

# Comparing Cerebellar and Motor Cortical Activity in Reaching and Grasping

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**ABSTRACT:** The activity of single cells in the cerebellar and motor cortex of awake monkeys was recorded during separate studies of whole-arm reaching movements and during the application of force-pulse perturbations to hand-held objects. Two general observations about the contribution of the cerebellum to the control of movement emerge from the data. The first, derived from the study of whole arm reaching, suggests that although both the motor cortex and cerebellum generate a signal related to movement direction, the cerebellar signal is less precise and varies from trial to trial even when the movement kinematics remain unchanged. The second observation, derived from the study of predictable perturbations of a hand-held object, indicates that cerebellar cortical neurons better reflect preparatory motor strategies formed from the anticipation of cutaneous and proprioceptive stimuli acquired by previous experience. In spite of strong relations to grip force and receptive fields stimulated by preparatory grip forces increase, the neurons of the pericentral motor cortex showed very little anticipatory activity compared with either the premotor areas or the cerebellum.

**RÉSUMÉ:** Comparaison de l'activité corticale cérébelleuse et motrice dans les mouvements pour atteindre et saisir une cible. L'activité de cellules isolées dans le cortex cérébelleux et le cortex moteur de singes en état d'éveil a été enregistrée pendant des études de mouvements de tout le bras pour atteindre une cible et pendant l'application de perturbations de force pulsée à des objets tenus dans la main. Deux observations générales à propos de la contribution du cervelet au contrôle du mouvement ressortent de ces données. La première, qui découle de l'étude des mouvements de tout le bras pour atteindre une cible suggère que, bien que le cortex moteur et le cervelet génèrent un signal en relation avec la direction du mouvement, le signal cérébelleux est moins précis et varie d'essai en essai, même quand la cinématique du mouvement demeure inchangée. La seconde observation, qui découle de l'étude des perturbations prévisibles d'un objet tenu dans la main, indique que les neurones corticaux cérébelleux reflètent mieux les stratégies motrices préparatoires formées à partir de l'anticipation des stimuli cutanés et proprioceptifs acquis par expérience antérieure. Malgré les relations étroites à la force de préhension et aux territoires réceptifs stimulés par une augmentation préparatoire des forces de préhension, les neurones du cortex moteur précentral ont manifesté peu d'activité anticipatrice comparés à ceux des zones prémotrices ou à ceux du cervelet.

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Traditionally, neurology has derived its impressions about cerebellar and motor cortical functions from the clinical syndromes following lesions. Damage to motor cortex leads to an initial contralateral hemiparesis and the recovery from this paralysis is generally less certain among primates as compared with other species.<sup>1</sup> In contrast, lesions of the cerebellum are never associated with paralysis although voluntary movements are severely ataxic and dysmetric.<sup>2</sup> Recovery from motor cortical lesions is generally associated with heightened reflexes and spasticity whereas recovery from small cerebellar lesions can often be quite complete.

Although less frequently cited, punctate electrical stimulation of the motor cortex and cerebellar nuclei also reveals some striking differences. Microstimulation of the motor cortex produces discrete movements frequently involving activation of a

single muscle<sup>3</sup> and apparent reciprocal inhibition of antagonist muscles.<sup>4</sup> Moreover, movements evoked by microstimulation of the motor cortex at intensities greater than 30 $\mu$ A in monkeys disappear after bilateral pyramidotomy (Smith, Hepp-Reymond and Wyss, unpublished observations). It would appear that the movement evoked in the intact monkey by intracortical microstimulation at less than this intensity is probably conveyed by the corticospinal tract. Electrical stimulation of the corticospinal tract is known to activate recurrent collaterals to inhibitory intracortical interneurons which may explain why this stimulation also produces both relaxation of the antagonist muscles as well as activation of the agonists.<sup>5</sup> In addition, it is known that blocking intracortical inhibition with local injections of bicuculline transforms a reciprocally-organized command into a co-contraction of antagonist muscles.<sup>6</sup> These two observations taken

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together seem to suggest a hard-wired system for insuring reciprocal inhibition of antagonist muscles by the corticospinal tract.

In contrast, stimulation of the deep cerebellar nuclei invariably evokes co-contraction of antagonist muscles, and generally requires higher stimulation currents to evoke movement.<sup>7</sup> Also, stimulation at particular points in the dentate nucleus yields synergistic muscle activations at multiple joints and in both the arm and leg of primates.<sup>7</sup> Although the cerebellum acts on corticospinal neurons through the cerebello-thalamocortical pathway there are several other brainstem motor pathways which receive cerebellar excitation and which may mediate these co-contractions and synergies.

Unlike the effect of lesions or electrical stimulation, single unit recording studies of cerebellar and motor cortical activity in identical behaviors, indicates greater similarity than difference in the discharge patterns.<sup>8-15</sup> Some neurons in both areas have discharge patterns related to force, muscle activity, position and the next intended movement.<sup>15</sup> In spite of extensive study, single unit recording has still not demonstrated unique contributions of the cerebellum and motor cortex to the planning and execution of movement.

