Cerebellar Control of Constrained and Unconstrained Movements. II. EMG and Nuclear Activity

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Goodkin HP and WT Thach. Cerebellar control of constrained and unconstrained movements. II. EMG and nuclear activity. J Neurophysiol 89: 896–908, 2003; 10.1152/jn.00115.2002. The aim of this study was to see in monkeys if neurons in dentate and lateral interposed deep cerebellar nuclei are preferentially active in relation to certain movements relative to others. Simple and compound digit movements were trained with digits, hand, and elbow constrained in a cast. The constrained simple movement was flexion of Thumb or Index; the constrained compound movement, flexion of Thumb + Index. An unconstrained compound movement consisted of a reach to, pinch of, and retrieval of a small food reward (Reach + Pinch). Electromyographic (EMG) recording showed that many muscles in the upper extremity, shoulder girdle, and trunk were active in all movements. EMG/muscle stimulation during the constrained digit movements showed that the digit prime movers were active during, sufficient for, and necessary for performance of these digit tasks. By contrast, EMG/muscle stimulation showed that the proximal muscles (though co-active during the tasks) were neither sufficient nor necessary for performance of the digit tasks. A fraction of those neurons that were active during both the constrained and the unconstrained movements fired at a higher frequency during the unconstrained task. Some neurons were active during Reach + Pinch only; a few others were active during one or more of Thumb, Index, Thumb + Index only. There was no distinct preferential discharge relationship to the compound Thumb + Index as compared with the simple Thumb or Index. These correlational data are consistent with an interpretation that the cerebellar discharge influenced all of these movements—simple and compound, constrained, and unconstrained—no one type seemingly more than any other.

INTRODUCTION

This and the companion paper address the question of what specific aspects of movements are controlled by the cerebellum. Historical suggestions have included all muscles in all movements (Holmes 1939; Luciani 1915), muscle combinations in all compound movements (Babinski 1899; Flourens 1824), and muscle combinations preferentially in unconstrained movements (Bastian et al. 1996). Rhesus monkeys (Macaca mulatta) were seated in a chair with digits, elbow, and head constrained. They were trained to make movements of thumb and index digits: “simple” movements were flexion of thumb or index; “compound” movements were simultaneous flexion of the thumb and the index digits. An unconstrained compound movement consisted of a reach for and precision pinch of fruit from a food well. Our hypotheses were as follows: If cerebellar nuclear neurons control all muscles in all movements, they should discharge equally in relation to Thumb, Index, and Thumb + Index movements. However, if cerebellar nuclear neurons control compound movements preferentially, they should discharge preferentially in relation to the Thumb + Index combined movement. Last, if cerebellar neurons control compound movements preferentially when unconstrained, they should fire preferentially during Reach + Pinch.

In this paper, we show that digit prime mover muscles (Beevor 1903) did indeed act singly in the constrained Thumb, Index, and in combination in Thumb + Index movements. Cerebellar nuclear discharge related almost equally to simple and to compound movements, without a categorical preferential relationship to the compound movements, constrained or unconstrained. Contrary to our expectations, many more muscles were active over arm and trunk than were necessary to perform the constrained digit tasks. Further, muscles active in the constrained movements were comparable in number and intensity to those active in the unconstrained movement, despite large differences in movement range and force. Similar to electromyographic (EMG) recordings, cerebellar neural discharge related to all movements, yet with a 55% higher mean frequency in the unconstrained movements.

In the previous paper we found that cerebellar nuclear inactivation impaired all movements, but the unconstrained movements were impaired apparently more than the constrained. We discuss here the limitations of recorded neural discharge/EMG/movement correlation and of neural inactivation/movement-deficit correlation when used singly, and their complementary strengths when used together.

METHODS

All aspects of this study were approved by the Internal Review Board of Washington University School of Medicine and performed in compliance with Animal Welfare guidelines.

EMG

Intramuscular EMGs (Figs. 1 and 2) were recorded from the muscles of the right upper extremity and trunk during the constrained digit movements in the first and second monkeys and the unconstrained...
Reach+Pinch movement in the second monkey. These muscles included the flexor pollicus brevis, flexor digitorum profundus and superficialis, abductor pollicis longus and brevis, opponens pollicis, adductor pollicis, interossei, hypothenar muscles, flexor carpi radialis and ulnaris, extensor carpi radialis and ulnaris, brachioradialis, extensor digitorum communis, extensor digitorum IV and V and extensor digitorum II and III, supinator, brachialis, biceps brachii, triceps, supraspinatus, infraspinatus, teres major, deltoid, latissimus dorsi, and rhomboids.

