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

Output Organization of Intermediate Cerebellum of the Monkey

PETER L. E. VAN KAN, JAMES C. HOUK, AND ALAN R. GIBSON
Department of Physiology, Northwestern University Medical School, Chicago, Illinois 60611; and Division of Neurobiology, Barrow Neurological Institute, Phoenix, Arizona 85013

SUMMARY AND CONCLUSIONS

1. The goal of this study was to investigate the motor organization of monkey nucleus interpositus (NI) and neighboring regions of the lateral nucleus (NL) by correlating discharge of single neurons with active movements. Neurons were surveyed during free-form movements as well as during operation of six devices that required movement about specific forelimb joints. The paradigm allowed us to test the hypothesis that discharge of individual cells relates to movements about individual joints.

2. One hundred sixty-two isolated nuclear neurons from two monkeys were studied. Eighty-three percent showed large increases in discharge (an average of 3 times resting rate for forelimb neurons) during movement of one body part, either forelimb, hindlimb, mouth/face, or eyes.

3. Anterior interpositus contains neurons related to hindlimb movement in anterior regions and neurons related to forelimb movement in posterior regions. A mouth/face-related area exists in the dorsal-posterior regions and is continuous with a mouth/face area in the dorsal regions of NL. Posterior interpositus (NIP) showed no clear separation between forelimb and hindlimb neurons: forelimb neurons were encountered throughout the nucleus, and hindlimb neurons were encountered in the medial-anterior two thirds. A distinct eye movement area exists in lateral, posterior, and ventral regions of NIP. This area borders regions of NL that also contain eye movement–related neurons.

4. Forelimb interpositus neurons discharged strongly during reach and grasp; discharge rates were recorded for 41 neurons during a stereotyped reach and the average depth of modulation was 149 imp/s. Nineteen neurons that modulated during device tracking were also tested during reaching, and the depth of modulation was much greater during reaching.

5. Fifty-nine forelimb neurons were tested with device tracking. Twenty-seven (46%) produced no audible modulation, regardless of the joint being exercised. The remaining 32 neurons modulated during movement on at least one device (mean depth of modulation = 84 imp/s). Comparison of discharge during use of different devices revealed no strong evidence for device-specific discharge.

6. Discharge modulations during device tracking were phasic, preceded movement, and, for a small number of cells, showed consistent parametric relations to duration, amplitude, and velocity of movement.

7. Despite a clear somatotopy within NI and NL, there is no finer mapping based on active movements about individual joints within forelimb regions. Discharge modulation depends on movements involving the whole limb. Progress in understanding the function of intermediate cerebellum depends on determining the variables required to elicit consistent and high modulation of neural discharge. A reach and grasp produces such modulation: further analysis of this complex motor task will be useful.

INTRODUCTION

The cerebellum provides a major site for interfacing sensory information with the motor system (Evarts and Thach 1969). Although this structure has been the object of numerous anatomic and physiological studies, we still do not understand its mode of information processing, i.e., how information carried by sensory inputs is used to generate motor outputs. To gain a better understanding of this problem, we have undertaken a series of studies using similar experimental paradigms to allow a direct comparison of cerebellar input and output.

The focus of our analysis is the intermediate region of the cerebellum, which is known to be important for the control of limb movements (Harvey et al. 1977, 1979; Strick 1983; Thach 1968, 1970a,b, 1978). The intermediate cerebellum includes paravermal cerebellar cortex and its output nucleus, nucleus interpositus (NI). NI consists of two parts, nucleus interpositus anterior (NIA) and posterior (NIP). Both divisions of NI target the same extracerebellar nuclei, the magnocellular red nucleus (RNm) and the thalamic nucleus, ventralis lateralis posterior (VLp, Jones 1989). Both RNm and VLp provide intermediate cerebellum access to spinal mechanisms: RNm directly via the rubrospinal tract and VLp indirectly via precentral cortex and the corticospinal tract.

In previous work (Gibson et al. 1985a,b), we have characterized the properties of single units in RNm by recording discharge while monkeys made free-form movements and while they operated devices that required movements about specific forelimb joints. The experimental design allowed a general movement survey as well as a detailed quantitative analysis of forelimb neurons. In this study, we report the results of interpositus recordings using a similar paradigm, and in the immediately following report we utilize the same paradigm to characterize movement relations of mossy fibers within intermediate cerebellar cortex. As a whole, the results allow direct comparisons between three successive stages of neural processing involving intermediate cerebellum.

Within the forelimb region of RNm, movement representation is highly biased to favor movements involving hand use: single units show a preference for movements of a twisting device involving both fingers and wrist, whereas few units fire strongly during use of tracking devices requiring movement about isolated proximal joints (Gibson et al. 1985a,b).

Previous recording studies of NI suggest a very different movement organization than that found in RNm. Single neurons have been reported to discharge in relation to movements about specific upper limb joints (Harvey et al. 1979; Thach et al. 1982). These results on NI might be reconciled with the RNm results if the distal emphasis within RNm is the product of selective input from NI cells that are concerned with distal movement.

The device testing in NI yielded only a small number of

cells that had consistent relations between discharge and movement (as was the case for RNm); the properties of these cells were similar to RNm cells, and, therefore RNm properties are probably not the result of highly selective NI input.

Perhaps more importantly, many forelimb interpositus cells failed to discharge during device tracking. The cells that did modulate during tracking showed little specificity for particular devices and modulated over twice as strongly during a reach and grasp. Movement organization within interpositus is not based on a simple representation of individual forelimb joints: it may be based on coordinated movements involving several joints.

A preliminary account of this work has been reported (Van Kan et al. 1986).

METHODS

Behavioral training

Two male monkeys (*Macaca mulatta*) were trained to operate six manipulanda (Fig. 1) in a visually cued tracking paradigm. The manipulanda were designed to isolate movements behaviorally without the necessity of constraining the forelimb during task performance. Three devices, the shoulder, elbow, and wrist, elicited movements primarily about single joints, and the pivot points of these devices corresponded to the pivot points of the appropriate joints of the monkey's arm. The finger device required simultaneous movement of the metacarpophalangeal joints. The remaining two devices, the twister and supination-pronation devices, required coordinated movement across several forelimb joints. The twister, which was particularly effective for eliciting RNm discharge, required the combined use of the fingers and wrist, much like the operation of a motorcycle throttle.

All devices had a small amount of friction, and the finger device had a weak elastic restoring force in the extension direction. The shoulder, elbow, and wrist devices were equipped with freely rotating handles so that grip changes were not necessary for their operation, thereby ensuring relatively uncontaminated simple movements about individual joints. The shoulder and elbow devices included a counter weight to minimize the forces required to maintain a stable limb position. The wrist and finger devices included a support surface for the forearm to reduce undesired involvement of shoulder and elbow joints (and wrist joint in case of the finger device).

The tracking display consisted of an oscilloscope screen on which two horizontal lines defined a target zone. A third horizontal line, the position feedback trace, was controlled by the output of a potentiometer mounted on the rotation axis of each of the manipulanda. To initiate a trial, the animal was required to keep the position feedback trace in the target zone for a random interval between 1 and 2 s. Then the target jumped to a new location (1 of 3 fixed positions), and the animal was reinforced for moving the device so as to position the feedback trace in the target zone at the new location. Although reinforcement was not contingent on rapid reaction times, the monkeys learned to respond rapidly after each target change. The target display remained stationary for 5 s, during which the animal received a water reward.

When we desired to test with a different device, the control of the cursor was switched to the new device, and the device was positioned within reach of the monkey. The monkeys quickly learned to quit operating a device as soon as it lost control of the cursor and would rapidly try other devices until the one controlling the cursor was found. The preferred tracking device was defined as the device that resulted in the largest modulation in firing rate of the unit under study.

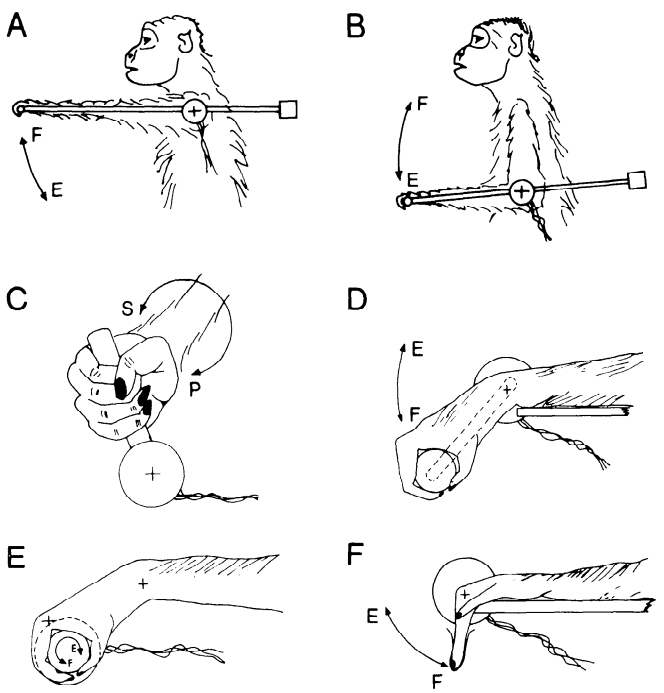

FIG. 1. Manipulanda used in the visual cued tracking task. Relatively pure rotations about the shoulder, elbow, wrist, and metacarpophalangeal joints were obtained by operation of the shoulder (*A*), elbow (*B*), wrist (*D*), and finger (*F*) device. Supination and pronation of the forearm were studied during operation of the supinator/pronator device (*C*). The twister (*E*) required the monkey to make a coordinated hand movement involving a combined action about wrist and finger joints.

Surgical preparation

After training, a stainless steel recording chamber and head holder were implanted under surgical anesthesia (intravenous pentobarbital sodium) and aseptic conditions. A craniotomy was centered above the right cerebellar hemisphere (Horsley-Clarke P 6.0, L 5.0), and the recording chamber was mounted above the opening at a 15° angle from the vertical stereotaxic position in the coronal plane. Wound margins and the recording chamber were treated daily with a providone-iodine solution, which effectively prevented infection.

Free-form testing

During the recording sessions, monkeys were seated in a primate chair. A head holder, neck collar, and a belt around the waist restricted movement of the head and trunk but allowed relatively unconstrained movements of the forelimbs, hindlimbs, mouth, and eyes. Neurons were routinely tested for relations between discharge and movement of specific body parts by visual observation and videotaping. Movements of the forelimbs and eyes to particular positions in space were elicited by holding raisins in different positions, and mouth movements could be studied during ingestion of the raisins or during licking of the water tube. Hindlimb movements were elicited by lightly touching the toes or hairs of the foot.

Data recording

Data recording relied on both computer collection and video recording. The computer collection allowed accurate collection of movement/discharge relations during device operation, and the

video recording allowed records to be made of discharge during movements not tested by devices. Slow-motion review aided judgements of movement/discharge relations, and for some cases the video records were used for off-line data analysis utilizing computerized digitizing (see below).

Cerebellar nuclear neurons were recorded with tungsten microelectrodes (impedance 0.5–1.0 MΩ at 1 kHz) during daily recording sessions lasting ~2 h. We modified a Narashige microdrive to minimize deflection of the microelectrode by installing a stainless steel guide tube that extended to the surface of the dura. When the dura became too thick to be easily penetrated by the microelectrode, a 19-gauge hypodermic needle was fitted inside this guide tube and was inserted through the superficial 2–3 mm of cerebral cortex. The microelectrode was then lowered through the hypodermic needle. This system considerably improved the accuracy of stereotaxic placement of microelectrodes. Reproducibility of stereotaxic coordinates was achieved by cross-referencing microelectrodes with an optical zeroing device (Gibson et al. 1985a).

Action potentials were amplified with a half-amplitude bandwidth of 300–10,000 Hz. For computer records, potentials were discriminated and collected as interspike intervals with 0.1-ms accuracy, and analog position records were sampled at 250 Hz. During videotaping, action potentials were recorded on an audio channel of a ¾-in. video tape recorder.

Data analysis

Data collected during device use were analyzed by grouping similar movement trials for each unit. Each trial was computer analyzed by marking the time of movement onset on the position trace with a trackball-controlled cursor. Movement onsets were then used as synchronization points for the generation of averaged records and trial rasters. Histograms of average discharge were constructed with a binwidth of 12 ms. The depth of modulation (DOM), defined as the difference between average discharge rate during movement and the average resting rate during a stationary period before target change, was calculated from discharge records of successive trials.

For comparison with the free-form discharge rates, a somewhat different method of calculating device DOM was used. Rates during free-form movement were obtained from a rate meter that recorded the highest discharge that occurred over 100-ms intervals of time. DOM was calculated from this rate by subtracting the highest discharge that was measured while the monkey was motionless. Similar rate meter measurements were also made before and during device movement, and these measurements were used to calculate device DOM for comparison with reach and grasp movement DOM (Fig. 10).

Depth of modulation estimates for flexion and extension movements were used to calculate a directional index by dividing the depth of modulation in the nonpreferred direction by that in the preferred direction and subtracting the resultant value from 1. A value of 1 indicates a purely unidirectional modulation, a value of 0 indicates equal modulations in both directions, and a value above 1 indicates an increase in discharge in one direction of movement and a decrease in the opposite direction. Cells with indexes >0.5 were considered directionally selective.