The following brief comparison of cerebellar and motor cortical discharge patterns in reaching and grasping attempts to gather preliminary evidence about the unique contributions of each of these motor structures.

## EXPERIMENT #1

### Methods

Single cells were recorded in the cerebellar cortex, the interpositus and dentate nuclei as well as in the central sulcus of the primary motor cortex of primates trained to make accurate, visually-guided movements to 8 radially arranged targets. Details of the task, recording procedures and data analysis can be found in earlier publications.<sup>16,17</sup> Briefly the task was divided into 4 distinct epochs. The first was a center hold time (CHT) in which the monkey held a handle over a central starting position before one of the 8 light emitting diodes was illuminated. The second epoch was the reaction time (RT) which consisted of the interval between the appearance of a target stimulus and the initiation of movement toward the target. Third was the movement time (MT) comprising the time from movement onset until the handle was stabilized within the target zone. Finally the target hold time (THT) was the time the monkey maintained a steady arm position over the target stimulus.

It was assumed that all the cells included in the present study were related to the shoulder or the elbow. This assumption was based on the presence of receptive fields related to imposed movements of the shoulder and elbow or the discharge recorded outside the task while the animals reached for raisins in different directions or at varying distances from the body. Cells with receptive fields on the hand or trunk were specifically excluded from the sample. Since it was generally more difficult to identify the sensory or motor field or cerebellar neurons, the selection criterion was used to compare only cells that were strongly related to movements in the task. However, these criteria did not include directional tuning or response variability which were the 2 measures examined in this study.

A classification scheme described by Fortier et al.<sup>16</sup> was used to sort motor cortical and cerebellar neurons into reciprocal,

graded and non-directional categories. A reciprocal cell showed a maximum increase in activity for movements in a single preferred direction and a statistically significant decrease in activity in the opposite direction. Cells with graded response patterns had increased activity in the preferred direction but no decreased activity in the opposite direction. Non-directional neurons had firing rates which were statistically different from the rate associated with the initial posture, although these responses did not differ across the various directions of movement.

As a measure of the degree of directional tuning we calculated *directional sector widths* for each neuron for the RT and MT epochs. This is a measure of the dispersion of neuronal discharge about the preferred direction. The sector width is defined as :

$$2 * \text{mean angular deviation,}$$

that is,

$$2 * 180^{1/2} / D * [2(1 - r)],$$

where r is the mean length,

$$r > > = \frac{(\text{preferred direction vector}) > >}{(\text{sum of 8 direction vectors}) > >}$$

a measure of concentration of data arrayed circularly about its mean preferred direction.<sup>18</sup> The mean angular deviation is analogous to the standard deviation of scalar data, and the greater the dispersion of cell activity about its preferred direction, the wider the sector width.

Absolute and movement-related directional sector widths were calculated for each cell because the absolute discharge is composed of two constituent parts; a direction-related variation in discharge and an unmodulated component. The size of the unmodulated component is determined by the minimal response frequency observed during the 8 directions of movement, and represents the offset of the movement-related curve from zero. Since the minimum response could be either an increase or decrease in the discharge rate observed at the center hold position, the unmodulated component should not be confused with the center hold activity. The absolute sector width reflects both the dispersion of the direction-related discharge about the preferred direction plus the unmodulated component. Therefore the larger the unmodulated component, the wider the sector width. For this reason, a movement-related directional sector width was also calculated by subtracting the unmodulated component of the cell activity.

An alternative measure of temporal variability is the variation of preferred direction across replications for a given cell. For each replication of a block of 8 directions, a replication preferred direction can be calculated. The experimental design involved 5 replications from which 5 replication preferred directions were calculated. The replication preferred direction should be distinguished from the mean preferred direction, which was calculated from the mean discharge recorded for the 5 replications of each of the 8 directions. The degree of variation of the 5 replication preferred directions was then measured by calculating the sector width of their distribution, which we have called the "replications sector width". The replication sector width measures the dispersion of the 5 replication preferred direction values rather than the dispersion of cell discharge in the 8 directions (i.e., directional sector width).

## RESULTS — EXPERIMENT #1

## Directional Tuning Curves

Almost all motor cortical neurons demonstrated either the reciprocal (58%) or the graded (41%) discharge pattern to the 8 target directions. Although a higher proportion of graded responses were found in the cerebellum compared to motor cortex, the graded responses were similarly distributed in Purkinje (68%) interpositus (71%) and dentate cells (67%). The lower incidence of reciprocal cells (26%) and higher incidence of non-directional cells (18%) in the cerebellum was statistically significant, and was another important difference.