We used bipolar electrodes consisting of twisted pairs of Teflon-insulated 34-gauge stainless steel wire bared at the tip. An electrode was inserted percutaneously via a hypodermic needle into the muscle.

FIG. 1. Electromyographic (EMG) activity shown as average frequency histogram (top), voltage-to-frequency dot raster (middle), and raw amplified EMG traces (bottom) for 5 correct trials of the Thumb (left), Index (middle), and Thumb+Index (right) for (A) Flexor Pollicus Brevis and (B) Flexor Digitorum Profundus. Trials are aligned on the start of digit movement.

A Flexor Pollicus Brevis

B Flexor Digitorum Profundus
FIG. 2. EMG activity across muscles and tasks. A: EMG average frequency histograms of selected muscles across Thumb (left), Index (middle), and Thumb+Index task (right column). Histograms are aligned on the start of digit movement. B: graphical summary of EMG activity during Thumb, Index, Thumb+Index, and Reach+Pinch tasks. ○, first monkey; ●, second monkey. See text for details. C: Venn diagram of number of EMG recordings related exclusively to Thumb, Index, Thumb+Index, and combinations of these tasks.
The impaled muscle was identified by reference to surface landmarks, published description of muscular anatomy (Fetz and Cheney 1980; Hartman and Straus 1933; Szelenyi 1969), and by observation of the movements produced by stimulation (100-ms trains of 10-Hz, 0.1-ms duration, 0.1- to 1.0-mA current pulses). During stimulation, an attempt was made to allow for the fact that axons close to the electrode may be excited at lower thresholds than the impaled muscles (Loeb and Gans 1986). The bipolar signal was amplified \( \times 1000 \), filtered (band-pass of 100–10,000 Hz) to further reject low-frequency distant components, displayed on an oscilloscope, full-wave rectified, and passed to a voltage-to-frequency converter whose output pulses were recorded and processed (Schieber and Thach 1985a,b).

**Single units**

Single-unit activity in the deep cerebellar dentate and lateral portions of the interpositus nuclei were recorded during performance of the constrained and unconstrained tasks in both monkeys. Glass-coated platinum/iridium microelectrodes (impedance 1 to 6 M\( \Omega \)) were mounted on a mechanical XYZ microelectrode positioner/advancer. During recording sessions, a bevel-tipped guard tube was lowered through the cerebral dura mater. The microelectrode was then lowered through the guard tube to a position just above the cerebellar cortex. In searching for units, the microelectrode was advanced from this position with a Trent-Wells hydraulic microdrive as the monkey performed the constrained digit tasks. The signal from the electrode was amplified, filtered (band-pass 0.3 to 3.0 kHz), and sent 1) to a storage oscilloscope so that the waveforms could be observed, 2) to an audio system, and 3) to a two-window spike discriminator which sent a TTL pulse to the CED 1401 (Cambridge Electronic Design, UK) interface. All nuclear cells with discriminable action potentials were recorded during the performance of the constrained digit tasks and the unconstrained Reach+Pinch task. For each isolated nuclear unit, its size, duration, shape, coordinates, and presumed anatomical location were noted (Thach 1968).

**Data analysis**

Neural unit discharge was examined off-line in dot rasters and average frequency histograms. Moving histograms were averaged using 5-ms bins and were smoothed with a moving average window. The histograms were used to determine instantaneous firing frequency. In these task performances we found no systematic differences between neurons in dentate and those in interpositus and therefore no distinctions are made in presenting the neural data.

**Constrained digit tasks**

Unit discharge for all correctly performed trials was aligned trial-by-trial on the start of movement for the Thumb task and the Index task and on the time of the first digit movement for the Thumb+Index task. The following four variables were measured: 1) time of first activity change, 2) level of significance of activity change, 3) time of peak activity change, and 4) magnitude of peak activity change. The time of first activity change (relative to movement onset) was determined using a method similar to that described previously (Thach 1975). Briefly, if a cell showed a significant change \( (P = 0.0001) \) in firing frequency from its baseline activity, then the time at which the significance level first reached \( P = 0.01 \) was called the “time-of-first-change.” The level of significance was determined using a \( t \)-test to compare baseline activity with test range activity (the first 50 ms after the time-of-first-change); this was done only for those tasks in which a time-of-first-change was found. If the \( t \)-test was significant at a \( P < 0.05 \) level, the neuron was considered related to that task and included in the data set. For each neuron related to a constrained digit task, the time of peak activity change (relative to the movement onset) was determined. Peak activity change was the highest or lowest level of neural discharge measured from the start to the stop of movement. The magnitude of peak activity change (relative to the baseline activity) was also determined only for those neurons found to be related to a constrained digit task. The magnitude of peak activity was the highest or lowest level of neural discharge reached during the time of peak activity change.