Relations between discharge during limb holding phases and joint angle and between detailed parameters of movement and corresponding discharge were evaluated by regression analysis using the Pearson product moment correlation (r). For each cell, the joint angle dependency of unitary discharge was evaluated by plotting for each trial the tonic firing rate as a function of joint angle. Tonic firing rate was defined as the mean frequency measured over a 400-ms interval during which the monkey held the limb steady at one of three target positions.

Relations between parameters of individual tracking movements and corresponding modulations were derived from estimates of movement and modulation onset and offset times measured from records of angular position and integrated spikes for each trial. The integrated spike plot is a cumulative count of the number of action potentials versus time. An interactive display program was used to determine onset and offset times of modulations by aligning cursors to the corresponding inflection points in the integrated spike records. Analogously, movement onset and offset times were estimated from inflection points in the corresponding position records. The measurements were used to calculate mean lead or lag times for individual trials of a given unit, and t statistics were used to determine whether modulation onset differed from movement onset. Movement and discharge onset and offset times also allowed us to correlate movement duration with the duration of discharge modulation.

Measurements of position and integrated spikes at movement and modulation onset and offset times were used to calculate correlations between movement amplitude and modulation amplitude and between movement velocity and discharge rate. Modulation amplitude was calculated by subtracting the cumulative sum of spikes at modulation offset from that at onset. Movement velocity was derived from measurements of the slope of the angular position record between movement onset and offset times. Movement-related discharge rate was derived from estimates of the slope of the integrated spike record between modulation onset and offset times.

Relations between discharge and reaching movements were analyzed from the movement sequences, and raw action potentials stored on videotape. During video playback, action potentials were discriminated and their time of occurrence was collected on an IBM compatible computer by a CED 1401 interface (Cambridge Electronics Design). Reach onset, defined as the first instance where the limb could be seen to change position, was manually marked and collected on an event channel to provide an approximate synchronization point for generating peristimulus time histograms.

Verification of recording sites

Although final confirmation of recording sites relied on histological reconstruction, during recording the cerebellar nuclei could be identified as groups of negative-positive potentials separated from the cerebellar cortex by an interval of white matter. Because each electrode was adjusted to a standard length, the depths at which units were encountered proved to be a useful guide for identifying nuclear neurons. The durations of unitary potentials were ~1 ms, and amplitudes were on the order of 1 mV, thereby suggesting that the potentials represented cellular rather than fiber recordings (see Harvey et al. 1979; Van Kan et al. 1993).

Near the end of the recording period, small electrolytic lesions (−10 μA for 10 s) were made at selected sites through the recording electrodes (see Fig. 2), and larger lesions (+50 μA for 30 s) were placed at the corner positions of a rectangular volume that included all recording tracks. The large lesions were placed after recording, before perfusion. A total of 10 small lesions were made in *monkey MAX* during the last fourth of the recording tracks, whereas *monkey OSC* had 5 small lesions placed during the last fifth of the recording tracks. Most of the lesions were made at the end of specific tracks, and no obvious functional compromise resulted from the lesions.

Before perfusion, the monkeys were administered a lethal dose of pentobarbital sodium and perfused with physiological saline followed by 10% formalin. After post-fixing in 30% sucrose-10% formalin, brains were frozen and sectioned at 40 μm. All sections through the cerebellum were mounted and stained with cresyl violet or cresyl violet-luxol fast blue. Sections were enlarged and traced and, with the aid of stereotaxic coordinates, electrode paths, and lesions, recording sites were reconstructed.

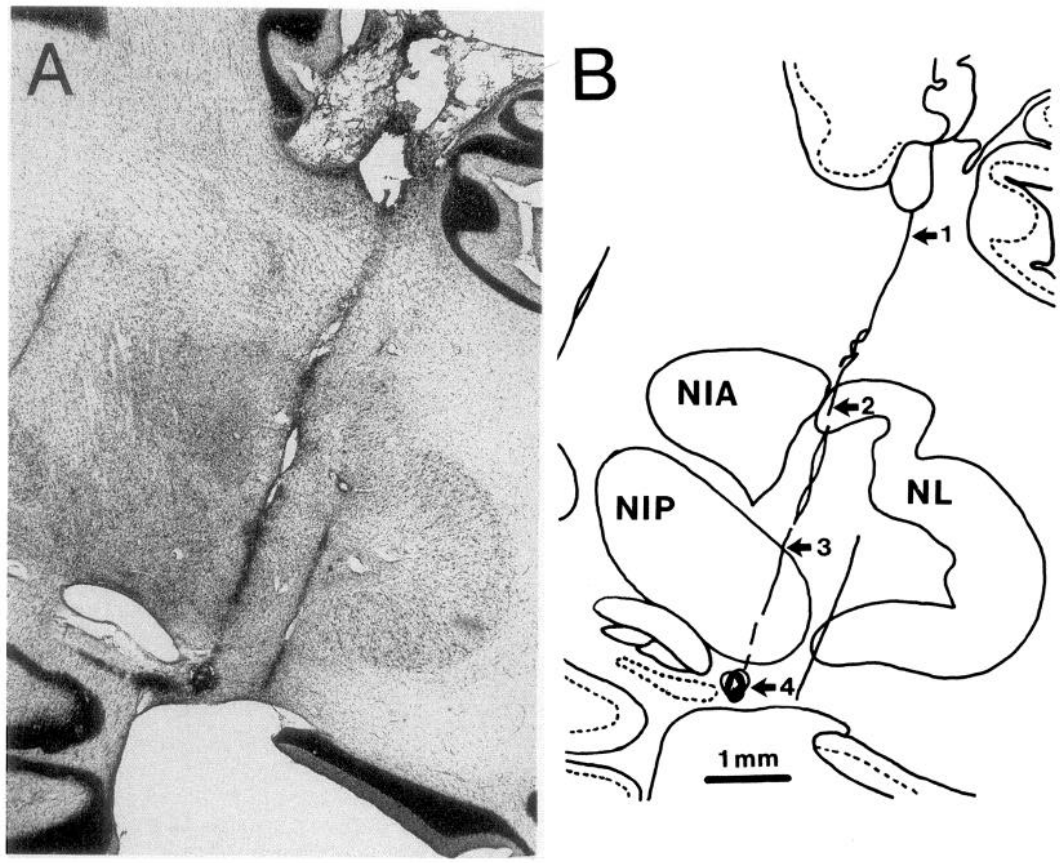

FIG. 2. Histological verification of recording sites. *A*: photomicrograph of a transverse section through the cerebellar nuclei of *monkey OSC* illustrating gliosis from 3 microelectrode penetrations. A marking lesion is visible at the bottom of the middle penetration. *B*: reconstruction showing the sites of 3 nuclear cells recorded along a single penetration. One cell, related to movement of the ipsilateral hindlimb, was recorded at the border between nucleus interpositus anterior (NIA) and lateral nucleus (NL) (arrow 2). Two cells related to eye movements were recorded in nucleus interpositus posterior (NIP) between arrows 3 and 4. An electrolytic lesion (arrow 4) marked a transition from cerebellar nuclear to cerebellar cortical eye movement-related activity. Arrow 1 points to the recording site of a fiber in white matter underlying cerebellar cortex that was related to movement of the ipsilateral hindlimb.

RESULTS

Spatial distribution of neural properties

Single-unit recordings in the cerebellar interpositus and nearby lateral nucleus were made while monkeys performed a variety of movements, including movements limited to specific joints and free-form movements such as reaching for and grasping raisins. Recording sites were then used to generate a map of movement relations in the nuclei. We determined movement relations for 134 neurons; 96 were located in NI and 38 in neighboring regions of lateral nucleus (NL). During free-form testing, we were unable to detect clear differences between the movement-related discharge of neurons in different divisions of the deep nuclei. For example, forelimb neurons appeared to fire in similar ways, whether they were localized to NIA, NIP, or dorsal NL.

Generally, it was easy to associate discharge with movement of a particular body part because audible modulation only occurred during use of that body part. The exceptions are described under the heading BILATERAL AND MIXED MOVEMENT RELATIONS. During free-form movement, discharge peaked between 200 and 400 imp/s (measured over 100-ms intervals), which usually exceeded resting rate several times. Although resting rates could be quite high, only one neuron (located in NL) showed a decrease in discharge as its primary modulation.

Figure 2 illustrates recordings along one of the electrode penetrations marked with an electrolytic lesion. At arrow 1, a unit related to hindlimb movement was recorded in the white matter. We identified this unit as a fiber by its location and wave shape (Van Kan et al. 1993): the action potential was triphasic, brief in duration, and relatively small in amplitude (0.3 mV). At arrow 2, the electrode entered NL and a neuron related to hindlimb movement was recorded. Between arrows 3 and 4, two isolated neurons related to eye movements were recorded from a background of eye movement units. At arrow 4, a transition from the relative silence of white matter to the high activity characteristic of cerebellar cortex occurred, and we made a lesion at this point. The high activity was related to eye movements, and examination of neighboring sections showed that the electrode had entered the granular layer of the underlying cerebellar cortex. To avoid confusion, lesions were made on selected, well-separated tracks. Reconstruction of unmarked electrode tracks relied on relative stereotaxic coordinates to the marked tracks as well as to larger lesions marking the borders of the recording volume.

The reconstructed locations of all neurons from two monkeys are plotted in the series of frontal sections shown in Fig. 3. This figure illustrates only the locations of isolated neurons; however, in most cases the background activity indicated that many units in the region modulated during the same movements. Outlines were drawn from transverse sections of one monkey, and locations from both monkeys were plotted on the most closely matching outline.

The tracks were driven at a 15° angle from lateral to medial, as is indicated by the lines in the second and third sections of Fig. 3. Tracks were continued until we had traversed all nuclear regions, so that extending the 15° through the plotted cells provides an estimate of nuclear areas sampled. The ventral-lateral regions of NL were not well sampled.

EYE MOVEMENT RELATIONS. Eye movement neurons formed a distinct region within ventral and lateral NIP and the neighboring NL. By observation and slow-motion video review, a variety of eye movement discharge types could be discerned qualitatively. Nine neurons discharged in high-frequency bursts (250–700 imp/s) related to saccades: both directional and nondirectional neurons were observed. Five neurons fired preferentially when the monkeys visually pursued a raisin moving slowly in front of them. Some of the neurons appeared to fire in combination with limb movements. For example, one unit reliably increased discharge when the raisin came within arm reach. One neuron whose firing was related to saccades fired during blinking, and two units fired to blinking alone. One unit had a tonic firing pattern related to eye position and showed an increase in discharge rate as the eyes moved slowly in an upward direction.

LIMB MOVEMENT RELATIONS. Limb movement neurons were recorded in all divisions of the deep nuclei studied. The locations of neurons related to limb movement show a rough somatotopic order within NIA and NL: hindlimb neurons were found in the most anterior sections and forelimb neurons were found in posterior regions with some intermixing of hindlimb and forelimb neurons at the transition between the regions. In the region of overlap, hindlimb NIA neurons lie medial to forelimb (except for 1 case in the 6th section). The distribution of limb-related neurons was not as clearly demarcated in NIP: hindlimb neurons tended to be located in the medial and anterior regions of NIP, but forelimb neurons were located throughout the nucleus.

MOUTH/FACE RELATIONS. Neurons related to movements of the mouth, tongue, jaw, and/or face were observed during chewing or drinking. Because these movements could not be dissociated easily, we have chosen to label them as mouth/face neurons.

As with limb movement neurons, mouth/face neurons were encountered in all nuclear divisions and no differences were noted in discharge properties from different divisions. Most of the mouth/face neurons were located in caudal and dorsal regions of NIA and adjoining NL. Only two mouth/face neurons were localized to NIP, and they lay in its most caudal sections.

BILATERAL AND MIXED MOVEMENT RELATIONS. Most limb movement neurons modulated only during use of the limb ipsilateral to the recording site. One NL and six NI neurons also modulated during use of the corresponding contralateral limb, although modulation during ipsilateral limb use was stronger.

