# Cerebellar Unit Activity and the Movement Disruption Induced by Caudate Stimulation in Rats

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**Abstract**. Movement-triggered electrical stimulation of the head of the caudate nucleus (Cd) in rats impairs lateralized reaching for food with the contralateral forepaw. In an attempt to analyze the nature of this effect, unit activity changes elicited by the reaching movement, electrical stimulation of Cd and movement--triggered Cd stimulation were recorded in cerebellar cortex and dentate nucleus of 16 rats using a miniature microdrive and capillary electrodes. Cerebellar recording was ipsilateral and Cd stimulation contralateral to the preferred forepaw. Unit activity and reaching, monitored photoelectrically, were recorded on an analogue tape and processed off-line with a computer programmed for spike recognition and perireach histogram analysis. About 75% of cerebellar neurons reacted to reaching, mostly with an activity increase culminating in about 80 ms before reach onset. Activity of 50% of cerebellar units was inhibited by low rate (0.2 p.p.s.) stimulation (0.1 ms, 5 to 20 V) of contralateral Cd. Movement-triggered stimulation blocked the second part of the reaching response. In 64 units examined under all three conditions, neurons, reacting to both reaching and Cd stimulation were encountered significantly more frequently than would correspond to independent reactions. The prestimulus part of perireach histogram was often modified by continued movement-triggered stimulation. The steeper and higher excitatory reactions probably reflected the effort of the animal to overcome the anticipated disruptive effects of stimulation. Although the exact pathways mediating the cerebellar activity changes induced by Cd stimulation are not yet known, the distortion of the cerebellar activity patterns is serious enough to account for the disruption of the preprogrammed ballistic reaching.

**Key words**: Handedness — Instrumental reactions — Cerebellum — Dentate nucleus — Unit activity — Brain stimulation — Caudate nucleus

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## Introduction

Recent research into the neurophysiological mechanisms of skilled movement has led to the formulation of a comprehensive hypothesis (Allen and Tsukahara 1974; Kornhuber 1974), attributing to various brain structures specific roles in the elaboration of the motor command. According to this hypothesis cerebellum is responsible for the pre-programmed ballistic movements, while caudate nucleus is mainly concerned with the slow ramp movements. Both structures converge through the ventrolateral nucleus of thalamus upon the motor cortex, the activity of which controls specific motor acts through the pyramidal pathway. Supporting evidence for these ideas has been obtained mainly from experiments on monkeys, trained to perform various instrumental reactions (Brooks et al. 1973; Evarts 1973; Kozlovskaya 1976; Thach 1970a, b, 1978), but analogous results have been also reported in cats (Amassian et al. 1972; Kotlyar et al. 1979) and rats. In the latter species the so called "handedness" (Peterson 1934), the preference of rats to use one forepaw to reach for food objects inside a narrow tube, has proved to be a particularly suitable experimental model of an acquired ballistic movement, well amenable to electrophysiological analysis. Dolbakyan et al. (1977) and Hernandez-Mesa and Bureš (1978) demonstrated characteristic unit activity changes in the motor cortex, caudate nucleus and cerebellum accompanying lateralized reaching with the ipsilateral or contralateral forepaw. The functional importance of these unit activity changes has been confirmed by experiments showing that reaching can be disrupted by movement triggered electrical stimulation of any of the above structures (Hernandez-Mesa and Bureš 1977). Especially the stimulation of the caudate nucleus contralateral to the preferred forepaw prevented the rat from completing the movement and caused long trains of ineffective reaches. Disruption could be due not only to the disorganization of the caudate activity by electrical stimulus (Doty 1969), but also to interference with the organized activity of the ventrolateral thalamic nucleus, motor cortex, and cerebellum. Whereas the caudato-cortical influences mediated through thalamic nuclei are well documented (Kemp and Powell 1971; Sakata et al. 1966) less is known about caudato-cerebellar connections. Fox and Williams (1968, 1970) described evoked potentials elicited in the cerebellar cortex of cats by electrical stimulation of the caudate nucleus. Cerebellar unit activity changes induced by caudate stimulation were demonstrated in cats by Hablitz and Wray (1977) and Bratus and Moroz (1978, 1979). The purpose of the present paper is to examine the responses of cerebellar units (both in cortex and dentate nucleus) during reaching, continuous low frequency caudate stimulation and caudate stimulation, triggered by reaching; and to assess in this way the role of cerebellum in the movement disruption induced by caudate stimulation.