**Unconstrained Reach+Pinch task**

Unit discharge for all correctly performed trials was aligned on the following: 1) removal of the investigator’s hand from placement of the fruit reward onto the cantilever, 2) monkey’s initial touch of the food reward, and 3) monkey’s removal of the food reward from the cantilever. The baseline range was defined as the 250-ms interval centered on placement of the fruit reward. This baseline range was compared with test ranges defined as follows: 1) the 250-ms interval prior to the monkey’s first touch of the fruit, 2) the 250-ms interval just after the first touch, and 3) the 250-ms interval after the monkey removed the fruit from the cantilever. The baseline range and these three test ranges were compared using the Student-Newman-Keuls (SNK) test of multiple comparisons of means. If one or more of the test ranges were significantly different from the baseline range at a level of \( P < 0.05 \), the neuron was considered related to the unconstrained Reach+Pinch task and was included in the final data set. The magnitude of peak modulation was then determined.

**Histology and localization of electrode penetrations**

At the completion of recording and inactivation (described in the companion paper), the animals were given an overdose of thiopental sodium and were perfused with 0.9% saline followed by isotonic 10% Formalin in a phosphate buffer. The calvarium was removed; the cerebellum was exposed, marked stereotaxically, and prepared for histologic examination. The location of electrode penetrations into the dentate and lateral interpositus nuclei are shown in Fig. 3. A (the first monkey) and B (the second monkey).

**RESULTS**

**EMG activity**

EMG recordings were made from 28 muscles in two monkeys. A “prime mover” muscle was defined as one whose activity was present during a movement and was both necessary and sufficient to cause that movement. Figure 1 shows the raw amplified EMG traces, corresponding dot rasters, and average frequency histograms during correct trials of the constrained digit tasks for the two muscles that met the criteria of prime movers: the short flexor of the thumb (flexor pollicis brevis, FPB), and a flexor of the index digit (flexor digitorum profundus, FDP). These two muscles were consistently active in the data set. For each neuron related to a constrained digit task, the time of peak activity change (relative to movement onset) was determined. Peak activity change was the highest or lowest level of neural discharge measured from the start to the stop of movement. The magnitude of peak activity change (relative to baseline activity) was also determined only for those neurons found to be related to a constrained digit task. The magnitude of peak activity was the highest or lowest level of neural discharge reached during the time of peak activity change.

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in both monkeys across trials (Fig. 2B). FPB was active during the Thumb and Thumb+Index tasks and not the Index task (a pattern categorized as "T, T+I"). FDP was active during the Index and Thumb+Index tasks and not the Thumb task ("I, T+I"). Electrical stimulation through the recording EMG electrodes produced Thumb or Index movements, respectively.

Nonprime mover muscles were defined as those that were neither necessary nor sufficient to cause these movements. Thus defined, nonprime mover muscles showed a variety of different activity patterns. The EMG activity of nine such muscles of the right upper extremity is shown in Fig. 2A. One was active in the pattern of the thumb prime mover, FPB (T, T+I); extensor digitorum 4 and 5. Another three were active in the pattern of the index prime mover, FDP (I, T+I); biceps brachi (Biceps), flexor carpi radialis (FCR), and Abductor Pollicis Longus (AbPL). By contrast, three were commonly active across all tasks (T, I, T+I): Deltoid, Supinator, and Flexor Digitorum Sublimis (FDS).

Figure 2B summarizes the EMG recordings from all muscles during all tasks in both monkeys. The EMG recordings are shown vertically for 28 muscles of the hand, forearm, upper arm, and shoulder girdle/trunk, respectively. The activity of the different muscles for the different tasks are shown horizontally for prime mover patterns (T, T+I; I, T+I), the common pattern (T, I, T+I) and "other" (T; I; T; I; T+I), and during the Reach+Pinch task (R + P). Open circles represent EMG from the first monkey and filled circles from the second.