By aligning the discharge profiles of all cells about their preferred direction for the combined RT and MT epochs it was possible to establish mean population tuning curves for the motor cortex and cerebellum for reciprocal and graded cells separately shown in Figure 1. The combined cerebellar and motor cortex population tuning curves showed an excellent fit to a cosine function ( $R^2 = 0.99$  for the cerebellum and  $0.98$  for the motor cortex).

The mean tuning curve for graded cerebellar neurons shown in Figure 1B was shifted above the center-hold rate indicating an increase in discharge rate for movements in all directions - even those opposite to the preferred direction. In contrast, the mean population curve for graded motor cortex cells did not increase from the center-hold rate. The reciprocal cerebellar and motor cortical neurons shown in Figure 1A had nearly identical tuning properties although the cerebellar neurons had a higher mean center-hold tonic frequency as well as a higher mean movement-related discharge rate. The half-wave directional modulation, which is simply a measure of the depth of modulation of cellular activity, was different for reciprocal and graded neurons. The modulation was 17.3 imp/sec for reciprocal cerebellar cells and 14.5 imp/sec for reciprocal motor cortical neurons. The half-wave modulation of graded neurons was 12.5

imp/sec for cerebellar neurons and 11.2 imp/sec for motor cortical neurons.

## Directional Sector Widths

The directional sector widths provided a measure of the dispersion of cellular discharge about the preferred direction. The directional sector widths were significantly greater for cerebellar cells compared with motor cortex neurons. Also, graded cells had significantly greater directional sector widths than reciprocal cells in the cerebellum but not the motor cortex. The absolute and movement-related sector widths of reciprocal cerebellar cells were significantly narrower than for graded cerebellar cells (Mann-Whitney test  $p < .01$ ). By comparison the sector widths of reciprocal and graded motor cortex cells were identical. The absolute sector widths of cerebellar neurons were significantly broader than for motor cortex neurons (Mann-Whitney test  $p < .01$ ). When the movement-related directional sector widths were calculated by subtracting out the unmodulated component, both populations shifted toward narrower sector widths and a much greater overlap was seen between the cerebellar and motor cortical distributions although the difference remained statistically significant (Mann-Whitney test  $p < .01$ ). The movement-related sector widths of reciprocal cerebellar cells were not significantly different from reciprocal motor cortical neurons. However, the movement-related sector widths of graded cerebellar neurons remained significantly broader than graded cortical neurons.

## Replications Sector Widths

Most motor cortical cells discharge in a consistent and stereotyped manner from trial to trial. In contrast, three anatomically distinct sub-populations of the cerebellar cells, interpositus, dentate, and Purkinje neurons, demonstrated greater variability. In order to demonstrate this intertrial variability, the preferred direction of each set of 5 repetitions of 8 directions of movement was derived, and from these a replications sector