**Method**

Sixteen male albino rats of the Wistar strain, about 3 months old, were reduced to 85 % of original body weight (200—250 g) and trained to reach for 20 mg pellets of Larsen's diet into a narrow (11 mm internal diameter) horizontal feeder attached to the front wall of a plexiglass chamber (Megirian et al. 1974). Only animals which succeeded in retrieving pellets placed 10—15 mm deep in the feeder consistently, using the left or the right forepaw on several successive days, were used in the electrophysiological experiments. Under Nembutal anaesthesia (40 mg/kg), the trained rats were implanted with stimulating electrodes (twisted stainless steel wires 200 μm in diameter) aimed, according to the atlas by Fifková and Maršala (1967), at the heads of both caudate nuclei (AP-2, L 2, V 4). A 3-mm trephine opening above the dentate nucleus (AP 11.0, L 3.0) was used for implanting of a stainless steel guiding cannula (2 mm internal diameter) above the cerebellar hemisphere ipsilateral to the preferred forepaw. A silver screw (2 mm in diameter) was implanted into the frontal bone 7 mm rostral to bregma. The electrodes were connected to a miniature 5-pin transistor socket and the whole implant was fixed to the skull bones by anchoring bolts and acrylate.

Two days after surgery the animal was connected to the isolation unit of the stimulator through a flexible cable and a miniature microdrive (Bureš et al. 1976), loaded with a capillary microelectrode (4 mol.l$^{-1}$ NaCl, 1 μm, 5—10 MΩ), was fixed to the guiding cannula. The microelectrode was inserted through the cerebellar cortex into the dentate nucleus and well isolated stable units were examined in both structures during spontaneous reaching, low frequency electrical stimulation (0.1 ms, 5 to 20 V, 0.2 Hz), and reach-triggered electrical stimulation. With the electrodes used, the stimulus current ranged from 0.1 to 0.4 mA. Extension of the forepaw into the feeder was detected with a photoelectric sensor connected to a Schmitt trigger circuit and recorded on one channel of a conventional tape recorder as a train of 1000 Hz pulses gated by the reaching. Synchronization pulses triggering the automatic electrical stimulation were recorded in the same way. Unit activity was picked up with a FET source follower probe mounted on the microdrive, amplified 1000 times with an IC instrumentation amplifier, displayed on the CRO and recorded in the other channel of the tape recorder.

Off-line processing of the records was performed using a LINC 8 computer. Spikes were detected with a pattern recognition program using amplitude, slope, and duration criteria (Stashkevich and Bureš 1981). The events detected during 512 ms before and 512 ms after the onset of reaching were stored at four memory locations (peak amplitude, peak-trough difference, event-reach time and serial number of the reach). After an accumulation of 512 spikes the program automatically displayed the peak versus peak-trough scattergram. Points corresponding to spikes of the same type formed dense elliptic clouds. Manually operated cursors were used to enclose groups of points into square boxes delineating the space occupied by a unit. Peri-reach histograms were constructed for units identified by the above procedure. Stationarity of responding was tested by raster displays in which rows corresponded to individual reaches and dots to the occurrence of spike. If necessary, several portions of the record, each with 512 spikes, were added in order to obtain cumulative peri-reach histograms for a period of activity during which parameters of the unit reamined stable.

The peri-reach histograms ( ± 512 ms around the onset of reaching, 64 bins of 16 ms) were evaluated on the assumption that the first 10 bins (160 ms) were relatively unaffected by reaching and could be considered, therefore, as a sample of a spontaneous activity. Average firing rate during this period was compared with the activity in at least 3-bin long (48 ms) continuous segments of the histograms, corresponding to the suspected excitatory or inhibitory reactions. A two-tailed Student's t-test was used to compute the statistical significance of the difference which was accepted as reaction when significant at the 0.01 level. The chronic use of a roving electrode precluded histological verification of the individual recording sites, the position of which was obtained from microdrive readings. After the conclusion of the experiments, a stainless steel wire electrode (100 μm in diameter) replaced the glass capillary and an electrolytic lesion was made in the lowest electrode placement. The

deeply anesthetized animals was killed by intracardial perfusion with physiological saline followed by 4 % formalin. The position of the caudate electrodes and of the cerebellar lesion was localized in Nissl stained serial sections and the microdrive data were corrected accordingly. Functional criteria were used to distinguish unit activity in the depth of cerebellar folia from the activity of nuclear neurons. High background activity and the presence of complex spikes within 200 μm from the recording site indicated electrode position in the cerebellar cortex.