While no EMG pattern changed during a recording session, patterns of the 19 nonprime mover muscles varied between monkeys and across recording sessions. Two different EMG patterns were seen for opponens pollicus, first dorsal interosseous, hypothenar, flexor digitorum superficialis, palmaris longus, extensor carpi radialis, extensor digitorum communis, brachialis, triceps, infraspinatus, teres major, deltoid, and three patterns for flexor carpi ulnaris, extensor carpi ulnaris, latissimus dorsi, and supraspinatus. Thus a muscle that was active during all of the constrained tasks (T, I, T+I) during one recording session (e.g., supraspinatus in the first monkey) may have also acted in a pattern similar to one of the prime movers during another recording session. For the flexor digitorum superficialis this variation was predictable in that it was dependent on the location of the recording (ulnar side of muscle active in a pattern similar to FPB and radial side of muscle active in a similar pattern across constrained tasks). However, for most muscles, the variation was not predictable.

Figure 2 also summarizes the activity recorded during Reach+Pinch of 24 muscles recorded in the second monkey. During this task, proximal and distal muscles were active. With the exception of the rhomboids, all of the muscles active in Reach+Pinch were also active in one or more of the constrained single digit tasks.

In sum, we had hoped that training in the constrained simple tasks might restrict activity to those muscles acting on the digits (Schieber and Thach 1985b). Nevertheless, all sampled muscles were active across constrained Thumb, Index, Thumb+Index, and unconstrained Reach+Pinch tasks.

Dentate neuron activity during the constrained digit tasks

The activity of 193 neurons was recorded during the performance of the constrained digit tasks—55 neurons in the first monkey and 158 neurons in the second monkey. One hundred eight (56%) neurons discharged in relation to at least one of the constrained digit tasks—17/35 (49%) in the first monkey and 91/158 (58%) in the second monkey. These task-related neurons were recorded over a large area of the dentate nucleus, spanning its entire rostral-caudal extent (Fig. 3, A and B).

Eighteen of the 108 (17%) movement-related neurons had a "digit-specific" discharge pattern similar to the EMG pattern of the digit prime movers. These neurons discharged whenever one of the digits was moved, singly or in combination with the other digit. In Fig. 4A, one such unit increased its activity in relation to Index and Thumb+Index tasks. Of the 18/108 neurons that showed digit-specific prime mover patterns, four showed the pattern T, T+I; 14 showed the pattern I, T+I. In Fig. 4B, plots show the times of first activity change, times of peak activity change, and magnitude of peak activity change. The striking result in Fig. 4B is that for these prime mover-like neurons the discharge characteristics for the simple tasks are essentially the same as for the compound tasks. Although one cannot be certain that these neurons do in fact control prime movers, from the inactivation results (companion paper), it would seem that some of them must have.

Most of the neurons (79/108, 73%), similar to most of the muscles (Fig. 2: 20/28 muscles), discharged in a similar "common" pattern (T, I, T+I) across all of the constrained digit movements. In Fig. 5B the neuron increased and in Fig. 5C the neuron decreased discharge frequency during all the tasks. Figure 6 shows for these units plots of J) times of first activity change; 2) times of peak change, and 3) magnitudes of peak change. On the ordinate of each graph is the measure of interest for one of the tasks. On the abscissa is the corresponding measure of interest for another of the tasks. These plots show that these neurons discharged in a similar pattern across tasks. Most had similar discharge measures across all constrained digit tasks.

Eleven neurons (11/108, 10%) did not discharge in either the prime mover or the common pattern and were labeled "other." In Fig. 5A, one such neuron decreased firing during the Thumb task and increased firing during both the Index and the Thumb+Index tasks. However, the parameters for the Index task (239.4 Hz, time of change, −80 ms) and the Thumb+Index task were very different (81.9 Hz, time of change, +25 ms). Of the neurons labeled other, seven changed only during Thumb; one only during Index; and three only during Thumb+Index tasks. Similar patterns were sometimes seen in EMG recordings (Fig. 2).