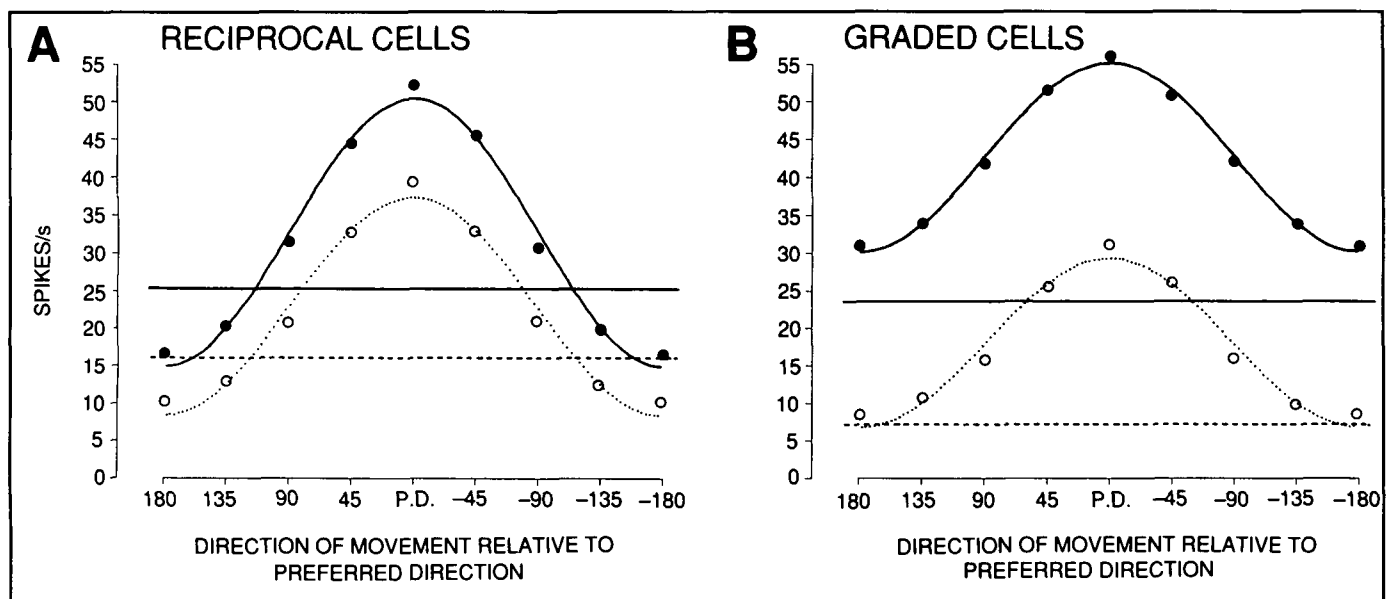


Figure 1 — Population tuning curves of activity changes with direction of reaching for cerebellar (solid line) and motor cortical neurons (hatched line). (A) Cerebellar and motor cortical neurons with reciprocal discharge pattern, and (B) Cerebellar and motor cortical neurons with graded levels of excitation. The solid horizontal line represents the mean discharge frequency of cerebellar neurons during the center hold period, and the horizontal hatched line represents the mean discharge frequency of motor cortical neurons during the same period.

width was to be calculated for each cell. Although the replication sector widths of reciprocal cerebellar neurons were nearly identical to those of reciprocal motor cortical neurons, the graded cerebellar cells were considerably more variable than graded motor cortical neurons. An example of the replication variability is shown in Figure 2. The directional vector changes markedly on each of the five replications for a typical cerebellar neuron shown on the left, whereas for a typical motor cortical neuron shown on the right the directional vectors show relatively little dispersion.

### Latency of Response Onset

To compare the temporal recruitment of cerebellar cells with those of motor cortex, the response latencies of cells which showed significant changes in activity during the reaction time (i.e., prior to movement onset) were compared. There was complete overlap of the distribution of cerebellar and motor cortical response latencies. A Kruskal-Wallis one-way analysis of variance failed to show any significant difference between these distributions. The cumulative recruitment histograms of the activity onsets of cerebellar and motor cortical cells (not shown) indicated that the initial rising phases also virtually overlapped one another. This observation implies that motor cortical and cerebellar neurons are recruited essentially simultaneously during whole-arm visually-guided reaching movements.

## EXPERIMENT #2

### Methods

In the second behavioral task, single cells were recorded from cerebellar and cerebral motor cortex of monkeys trained to grasp a test object between the thumb and index finger and lift it a distance of 1 to 2 cm, and hold it stationary for one second. Slip of the object between the fingers could be simulated by applying a 100 ms force pulse to the hand-held device. A complete description of the task, recording procedures and data analysis can be found in Espinoza and Smith<sup>19</sup> and Dungas and

Smith.<sup>20</sup> Cerebellar neurons were recorded in the hand area of the paravermal region of the anterior lobe. Purkinje cells were identified by the presence of both complex and simple spikes. Motor cortical neurons were recorded from area 4 either within the rostral bank of the central sulcus or on the adjacent convexity in areas from which microstimulation evoked discrete finger and wrist movements at intensities less than 30 $\mu$ A.

Whenever possible, an attempt was made to identify the receptive field of each recorded neuron by stroking the skin with a camel-hair brush, passively displacing the fingers and wrist and tapping the skin overlying muscle bellies.

After a 20-trial block of unperturbed trials had been recorded, the effects of object slip were examined by applying a 100 ms downward force pulse to the manipulandum after it had been stabilized in the force window for 750 ms. The perturbations were repeated on every trial until approximately 30 rewarded trials had been accumulated and then an additional series of unperturbed trials were given as a second control. If the perturbations were unopposed the object would be displaced out of the position window and the trial would go unrewarded and unrecorded.

## RESULTS — EXPERIMENT #2

### Receptive Fields

As a general rule the receptive fields of neurons both in the cerebellum and in the motor cortex could be classified as originating from either cutaneous or proprioceptive mechanoreceptors, although a few (less than 5%) of the neurons in both areas received converging input from clearly distinct and separate proprioceptive and cutaneous sources. Approximately 46% (83/180) of the neurons in the paravermal cortex received proprioceptive input and were more strongly excited by quick dynamic stretches of the wrist and finger muscles than by imposed static limb positions. Approximately 31% (56/180) of the cerebellar cortical neurons had cutaneous input from the