### Results

Post-stimulus or perievent histograms were obtained from 305 units which satisfied the conditions of spike detection and of the computer identification program. Low resistance capillary electrodes favoured the recording of cell activity. Both simple and complex spikes were recorded in the cerebellar cortex. On the basis of functional criteria and histologically validated microdrive readings, 147 units were localized in the cerebellar cortex overlying the dentate nucleus, i.e. in the cerebellar hemisphere at the level of sulcus intercruralis (Zeman and Innes 1963) and 158 units in the dentate nucleus, forming the most lateral part of the nuclear complex. Units of uncertain localization were not included in the final evaluation of results. All cerebellar recordings were made in the hemisphere ipsilateral to the reaching fore-paw.

*Activity changes induced by reaching.* Periods of excitation or inhibition, statistically significant ($p < 0.01$) with respect to the first 10 bins of the histogram, were found in 145 out of the 210 units examined during reaching. The responses were similar to those described by Hernandez-Mesa and Bureš (1978). Typical ones consisted of phasic excitation culminating in some 50—80 ms before the reach onset, and were sometimes preceded and/or followed by less prominent periods of inhibition. Histograms of this shape were found both in the cerebellar cortex and the dentate nucleus (Fig. 1A). Tonic activity changes were less common (Fig. 1B). Their incidence was relatively higher in the cerebellar cortex than in the dentate units. The overall distribution of the excitatory and inhibitory responses in the neuronal population examined is reflected in the population response profiles (Fig. 2), closely resembling those reported by Hernandez-Mesa and Bureš (1978).

*Activity changes induced by caudate stimulation.* Single pulse stimulation of the contralateral caudate nucleus, subthreshold for eliciting overt movement, but strong enough to induce slight impairment of reaching, elicited significant responses in 93 our of 177 cerebellar units. The number of responding neurons was similar in cerebellar cortex and dentate nucleus. The distribution of various types of responses was also similar in both structures. Typical responses shown in Fig. 3 consisted in short latency inhibition (Fig. 3A, C), sometimes interrupted by a period of excitation (Fig. 3B, C). Purely excitatory responses were rather exceptional (Fig. 3D). The population response profiles (Fig. 4) indicate that the
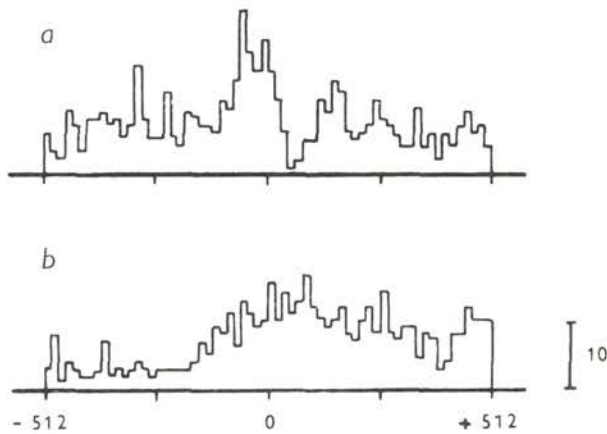
**Fig. 1.** Examples of the basic types of perireach histograms. Abscissa: time (ms) before (negative values) and after (positive values) reach detection (zero of the time axis). The histogram consists of sixty four bins of 16 ms. Calibration: 10 spikes/bin. A. phasic response of a dentate nucleus neuron. B. tonic response of a cerebellar cortex neuron.
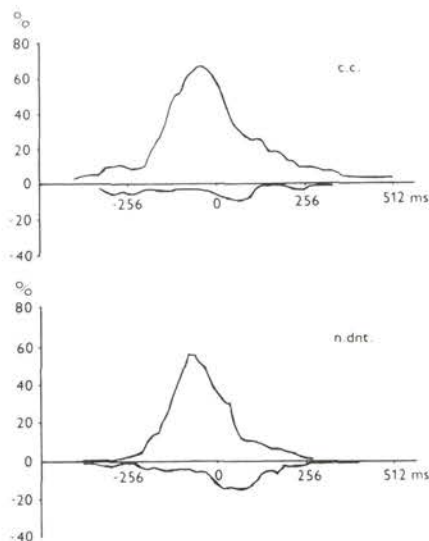


