

DENTATE CONTROL PATHWAYS OF CORTICAL MOTOR ACTIVITY. ANATOMICAL AND PHYSIOLOGICAL STUDIES IN RAT: COMPARATIVE CONSIDERATIONS

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INTRODUCTION

It is well known that the cortical motor activity is under the control of the cerebellar dentate nucleus (see review of the question in 3). More particularly, the action of the dentate nucleus would be determinant for correct execution of skilled movements (see in particular 4, 15). One motor operation is specifically dependent on the activity of the corticospinal tract: it concerns the discrete movements of fingers (7, 35, 36, 53). Actually, this specific motor behaviour is related to the development of a particular component of the corticospinal tract, i.e. pyramidal tract fibres that monosynaptically impinge upon motoneurons of the intrinsic hand muscles, responsible for independent finger movements (37, 40, 44). These features have been considered to be associated to the existence of an opposable thumb in the hand, and therefore to be a privilege of primates and human (see discussion of this point in 24). However, monosynaptic linkage of pyramidal tract fibre terminals with motoneurons of the distal musculature also exists in the cervical spinal cord of rodents, and particularly the rat which also presents to some degree the aptitude to manipulate (9, 16, 23).

To which extent skilled motricity is under a specific control from the neocerebellum is not yet clearly documented. It is known that the neocerebellar efferent, the dentate nucleus, is the source of a major nervous pathway to the motor cortex, via a relay in the ventrolateral, or "motor", thalamus. The main anatomical features of the dentate output to the motor cortex have been investigated in a variety of mammals (for a review, see 3, 34). On the other hand, the differential role exerted by the dentate nucleus upon the various steps of the voluntary movement has been repeatedly investigated (4, 5, 6, 52, 55). The informations thus collected clarify important aspects of the influence of the dentato-thalamocortical pathways upon the cortical motor activity. Nevertheless, several important anatomical and functional features of the dentatocortical influences are still ill known. As the rat discloses in its motor behaviour the functional similarities with primates mentioned above, and because of its relative phylogenetic proximity to the root leading to insectivora and primate orders, we thought that the rat might represent a simple model that would help understand the anatomical substrate and functional features

of dentate influences upon "cortical motricity". Specific questions that were addressed here concerned: *i*) whether the dentate control of skilled motor activity, which has been demonstrated in monkeys (48), is a prerogative of the primates, or whether it might be present in "lower" mammals and *ii*) whether "skilled motricity" in rat segregates to movements of digits and the eyes, as was shown in primates (47, 48), or whether it might concern different body regions. Our approach has been two-sided: first, an experimental anatomical analysis of the dentato-thalamocortical pathways has been carried out, using electrophysiological landmarks to functionally identify the foci involved in the motor cortex (2, 10). The corticothalamic projections from the motor cortex, which stand as important feed-back systems, have been concurrently analysed (12). Second, an electrophysiological analysis has been made by testing the motor consequences of direct intradentate microstimulations in normal rats and following ablation of the motor cortex (11).

METHODS

Both the anatomical and the physiological approaches have been carried out on adult Wistar rats.

The anatomical analysis. The study of the dentate control pathways upon the thalamocortical system has been three-stepped. The first step concerned the dentatothalamic projection. This has been analysed anterogradely by means of the autoradiographical tracing. Micro-injections of tritiated leucine or proline were made within the cerebellar nucleus lateralis (NL), which, in "lower" mammals, corresponds to the nucleus dentatus of the primates. The NL has been successfully injected without involving the neighbouring nucleus interpositus (NI) in 13 animals. A detailed description of the techniques employed has been given in 2. Terminal labelling was mapped at the thalamic level using bright field illumination. The observation was reported on standard drawings of transverse sections. The second step concerned the thalamocortical projection. This has been studied retrogradely using horseradish peroxidase (HRP) in 14 animals. Each cortical injections site had been selected on the basis of the motor effects of an intracortical microstimulation applied to it. These latter physiological tests were made under alcoholic anaesthesia (details of the procedure followed are given in 10, whereas the use of ethilic alcohol as anaesthetic was extensively discussed in 11). The sections of the "motor" thalamus were examined using bright field illumination or polarized light. Retrograde cellular labelling was reported on standard drawings of transverse sections of the ventral thalamus. The third step concerned the corticothalamic feedback pathways, i.e., both the direct projections and those that relay in the nucleus reticularis thalami (RT). In a first contingent of animals (14 rats), cortical microinjections of HRP-wheat-germ agglutinin compound (WGA-HRP) were made in the motor cortex, using the same electrophysiological landmarks for placing of the injections as just described. In these animals, anterograde terminal labelling has been mapped within the "motor" thalamus and the RT. In a second contingent of animals (16 rats), localized injections of WGA-HRP were made in the "motor" thalamus, and retrograde labelling was looked for within the RT and at the cortical level. Details of the approach followed are to be found in 12.