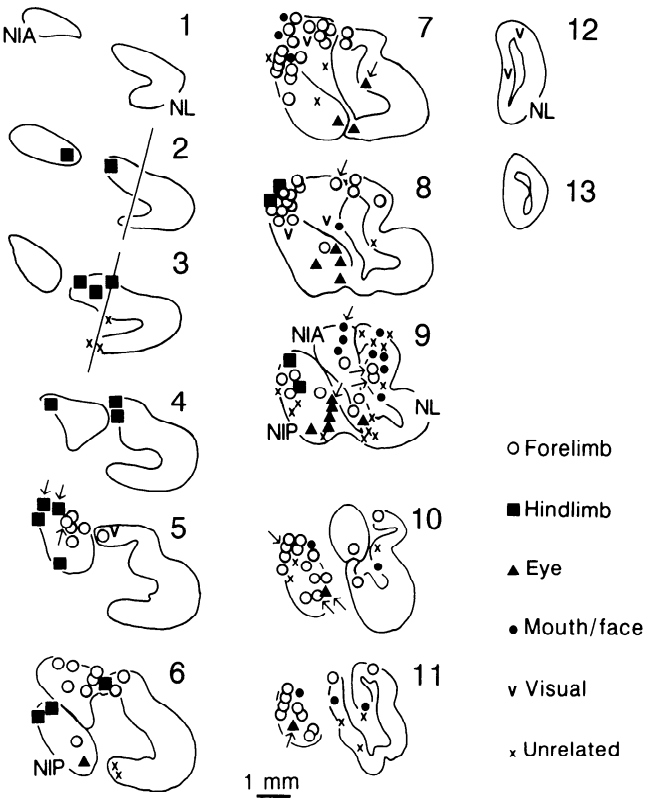

FIG. 3. Recording sites of 134 movement-related neurons from 2 monkeys plotted on equally spaced transverse sections through the cerebellar nuclei from P6.4 (section 1) to P11.2 (section 13). Forelimb neurons (n = 82) are indicated by open circles, hindlimb neurons (n = 19) by solid squares, eye neurons (n = 16) by solid triangles, and mouth/face neurons (n = 17) by solid circles. Of the 82 forelimb neurons, 29 were located in nucleus interpositus anterior (NIA), 37 in nucleus interpositus posterior (NIP), and 16 in lateral nucleus (NL). Locations of neurons with mixed movement relations are indicated by arrows. Neurons that modulated to movement of both forelimb and hindlimb are located in section 5, those that modulated to forelimb and eye movement in sections 7, 9, 10, and 11, and those that modulated to forelimb and face movement in sections 8 and 9. Locations of 6 neurons responsive to visual stimuli are indicated by Vs, and locations of 28 well isolated neurons that could not be associated with any property are indicated by ×s. Lines through sections 2 and 3: 15° angle of the miroelectrode penetrations.

Occasionally neurons fired during movements of noncorresponding body parts. Three forelimb NIA neurons modulated during movement of the ipsilateral hindlimb, and four forelimb neurons (1 NIA and 3 NL) modulated during mouth/face movements. Five neurons related to eye movements also fired during forelimb use. Neurons showing modulation during movement of more than one body part tended to occur at the border zones between body part representations, and their locations have been marked with arrows in Fig. 3 (see legend for properties).

VISUAL RESPONSES. During our efforts to determine movement relations, it became clear that some neurons responded to visual movement alone. Visual neurons were not localized to any particular region of the deep nuclei. Their locations are indicated by Vs in Fig. 3. A total of six neurons, three in NI and three in NL, responded well to

TABLE 1. *Number of interpositus neurons studied on each device*

Shoulder	Elbow	Sup/Pro	Wrist	Twister	Finger
32 (54)	40 (68)	10 (17)	22 (37)	48 (81)	35 (59)

Numbers in parentheses are percentages. Percentages are based on a total of 59 neurons that were tested on one or more devices. Forty-seven neurons were tested on multiple devices and are included in more than one column. Sup/Pro, supination/pronation.

movement of the experimenter's arm or pieces of paper moved in particular parts of the visual field. A careful review of close-up video recordings of eye movements demonstrated that the discharge could not be attributed to eye movements. By presenting stimuli while the monkeys attended the tracking display, we were able to make estimates of receptive field size. The fields were large, on the order of 20–50° of arc, and were confined to the ipsilateral hemifield. Two of the visual neurons, one in NIP and one in NL, seemed to modulate discharge also during arm use. Movement of the monkeys arm within the visual field appeared to be a particularly effective stimulus for these cells. None of the visual cells responded to a flash stimulus.

It is surprising that visual responsiveness can be seen at this relatively late stage of motor processing, but a similar observation has been made by MacKay (1988b). Visual responses in the deep nuclei probably reflect visual input to cerebellar cortex arriving via mossy fibers from the pontine nuclei (Brodal 1978; Glickstein et al. 1985), and visually responsive neurons in the deep nuclei may provide the basis for visual responses seen in monkey motor cortex (Wannier et al. 1989).

UNRELATED NEURONS. If we were unable to determine clear movement or sensory relations for a well-isolated neuron during testing, we recorded the neuron as being unrelated. The actual number categorized as being unrelated is certainly an underestimate, because less effort was devoted to isolating neurons that failed to show clear relations. The relative number between regions, however, is approximately proportional to the frequency of encountering unrelated neurons.

Of the 28 unrelated neurons, 1 was located within NIA, 8 in NIP, and 19 in NL. The locations of these neurons is shown by ×s in Fig. 3. The relatively high number in ventral NL is striking because fewer tracks traversed this region. Thirteen well-isolated neurons were studied in ventral NL, and all were classified as being unrelated. Because very few related neurons were localized to ventral NL but many were localized to dorsal NL, dorsal and ventral NL probably serve different functions.

In summary, there is a parallel organization of movement relations in NI and NL. Cells firing during hindlimb movements are located in the rostral portion of NIA, NIP, and NL. Forelimb cells are located in the intermediate and caudal regions of NIA, throughout NIP, and dorsal and caudal in NL. A mouth/face region is located in the caudal region of NIA and in the adjoining dorsal regions of NL. Finally, a distinct eye movement area is located in ventral and caudal NIP and ventral NL.

Discharge related to device tracking

In addition to free-form testing, we routinely tested cells for modulation during tracking on six devices (see Table 1). Fifty-nine of the 66 forelimb interpositus neurons were tested during tracking. All neurons that fired during device use also fired during reach and grasp. *Typically, the modulation during the reach and grasp was considerably stronger than during device use, and only a small number of neurons provided device data suitable for parametric analysis.*

In agreement with our qualitative observations, quantitative analysis of NIA and NIP forelimb neurons revealed no differences between these nuclear divisions. Table 2 shows various measurements for cells located in NIA and NIP; none of the differences between means approach statistical significance ($P > 0.05$). In the figures and tables, we have identified the neurons as being from NIA or NIP with an A or P after the unit identification number to allow the reader to compare between divisions. In no case did we find differences that justified a separate data analysis, and the data from NIA and NIP have been pooled for the presentation of frequency distributions.

Thirty-two (54%) of the forelimb neurons showed modulations of discharge of ~50 imp/sec or greater during tracking on at least one of the devices, and the following descriptions are based on this population.

DEVICE SPECIFICITY. During device testing, we first made a qualitative judgement of a neuron's movement relation and began testing with the device that seemed most likely to elicit a high modulation. In this fashion, we sought to maximize the likelihood of observing strong device modulations, because isolated neurons were sometimes lost as testing progressed. The devices producing the strongest modulations for 32 neurons were the elbow (12), twister (10), shoulder (6), finger (3), and supinator/pronator (1).

We were able to test 23 forelimb neurons on two or more devices. Although the preferred device was by definition the device that produced the strongest discharge modulation, many neurons modulated with nearly equal strength for more than one device. Figure 4 shows examples of the strongest modulations from multiple device testing for four neurons. Some of the neurons (*A*, *B*, and *D*) showed strong modulations on a number of, but not all, devices. For example, the neuron illustrated in Fig. 4*A* showed strong and approximately equal modulations during elbow extension and supination but a weak modulation during shoulder extension. Clear but weaker modulations were seen with

TABLE 2. *Parametrics of forelimb NIA and NIP neurons*

	NIA	NIP
DOM device, imp/s	88 ± 39 (17)	80 ± 25 (15)
DOM reach, imp/s	162 ± 81 (11)	182 ± 55 (9)
Directional index	0.7 ± 0.4 (17)	0.9 ± 0.5 (15)
Lead time, ms	81 ± 99 (17)	135 ± 73 (15)

Values are means ± SD. Numbers in parentheses indicate number of neurons. Neurons included in the discharge modulation during reach and grasp are a subset of those that modulated during device use. Values for NIA neurons are not significantly different from those for NIP neurons ($P > 0.05$). NIA, nucleus interpositus anterior; NIP, nucleus interpositus posterior; DOM, depth of modulation in discharge.

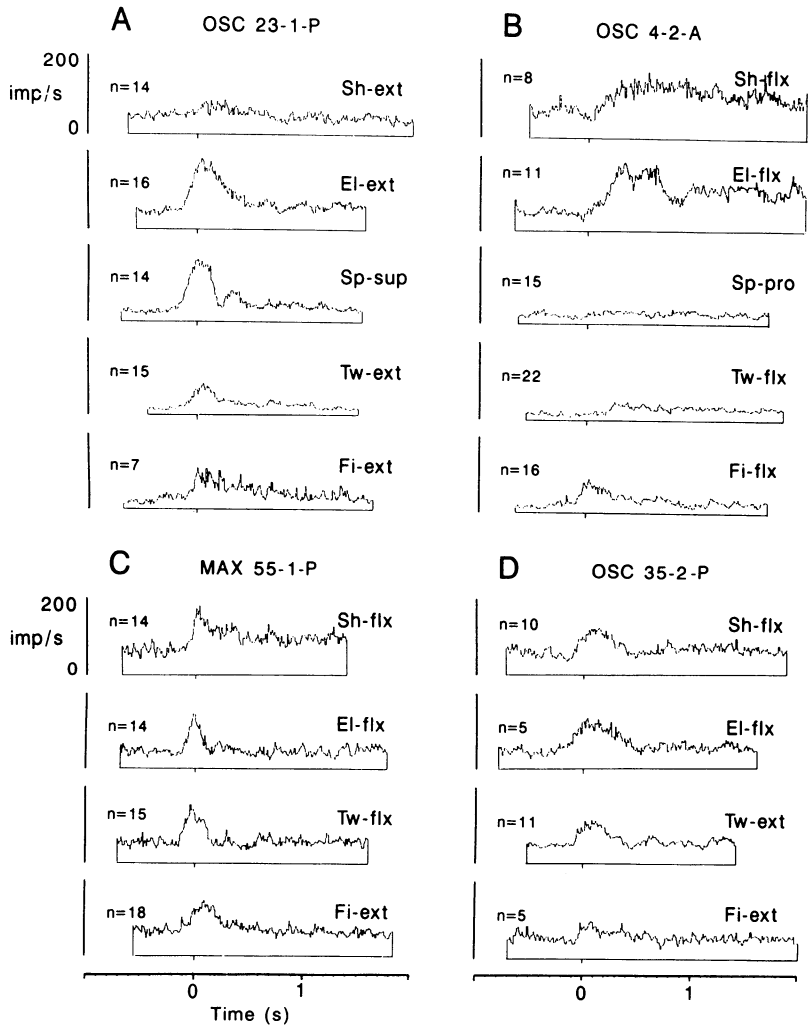

FIG. 4. Discharge of 3 nucleus interpositus posterior (NIP) (*A*, *C*, and *D*) and 1 nucleus interpositus anterior (NIA) neuron (*B*) during operation of multiple devices. Records are averaged over *n* trials of movement in the preferred direction and are synchronized on movement onset (time 0). flx, flexion; ext, extension; sup, supination; pro, pronation; Sh, shoulder; El, elbow; Sp, supinator/pronator; Tw, twister; Fi, finger.

finger and twister extension. Other neurons, such as that illustrated in Fig. 4*C*, had modulations of approximately equal strength for all devices tested.

Table 3 lists the modulation ratings for multiple device testing for all 23 neurons. We have grouped the modulations into categories by using ++ for the strongest modulations, + for weaker but clear modulations, +/− for weak and variable modulation, and 0 for no modulation. For the most part, the judgments were made by reviewing averaged data records of cell discharge and device movement, but data files were not always collected when no modulation could be heard. Averaging in these instances might have revealed a slight modulation (Fig. 9 illustrates 2 neurons that received 0 device ratings). An appreciation for the categorization may be gained by comparing the ratings with the discharges for the cells illustrated in Fig. 4 (also see Figs. 6 and 8). For instance, the cell in Fig. 4*A* (*OSC* 23-1) was given ++ for both elbow extension and supination, a + for twister and finger extension, and a +/− for shoulder extension.

The ratings in parentheses in Table 3 are the strongest modulations, and the cells have been ordered from the strongest modulations on the most proximal device (shoulder) to the most distal device (finger). Notice, however, that there is little specificity for individual devices. Cells rated ++ for the shoulder device often were rated ++ or + for the finger device and vice versa. Because the proximal arm rested on a support during finger device use (see Fig. 1), there was little or no common joint movement between these devices. Nineteen neurons were tested on at least one proximal (shoulder/elbow) device and one distal (wrist/twister/finger) device, and all received ++ or + ratings for both.

PARAMETRIC RELATIONS BETWEEN DISCHARGE AND MOVEMENT. The depth of modulation was calculated for 32 cells from the averaged discharge on the preferred device (Tables 1 and 3) during movement in the direction producing the largest modulation. The modulations were phasic; no neuron exhibited tonic discharge related to device position (contrast with the position-related discharge of mossy fibers in the following paper). In some instances, the averaged discharge records showed apparent differences in tonic discharge before and after movement (i.e. Fig. 4*B*), but examination of individual trials showed that the additional discharge was due to position adjustments after movement. A period of steady holding was required before the onset of the next trial, which favored a low discharge rate before movement. The distribution of modulations, shown in Fig. 5*A*, was broad, with a peak of ~70 imp/s.