**Fig. 2.** Population response profiles elicted in cerebellar cortex (c.c., n = 102) and dentate nucleus (n.dnt., n = 108) by reaching. Abscissa: time (ms) before (negative values) and after (positive values) reach detection (zero of the time axis). Ordinate: percentage of neurons showing in the respective bins statistically significant activity increase (+) or decrease (−) with respect to the first 10 bins of the peri-event histogram.
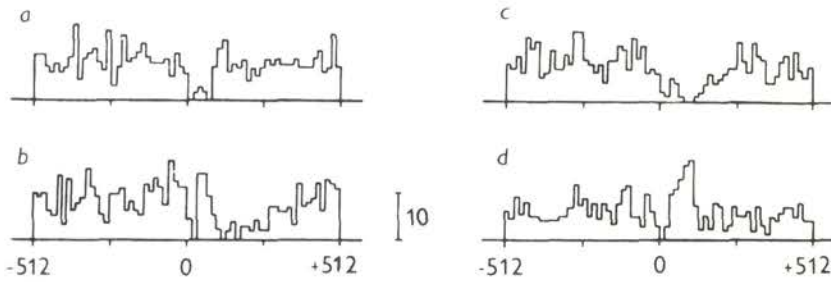
**Fig. 3**. Reactions of dentate nucleus neurons to single pulse stimulation of the caudate nucleus. Regular stimulation (0.2 p.p.s.) occurred at time zero. Other details as in Fig. 1. Predominantly inhibitory responses (A, C) were sometimes interrupted by excitatory peaks (B, D).
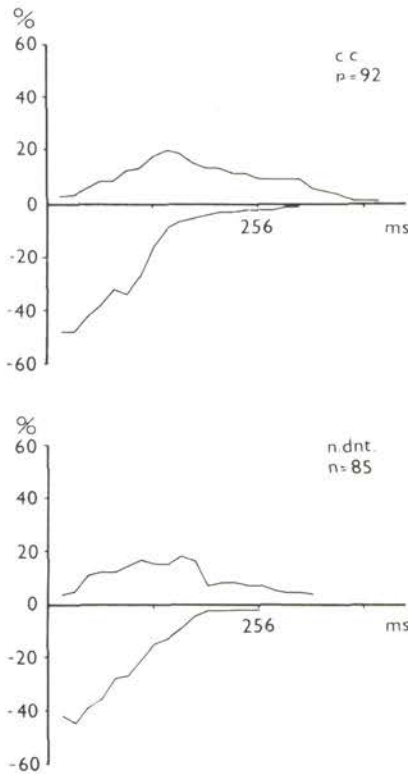


**Fig. 4**. Population response profiles elicited in the cerebellar cortex (c.c., n = 92) and dentate nucleus (n.dnt. n = 85) by single pulse stimulation of the caudate nucleus. Only the poststimulus effect is shown. Other description as in Fig. 2.

individual responses are sufficiently uniform to generate smooth distributions. Similar but less pronounced inhibitory responses were also elicited by the stimulation of the ipsilateral caudate nucleus (n = 18).

*Activity changes induced by stimulation of the caudate nucleus triggered by reaching.* The pre-reach part of the perievent histogram was little affected by the movement-triggered stimulation. The second part of the histograms reflected the interaction of the movementrelated activity with the electrically elicited response. The population response profile (n = 124) was not a sum of the population responses to reaching alone and to electrical stimulation alone, but rather resembled the response to the electrical stimulus alone (Fig. 5).
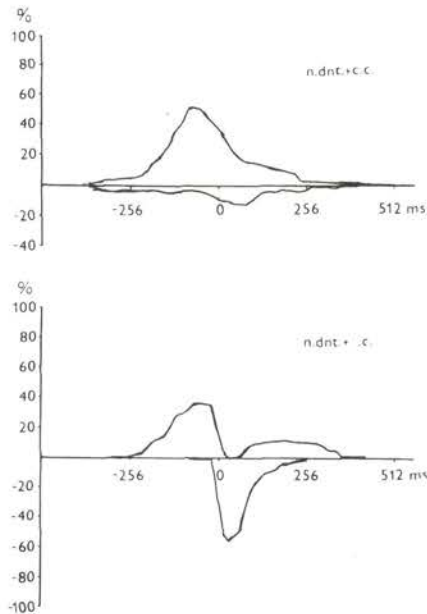


**Fig. 5**. Population response profiles of cerebellar neurons (from both cerebellar cortex and dentate nucleus) during reaching alone (above, n = 210) and reaching-triggered caudate stimulation (below, n = 124). Other description as in Fig. 2.

*Comparison of movement and stimulation induced changes in the same neuron.* In 82 neurons movement-induced and stimulation-induced responses were elicited in immediate succession. The contingency Table 1 shows the distribution of reacting and non-reacting neurons under these conditions. The percentage of neurons affected by both stimuli was significantly higher than the expected random distribution ($\chi^2 = 47.86$, p < 0.001). It was more difficult to assess the relationship