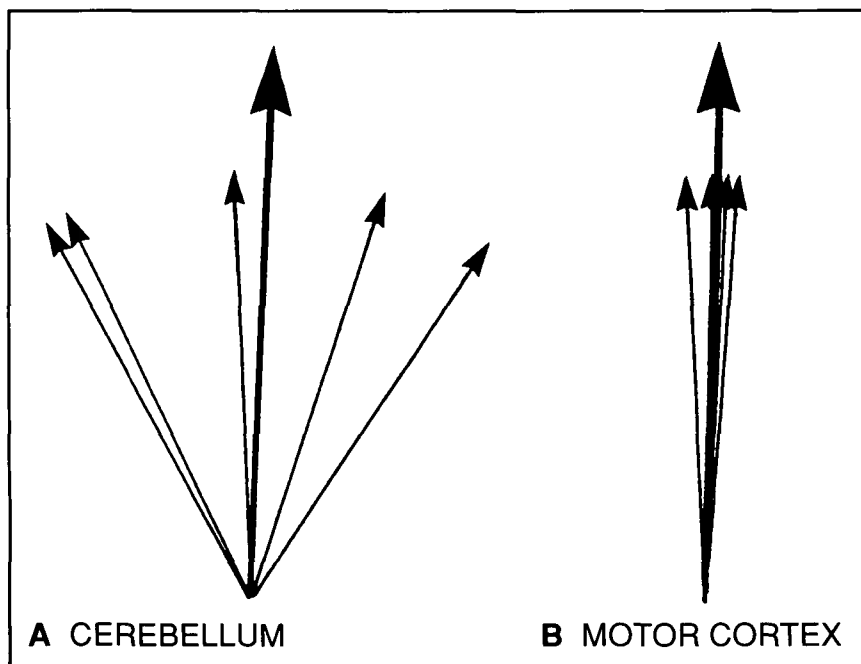


Figure 2 — The mean preferred direction during the RT+MT epoch (long arrow) and the distribution of replication preferred directions (shorter arrows) are shown for a typical cerebellar neuron (A) and motor cortical cell (B). The arrow lengths have no relation to response strengths but dispersion about the preferred direction (i.e., over 360 degrees) indicates the replication variability of the neuronal discharge.

glabrous skin of the hand. Virtually none of the cells in this sample were excited by the hairy skin.

The cutaneous receptive fields of cerebellar cells were generally larger than those of either the sensory or motor cortex. These frequently but not invariably, included the entire territory of the median or ulnar nerve distal to the wrist. That is, they usually encompassed either the medial or lateral half of the palm. Occasionally smaller receptive fields restricted to either a single digit or the palm were also encountered. Some of the cells had multiple receptive fields on the fingertips which would imply convergent afferents from both the median and ulnar nerves. The foliated nature of the cerebellar cortex made it impossible to determine whether proprioceptive and cutaneous afferents were spatially segregated in the paravermal anterior lobe.

Overall, the neurons of the motor cortex were about equally divided between cutaneous (46% or 96/208) and proprioceptive (39% or 82/208) receptive fields. The cutaneous afferents were more frequently encountered in the rostral bank of the central sulcus where 61% of the recorded neurons received cutaneous input. In contrast, only 31% of the cells on the cortical convexity received cutaneous input. In general, the motor cortex had a greater proportion of cutaneous afferents than the cerebellum (46% vs 27%) whereas the proportion of proprioceptive afferents appears to be about the same in both areas (39% vs 42%). The cutaneous fields were, as a rule, smaller in area 4 than those encountered in the cerebellum. The fields were for the most part restricted to the volar glabrous skin and region about the finger pads. Only one neuron in the motor cortex responded to hair displacement. The fields were usually restricted to a single phalangeal segment although the largest fields were similar to those found in the cerebellar cortex. The smallest fields resembled the size of receptive fields in the postcentral cortex (Picard and Smith, unpublished observations).

Despite different proportions of proprioceptive and cutaneous neurons found in the cerebellum and motor cortex, the discharge patterns of neurons receiving these afferents during grasping and holding were very similar. Typically, both cerebellar and cortical neurons discharged with higher frequency during the dynamic phase of grasping and lifting compared with static holding. It appears that peripheral afferents provide positive feedback to neurons of both the cerebellum and motor cortex, and that this feedback would appear to be transformed into a similar output signal. The similar cosine functions found between cerebellar and motor cortical cells in experiment 1 may reflect similar feedback excitation from peripheral receptors.

#### Perturbation Latencies

The force pulse perturbations produced excitatory responses in both the cerebellar and motor cortex. Perturbation response latencies in the motor cortex ranged from less than 15 ms to 95 ms with a mean latency of 39.5 ms (shown in Figure 3). Cerebellar cortical response latencies varied from less than 15 ms to 85 ms with a mean of 42.5 ms. Overall similar proportions of neurons with cutaneous as opposed to proprioceptive receptive fields in both the cerebellum and motor cortex responded to the perturbation. There was no significant difference between the response latencies of cutaneous neurons compared to proprioceptive neurons in either the cerebellum or the motor cortex.

In spite of the similar mean response latencies to the perturbation in the cerebellar and motor cortex, the shape of the

latency distributions differed markedly. Figure 3 shows that the cerebellar responses formed an unimodal Gaussian distribution whereas the distribution of responses in the motor cortex was skewed to the left and were broader. The median response latency of the motor cortical cells was between 30 and 35 ms and was approximately 10 ms shorter than the median cerebellar response latency.