TABLE 3. *Device specificity of interpositus neurons*

Unit	Shoulder	Elbow	Sup/Pro	Wrist	Twister	Finger
OSC 4-1-A	(++)	++	++		+	+
MAX 1-1-P	(++)			+	0	0
MAX 52-2-P	(++)	++				
OSC 4-2-A	+	(++)	0		+	++
OSC 23-1-P	+/0	(++)	++		+	+
OSC 26-6-P		(++)			+	
OSC 35-2-P	++	(++)			++	+
OSC 59-3-P	0	(++)			+	
MAX 12-6-A	0	(++)		+	0	0
MAX 29-6-A		(++)			+	+/0
MAX 51-4-A	+	(++)		+	+/0	0
MAX 36-2-A	++	++	(++)	+	++	++
MAX 13-5-A				+	(++)	
OSC 4-3-A		+/0			(++)	+
OSC 4-4-A	+	+			(++)	+
OSC 5-5-P	+/0	+	++		(++)	
OSC 28-1-P	+				(++)	0
MAX 31-5-A				+/0	(++)	
MAX 43-4-A		++			(++)	
MAX 55-1-P	++	++			(++)	+
OSC 36-1-P		++	+		+	(++)
MAX 28-7-A		+		0	+/0	(+)
MAX 60-1-A					0	(++)

The 23 neurons included are a subset of 32 that showed modulation in discharge during use of at least one of the devices. Sup/Pro, supination/pronation; ++, strong modulation; +, clear modulation; +/0, weak or no modulation; 0, no modulation. Parentheses indicate device associated with strongest modulation. The A and P following the cell identification number indicate recording sites in nucleus interpositus anterior (NIA) and nucleus interpositus posterior (NIP), respectively.

The directionality of modulations during preferred device use varied from cell to cell: Fig. 6 illustrates discharge of three units during movement of different directions on their preferred device. The unit illustrated in Fig. 6, *A* and *B*, modulated about equally during extension or flexion and was classified as bidirectional. The unit shown in Fig. 6, *C* and *D*, increased discharge in one direction and decreased in the other and was classified as reciprocal, whereas the unit in Fig. 6, *E* and *F*, increased in one direction with no change in the other and was classified as unidirectional. Directional indexes (see METHODS) were calculated for all 32 neurons that modulated during device use and are plotted in Fig. 5*B*. Notice that most (72%) of the cells were directional, being either in the unidirectional or reciprocal categories.

Average onset times of movement and discharge modulation were calculated from individual trials for each of the neurons. Most cells began discharge before movement onset, as illustrated for the three cells in Fig. 6. A histogram of the mean lead or lag times for all cells is shown in Fig. 5*C*. Only 1 cell had a discharge modulation that significantly followed movement onset; the average lead time for all 32 cells was 107 ± 91 (SD) ms.

A more detailed quantitative analysis of relations between parameters of individual tracking movements and corresponding neural discharge was performed on a subset of 11 neurons that were selected from the larger population of device-related neurons. The neurons were selected on the basis of showing the most consistent modulations on a trial-by-trial review. Preferred devices were the twister (7), supinator/pronator (2), elbow (1), and finger devices (1). The cells had modulations >49 imp/s and led movement onset by an average of 121 ± 62 ms. Figure 7 illustrates scatter plots and regression analysis of modulation versus movement duration (*A* and *B*), modulation versus movement amplitude (number of spikes) (*C* and *D*), and firing rate versus movement velocity (*E* and *F*) for two of the well-related neurons.

Duration of discharge modulation was highly correlated with movement duration for all 11 neurons, and all correlations were statistically significant ($P < 0.05$). The linear correlation coefficient averaged $r = 0.78 \pm 0.11$. The slopes of the relations for most neurons were close to 1, with an average of 1.02 ± 0.28. Regression lines fitted to the data had offsets that averaged 71 ± 67 ms, indicating that the duration of modulation was greater than the duration of the movement.

The amplitude of the discharge was calculated by taking the increment in the number of spikes associated with movement. The integrated spike trace showed a change in slope during the discharge so that inflection points could be

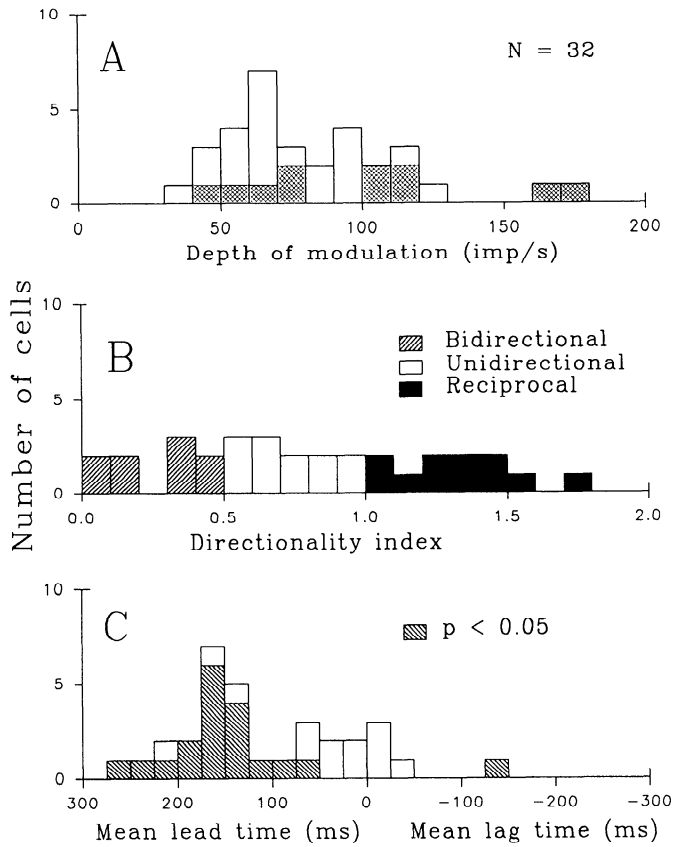

FIG. 5. Distribution of average depth of modulation, directional specificity, and average lead or lag time for 32 interpositus neurons that modulated discharge during tracking. All measurements were made from modulations on the preferred device. *A*: average depth of modulation was calculated for the direction that was associated with the largest modulation in discharge (preferred direction). Shaded areas: measurements from neurons analyzed for relations between parameters of individual tracking movements and corresponding neural modulation. *B*: cells with indexes >0.5 were considered direction specific, whether unidirectional or reciprocal. *C*: measurements of the difference between movement and modulation onset times were averaged for 3–14 movements in the preferred direction. Neurons with statistically significant ($P < 0.05$) lead and lag times are shaded.

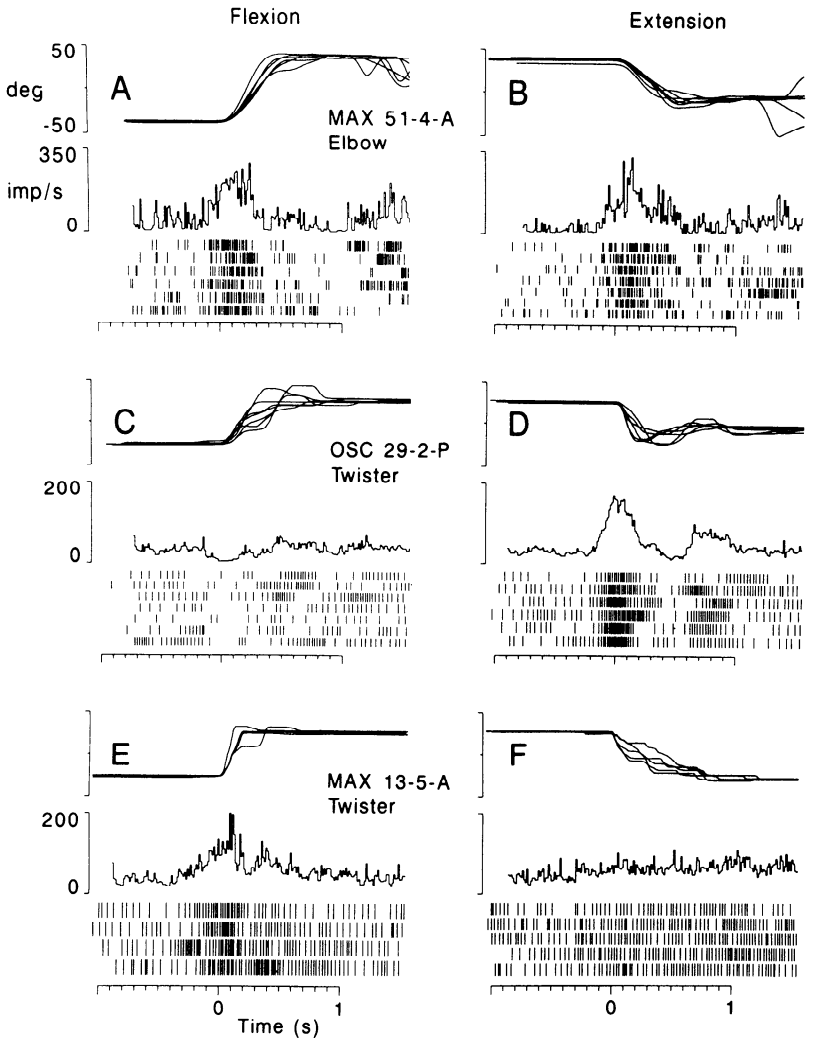

FIG. 6. Directionality and timing relations of discharge of 2 nucleus interpositus anterior (NIA) neurons (*A* and *B*, *E* and *F*) and 1 nucleus interpositus posterior (NIP) neuron (*C* and *D*) during flexion (*A*, *C*, and *E*) and extension (*B*, *D*, and *F*) on the indicated devices. Movement records for each trial have been overplotted, and average discharge rate is plotted in the histogram. Successive rows in the rasters represent individual trials aligned on movement onset, illustrating the repeatability of successive trials. Later movements in *A* and *B* are the result of experimentally induced perturbations of device position. For clarity, every 3rd (*A* and *B*), or 2nd (*C*–*F*) spike is plotted. Directional indexes: *MAX* 51-4-A, 0.05; *OSC* 29-2-P, 1.21; *MAX* 13-5-A, 0.66. All modulations in discharge preceded movement onset (*A*, 154 ± 47 ms, mean ± SD; *D*, 173 ± 46 ms; *E*, 244 ± 112 ms).

marked to define the period of modulation. The correlation between modulation amplitude and movement amplitude averaged 0.72 ± 0.11. Regression lines fitted to the data had an average slope of 0.89 ± 0.36 imp/deg of rotation at device pivot point and an average offset of 16 ± 7 impulses.

Discharge rate of seven neurons correlated well with movement velocity; correlations for the remaining four were not statistically significant ($P > 0.05$). The significant velocity correlations averaged 0.57 ± 0.13. The offset of the regression lines averaged 97 ± 57 imp/s compared with an average background discharge unrelated to movement of 64 ± 44 imp/s. The slope of the significant velocity relations averaged 0.29 ± 0.16 (imp/s)/(deg/s).

Although a few units had significant velocity correlations, it is possible that other phasic components such as force or change in force (dF/dt) were responsible for the correlation. Additional testing with various loading conditions would be required to tease apart such variables, but the generally poor parametric relations suggest such studies would not be particularly conclusive or relevant.

Discharge related to perturbations

Eight neurons were evaluated for sensory responsiveness by perturbing the device position during the limb holding phase of the tracking task. Mechanical disturbances were induced by a tap on the shoulder ($n = 4$), elbow ($n = 3$), or finger ($n = 1$) device. Seven of the eight neurons failed to respond to the perturbations, although all modulated strongly during free-form movements and five (including the 1 that did respond to perturbations) discharged during active tracking movements on the perturbed device.

The responsive neuron (*MAX* 51-4) fired briskly to perturbations of the elbow device. The peak response was ~250 imp/s for perturbations in the extension direction and 200 imp/s for flexion, and response latency averaged 37 ± 14 ms ($n = 8$). The latency is in the middle of the range of those reported by Strick (1983) for interpositus responses to perturbations. The average discharge during active movement was ~200 imp/s for both flexion and extension and commenced 154 ± 47 ms before movement onset (Fig. 6, *A* and *B*).