**Table 1**. Incidence of movement-related and caudate stimulation-induced reactions in 82 cerebellar neurons

|  |  | Movement | | |
| --- | --- | --- | --- | --- |
|  |  | reacting | non-reacting | total |
| caudate stimulation | reacting | 37 | 7 | 44 |
|  | non-reacting | 2 | 36 | 38 |
|  | total | 39 | 43 | 82 |

between the reactions elicited by movement and by stimulation. As shown in Fig. 6, neurons displaying phasic (Fig. 6A) or tonic (Fig. 6D) response during movement reacted with the same inhibitory reaction to the electrical stimulation of the caudate nucleus (Fig. 6C and F).
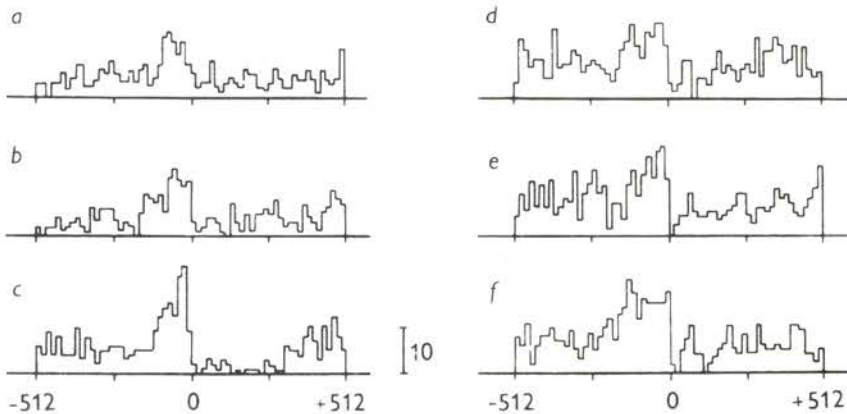


**Fig. 6**. Perireach and post-stimulus histograms of dentate nucleus (A, B, C) and cerebellar cortex (D, E, F) neurons during reaching (A, D), reach-triggered (B, E) and continuous (0.2 p.p.s.) (C, F) caudate stimulation. Other description as in Fig. 1 and 3.

*Changes induced by movement, continuous stimulation and movement-triggered stimulation in the same neuron.* In 64 neurons it was possible to examine all three experimental conditions and to compare the movement-stimulus combination with the effects of movement and stimulus separately. Typical results are shown in Figs. 6 to 8. In most cases the interaction was manifested by the powerful effect of electrical stimulation and by serious distortion of the movement pattern. A rather common observation was an anticipatory change of the pre-reach activity. The excitatory peaks were higher and started more abruptly (Fig. 6B, E) than in the

reach alone conditions (Fig. 6A, D). This is clearly reflected also in the raster displays (Fig. 7). With continued movement-triggered stimulation, the pre-reach
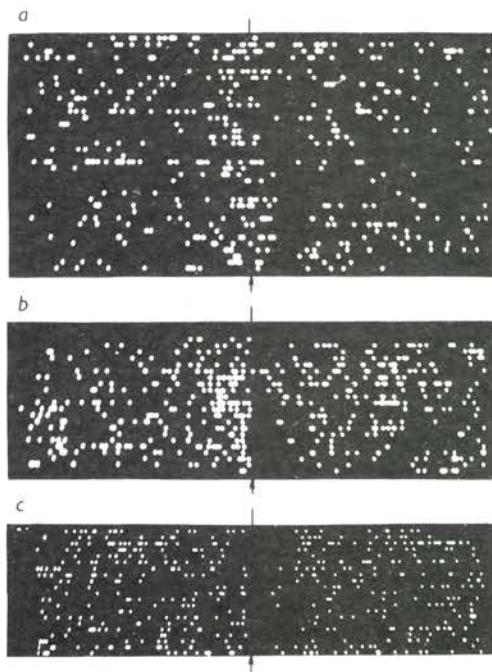


**Fig. 7.** Raster displays of the responses of a dentate nucleus neuron to reaching alone (A), reach-triggered stimulation (B) and continuous (0.2 p.p.s.) stimulation (C). Abscissa: The ±512 ms interval around reach detection. Ordinate: the rows represent individual reaches. Each dot indicates occurrence of an identified spike in the corresponding peri-reach interval (bin width 2 ms).

activity was gradually enhanced (Fig. 8). This change was also reflected in the population response profiles plotted for the 31 neurons displaying significant reactions to movement and examined under all three experimental conditions (Fig. 9). Between 160 and 48 ms before reach detection the percentage of activated cerebellar neurons was higher in the non-stimulated than in the stimulated reaches. Binomial probability tests showed that the difference was significant at the $p < 0.05$ level.