Figure 7, A and B, summarizes the relations among constrained task type, muscle, and neural activities. The active neurons were sorted based on the constrained tasks to which they were related (Fig. 7A). Figure 7B compares the fractions of all movement-related EMG recordings (n = 68) and all movement-related neurons (n = 108) to each of the constrained tasks. Most muscles and most neurons were related to Thumb, Index, Thumb+Index. A smaller fraction were related to Index, Thumb+Index, and Thumb, Thumb+Index. Still smaller fractions were related to Thumb or Index or Thumb+Index.
Dentate neuron activity during the unconstrained Reach+Pinch task

Figure 8A shows the activity of a neuron that changed during Reach+Pinch. The top raster labeled “Cue to Reach” is aligned on the time when the examiner’s hand left the fruit on the strain-gauge-monitored cantilever and withdrew from blocking the food well. Reach began within around 500 ms after the cue, although the time of onset of movement was not routinely determined. The middle raster labeled “Pinch Onset” is aligned on the time when a digit first touched the fruit on the strain-gauge-monitored cantilever. The bottom raster labeled “Retrieval Onset” is aligned on the time of the monkey’s removal of the fruit from the strain-gauge-monitored cantilever. During this time, the pinch persisted as the monkey withdrew its arm from the food well up until the time when the fruit was placed in its mouth. Figure 8A shows an increase in discharge 300 ms after the cue to reach and 200 ms prior to onset of pinch. Discharge remained elevated after the onset of retrieval—during the persisting pinch and the withdrawal of the arm. Figure 8B shows the discharge of another neuron that increased 450 ms after cue to reach and 150 ms before onset of pinch, peaked after pinch onset, then decreased after onset of retrieval, but still remained above baseline.

The activity of 125 neurons was recorded during both the constrained and the unconstrained tasks: 100/125 neurons changed activity in relation to movement in one or more tasks; 13/15 (87%) in the first monkey, 87/110 (79%) in the second monkey. Neurons that changed discharge in relationship to the Reach+Pinch were categorized based on the “portion” of the task (cue to reach, onset of pinch, onset of retrieval) during which they were active compared with a 100-ms baseline period prior to the cue to reach. To be related to a particular task portion, criteria for a task-related change in discharge were as follows: cue to reach, within 500 ms after alignment; onset of pinch, within 250 ms prior to alignment; onset of retrieval, within 250 ms prior to or after alignment. We emphasize that this categorization cannot indicate nor is it meant to imply that the discharge specifically related to a particular aspect of the task (cue, reach, prehension, pinch, retrieval) or to specific muscles involved. Nevertheless, the discharge patterns varied considerably across the monitored conditions, and the
categorization shows that variety. Based on this categorization, the neuron in Fig. 8A was active during all three conditions and the neuron in Fig. 8B was active only during the second two conditions. The categorization of all the neurons is summarized in the Venn diagram in Fig. 8C.

Comparison of unit activity during the constrained digit tasks and the unconstrained Reach + Pinch task

The patterns of discharge varied widely across performance of the different tasks. Figure 9A shows the discharge pattern of a neuron with increased activity across all tasks (only T/I shown of the digit tasks). During and after onset of pinch in Reach + Pinch, firing rose to 225 spikes/s. During T/I, firing frequency was less at 125 spikes/s. Figure 9B shows the discharge pattern of another neuron that had a different direction of change depending on the task. The neuron decreased firing before and after pinch onset in Reach + Pinch, but increased during all of the constrained digit tasks (only T/I shown). Figure 9C shows the discharge pattern of a neuron that increased prior to onset of pinch in Reach + Pinch, but decreased slightly during T, I, T+I (only T+I shown). We wondered whether muscles used only during the unconstrained Reach + Pinch task and not during the unconstrained digit movements could have accounted for these neurons. However, of the muscles recorded, only the rhomboids were uniquely active during the unconstrained Reach + Pinch task. Moreover, these neurons were located over the entirety of the dentate nucleus, medial and lateral, rostral and caudal, and not to shoulder and elbow regions as demonstrated by Asanuma et al. (1983a,b) and Thach et al. 1992. Figure 9D shows the discharge pattern of a neuron that increased slightly during cue to reach of Reach + Pinch and Thumb but not during any other task.

Figure 10A summarizes in a table and Venn diagram the categorization of neurons across constrained and unconstrained tasks. Of the 125 neurons recorded during both types of tasks, 102 were related to at least one of the constrained digit tasks or the unconstrained Reach + Pinch task or both (Fig. 10A). Most of these neurons (80/120) were related both to the constrained and the unconstrained tasks, increased firing frequency during one type of task and decreased firing frequency during the other type of task. Twenty-one of these 80 neurons that were related to both the constrained and the unconstrained tasks increased firing frequency during one type of task and decreased firing frequency during the other type of task. Twenty neurons were active only during the unconstrained Reach + Pinch task and not during any of the constrained digit tasks. Two neurons changed only
during the constrained digit movements and not the unconstrained Reach+Pinch task.