Discharge of forelimb neurons in NL

Sixteen forelimb neurons were recorded in NL with 13 located at the border of caudal NIA and dorsal NL (Fig. 3). Neural modulations during reach and grasp were stronger than during device use (121 ± 40 vs. 93 ± 57 imp/s; $n = 9$), but the difference was not as large as that seen for NI neurons. Seven of nine NL neurons showed a modulation during operation of at least one device. The two unmodulated

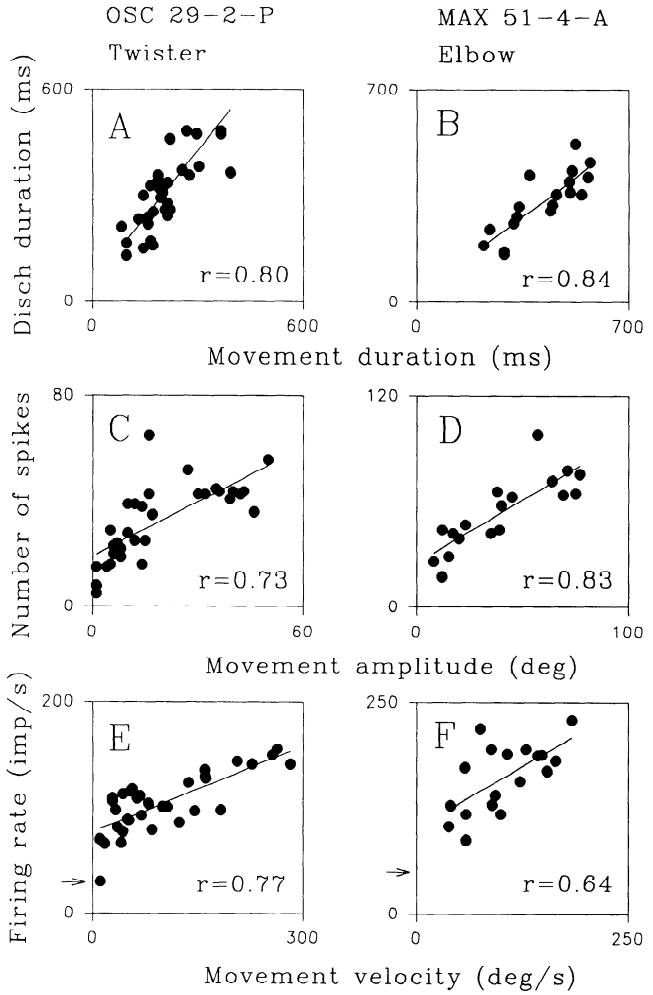

FIG. 7. Scatter plots showing correlations between parameters of individual tracking movements and corresponding modulations in discharge for a nucleus interpositus posterior (NIP) neuron (*A*, *C*, and *E*) and a nucleus interpositus anterior (NIA) neuron (*B*, *D*, and *F*). *A* and *B*: duration of the modulation as a function of movement duration. *C* and *D*: modulation amplitude as a function of movement amplitude. *E* and *F*: discharge rate as a function of movement velocity. Arrows: spontaneous rate. Slopes of the regression lines from *A*–*F* are 1.25 (1 point, 348–758, is off scale), 0.75, 0.69, 0.72, 0.27, and 0.59.

neurons discharged during reach and grasp with modulations of 150 and 70 imp/s. Four NL neurons were tested on at least one proximal and one distal device, and three showed specificity. One of four neurons tested responded to perturbations.

In summary, it seems that the NL neurons are similar to NI neurons in that they discharge more strongly during reach and grasp than during device use, and some forelimb NL neurons do not discharge at all during device use. The NL population, however, did show a tendency for stronger device discharge and greater specificity. Whether this is due to a sampling error or represents a true difference between NI and NL remains to be tested by a study of a larger number of NL neurons.

Discharge during free-form movement

Essentially all forelimb neurons fired more strongly during free-form movements than during device use. The contrast between free-form and device use became apparent as the animal switched between devices during testing: vigorous firing occurred as a monkey released one device, repositioned the arm and hand, and gripped the new device. As the monkey commenced the tracking task, modulations decreased dramatically or ceased. Occasionally, the monkeys would readjust the grip or hand position, and it was common for bursting to accompany these readjustments.

For 41 of the 66 forelimb interpositus neurons, discharge rate (based on 100-ms sample intervals) was measured during a more or less stereotyped reach and grasp movement. The movement began with the monkey holding a device handle near the waist; then the monkey extended the arm and hand to grasp a raisin held in front at shoulder height. The monkey then retrieved the raisin to the mouth, placed it in the mouth, and returned to the device handle. Discharge during the movement increased more than threefold from a mean rate of 64 ± 44 imp/s before movement to

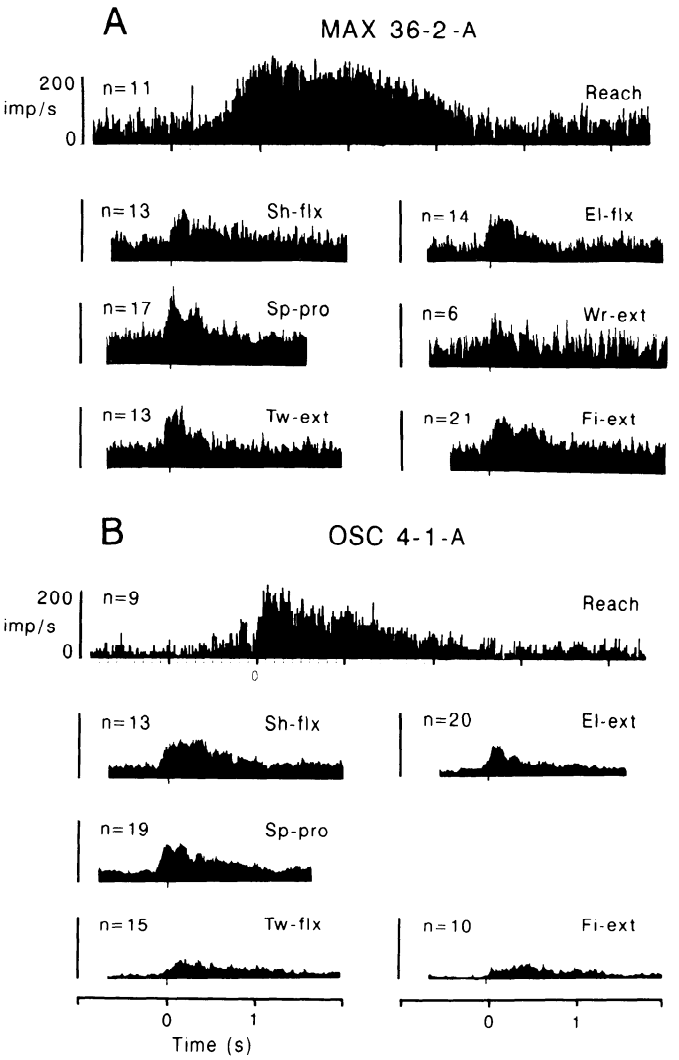

FIG. 8. Discharge of 2 nucleus interpositus anterior (NIA) neurons (*A* and *B*) that exhibited strong modulation during operation of the indicated devices compared with even stronger discharge during free-form reaching. Reach-related modulations are aligned on reach onset as determined from videotaped movements. Discharge records during device operation are averages for the direction of movement that elicited the largest modulation.

215 ± 71 imp/s during the movement (DOM = 149 ± 68 imp/s).

Figure 8 shows the discharge of 2 of the 32 device-related neurons that fired well during device use but fired more strongly when the monkeys reached for, grasped, and retrieved a raisin. The remaining forelimb neurons (27, or 46% of the forelimb population tested) had either no or very weak modulations during device use. Two of the neurons that were classified as not having device discharge are shown in Fig. 9. Despite the lack of discharge modulation during device use, there is a prominent increase in discharge during a reach and grasp. The lack of modulation during device use was not due to averaging over unsynchronized trials, because inspection of individual trials indicated a uniformly low discharge modulation during device use.

The population of neurons that modulated during device use modulated more strongly during reaching than the population of neurons that failed to modulate during device use

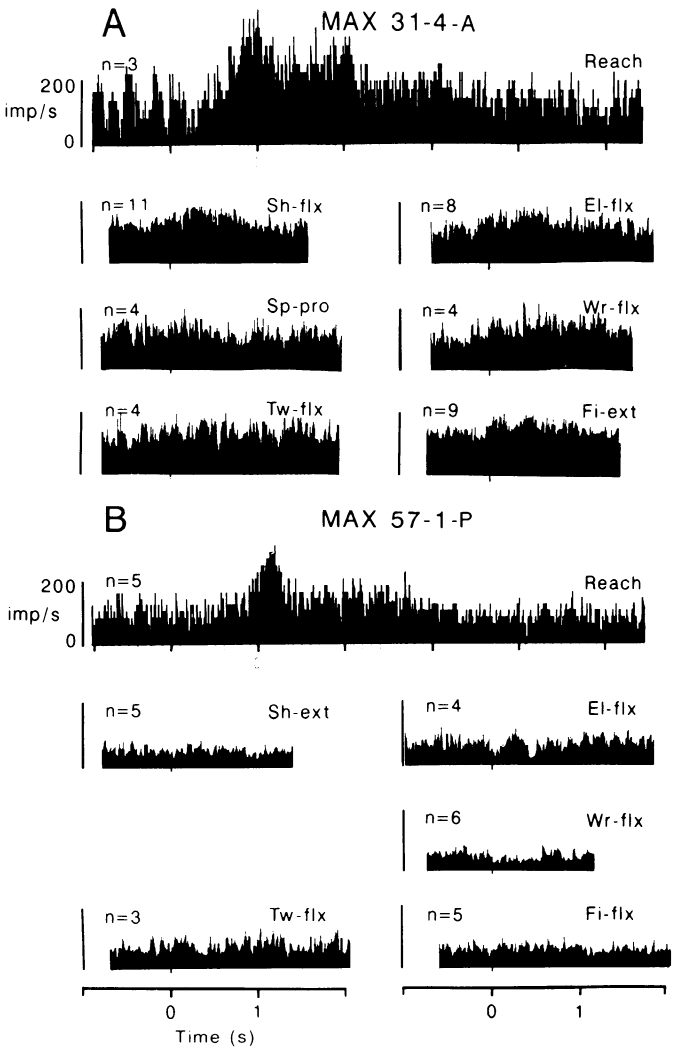

FIG. 9. Discharge of a nucleus interpositus anterior (NIA) (*A*) and a nucleus interpositus posterior (NIP) neuron (*B*) that revealed weak or no modulation during operation of the indicated devices is compared with strong reach-related discharge. Reach-related discharge is aligned on reach onset as determined from videotaped movements. Discharge records during device operation are averages for the direction of movement that elicited the largest modulation.

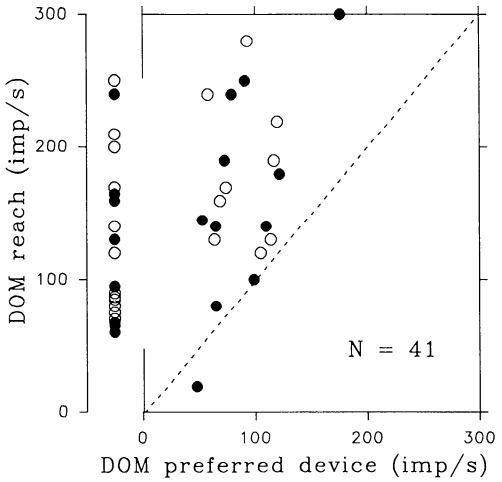

FIG. 10. Depth of modulation of interpositus neurons during reaching vs. that during operation of the preferred device in the preferred direction. Each data point represents an average value obtained for a single nucleus interpositus anterior (NIA) (●) or nucleus interpositus posterior (NIP) (○) neuron. Reach-related modulations for 21 neurons that did not modulate discharge during device use are plotted to the left of the *x*-axis.

(171 ± 70 vs. 128 ± 61 imp/s). The difference between the populations is statistically significant ($P < 0.05$) and suggests that neurons modulating during device use were generally more excitable. The average modulation during reach and grasp was more than two times greater than during device use (171 vs. 84 imp/s).

The sizes of modulations for forelimb neurons during reach and grasp are plotted in Fig. 10. For neurons that modulated during device use, modulation during reach and grasp is plotted against the strongest modulation seen on any device. For this comparison, modulation during device use was measured with a rate meter that recorded the highest discharge rate over 100-ms intervals. Neurons that failed to modulate during device use are plotted as a single row to the left of the *x*-axis. Only one forelimb neuron showed a stronger modulation during device use than during reach and grasp, and the modulation was low for both movements.

Although high discharge modulation during reach and grasp was a common property for NI and dorsal NL neurons, the patterns of discharge during the reach and grasp varied between cells. Figures 8 and 9 illustrate that modulations during reach and grasp showed a variety of shapes. Using slow-motion video review of the movements, discharge of the neurons appeared to be correlated with phases of the movement involving hand or finger use. However, device testing did not reveal any preference for greater modulations during use of the finger device as opposed to other devices.

DISCUSSION

Our results demonstrate a movement-related organization within interpositus based on discrete but relatively large divisions of the body. Most neurons discharge preferentially during movement of the forelimb, hindlimb, mouth/face, or eyes. Cells with similar movement relations tend to group together to form subregions within the nuclei.

More intensive study of forelimb neurons using devices that limit movement to specific joints produced surprising

results: many forelimb neurons failed to modulate during isolated movement about any forelimb joint, and the cells that did modulate showed little specificity for particular joints. Yet, essentially all units fired strongly during reaching out and retrieving a raisin. Reaching for and grasping an object appears to be qualitatively different from making movements during a tracking task.

The following discussion argues that in many ways our findings are similar to those of previous studies. We then discuss several possibilities for the dramatic differences in firing rate during reach and grasp versus tracking movements.