#### Preparatory Reactions

The perturbations were delivered consistently at the same time in blocks of 20 - 30 trials such that the monkeys were able to anticipate the arrival of the perturbation which encouraged the development of an appropriate strategy for stabilizing the position of the wrist and fingers. Although preparatory changes in the dynamics and kinematics of the grasping and lifting sequence were sometimes seen during the dynamic period, only the mean forces and associated activity changes during static holding (i.e., after movement had ceased) were analyzed. By comparing the average grip forces of perturbed trials with the average grip forces on trials prior to the introduction of the perturbation, it was possible to determine the approximate point at which the mean force traces diverged due to the anticipation of the perturbation.

For each cell, the mean firing frequency and standard deviation were calculated for the one second of static holding during

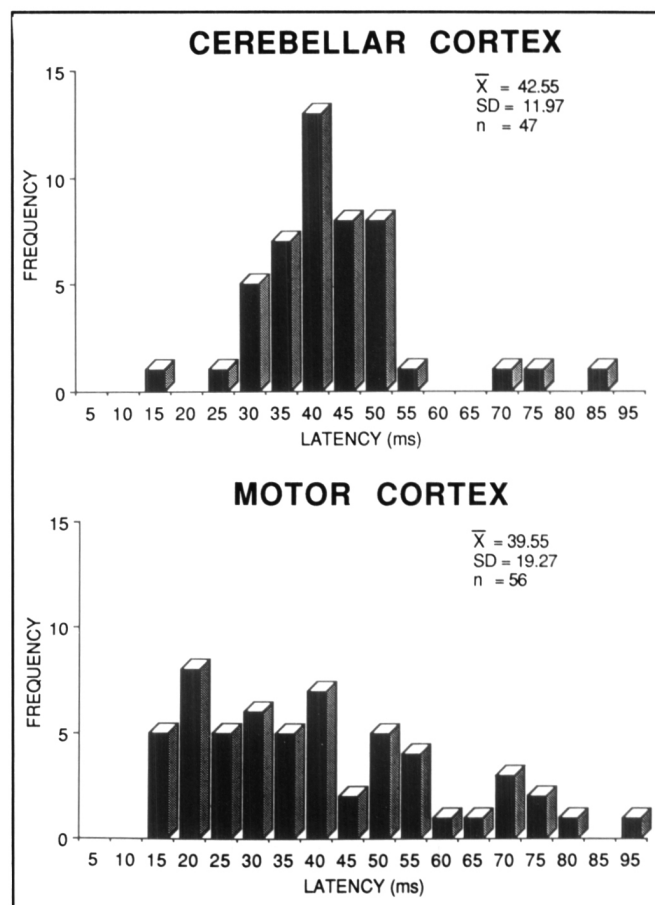


Figure 3 — The response latency histograms of cerebellar and motor cortical neuronal responses to the force-pulse perturbation applied to the hand-held object.

the first control period before the perturbation was introduced. The mean activity during static holding with the perturbation was sequentially examined every 20 ms to find the point at which the discharge exceeded the control frequency by 2 standard deviations, and this point was taken as the onset of preparatory activity for the cell.

According to this criterion, 13 Purkinje cells and 22 unidentified neurons (25%) of 140 neurons in the cerebellar cortex with grasp-related discharge increased their firing frequency during the holding period in preparation for the perturbation. An example of this preparatory discharge is shown in Figure 4. The perturbation failed to evoke complex spike responses from any of the recorded Purkinje cells either as a preparatory discharge or as a reflex response to the perturbation. That is, all the perturbation-evoked activity changes involved modulation of the simple spike discharge only. The simple-spike preparatory activity appeared gradually and was strongest after twenty or thirty repeated perturbations. When the perturbation was withdrawn, the preparatory discharge diminished slowly and was generally extinguished within 20 or 30 trials.

In contrast to neurons of the cerebellar cortex very few neurons of the rostral bank of the central sulcus demonstrated preparatory discharge activity. Of 189 hand area neurons of the motor cortex only 14 (7%) had a preparatory discharge when evaluated by the same criterion as the cerebellar cortical neurons. A motor cortical cell which failed to show a preparatory discharge despite a clear anticipatory increase in grip force is shown in Figure 4. This was an unexpected finding since the majority of cells had receptive fields that would clearly have been stimulated by the preparatory force increase prior to the perturbation, and their activity was significantly correlated with the grip force itself. The motor cortical region from which the recordings were made could be readily identified by microstimulation and all these neurons appeared to be related to muscles active during grasping and the majority had cutaneous receptive fields on the thumb or index finger or responded to stretch of one of the thenar muscles.