Figure 10B shows in open squares the peak change in neural discharge during Reach+Pinch compared with that during whichever was greatest of Thumb, Index, Thumb+Index for neurons whose discharge changed in the same direction during both types of task. Filled squares represent peak discharge for those neurons related only to Reach+Pinch. The peak discharge frequency varied greatly. Discharge of the two neurons that changed only during the constrained digit tasks is plotted as filled circles; change in firing frequency was slight. Most of the neurons related both to Reach+Pinch and to at least one of T, I, T+I had similar discharge frequencies during both types of task. However, 13/80 of these neurons had 55% higher firing frequency during Reach+Pinch. Firing rate means ± standard deviation (SD) were 42.47 ± 35.11 for constrained and
65.89 ± 49.41 for unconstrained movements. The difference was significant at $P < 0.001$ (paired $t$-test, $t = -5.14$, df = 56). No neuron that changed discharge in the same direction across Reach+Pinch and at least one of T, I, T+It had its highest frequency during a constrained digit task.

**DISCUSSION**

*Cerebellar nuclear discharge during the constrained digit movements*

One hypothesis is that the cerebellum controls all muscles in all movements (Holmes 1939; Luciani 1915). A small proportion (18/108) of the neurons discharged during constrained tasks as if in preferential relation to digit prime mover muscles during both simple movements and compound movements: Thumb and Thumb+Index(4), Index and Thumb+Index(14). For each of these neurons, the time of first change, time of peak change, and magnitude of peak change were similar during the simple and the compound movements. Such patterns could be interpreted as consistent with the hypothesis that the cerebellum exerts equal control over all individual muscles in all movements. However, 19/28 synergist and antagonist muscles were also active in patterns similar to those of digit prime movers. While it is impossible to know from these data whether deep cerebellar nuclear activity was related to the prime movers, it seems likely that at least some of these neurons were. Given that all neurons with digit-specific discharge patterns had similar discharge for the constrained single and the constrained compound movement (Fig. 4B), and that these constrained digit movements were often delayed by cerebellar nuclear inactivation, it would thus seem likely that some nuclear neurons control prime movers in all movements. From these considerations, one could conclude that this result is consistent with the hypothesis that the cerebellum contributes *equally* to both simple and compound movements, and that the cerebellum exerts *equal* control over *all* individual muscles in *all* movements.

Another hypothesis is that the dentate/interposed output is preferentially related to compound movements as opposed to simple movements (Babinski 1899; Fluorens 1824). If this were so, then neural discharge might have been systematically greater during compound Thumb+Index than simple Thumb or Index. Three such Thumb+Index neurons were actually recorded, all in the second monkey. Although the training of Thumb+Index was given special attention in the second monkey to ensure that the combined movement had a unique and unambiguous triggering stimulus, the modulation of these few neurons was weak. Moreover, eight units discharged preferentially in relation to Thumb(7) only or Index(1) only.

Most neurons discharged equally across all three tasks: 79/108 task-correlated neurons had a common pattern across *all* the constrained digit movements, Thumb, Index, and...
This pattern was also shared with synergist and antagonist muscles during the constrained simple and the compound tasks.

One aim of this experiment was thwarted by our inability to dissociate the EMG of simple from compound movements (Beevor 1903). Our EMG results are similar to those of previous studies of simple movements, constrained and unconstrained, in which EMG was recorded. Proximal “synergist” muscles were active along with “prime movers,” and often “bidirectionally,” co-contracting during reciprocal movements (Brooks et al. 1973; Conrad and Brooks 1974; MacKay 1988a,b; Schieber and Thach 1985b; Thach 1968, 1970, 1975, 1978).