The overall outlines of the cerebellar nuclei conform to the description of Korneliussen (28). However, as will be explained in the next paragraph, we consider the "dorsolateral hump" (dlh, of Goodman *et al.*, 19) as part of the NL and not of the NI. In the "motor"

thalamic zone, the nuclear delineation conforms to that of Jones and Leavitt (26). With regard to the extent and arrangement of the "motor area" over the surface of the rat cortex, our observations confirm those of Hall and Lindholm (20), Donoghue and Wise (14) and Kartje-Tillotson *et al.* (27). A "rostral forelimb area" has also been observed, in agreement with 41, 42. In our experiments, not only movements of the distal forelimb, but also vibrissal activations were obtained from this "rostral forelimb area".

The physiological analysis. The motor effects of microstimulation applied to various regions of the NL have been explored in 28 intact rats. The stimulating electrode (a monopolar tungsten micro-electrode) was stereotaxically descended into the NL. The indifferent electrode consisted of a silver wire placed under the skin. Myographic electrodes were inserted in forelimb muscles. Under alcoholic anaesthesia, microstimulations were applied to the lateral cerebellar nucleus. For each nuclear locus tested, thresholds were searched for and the various parameters of the movements obtained were recorded myographically and through videotape. Post mortem control of the electrode placement was systematically carried out. In 17 other rats, the motor cortical region contralateral to the stimulated NL was removed prior to the session of NL stimulations. The experimental protocol was the same as that followed in intact animals. Finally, in 15 more rats, electrolytic destruction of the rubral region were performed prior to the session of NL stimulations. Further details of the techniques used are given in 11.

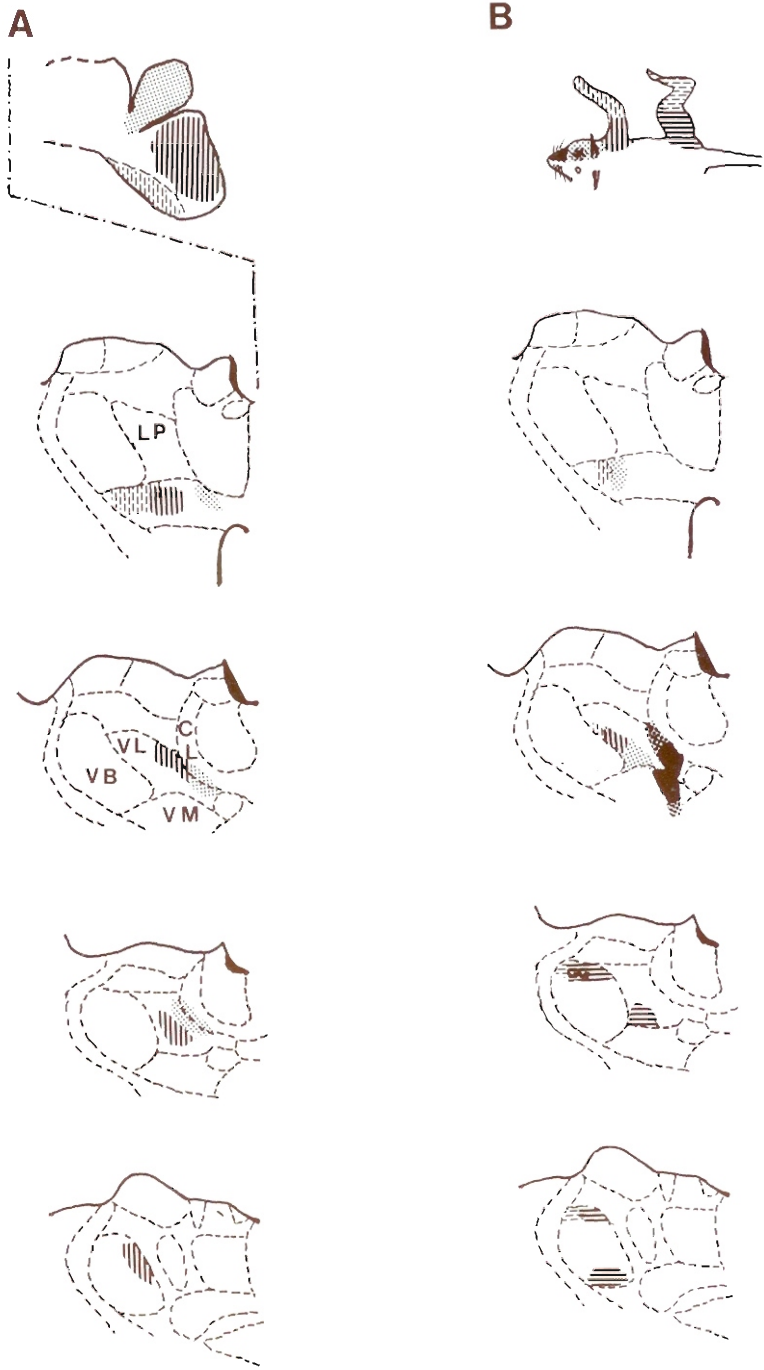
RESULTS

1. *Morphological organization of the dentato-thalamocortical pathways in the rat.*

The dentatothalamic projections. — It may be appropriate to detail here the three cytoarchitectonic subdivisions that we have differentiated within the NL of the rat, since only two subdivisions had been classically distinguished (28): these were a main, large-celled, subregion (NLI) and a ventral, small-celled, subregion (corresponding to the "subnucleus lateralis parvocellularis", slp, of Flood and Jansen, 18). On the basis of its olivary projections (1) as well as its cerebellocortical connections (8), we have seen that the "dorsolateral hump" (dlh) of Goodman *et al.* (19), which appears as wedged between the NLI and the NI, was also to be considered part of the NL.