## DISCUSSION

### Reaching

Single unit recordings from the cerebellum and motor cortex of awake primates performing reaching movements revealed some similarities as well as some surprising differences which would not necessarily have been predicted from the behavioral deficits after lesions. Perhaps the most important similarity between the cerebellum and the motor cortex is the identical bell-shaped mean population response curve when all cell activities are grouped about their preferred direction as shown in Figure 1. Both population curves showed a very close fit ( $R^2 > .98$ ) to a cosine function. A second important similarity concerns the overlapping temporal recruitment of cerebellar and motor cortical neurons prior to movement onset. This suggests that during visually-guided reaching movements the cerebellum and motor cortex are simultaneously recruited rather than

sequentially with one structure initiating and the other following. In addition, the similarity of the population tuning curves implies that both structures are related to parameters covarying with movement direction, although these parameters are very probably not identical for reasons which will be discussed below.

One potentially significant distinction between cerebellum and motor cortex appears to be the higher proportion of reciprocal discharge patterns among cells of the motor cortex compared to a greater proportion of graded cells in the cerebellum. Paradoxically, subtotal lesions of the dentate and interpositus nuclei have been shown to increase the co-contraction of elbow antagonists and decrease the number of reciprocal cells in the motor cortex.<sup>21</sup> It is possible that the graded cerebellar nuclei neurons not only excite corticospinal neurons via thalamic relays, but they also may activate intracortical inhibitory neurons mediating reciprocal inhibition as well.

The higher proportion of graded neurons in the cerebellum coupled with the observation that the mean population tuning curve for cerebellar neurons was shifted above the center-hold rate indicates an increase in discharge frequency for movements in all directions including an increase in activity for movements opposite to the preferred direction. Since both Purkinje and nuclear cells increased activity for movements in a particular direction, one wonders whether the Purkinje cells and their target nuclear cells are excited in or out of phase with respect to one another. The fact that both Purkinje cells and nuclear cells increase activity for movements opposite to the preferred direction is also puzzling, and defies any simple relation to movement dynamics or kinematics.

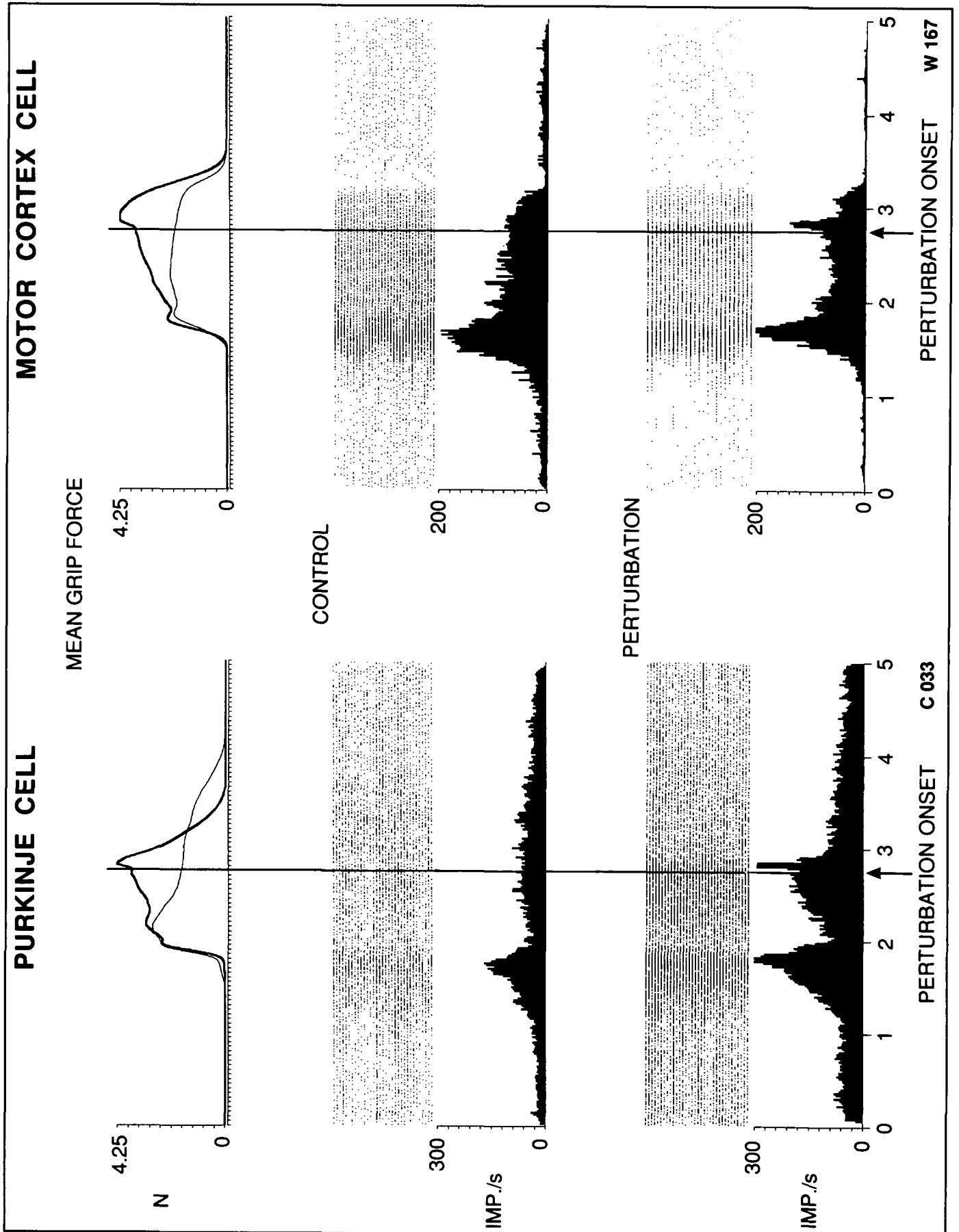
Another major difference between the cerebellar cells and motor cortical neurons was the narrower, more selective, directional tuning of the latter group. This difference persists even after the higher discharge rate of cerebellar neurons during the initial starting posture was subtracted out. For the graded cerebellar cells both the absolute directional sector widths and the movement directional sector widths were broader than motor cortical neurons. Exactly why graded cerebellar cells have broader tuning curves remains unclear since there is no "a priori" reason why cells with graded activity cannot be as narrowly tuning as any reciprocal cell.