## Discussion

The main finding in the present paper is that 52.5% of units in the cerebellar hemispheres and in the dentate nucleus of freely moving rats respond to single
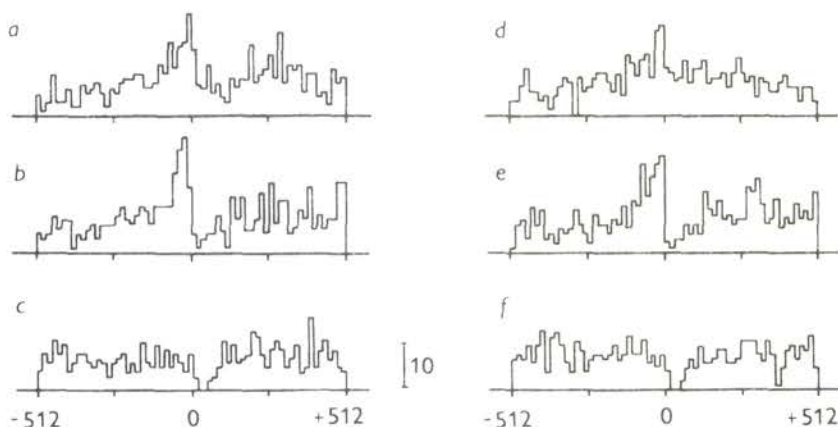
**Fig. 8**. Responses of two dentate neurons (A, B, C and D, E, F) to repeated reach-triggered caudate stimulation. Other details as in Fig. 1 and 3. Note that the pre-reach activity gradually increases from the first (A, D) to the third (C, F) histogram, each based on 30 to 40 reaches.

pulse stimulation of the caudate nucleus at intensities which do not elicit overt movement. The predominantly inhibitory reactions resembled the tonic responses of Purkyně cells evoked by caudate or pallidal stimulation in anesthetized cats (Bratus and Moroz 1978).

Closer inspection of the records showed brief excitatory reactions superimposed on prolonged inhibition. Although the exact path mediating the above effect is not known, analysis of cerebellar evoked potentials (Gresty and Paul 1975; Fox and Williams 1968, 1970) and unit activity changes (Hablitz and Wray 1977; Bratus and Moroz 1978, 1979) in cats indicate that caudate impulses reach the cerebellum via substantia nigra and inferior olive (by climbing fibre input) and through a region dorsal to the red nucleus (by mossy fibre input). A monosynaptic projection from the caudate nucleus to inferior olive was described by Sedgwick and Williams (1967). Possible spread of the stimulus current to cortico-pontine or cortico-olivary fibres must be also considered. According to Oka and Jinnai (1978) activation of collaterals of the above pathways to the head of the caudate nucleus accounts for the close similarity of the cerebellar responses elicited by the stimulation of the caudate nucleus and of the motor cortex (Armstrong and Harvey 1966). The uncertain mediation of cerebellar inhibition in the above experiments precludes an unequivocal interpretation of results. Although the stimulating electrodes were in the caudate nucleus, the cerebellar response could be due to cortico-cerebellar rather than to caudato-cerebellar influences. The stimulation induced cerebellar inhibition is perhaps reflected in the reciprocal relationship between cortical (or caudatal) and cerebellar unit activity during reaching. Hernandez-Mesa and Bureš (1977) reported that the cortical activation is about 60 to
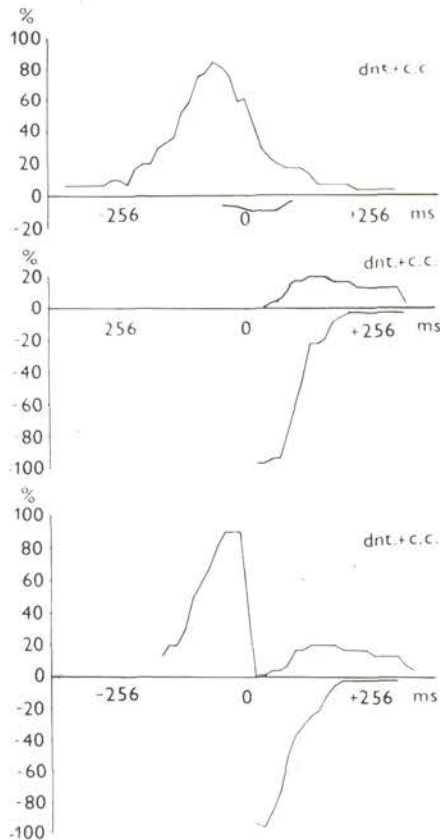
**Fig. 9**. Population response profiles of a group of 31 neurons (from both dentate nucleus and cerebellar cortex) which displayed statistically significant responses to reaching (above) and were also tested with clock-triggered (middle) and reach-triggered caudate stimulation (below). Note shorter and steeper activation of the examined population in the reach-triggered responses.