By contrast, other EMG and unit recording studies have succeeded in dissociating simple, compound, constrained, and unconstrained movements in the monkey. Smith and colleagues (Fryssinger et al. 1984; Smith and Bourbonnais 1981; Wets et al. 1985) recorded Purkinje and cerebellar nuclear cell activity during constrained reciprocal wrist movements (forearm agonists active, antagonists suppressed) and constrained pinching movements (agonists and antagonists co-active). From patterns of EMG and unit recordings, they suggested interposed nuclear output controls antagonists and not agonists. Schieber and Thach (1985a,b) trained monkeys to minimize antagonist-synergist muscle activity while performing constrained slow wrist tracking movements with and against loads (Schieber and Thach 1985a,b). None of the prime mover muscles had patterns shared with synergists and none of the cerebellar dentate or interposed neurons correlated with prime mover muscle activity. Instead, all cerebellar nuclear neurons had a discharge pattern similar to that seen also in la afferents from prime movers (both anatomic agonists and antagonists, although the EMG of only one of the muscle pair was active under load), and a few synergist muscles at the shoulder. Yet in motor cortex, 50% of the movement-related neurons fired in patterns similar to those of the wrist prime mover muscles.

**FIG. 8.** Neural firing patterns for correct trials across Reach+Pinch. Conventions are the same as in Fig. 4. Alignments of histograms and rasters: top (cue to reach): on removal of the examiner’s hand from the food bit on the strain-gauge bearing cantilever; middle (pinch onset): on monkey’s first touch of the food bit; bottom (retrieval onset): on monkey’s removal of food bit. The bottom raster and histogram are aligned on the removal of the food bit from the cantilever. A: neuron active during all of the phases of cue to reach, pinch onset, and retrieval onset. B: neuron active during the pinch onset and retrieval onset only. C: Venn diagram of classification of activity during 3 phases of the Reach+Pinch task. The number in each circle represents the number of neurons uniquely related to each phase of Reach+Pinch. Thus 65 neurons were active during cue to reach: 27 only during cue to reach; 18 during cue to reach and pinch onset; 11 during cue to reach and retrieval onset; and 19 during all 3 phases.

**Thumb + Index.** This pattern was also shared with synergist and antagonist muscles during the constrained simple and the compound tasks.

One aim of this experiment was thwarted by our inability to dissociate the EMG of simple from compound movements (Beevor 1903). Our EMG results are similar to those of previous studies of simple movements, constrained and unconstrained, in which EMG was recorded. Proximal “synergist” muscles were active along with “prime movers,” and often “bidirectionally,” co-contracting during reciprocal movements (Brooks et al. 1973; Conrad and Brooks 1974; MacKay 1988a,b; Schieber and Thach 1985b; Thach 1968, 1970, 1975, 1978).

By contrast, other EMG and unit recording studies have succeeded in dissociating simple, compound, constrained, and unconstrained movements in the monkey. Smith and colleagues (Fryssinger et al. 1984; Smith and Bourbonnais 1981; Wets et al. 1985) recorded Purkinje and cerebellar nuclear cell activity during constrained reciprocal wrist movements (forearm agonists active, antagonists suppressed) and constrained pinching movements (agonists and antagonists co-active). From patterns of EMG and unit recordings, they suggested interposed nuclear output controls antagonists and not agonists. Schieber and Thach (1985a,b) trained monkeys to minimize antagonist-synergist muscle activity while performing constrained slow wrist tracking movements with and against loads (Schieber and Thach 1985a,b). None of the prime mover muscles had patterns shared with synergists and none of the cerebellar dentate or interposed neurons correlated with prime mover muscle activity. Instead, all cerebellar nuclear neurons had a discharge pattern similar to that seen also in la afferents from prime movers (both anatomic agonists and antagonists, although the EMG of only one of the muscle pair was active under load), and a few synergist muscles at the shoulder. Yet in motor cortex, 50% of the movement-related neurons fired in patterns similar to those of the wrist prime mover muscles.

**FIG. 8.** Neural firing patterns for correct trials across Reach+Pinch. Conventions are the same as in Fig. 4. Alignments of histograms and rasters: top (cue to reach): on removal of the examiner’s hand from the food bit on the strain-gauge bearing cantilever; middle (pinch onset): on monkey’s first touch of the food bit; bottom (retrieval onset): on monkey’s removal of food bit. The bottom raster and histogram are aligned on the removal of the food bit from the cantilever. A: neuron active during all of the phases of cue to reach, pinch onset, and retrieval onset. B: neuron active during the pinch onset and retrieval onset only. C: Venn diagram of classification of activity during 3 phases of the Reach+Pinch task. The number in each circle represents the number of neurons uniquely related to each phase of Reach+Pinch. Thus 65 neurons were active during cue to reach: 27 only during cue to reach; 18 during cue to reach and pinch onset; 11 during cue to reach and retrieval onset; and 19 during all 3 phases.
remaining motor cortex neurons had the pattern of synergists and Ia afferents (Schieber and Thach 1985b). A tentative conclusion was that the "nonprime mover" cerebellar and motor cortex neurons controlled the few bidirectional alpha motor neurons to shoulder synergists and the many more gamma motor neurons bidirectionally active in both forearm agonist (active) and antagonist (silent) muscles. A further suggestion since offered was that there may be no cerebellar control over alpha motor neurons when they are restricted to the simplest of movements: prime mover muscle action at a single joint (Thach et al. 1993).