Movement organization within interpositus

Current views of cerebellar somatotopy incorporate multiple representations of the body, one vermal, one intermediate, and one lateral (Asanuma et al. 1983; Thach et al. 1992). In certain aspects, our data agree with this schema: within interpositus, we found one eye movement area, one mouth/face area, and, although both forelimb and hindlimb-related cells are found in NIA and NIP, the forelimb and hindlimb representations might be functionally continuous across interpositus divisions. However, the same functional argument that would make limb representations continuous across divisions of NI would also require making regions of NL continuous with NI.

EYE MOVEMENT REPRESENTATION. Eye movement–related neurons are found in a discrete region in the ventral and lateral parts of NIP. On its lateral border, the region appears to be continuous with an eye movement area in ventral NL. Despite the relatively large size of the region, there has been only brief mention of eye movement neurons within interpositus (Hepp et al. 1982; MacKay 1988b). In contrast, eye movement neurons in NL have been well characterized (Chubb and Fuchs 1982; Gardner and Fuchs 1975; Hepp et al. 1982).

The presence of an eye movement area is further supported by anatomic evidence: ventral-lateral NIP projects heavily to the superior colliculus (and possibly oculomotor nucleus) in monkey (Gonzalo-Ruiz et al. 1988; May et al. 1990) as well as other species (Hirai et al. 1982; Kawamura et al. 1982; Martin et al. 1974; May and Hall 1986; Roldan and Reinoso-Suarez 1981; Uchida et al. 1983). The anatomic location of NI and NL cells projecting to the superior colliculus coincides well to the regions that we identified as containing eye movement neurons.

In complement to their tectal projection, ventral-lateral NIP and ventral NL have little projection to the magnocellular red nucleus (Kennedy et al. 1986; Stanton 1980), which contains head and limb but no eye movement–related neurons (Gibson et al. 1985a). Ventral regions of NL do connect to regions of the thalamus related to the frontal eye fields (Stanton 1980; Stanton et al. 1988) as well as to caudal ventral anterior nucleus (VA), where Anderson and Turner (1991) have identified eye movement neurons that receive cerebellar input.

It is likely that eye movement neurons in NIP/NL are functionally distinct from those of the medial nucleus, because the NIP/NL projection onto the superior colliculus includes the entire visual field representation whereas the medial nucleus projection is limited to foveal areas (May et al. 1990). Although our description of the area is qualitative, the observations do demonstrate a substantial, largely unrecognized, eye movement area within NIP that merits detailed study.

MOUTH/FACE AND LIMB REPRESENTATIONS. One other study, that of Thach et al. (1982), has generated a comprehensive map of movement-related neural discharge in interpositus based on single-unit recordings. A comparison of the maps shows that both place mouth/face neurons in more caudal areas of interpositus and hindlimb neurons in more rostral areas. Thach et al. (1982) and Schieber and Thach (1985), however, found forelimb neurons throughout interpositus, whereas we found no forelimb neurons in the rostral areas of NIA or NL. Our distribution of forelimb recording sites agrees with the distribution shown by Harvey et al. (1979).

Our data confirm the observation of Thach et al. (1982) that body representation within interpositus is paralleled by representation in the adjoining areas of NL. It is difficult to distinguish between NI and neighboring dorsal NL on the basis of movement relations, which suggests functional continuity across these areas. Using quantitative analysis of neural discharge during wrist movements and finger prehension, Wetts et al. (1985) report similar discharge properties in NI and neighboring NL. Some anatomic support for a functional continuity comes from studies of cerebellar projections to RNm, because wheat germ agglutinin-horseradish peroxidase (WGA-HRP) injections into RNm retrogradely label cells in dorsal NL as well as NI [Kennedy et al. (1986) in monkey; Robinson et al. (1987) in cat].

In contrast to the dorsal regions of NL, we were unable to determine clear movement relations for neurons in ventral regions of NL [the neurons studied by Wetts et al. (1985) were also confined to the dorsal half of NL]. Ventral NL neurons may be more dependent on such variables as response set [as demonstrated for dentate neurons by Strick (1983)]. In any case, it is clear that NL is not functionally homogeneous.

As is the case for NIA and dorsal NL, no obvious differences in recordings could be discerned between forelimb units located in NIA and NIP, and one could argue that the nuclear divisions contain only one somatotopy. The border between hindlimb and forelimb slants so that in more caudal sections hindlimb is confined to the medial borders of NIA and NIP. Support for a slanted border zone between limb representations comes from studies of interpositus projections to hindlimb and forelimb regions of RNm in the cat (Robinson et al. 1987).

However, from recording locations one could also argue that there are independent limb representations in NIA and NIP. There is a hint of a gap between hindlimb representation in NIA and NIP, and the forelimb neurons are not clearly separated from hindlimb neurons in NIP. This limb mapping fits well with the data of Allen et al. (1977) from recordings of nuclear responses to stimulation of motor cortex in anesthetized monkeys; they show a reasonably clear separation of hindlimb and forelimb in NIA (with hindlimb more anterior) but a mixed representation of hindlimb and forelimb in NIP.

Two major anatomic considerations, discussed in the fol-

lowing paragraphs, strengthen the argument that NIA and NIP contain functionally separate representations of the body: first, there is a mirror image representation of the body in intermediate cerebellar cortex that is preserved in its nuclear projection; second, different divisions of the inferior olive with distinct properties project to NIA and NIP and their associated cortical areas. The anatomic data are from both monkey and cat, but, to date, there is little evidence that the organization of intermediate cerebellum differs between these species.

A double representation of the body, one in anterior lobe and one in posterior lobe, seems to exist in intermediate cerebellar cortex for both cat and monkey (Hampson et al. 1952; Snider 1950; Snider and Stowell 1944). The double cortical representation is preserved in the cortical projection to the deep nuclei, although the mapping is complex and follows the zonal organization described by Voogd (Groenewegen and Voogd 1977; Groenewegen et al. 1979; Voogd 1969; Voogd and Bigaré 1980). Anterograde tracers injected into forelimb cerebellar cortex label adjacent areas in interpositus, caudal NIA and rostral NIP (Bishop et al. 1979; Trott and Armstrong 1987a,b), whereas injections into hindlimb cortex label separated regions, one rostral in NIA and one caudal in NIP (Bishop et al. 1979).

Consideration of olivary input to intermediate cerebellum adds support for a dual limb representation and suggests a possible explanation for an unclear hindlimb/forelimb separation in NIP. NIA and NIP and their associated cortical zones receive input from different divisions of the inferior olive in both monkey and cat (Groenewegen et al. 1979; Kalil 1979). Rostral dorsal accessory olive (rDAO), which contains a representation of the entire body surface (Berkley and Hand 1978; Boesten and Voogd 1975; Gellman et al. 1983), projects in a topographic pattern to NIA (Gibson et al. 1987). The resulting somatotopy in the cat NIA is similar to the motor representation that we found in the monkey.

NIP receives input from the rostral medial accessory olive (rMAO). The somatotopic organization within cat rMAO is less clear than that of rDAO, emphasizes the forelimb, and contains little or no facial representation (Gellman et al. 1983, 1985), resembling the motor representation that we found in NIP. In addition to the differences in mapping, rMAO cells have larger and more complex fields than rDAO cells and often include more than one limb. Complex properties might account for the relatively high number of unrelated cells noted in NIP as well as for the lack of a clear forelimb/hindlimb somatotopy.

In summary, from discharge/movement relations alone we cannot make a case for more than one motor representation within NIA, NIP, and NL. However, a conclusion of functional continuity across nuclear divisions is qualified by two major considerations. First, we were unable to specify movement relations beyond forelimb, hindlimb, mouth/face, and eyes. There are certainly many functional characteristics for which our testing was not sensitive; this qualification is further strengthened by anatomic evidence supporting different functions for NIA and NIP. Second, our testing in NL was largely limited to dorsal areas neighboring NIA; other areas of NL may contain additional motor representations.

Movement relations of forelimb neurons

This section of the discussion deals with the more detailed information gained from device and free-form testing of neurons that fired during forelimb movement. Two major issues are addressed; one is the comparison of interpositus discharge characteristics to those of its target nuclei, the RNm and thalamus; the other is the nature of movement representation within interpositus.

Cellular properties of interpositus projection targets

Interpositus selectively targets the RNm (Flumerfelt et al. 1973) and regions of the ventral lateral thalamus (Asanuma et al. 1983) referred to as VLp (Jones 1989). Several chronic recording studies in monkeys have investigated discharge properties of RNm and VLp thalamic neurons during movement. The following discussion compares and contrasts the findings of those studies with the present results.

INTERPOSITUS VERSUS RNm DISCHARGE. The multiple-device testing paradigm used for interpositus testing was adapted from an earlier study of RNm by Gibson et al. (1985a,b), and, therefore, the results from the two studies are directly comparable.

The qualitative description of RNm neurons during reaching and grasping is very similar to what we found for NI neurons. RNm cells discharge at high rates during free-form (usually reaching and grasping) movements, and discharge usually could be associated with movement of specific limbs (Gibson et al. 1985a). Observation aided by video taping indicated that most RNm cells, like NI cells, are active during phases of reaching that involve hand use or, in the case of the hindlimb, toe use (Gibson et al. 1985a). Kennedy (1987) and Houk et al. (1988) have also reported that RNm discharge is well-related to hand use.

Additional similarities, as well as some differences, become apparent when relations to device use are considered. Our best-related NI cells (11 neurons) increased firing rates before movement and were directionally selective, and the preferred device for seven of the cells was the twister, characteristics shared by RNm neurons (Gibson et al. 1985b).

Despite less complete testing on multiple devices, RNm neurons showed stronger specificity for particular devices (especially the twister device) than did NI neurons. NI neurons, like RNm neurons, had high correlations between modulation duration and movement duration as well as between the number of spikes and movement amplitude. Discharge rate of 7 of 11 NI neurons was significantly correlated also with movement velocity; however, the highest velocity correlations were lower than the highest seen for RNm neurons.

Several possibilities exist why RNm neurons might show stronger parametric relations to movement than NI neurons. One possibility is that motor cortical input to RNm could play an important modulatory role in the generation of RNm motor signals (Humphrey and Reitz 1976). However, both anatomic and physiological evidence indicate that the dominant RNm input originates in NI and that cortical input is relatively weak (Humphrey and Reitz 1976; Humphrey et al. 1984; Kennedy et al. 1986). Also,

RNm neurons fire at high rates in the absence of cortical input (Houk et al. 1988). Another possibility is that RNm activity reflects the combined action of many NI neurons. It has been estimated that ~50 NI neurons converge on each RNm neuron (Toyama et al. 1970). A large degree of both convergence and divergence is supported anatomically because axons from NI neurons branch extensively within RNm (Shinoda et al. 1988), and RNm neurons have large dendritic fields (Wilson et al. 1987). Individual NI units might be active during only a subset of conditions that elicit discharge from a given RNm neuron.

INTERPOSITUS VERSUS THALAMIC DISCHARGE. Four studies have investigated the properties of thalamic neurons in awake monkeys (Anderson and Turner 1991; Horne and Porter 1980; MacPherson et al. 1980; Strick 1976b), and all have reported strong neural discharge during active movements. Methodological variations and anatomic considerations do not allow as strong comparisons with interpositus as is the case with RNm. The anterior portions of VL receive input from the globus pallidus rather than the cerebellar nuclei, and one cannot be sure that the studies of the thalamus were dealing exclusively with cerebellar receiving areas. However, all studies included recordings from cerebellar receiving areas, and Anderson and Turner (1991) identified the sources of input to the thalamic cells.

There seems to be an overall movement somatotopy within thalamus that agrees well with its projection to cortex as well as with its input from cerebellum (Asanuma et al. 1983; MacPherson et al. 1980; Strick 1976a). Head is located medially, forelimb intermediately, and hindlimb laterally. Despite a general agreement with this scheme there is little evidence for a finer somatotopy within a limb region. MacPherson et al. (1980) used an isolated wrist movement and found related cells throughout the forelimb region of thalamus. Anderson and Turner (1991) report units with relations to individual joints, but the somatotopy is complex and suggests the possibility of multiple maps.

Horne and Porter (1980) also have reported thalamic discharge associated with movements about specific joints —the behavioral task employed included reaching out, grasping a knob, and pulling. Discharge was associated with specific joints by relating its timing to the timing of components of the complex movement. Their results indicate that all forelimb joints are represented with a bias to the distal joints (no joint somatotopy is shown). However, Harvey et al. (1979) used a similar, perhaps identical, task in their study of interpositus and reached the conclusion that most NI units were related to proximal joints. A comparison of records shown in Fig. 2 of Harvey et al. to Fig. 3 of Horne and Porter (1980) indicates that units with similar discharge patterns are attributed to shoulder movements in the first case and finger movements in the second. Our results suggest that the complex reaching task may be more important for eliciting discharge than involvement of specific joints.

The reports on VL thalamus include some striking differences as compared with NI. Horne and Porter (1980), for example, find that 52% of VL cells modulated to movements of either limb. We saw a few cells with bilateral modulations in NI but certainly not enough to explain the percentage in thalamus. MacPherson et al. (1980) report that 80% of thalamic cells fired as strongly after presentation of the visual target whether or not a wrist movement ensued. We saw evidence for visual responsiveness in a few cells, but modulation of most NI cells was always associated with active movement, and no cell discharge in our paradigm was time-locked to the visual target movement [although MacKay (1988a) has reported a few nuclear responses timed to target onset]. Strick (1976a) synchronized the discharge modulation of thalamic cells with either the target or arm movement and found a tight coupling to arm, but not target, movement.