80 ms delayed after the cerebellar one, and that the excitatory peak of the cortical population response coincides with the decline of the cerebellar excitatory response. The effect is less pronounced, but this is not surprising when we take into account that the activity of the cortical and/or caudate neurons during reaching is less synchronous, less uniform and weaker than during electrical stimulation.

The large proportion of cerebellar neurons responding to caudate stimulation supports the notion that the resultant disruption of skilled movement might be due to the disorganization of the patterned activity already at the cerebellar level. Comparison of the movement-elicited and stimulation-elicited unit activity changes in the same neurons revealed marked convergence of both inputs: while the

incidence of units reacting to movement and to caudate stimulation was 47.6% and 52.4%, respectively, the incidence of units reacting to both stimuli was 45.1%, i.e. significantly higher than the expected random incidence of this combination (25.5%). This indicates that the cerebellar neurons participating in movement preprogramming are also more likely to receive feedback connections from higher centres. Under normal conditions information passed through this route is probably employed for the correction of the cerebellar output. Movement-triggered caudate stimulation may disrupt such feedback and generate an error signal interfering with the patterned activity in the cerebro-cerebellar loop. The deterioration of motor performance following caudate stimulation (Kitsikis and Rougeul 1968 ; Buchwald et al. 1961 ; Wilburn and Kesner 1974) can be due to interference at the level of basal ganglia, thalamic nuclei and motor cortex, but the distortion of the cerebellar output already seems to be serious enough to account for behavioral failure. This possibility is supported by the brief latency of the cerebellar inhibition which precedes the earliest possible modification of the motor output and can therefore be the cause, but not a consequence of movement disruption. On the other hand, changes of cerebellar activity may be an unimportant epiphenomenon occurring in parallel to the modification of cortical activity induced by antidromic and orthodromic (through the ventrolateral nucleus) routes.

Hernandez-Mesa and Bureš (1977) prevented successful reaching by electrical stimulation of dentate nucleus, which appeared, however, to have aversive properties: after a few frustrated reaches the rat left the feeder and did not approach it for several minutes. Reaching was only resumed after the stimulus intensity had been reduced below the interference threshold. Changes of cerebellar activity induced by caudate stimulation do not have aversive properties. Reaching was not stopped but the number of reaches per retrieved pellet was increased. Caudate stimulation was also reported to impair task execution rather than movement initiation in cats solving a version of the bentwire problem (Wilburn and Kesner 1974). In the present experiments the rats obviously attempted to modify the reaching strategy in a way which would make it less prone to interference. This was reflected in the PSHs of dentate and cerebellar units recorded during reaching alone and during reach-triggered stimulation. The pre-extension portion of the histogram showed a more abrupt and more intense activation which was further enhanced with continued stimulation. Rapid development of these anticipatory modifications of the cerebellar PSHs indicates striking flexibility of the system participating in the control of skilled movements. As soon as the success of a stereotype movement drops below the expected level, the motor command is modified until the performance improves again. As shown by Brooks et al. (1973) the modified strategy can completely by-pass the dentate nucleus: functional elimination of dentate nucleus by local cooling caused only transient impairment of

trained forelimb movements. Performance rapidly improved in spite of continued cooling as soon as the animal started to rely on target cues rather than on preprogramming. Both stimulation and cooling elicit reversible blockade of a part of the system the rest of which can be restructed to meet the demands of the task in a different way.

## References

Allen G. I., Tsukahara N. (1974): Cerebrocerebellar communication systems. Physiol. Rev. **54**, 957—1006

Amassian V. E., Weiner H. A., Rosenblum M. (1972): Neural system subserving the tactile placing reaction: a model for the study of higher level control of movement. Brain Res. **40**, 171—178

Armstrong D. M., Harvey R. J. (1966): Responses in the inferior olive to stimulation of the cerebellar and cerebral cortices in the cat. J. Physiol. (Lond.) **187**, 553—574

Bratus N. V., Moroz V. M. (1978): Responses of the cat cerebellar cortex units when stimulating nucleus caudatus, globus pallidus, substantia nigra. Neirofiziologiya **10**, 375—384 (in Russian)

Bratus N. V., Moroz V. M. (1979): Electrophysiological analysis of basal nuclei afferent influences on the cerebellar cortex neurones. In: Neural Mechanisms of the Integrative Activity of Cerebellum, pp. 124—129. Izdatelstvo Akademii Nauk Armyanskoi SSR, Erevan. (in Russian)

Brooks V. B., Kozlovskaya I. B., Atkin A., Horvath F. E., Uno M. (1973): Effects of cooling dentate nucleus on tracking-task performance in monkeys. J. Neurophysiol. **36**, 974—995

