be specified as the difference between the initial position of the limb and a desired final position, duration may be computed as

$$\text{Duration} = \frac{\text{Desired Final Position} - \text{Initial Position}}{\text{Commanded Velocity}}$$

Mossy fibers may provide information about the initial position of the limb, but our results provide no direct evidence as to how desired final positions might be specified. One possibility is that the desired final limb position may be specified by the tracking display, because the display specified the amplitude and direction of the required movement. Therefore, we anticipated discovering mossy fibers that discharged in relation to the tracking display, but none were found. This suggests that target information may be specified in a more processed manner. Such signals would be expected to lead movement onset but need not be time-locked to the tracking display. It is possible that some of the position signals we recorded specified targets in motor coordinates (e.g., Fig. 7*C*), thus commanding rather than monitoring limb position. The long lead times seen for about one

fourth of the population are compatible with this interpretation. This interpretation is also compatible with Stein's (1986) suggestion that the intermediate cerebellum is not the site where targets are selected and converted into motor coordinates but, instead, is more concerned with the implementation phase of movement.

Sensory responsiveness also seems to be lost, or markedly attenuated, at early stages of cerebellar processing. Most movement-related mossy fibers showed strong sensory responses, which are also apparent in Golgi cells (in awake animals). On the other hand, both Purkinje (Harvey et al. 1977) and nuclear cells (Harvey et al. 1979; but see Strick 1983) exhibit little responsiveness to sensory tests similar to the ones we performed on mossy fibers. Although we did not emphasize tests of sensory responsiveness in our study of interpositus neurons, our findings are consistent with a relatively low degree of sensitivity [1 of 8 neurons tested was responsive (Van Kan et al. 1993)]. The thalamic (Horne and Porter 1980; Strick 1976) and rubral (Gibson et al. 1985a,b) targets of interpositus outputs are also relatively insensitive to sensory stimulation. The limited sensory responsiveness of Purkinje and interpositus neurons and their downstream targets contrasts with the intense discharge accompanying active movement.

Although it seems intuitively clear that sensory information is used to formulate movement commands, the experimental evidence suggests that continuous sensory feedback is hardly used, if it is used at all, to shape the time course of these commands (Bizzi et al. 1976; Gibson et al. 1985b; Harvey et al. 1977, 1979). Instead, the cerebellum may use sensory inputs to preselect and initiate motor programs with appropriate movement parameters that are then executed in a feedforward manner (Houk 1989).

On the other hand, the information we found present in mossy fiber inputs about ongoing movements could be useful for feedback control of velocity commands. A computational scheme has been suggested whereby velocity commands would be initiated in a feedforward fashion and continue until evidence accumulates that the desired final position is imminent. At this point feedback would be used momentarily to switch off the command (Houk et al. 1990).

SPATIAL COORDINATION. The high discharge rates seen in the reaching and grasping task for mossy fiber inputs (present results) and for interpositus nucleus outputs (Van Kan et al. 1993) underscore the importance of the intermediate cerebellum in controlling multijoint hand and limb movements. However, mossy fibers and interpositus neurons discharged quite differently during the more isolated movements elicited by the tracking task. Mossy fibers modulated as strongly when the animal operated the preferred device in the tracking task as during reaching and grasping, and there was relatively little modulation in discharge on devices exercising motion about alternative joints. In other words, mossy fiber inputs discharged during relatively isolated single-joint movements with high sensitivity and considerable selectivity. In contrast, interpositus neurons showed appreciably smaller modulations on the tracking devices as contrasted with reaching and grasping, and they lacked device specificity. Thus interpositus neurons showed modest sensitivity and low selectivity for single-joint movements. What are the mechanisms that underlie these differences, and how do they relate to information processing in the cerebellum?

The high degree of joint selectivity of mossy fibers fits well with the restricted convergence of muscle afferents onto cuneocerebellar neurons. These cells receive input from single muscles or closely related synergists, and the population includes units that modulate discharge to both proximal and distal muscles (Cooke et al. 1971b; Holmqvist et al. 1963; Rosen and Sjolund 1973). In agreement with the present results, one would expect some units to show responsiveness to neighboring joints [due to input from muscles that extend across multiple joints (cf. Wei et al. 1986)] and cross-responsiveness between proximal and distal joints to be rare.

Conversely, the low degree of joint specificity of interpositus neurons and their high discharge during whole limb movement may relate to the appreciable divergence in the pathways from the interpositus nucleus to motoneurons in the spinal cord, as is evident from intra-axonal staining (Shinoda et al. 1982, 1986, 1988), spike-triggered averaging (Mewes and Cheney 1992; Miller et al. 1992), and from other electrophysiological studies (Shinoda et al. 1977, 1985a,b). Although these output pathways target both proximal and distal motor pools, there is a distinct preference for the pools innervating distal muscles (especially the digits), as corroborated by neuroanatomical tracing (Holstege 1987; Holstege et al. 1988; McCurdy et al. 1987; Ralston et al. 1988; Robinson et al. 1987). Additional support for a distal preference in the output pathways of the intermediate cerebellum derives from lesions of the red nucleus (Lawrence and Kuypers 1968; Sybirska and Gorska 1980) and rubrospinal tract (Alstermark et al. 1981b), from microstimulation within the magnocellular red nucleus (Gibson et al. 1985a; Larson and Yumiya 1980; Orlovski 1972), and from magnocellular red nucleus recording studies (Gibson et al. 1985b). Furthermore, recent studies of interpositus neurons during coordinated whole limb movements have also emphasized the importance of digit movements for interpositus discharge (Van Kan et al. 1990). As a whole, these results suggest that individual interpositus neurons activate groups of limb muscles with a weighted emphasis on the musculature of the hand, and that each neuron promotes simultaneous movement about many joints with an emphasis on the joints of the hand and fingers.

If the main function of the intermediate cerebellum is to operate the hand muscles, why would the mossy fiber population include a prominent representation from proximal in addition to distal joints? Proximal information may be necessary to plan appropriate hand movements or to time specific movement components to ongoing performance. The proximal information, for example, might inform the cerebellum about initial limb position and the progress of the limb in reaching a point in space where the hand can manipulate an object, whereas the distal information could inform about the hand movement itself and the initial hand position. Presumably, the cerebellum integrates this and much additional information to generate the activation functions and other control parameters for commanding

reaching and grasping. A major goal of future studies will be to understand the cerebellar cortical mechanisms that underlie these computations.

We thank D. Browdy and L. Miller for computer programming; C. Mason for technical assistance; N. Markovitz, B. Dyer, B. Zimmerman, and R. Meza for assistance in data analysis; and Dr. A. F. Fuchs for criticisms of an earlier version of this manuscript.

This research was supported by National Institute of Neurological and Communicative Disorders and Stroke Grants NS-27373 to P. L. E. van Kan and NS-17489 to J. C. Houk, and by the Office of Naval Research contract N00014-88-K-0339 to J. C. Houk.

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Received 6 November 1991; accepted in final form 11 September 1992.

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CORRIGENDA

Volume 69, January 1993

Pages 74–94: Peter L. E. van Kan, Alan R. Gibson, and James C. Houk, "Movement-related inputs to intermediate cerebellum of the monkey." Page 86, left column, Fig. 12 legend, the last 3 lines are printed incorrectly; they should read: The modulation in discharge during active finger extension (*E*) was considerably larger than the perturbation response (*F*). Every 4th spike is plotted in the rasters.