Considering the rather weak supporting evidence for visual responses in thalamus, it seems possible that the responses of MacPherson et al. (1980) to the cue may have reflected some preparatory adjustment, such as tightening grip on the manipulandum, made before wrist movement. Of course, it is also possible that the differences are due to other sources of thalamic input, such as the basal ganglia.

NATURE OF MOVEMENT REPRESENTATION. Our multiple device testing produced little evidence that NI discharge is related to movement about individual joints. Rather, discharge often occurred during use of more than one device and was not as strong as discharge during reaching and grasping.

An obvious hypothesis that might explain a lack of joint specificity is that neural discharge may be related to activation of particular muscles. Because many forelimb muscles have actions across multiple joints, movement about different individual joints could still involve a common muscle and, therefore, neural activation. For instance, extensor digitorum works across elbow, wrist, and finger joints and might be active during use of several devices. Similarly, several upper arm muscles, such as biceps and triceps, have actions across both shoulder and elbow joints.

The hypothesis that NI discharge relates to particular muscles, however, could only explain lack of specificity in certain cases. Some cells fired equally well to movements of the shoulder as to movements of the fingers with the forearm supported, yet no muscles act across all of these joints (although hand use is required by all devices). The immediately following paper (Van Kan et al. 1993), which used the same paradigm and included the same monkeys, demonstrates a much higher degree of joint specificity for mossy fiber afferents to cerebellar cortex. It is very likely that the mossy fiber input reflects afference from limb muscles, if so, the multiple device paradigm effectively separates the actions of specific muscles.

Perhaps more troubling to the hypothesis that NI discharge relates to activation of particular muscles is the fact that about half of the cells failed to fire at all during any device use, and the cells that did fire during device use fired much more strongly during a reach and grasp. If NI discharge relates to specific forelimb muscles, many cells should have discharged as strongly or more strongly during device use as during reach and grasp (as was the case for mossy fibers reported in the following paper). Again, a caveat must be made for the hand musculature: activation of

hand musculature is certainly more complicated and inclusive during a reach and retrieval than during constant grip on a device handle (although forces generated by grip during device movement may be substantial).

The study by Thach et al. (1982) is the only other study of interpositus movement relations that used a multiple-device approach. Although they do indicate that individual interpositus neurons can be associated with movements of specific joints, it is difficult to tell if the degree of specificity is stronger than that which we found. Discharge records for six NL neurons are illustrated during operation of various devices (see their Fig. 3). As in our data, a given neuron's discharge is specifically associated with movements of either the forelimb, hindlimb, or face. Within the forelimb cells, however, the records indicate that some cells fired to movement of more than one forelimb joint, and one showed modulation during both wrist and shoulder movement. The modulations appear lower than the modulations that we commonly observed during reach and grasp but may be similar to our device testing. Overall, it appears that the Thach et al. (1982) data are consistent with ours.

Our observation that interpositus neurons fire at substantially higher rates during reach and grasp has been made by several other investigators, although the interpretations differ. Harvey et al. (1979) reported that interpositus neurons increased discharge markedly when monkeys reached for a manipulandum or a food reward, but not when they actually used the manipulandum. For the one cell shown, discharge rate was 5 times higher during reach and grasp than during manipulandum use. Similarly, MacKay (1988a) shows interpositus rates of ~150–200 imp/s when monkeys reach out to press a button, but during an elbow flexion and extension task (MacKay 1988b), interpositus discharge was relatively weak, ~40–70 imp/s for the illustrated neurons. Also, MacKay reports that ~40% of interpositus neurons were active during reach and button press compared with 17% during device use.

Both Harvey et al. (1979) and MacKay (1988a) attributed discharge during reaching to involvement of proximal muscles. Harvey and colleagues made the judgement on the basis of visual observation with and without manual restraint of specific joints, whereas MacKay made the judgement because the time course of proximal muscle activation was similar to the time course of interpositus activation. Our testing singled out neither distal nor proximal movements and suggests that the nature of the task is more important for eliciting discharge than is the involvement of specific joints. The observation that reaching, whether to grasp a device handle, push a button, or grasp a raisin, is accompanied by high interpositus discharge rates is common to all three experiments. Weak or no discharge modulation during device use is also common to all three experiments.

Although many studies have recorded from interpositus neurons during device use, only a few examples of interpositus discharge have been illustrated. The examples display uniformly low discharge modulation, lower than modulations that we observed during reach and retrieval (149–176 imp/s) but within the range of modulations during device tracking. Thach (1978), testing with wrist movements under various loads, found increases in discharge of ~50 imp/s under the highest loading conditions. Modulations accompanying unloaded movements were either nonexistent or very small. Schieber and Thach (1985) illustrate three interpositus neurons during wrist tracking of slowly moving targets. Modulation for wrist movement was ~40 imp/s compared with 75 imp/s for prehension (1 cell). Loaded wrist movements for two other interposed cells produced modulations of only 30 and 12 imp/s. Finally, Fortier et al. (1989) show discharge records of two interpositus cells during "a whole-arm reaching movement" with modulations of ~60 imp/s, and a population (n = 65) modulation of ~30 imp/s.

The relatively low modulations reported by Fortier et al. (1989) seem to contradict our findings of high modulations during reach and grasp, but their reaching task is more directly comparable to our device testing because no grasp component is present. In the Fortier et al. (1989) task, monkeys were trained to move a pointer in a two-dimensional plane. The movement involved the shoulder and elbow, but there was no hand component other than the constant grip. It is an interesting possibility that the addition of the grasp is responsible for the much higher discharge during reach and grasp. Some support for hand involvement being a crucial factor comes from the finding that a prehension task produces relatively high modulation (Wetts et al. 1985) in NI and NL neurons.

As a whole, the experimental data indicate that NI discharge is strongly attenuated when monkeys are required to perform a task by moving a device as opposed to making a whole limb movement with a grasping component. Why might this be?

Much of our thinking has focused on the differences in the movements required by the tasks, but it may be that the tasks are fundamentally different. In one case, the monkey moves a device to effect a remote position change of a cursor; in the other case, the animal is using sensory information to guide his limb to a point in space. Device operation is clearly a less "natural" movement that requires extensive training. It may be that direct association of sensory information with the moving limb is critical for engaging cerebellar circuitry. We cannot separate this factor in our data, but the tight parametric relations of some NI and RNm (Gibson et al. 1985b) cells with movement suggests that a remote tracking task can, at least in some cases, effectively engage the circuitry of intermediate cerebellum.

Another possibility is that a free reach may simply require much more sensory guidance (visual, somesthetic, etc.) than moving a device limited in its degrees of freedom. However, the high firing rates with small limb adjustments, which often seemed to occur without attention from the monkeys, would seem to require no more guidance than device movements.

If sensory guidance is critical for engaging NI neurons, one might expect to find NI neurons with sensory responses. However, Chapman et al. (1986) report that task-related interpositus neurons modulated primarily to the movement; only few neurons were related to the cue to move, and in all cases these were selective for somesthetic cues. Dentate modulations, in contrast, depended more

strongly on the cue to move (most often visual) than on the movement.

Our observations lead us to conclude that a whole-arm movement is necessary for interpositus discharge. The cerebellum has classically been viewed as a structure for coordinating movement across joints (Flourens 1824), and recently Goodkin and Thach (1990) have presented data that single-joint movements are relatively unaffected by cerebellar damage, whereas coordinated movements are severely impaired. Essentially all NI neurons fire strongly during reach and grasp, and most of the small number of cells that showed consistent relations to device movement modulated during use of the twister, which required a coordinated movement of wrist and fingers. Together with our observation that discharge seemed to correlate with hand use during reaching, the results suggest that coordinated forelimb movements with a hand component are necessary to effectively engage NI neurons. A recent study (Van Kan et al. 1990) reports that hand use is critical for the high NI discharge rates accompanying reaching and grasping.

Anatomic data from cats and monkeys also suggest that NI might exert control over the entire limb, but with a special emphasis on digit movements. Spinal projections of the RNm terminate on interneurons at all spinal levels (Kuypers et al. 1962), but terminations occur selectively on motoneuron pools serving musculature of the hand (Holstege et al. 1988; McCurdy et al. 1987; Ralston et al. 1988; Robinson et al. 1987).

Movement organization within forelimb interpositus is not based on a simple joint (or muscle) representation. It seems likely that it is based on coordinated movements that include the hand. In the following paper, using the same experimental approach, we demonstrate that mossy fiber input to intermediate cerebellum represents movements of the forelimb in a very different fashion.

We acknowledge D. Browdy and C. Reckling for computer programming and R. Meza and Dr. K. Horn for assistance in data analysis. We thank Drs. A. F. Fuchs and M. Glickstein 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-21218 and NS-24042 to A. R. Gibson, NS-27373 to P. L. E. van Kan, and NS-17489 to J. C. Houk.

Address reprint requests to P. L. E. van Kan, Div. of Neurobiology, Barrow Neurological Institute, 350 W. Thomas Rd., Phoenix, AZ 85013.

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

REFERENCES

ALLEN, G. I., GILBERT, P. F. C., MARINI, R., SCHULTZ, W., AND YIN, T. C. T. Integration of cerebral and peripheral inputs by interpositus neurons in the monkey. *Exp. Brain Res.* 27: 81–92, 1977.

ANDERSON, M. E. AND TURNER, R. S. Activity of neurons in cerebellar-receiving and pallidal-receiving areas of the thalamus of the behaving monkey. *J. Neurophysiol.* 66: 879–893, 1991.

ASANUMA, C., THACH, W. T., AND JONES, E. G. Anatomical evidence for segregated focal groupings of efferent cells and their terminal ramifications in the cerebellothalamic pathway of the monkey. *Brain Res. Rev.* 5: 267–297, 1983.

BERKLEY, K. J. AND HAND, P. J. Projections to the inferior olive of the cat. II. Comparisons of input from the gracile, cuneate, and spinal trigeminal nuclei. *J. Comp. Neurol.* 180: 253–264, 1978.

BISHOP, G. A., MCCREA, R. A., LIGHTHALL, J. W., AND KITAI, S. T. An HRP and autoradiographic study of the projection from the cerebellar cortex to the nucleus interpositus anterior and nucleus interpositus posterior of the cat. *J. Comp. Neurol.* 185: 735–756, 1979.

BOESTEN, A. J. P. AND VOOGD, J. Projections of the dorsal column nuclei and the spinal cord on the inferior olive of the cat. *J. Comp. Neurol.* 161: 215–238, 1975.

BRODAL, P. The corticopontine projection in the rhesus monkey. Origin and principles of organization. *Brain* 101: 251–283, 1978.

CHAPMAN, C. E., SPIDALIERI, G., AND LAMARRE, Y. Activity of dentate neurons during arm movements triggered by visual, auditory, and somesthetic stimuli in the monkey. *J. Neurophysiol.* 55: 203–226, 1986.

CHUBB, M. C. AND FUCHS, A. F. Contribution of y group of vestibular nuclei and dentate nucleus of cerebellum to generation of vertical smooth eye movements. *J. Neurophysiol.* 48: 75–99, 1982.

EVARTS, E. V. AND THACH, W. T. Motor mechanisms of the CNS: cerebro-cerebellar interrelations. *Annu. Rev. Physiol.* 31: 451–498, 1969.

FLOURENS, P. *Recherches Experimentales sur les Proprietes et les Fonctions du Systeme Nerveux dans les Animaux Vertebres.* Paris, 1824. Translated in: Clarke, E. and O'Malley, C. D. *The Human Brain and Spinal Cord.* Los Angeles: Univ. of California Press, 1968, pp. 657–661.

FLUMERFELT, B. A., OTABE, S., AND COURVILLE, J. Distinct projections to the red nucleus from the dentate and interposed nuclei in the monkey. *Brain Res.* 50: 408–414, 1973.

FORTIER, P. A., KALASKA, J. F., AND SMITH, A. M. Cerebellar neuronal activity related to whole-arm reaching movements in the monkey. *J. Neurophysiol.* 62: 198–211, 1989.

GARDNER, E. P. AND FUCHS, A. F. Single-unit responses to natural vestibular stimuli and eye movements in deep cerebellar nuclei of the alert rhesus monkey. *J. Neurophysiol.* 38: 627–649, 1975.

GELLMAN, R., GIBSON, A. R., AND HOUK, J. C. Somatosensory properties of the inferior olive of the cat. *J. Comp. Neurol.* 215: 228–243, 1983.

GELLMAN, R., GIBSON, A. R., AND HOUK, J. C. Inferior olivary neurons in the awake cat: detection of contact and passive body displacement. *J. Neurophysiol.* 54: 40–60, 1985.

GIBSON, A. R., HOUK, J. C., AND KOHLERMAN, N. J. Magnocellular red nucleus activity during different types of limb movement in the macaque monkey. *J. Physiol. Lond.* 358: 527–549, 1985a.