Buchwald N. A., Wyers E. J., Lauprecht C. W., Heuser B. (1961): The "caudate spindle" IV. A behavioral index of caudate-induced inhibition. EEG Clin. Neurophysiol. **13**, 531—537

Bureš J., Burešová O., Huston, J. P. (1976): Techniques and Basic Experiments for the Study of Brain and Behavior. Elsevier Scientific Publishing Company, Amsterdam and New York

Dolbakyan E., Hernandez-Mesa N., Bureš J. (1977): Skilled forelimb movements and unit activity in motor cortex and caudate nucleus in rats. Neuroscience **2**, 73—80

Doty R. W. (1969): Electrical stimulation of the brain in the behavioral context. Ann. Review Psychol. **20**, 289—320

Evarts E. C. (1973): Brain mechanisms in movement. Sci. Am. **229**, 96—103

Fifková, E., Maršala J. (1967): Stereotaxic atlases for the cat, rabbit and rat. In: Electrophysiological Methods in Biological Research (eds. Bureš J., Petráň M. and Zachar J.) pp. 653—731, Academic Press, New York

Fox M., Williams T. D. (1968): Responses evoked in the cerebellar cortex by stimulation of the caudate nucleus in the cat. J. Physiol. (Lond.) **198**, 435—450

Fox M., Williams T. D. (1970): The caudate nucleus-cerebellar pathways: an electrophysiological study of their route through the midbrain. Brain Res. **20**, 140—144

Gresty M. A., Paul D. H. (1975): Responses of fastigial nucleus neurones to stimulation of the caudate nucleus in the cat. J. Physiol. (Lond.) **245**, 655—665

Hablitz J. J., Wray D. V. (1977): Modulation of cerebellar electrical and unit activity by low-frequency stimulation of caudate nucleus in chronic cats. Exp. Neurol. **55**, 289—294

Hernandez-Mesa N., Bureš J. (1977): Impairment of lateralized reaching by movement synchronized stimulation of motor centers in rats. Exp. Neurol. **57**, 67—80

Hernandez-Mesa N., Bureš J. (1978): Skilled forelimb movements and unit activity of cerebellar cortex and dentate nucleus in rats. Physiol. Bohemosl. **27**, 199—208

Kemp J. M., Powell T. P. S. (1971): The connexions of the striatum and globus pallidus: synthesis and speculation. Phil. Trans. Roy. Soc. London, Ser. B **262**, 441—457

Kitsikis A., Rougeul A. (1968): The effect of caudate stimulation on conditioned motor behavior in monkeys. Physiol. Behav. **3**, 831—837

Kornhuber H. H. (1974): Cerebral cortex, cerebellum and basal ganglia: an introduction to their motor functions. In: The Neurosciences: Third Study Program (eds. Schmitt F. O. and Worden G.) MIT Press, pp. 267—280

Kotlyar B., Maiorov V., Savchenko E. (1979): Neuronal mechanisms of conditioned placing reactions in cats. Acta Neurobiol. Exp. **39**, 517—536

Kozlovskaya I. B. (1976): Afferent Control of Voluntary Movements. Nauka, Moscow 1976 (in Russian)

Megirian D., Burešová O., Bureš J., Dimond S. (1974): Electrophysiological correlates of discrete forelimb movements in rats. EEG Clin. Neurophysiol. **36**, 131—139

Oka, H., Jinnai K. (1978): Common projection of the motor cortex to the caudate nucleus and the cerebellum. Exp. Brain Res. **31**, 31—42

Peterson G. M. (1934): Mechanisms of handedness in the rat. Comp. Psychol. Monogr. **9**, 1—67

Sakata H., Ishijima T., Toyoda Y. (1966): Single unit studies on ventrolateral nucleus of the thalamus in cat: its relation to the cerebellum, motor cortex and basal ganglia. Jap. J. Physiol. **16**, 42—60

Sedgwick E. M., Williams T. D. (1967): Responses of single units in the inferior olive to stimulation of the limb nerves, peripheral skin receptors, cerebellum, caudate nucleus and motor cortex. J. Physiol. (Lond.) **189**, 261—279

Stashkevich I. S., Bureš J. (1981): Correlation analysis of neuronal interaction in the motor cortex of rats during performance of a discrete instrumental reaction. Int. J. Neuroscience. **2**, 1—6.

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

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

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

Wilburn M. W., Kesner R. P. (1974): Effects of caudate nucleus stimulation upon initiation and performance of a complex motor task. Exp. Neurol. **45**, 61—71

Zeman W., Innes J. R. M. (1963): Craigie's Neuroanatomy of the Rat. Academic Press, New York — London