Miller et al. (1993) used a cross-correlation technique to relate magnocellular red nucleus discharge to the control of specific muscles. They showed that the magnocellular red nucleus discharge was most frequently correlated with distal muscle activity and with extensors more than flexors. A similar study could address the preferential dentate nuclear control of synergist and antagonist muscles.

**Dentate discharge during unconstrained reach and pinch task: support for an additional role for the cerebellum in unconstrained movements?**

The unconstrained Reach + Pinch task and the constrained digit tasks had overlapping patterns of muscle activity in the shoulder girdle, arm, forearm, and hand. Of the 80/120 neurons related to both the constrained digit movements and the Reach + Pinch, 13/80 had a higher firing frequency during the unconstrained Reach + Pinch. For these neurons, firing rate means ± SD were 42.47 ± 35.11 for constrained and 65.89 ± 49.41 for unconstrained movements; the difference was significant at $P < 0.001$ (paired $t$-test, $t = -5.14, df = 56$). Another subset of these neurons was modulated in different directions during these tasks—bursting during one of the tasks (constrained or unconstrained) and pausing during the other type of task. Only two neurons were related only to the constrained tasks, and these were weakly modulated. None of the 80/102
neurons related to both constrained and unconstrained movements had a higher firing frequency during the constrained digit movements. Twenty of the 102 task-related neurons changed only during Reach/Pinch and not the constrained digit tasks.

In sum, while there was on average greater neural activity related to unconstrained versus constrained movements, this could have been due to extra muscle activity associated with shoulder and elbow movement in the unconstrained Reach+Pinch. Moreover, that the difference was so small was surprising given that the torque needed for the shoulder muscles in unconstrained Reach was estimated to be 67 to 123 times greater than torques for constrained Thumb and Index, respectively, and the Reach range was 70 times greater than that for the digits.

Overall, these neural recording results resemble those of Van Kan and colleagues (1993). In monkeys trained to perform a series of constrained simple tasks and an unconstrained compound task, most of the interpositus neurons were more related to an unconstrained task than to the constrained tasks. Yet one neuron had a greater discharge during the constrained tasks. They interpreted their results to suggest that cerebellar control was greater over compound than simple movements. Our results during similarly constrained digit movements favor no such preferential control over constrained compound (Thumb+Index) than constrained simple (Thumb, Index) movements. We thus question the generality of the combination hypothesis (Babinski 1899; Fluorens 1824) as such.

Nevertheless, our results do raise the question of a preferential control of unconstrained as opposed to constrained movements. The following questions remain: Are unconstrained movements more controlled by the cerebellum than constrained? If so, why might unconstrained movements require more cerebellar control? Finally, allowing for the large
differences in torque and range requirements, why were EMG and neural discharge patterns so similar across movements?

There were differences in the patterns of EMG activity across the two tasks (Fig. 2), and the magnitude of EMG activation may not have been equal across constrained and unconstrained tasks. Nevertheless, the broad activation of distal and proximal muscles observed here during both the constrained single digit tasks and the unconstrained Reach±Pinch task makes the two tasks similar, at least as far as muscle activity is concerned. That cerebellar inactivation impairs unconstrained movements more than constrained is consistent with the interaction hypothesis, which has been corroborated in humans (Bastian et al. 1996; Topka et al. 1998) and cats (Cooper et al. 2000). We can only speculate that the pattern of EMG (and neural discharge) that was necessary for the unconstrained movements was retained for the constrained movements, even though excessive and unnecessary. We may further speculate that it was easier for the monkeys to keep and use a default “unconstrained movement program” throughout the constrained movements rather than to have to learn not to employ that program. These results thus caution against the interpretation that the presence of muscle and neural activation during a task means the activation is specific to and necessary for that task’s performance.

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REFERENCES