GIBSON, A. R., HOUK, J. C., AND KOHLERMAN, N. J. Relation between red nucleus discharge and movement parameters in trained macaque monkeys. *J. Physiol. Lond.* 358: 551–570, 1985b.

GIBSON, A. R., ROBINSON, F. R., ALAM, J., AND HOUK, J. C. Somatotopic alignment between climbing fiber input and nuclear output of the intermediate cerebellum. *J. Comp. Neurol.* 260: 362–377, 1987.

GLICKSTEIN, M., MAY, J. G., III, AND MERCIER, B. E. Corticopontine projection in the macaque: the distribution of labelled cortical cells after large injections of horseradish peroxidase in the pontine nuclei. *J. Comp. Neurol.* 235: 343–359, 1985.

GONZALO-RUIZ, A., LEICHNETZ, G. R., AND SMITH, D. J. Origin of cerebellar projections to the region of the oculomotor complex, medial pontine reticular formation, and superior colliculus in new world monkeys: a retrograde horseradish peroxidase study. *J. Comp. Neurol.* 268: 508–526, 1988.

GOODKIN, H. P. AND THACH, W. T. Mechanism of recovery from cerebellar incoordination. *Soc. Neurosci. Abstr.* 16: 1317, 1990.

GROENEWEGEN, H. J. AND VOOGD, J. The parasagittal zonation within the olivocerebellar projection. I. Climbing fiber distribution in the vermis intermediate and hemispheric parts of cat cerebellum. *J. Comp. Neurol.* 174: 417–488, 1977.

GROENEWEGEN, H. J., VOOGD, J., AND FREEDMAN, S. L. The parasagittal zonation within the olivocerebellar projection. II. Climbing fiber distribution in the intermediate and hemispheric parts of cat cerebellum. *J. Comp. Neurol.* 183: 551–602, 1979.

HAMPSON, J. L., HARRISON, C. R., AND WOOLSEY, C. N. Cerebro-cerebellar projections and the somatotopic localization of motor function in the cerebellum. *Res. Publ. Assoc. Res. Nerv. Ment. Dis.* 301: 299–316, 1952.

HARVEY, R. J., PORTER, R., AND RAWSON, J. A. The natural discharges of Purkinje cells in paravermal regions of lobules V and VI of the monkey's cerebellum. *J. Physiol. Lond.* 271: 515–536, 1977.

HARVEY, R. J., PORTER, R., AND RAWSON, J. A. Discharges of intracerebellar nuclear cells in monkeys. *J. Physiol. Lond.* 297: 559–580, 1979.

HEPP, K., HENN, V., AND JAEGER, J. Eye movement related neurons in the cerebellar nuclei of the alert monkey. *Exp. Brain Res.* 45: 253–264, 1982.

HIRAI, T., ONEDERA, S., AND KAWAMURA, K. Cerebellotectal projections

studied in cats with horseradish peroxidase or tritiated amino acids axonal transport. *Exp. Brain Res.* 48: 1–12, 1982.

HOLSTEGE, G., BLOK, B. F., AND RALSTON, D. D. Anatomical evidence for red nucleus projections to motoneuronal cell groups in the spinal cord of the monkey. *Neurosci. Lett.* 95: 97–101, 1988.

HORNE, M. K. AND PORTER, R. The discharges during movement of cells in the ventrolateral thalamus of the conscious monkey. *J. Physiol. Lond.* 304: 349–372, 1980.

HOUK, J. C., GIBSON, A. R., HARVEY, C. F., KENNEDY, P. R., AND VAN KAN, P. L. E. Activity of primate magnocellular red nucleus related to hand and finger movement. *Behav. Brain Res.* 28: 201–206, 1988.

HUMPHREY, D. R., GOLD, R., AND REED, D. J. Sizes, laminar and topographic origins of cortical projections to the major divisions of the red nucleus in the monkey. *J. Comp. Neurol.* 225: 75–94, 1984.

HUMPHREY, D. R. AND REITZ, R. R. Cells of origin of corticorubral projections from the arm area of primate cortex and their synaptic actions in the red nucleus. *Brain Res.* 110: 162–169, 1976.

JONES, E. G. Correlation and revised nomenclature of ventral nuclei in the thalamus of human and monkey. *Stereotact. Funct. Neurosurg.* 54: 1–20, 1989.

KALIL, K. Projections of the cerebellar and dorsal column nuclei upon the inferior olive in the rhesus monkey: an autoradiographic study. *J. Comp. Neurol.* 188: 43–62, 1979.

KAWAMURA, S., HATTORI, S., HIGO, S., AND MATSUYAMA, T. The cerebellar projections to the superior colliculus and pretectum in the cat: an autoradiographic and horseradish peroxidase study. *Neuroscience* 7: 1673–1689, 1982.

KENNEDY, P. R. Parametric relationships of individual digit movements to neuronal discharges in primate magnocellular red nucleus. *Brain Res.* 417: 185–189, 1987.

KENNEDY, P. R., GIBSON, A. R., AND HOUK, J. C. Functional and anatomic differentiation between parvocellular and magnocellular regions of red nucleus in the monkey. *Brain Res.* 364: 124–136, 1986.

KUYPERS, H. G. J. M., FLEMING, W. R., AND FARINHOLT, J. W. Subcorticospinal projections in the rhesus monkey. *J. Comp. Neurol.* 118: 107–137, 1962.

MACKAY, W. A. Unit activity in the cerebellar nuclei related to arm reaching movements. *Brain Res.* 442: 240–254, 1988a.

MACKAY, W. A. Cerebellar nuclear activity in relation to simple movements. *Exp. Brain Res.* 71: 47–58, 1988b.

MACPHERSON, J. M., RASMUSSON, D. D., AND MURPHY, J. T. Activities of neurons in "motor" thalamus during control of limb movement in the primate. *J. Neurophysiol.* 44: 11–28, 1980.

MARTIN, G. F., KING, J. S., AND DOM, R. The projections of the deep cerebellar nuclei of the opossum, *Didelphis marsupialis virginia. J. Hirnforsch.* 15: 545–573, 1974.

MAY, P. J. AND HALL, W. C. The cerebellotectal pathway in the grey squirrel. *Exp. Brain Res.* 65: 202–212, 1986.

MAY, P. J., HARTWICH-YOUNG, R., NELSON, J., SPARKS, D. L., AND PORTER, J. D. Cerebellotectal pathways in the macaque: implications for collicular generation of saccades. *Neuroscience* 36: 305–324, 1990.

MCCURDY, M. L., HANSMA, D. I., HOUK, J. C., AND GIBSON, A. R. Selective projections from the cat red nucleus to digit motoneurons. *J. Comp. Neurol.* 265: 367–379, 1987.

RALSTON, D. D., MILROY, A. M., AND HOLSTEGE, G. Ultrastructural evidence for direct monosynaptic rubrospinal connections to motoneurons in *Macaca mulatta. Neurosci. Lett.* 95: 102–106, 1988.

ROBINSON, F. R., HOUK, J. C., AND GIBSON, A. R. Limb specific relations of the cat magnocellular red nucleus. *J. Comp. Neurol.* 257: 553–577, 1987.

ROLDAN, M. AND REINOSO-SUAREZ, F. Cerebellar projections to the superior colliculus in the cat. *J. Neurosci.* 1: 827–834, 1981.

SCHIEBER, M. H. AND THACH, W. T. Trained slow tracking. II. Bidirectional discharge patterns of cerebellar nuclear, motor cortex, and spindle afferent neurons. *J. Neurophysiol.* 54: 1228–1270, 1985.

SHINODA, Y., FUTAMI, T., MITOMA, H., AND YOKOTA, J. Morphology of single neurons in the cerebello-rubrospinal system. *Behav. Brain Res.* 28: 59–64, 1988.

SNIDER, R. S. Recent contributions to the anatomy and physiology of the cerebellum. *Arch. Neurol. Psychiatry* 50: 196–219, 1950.

SNIDER, R. S. AND STOWELL, A. Receiving areas of the tactile, auditory, and visual systems in the cerebellum. *J. Neurophysiol.* 7: 331–357, 1944.

STANTON, G. B. Topographical organization of ascending cerebellar projections from the dentate and interposed nuclei in *Macada mulatta:* an anterograde degeneration study. *J. Comp. Neurol.* 190: 699–731, 1980.

STANTON, G. B., GOLDBERG, M. E., AND BRUCE, C. J. Frontal eye field efferents in the Macaque monkey. I. Subcortical pathways and topography of striatal and thalamic terminal fields. *J. Comp. Neurol.* 271: 473–492, 1988.

STRICK, P. L. Anatomical analysis of ventrolateral thalamic input to primate motor cortex. *J. Neurophysiol.* 39: 1020–1031, 1976a.

STRICK, P. L. Activity of ventrolateral thalamic neurons during arm movement. *J. Neurophysiol.* 39: 1032–1044, 1976b.

STRICK, P. L. The influence of motor preparation on the response of cerebellar neurons to limb displacements. *J. Neurosci.* 3: 2007–2020, 1983.

THACH, W. T. Discharge of Purkinje and cerebellar nuclear neurons during rapidly alternating arm movements in the monkey. *J. Neurophysiol.* 31: 785–797, 1968.

THACH, W. T. Discharge of cerebellar neurons related to two maintained postures and two prompt movements. I. Nuclear cell output. *J. Neurophysiol.* 33: 527–536, 1970a.

THACH, W. T. Discharge of cerebellar neurons related to two maintained postures and two prompt movements. II. Purkinje cell output and input. *J. Neurophysiol.* 33: 537–547, 1970b.

THACH, W. T. Correlation of neural discharge with pattern and force of muscular activity, joint position, and direction of intended movement in motor cortex and cerebellum. *J. Neurophysiol.* 41: 654–676, 1978.

THACH, W. T., KANE, S. A., MINK, J. W., AND GOODKIN, H. P. Cerebellar output: multiple maps and modes of control in movement coordination. In: *The Cerebellum Revisited,* edited by R. Llinas and C. Sotelo. New York: Springer-Verlag, 1992. In press.

THACH, W. T., PERRY, J. G., AND SCHIEBER, M. H. Cerebellar output: body maps and muscle spindles. In: *The Cerebellum—New Vistas,* edited by S. L. Palay and V. Chan-Palay. Berlin: Springer-Verlag, 1982, p. 440–454.

TOYAMA, K., TSUKAHARA, N., KOSAKA, K., AND MATSUNAMI, K. Synaptic excitation of red nucleus neurons by fibres from interpositus nucleus. *Exp. Brain Res.* 11: 187–198, 1970.

TROTT, J. R. AND ARMSTRONG, D. M. The cerebellar corticonuclear projection from lobule Vb/c of the cat anterior lobe: a combined electrophysiological and autoradiographic study. I. Projections from the intermediate region. *Exp. Brain Res.* 66: 318–338, 1987a.

TROTT, J. R. AND ARMSTRONG, D. M. The cerebellar corticonuclear projection from lobule Vb/c of the cat anterior lobe: a combined electrophysiological and autoradiographic study. II. Projections from the vermis. *Exp. Brain Res.* 66: 339–354, 1987b.

UCHIDA, K., MIZUNO, N., SUGIMOTO, T., ITOH, K., AND KANO, M. Direct projections from the cerebellar nuclei to the superior colliculus in the rabbit: an HRP study. *J. Comp. Neurol.* 216: 319–326, 1983.

VAN KAN, P. L. E., GIBSON, A. R., AND HOUK, J. C. Movement-related inputs to intermediate cerebellum of the monkey. *J. Neurophysiol.* 69: 74–94, 1993.

VAN KAN, P. L. E., HORN, K. M., AND GIBSON, A. R. The importance of combined arm and hand use for discharge of interpositus neurons (Abstract). *Eur. J. Neurosci., Suppl.* 3: 300, 1990.

VAN KAN, P. L. E., HOUK, J. C., AND GIBSON, A. R. Body representation in the nucleus interpositus of the monkey (Abstract). *Neurosci. Lett. Suppl.* 26: 231, 1986.

VOOGD, J. The importance of fibre connections in the comparative anatomy of the mammalian cerebellum. In: *Neurobiology of Cerebellar Evolution and Development,* edited by R. Llinas. Chicago: AMA, 1969, p. 493–541.

VOOGD, J. AND BIGARÉ, F. Topographical distribution of olivary and cortico-nuclear fibers in the cerebellum: a review. In: *The Olivary Nucleus. Anatomy and Physiology,* edited by J. Courville, C. de Montigney, and Y. Lamarre. New York: Raven, 1980, p. 207–234.

WANNIER, T. M. J., MAIER, M. A., AND HEPP-REYMOND, M. C. Responses of motor cortex neurons to visual stimulation in the alert monkey. *Neurosci. Lett.* 98: 63–68, 1989.

WETTS, R., KALASKA, J. F., AND SMITH, A. M. Cerebellar nuclear cell activity during antagonist co-contraction and reciprocal inhibition of forearm muscles. *J. Neurophysiol.* 54: 231–244, 1985.

WILSON, C. J., MURAKAMI, F., KATSUMARU, H., AND TSUKAHARA, N. Dendritic and somatic appendages of identified rubrospinal neurons of the cat. *Neuroscience* 22: 113–130, 1987.