Another difference between cerebellar and motor cortical neurons relates to the replication sector widths which measures intertrial variability. The replication sector widths show that the directional signal of cerebellar cells can vary widely over time whereas the directional signal for motor cortex remains stable. This difference might be due to feedback-related carry-over effects of preceding movements on succeeding ones. Alternatively, these results might reflect the greater impact of expectancy or anticipation on cerebellar neurons as suggested by the study of perturbations on grasping.

### Grasping

This study suggests that proprioceptive and cutaneous afferents are received and processed by parallel and independent neuronal networks in both the cerebellum and motor cortex.

Figure 4 — Neuronal responses to the force-pulse perturbation for a cerebellar Purkinje cell and a motor cortical neuron. Both cells have reflex responses to the perturbation but only the Purkinje cell shows a preparatory discharge. Time in seconds is indicated beneath each histogram.



Ostensibly this separate processing of proprioceptive and cutaneous afferents would allow each class of mechanoreceptors to provide independent positive feedback to the cerebellar and motor cortex. However, the force-pulse perturbation which is a relatively strong stimulus produced nearly identical excitatory responses in both cells with cutaneous and proprioceptive receptive fields. A potentially important distinction between motor cortex and cerebellum is suggested by the distribution of post-perturbation latencies shown in Figure 3. The skewed shape of motor cortical distribution implies that excitation arrives earlier and lasts longer in motor cortex than in the cerebellar cortex despite the fact that the mean latencies are nearly identical for each group at about 40 ms.

The physiological consequences of positive excitatory feedback to the motor cortex is quite different and much easier to understand than the same excitation in the cerebellar cortex. Assuming that corticospinal, and possibly corticomotoneuronal cells are among those responding to the perturbation, the activation of cutaneous receptors by surface slip or short stretches of the intrinsic hand muscles would increase the grip force to prevent the object from dropping. The relative absence of preparatory responses among neurons of the rostral bank of the central sulcus suggests they may be more intimately involved with compensatory increases in grip force after perturbations, and have less involvement with preparing appropriate anticipatory strategies. The evidence provided by Dum and Strick<sup>22</sup> suggests that the neurons deep in the central sulcus do not receive cerebellar afferents. Although the absence of preparatory activity in motor cortex has already been noted by Riehle and Requin,<sup>23</sup> its absence in the present study was nevertheless surprising for two reasons. First, the majority of motor cortical cells had receptive fields which would have been stimulated by the anticipatory increase in force and second, the activity of many of these same neurons was significantly related in grip force which increased in anticipation of the perturbation (see Figure 3). However, it seems almost certain that some other cortical motor areas such as premotor or supplementary motor areas may well provide this preparatory activity which ultimately contributes to the increases in grip force.<sup>20,24,25</sup>

Taken together what do these single cell recordings during reaching and grasping tell us about the different functions of the cerebellum and motor cortex? The similar mono-modal distribution of activity profiles in the cerebellum and motor cortex suggest a relation to a covarying parameter of movement direction. Moreover, the similar temporal recruitment of these structures implies a parallel activation. However, certain differences are equally striking and suggest these two structures may be controlling different parameters. The study of reaching suggests that the motor cortex provides a more precise directional signal that is temporally more stable than the cerebellum. It is known that the cerebellar signal is sensitive to movement direction and less sensitive static posture than the motor cortex. These results suggest that the cerebellum may be controlling other aspects of movement such as compensating for dynamic reaction forces produced by the movement rather than directing the movement per se. The results on predictable perturbations of grasping suggest that the cerebellum can provide adaptive compensation based on the anticipation of proprioceptive and cutaneous stimuli.

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