Due to the different placements of the injection sites, the various subdivisions of the NL have been explored. Thus, two of our injections specifically affected dlh whereas dlh was also diversely involved in several of the injections that concerned NLI. Although none of our injections specifically affected slp, this subregion was included in 4 injections in conjunction with dlh and/or NLI. By comparing the distribution of the terminal fields in the various cases, it has been possible to determine with a good confidence the respective projection areas of dlh, NLI and slp. Furthermore, a comparison was possible between the distribution of fibres arising from rostral and from caudal regions of the NL, respectively. These results have been schematically represented in Fig. 1A.

Three longitudinal cellular columns in the ventral thalamus receive dentate afferents. Each of them rather specifically represents the projection field of one of



the three dentate subdivisions. A *centrodorsal region of the nucleus ventralis lateralis (VL)* is supplied from the NLI. This projection zone is rostrocaudally extensive: it runs throughout the VL extent (Fig. 1A). A region consisting of the *lateral nucleus centralis lateralis (CL)* and the *adjoining medial VL* is supplied from the dlh (Fig. 1A). There exists some overlapping within the medial VL between this projection zone and that of NLI. Finally, a *dorsocaudal region of the nucleus ventralis medialis (VM)* is supplied from the slp (Fig. 1A). Furthermore, a rostrocaudal arrangement exists within the dentatothalamic projection: rostral regions of the NL project onto rostral thalamic regions, caudal regions of the NL onto more caudal thalamic regions. This topographical arrangement is specially clear within the projection zone of NLI onto the VL.

The thalamocortical projections of the "motor" thalamus. — In 14 rats, foci physiologically identified as inducing discrete movements of the distal or proximal segment of the forelimb, the hindlimb, as well as of the vibrissae or of the eyes, have been selectively concerned by individual HRP injections (see 10 for technical details). Most of the retrograde cellular labelling was localized within the "motor" thalamus (Fig. 1B) where it distributed over regions that largely overlapped those receiving dentate projections (compare Figs. 1A and 1B). In individual cases, only restricted nuclear zones disclosed retrograde labelling. The topographical arrangement is schematically represented on Fig. 1B. Extensive regions of the VL itself are linked to cortical sites responsible for the movements of limbs, with the forelimb being represented more caudally than the hindlimb. There exists a complex topical relation of the VL with the cortical sites respectively engaged in movements of the distal and the proximal parts of the limbs (see Fig. 11 in 10). Thus, a lateral zone in the caudal VL is specifically linked to the "distal forelimb area" of the cortex. A dorsomedial zone of the VL and the adjoining region of the CL are linked to the "proximal forelimb area". Furthermore, this dorsomedial CL-VL region is connected to cortical sites responsible for movements of the distal forelimb and for oral and vibrissal movements in the face. VM regions are in relation with cortical sites (the "rostral forelimb area") also in charge of face motricity, specially ocular movements, and movements of the distal forelimb.

Besides the "motor" thalamus, several other nuclear regions were found to

Fig. 1 A-B. — *Anatomical mapping of the dentato-thalamocortical pathways.*

A: distribution of the projections from the three subdivisions of the NL onto the ventrolateral thalamus (anterograde autoradiographic study), synthetically reported on 4 drawings of equally spaced transverse sections through the thalamus; from caudal, above, to rostral, below. B: origin of the thalamic projections to the motor cortex (retrograde WGA-HRP study). Cortical target sites are represented by the body region that is mobilised by their intracortical microstimulation.

Abbreviations for this and the next figures: *Thalamus*. CL: nucleus centralis lateralis; LP: nucleus lateralis posterior; RT: nucleus reticularis thalami; VB: ventrobasal complex; VL: nucleus ventralis lateralis; VM: nucleus ventralis medialis. *Cerebellum*. Cop: copula pyramidis; PM: lobulus paramedianus; Sim: lobulus simplex; NLI: nucleus lateralis cerebelli, large cell subdivision; slp: subnucleus lateralis pars parvocellularis (of Flood and Jansen, 18).

project to the motor cortex. The somaesthetic thalamic relay, the ventrobasal complex (VB), represented a major source of such projections. Specifically, a dense retrograde labelling was observed in the rostral region of the VB, dorsally, in relation to the "hindlimb area" of the cortex. This observation is to be related to the large overlap of hindlimb motor and somatosensory areas in rodents (13, 20, 25). Other, more discrete, projections to the motor cortex were found to arise within regions of the mediodorsal nucleus and the lateral posterior-posterior nuclear complex.

The corticothalamic projections of the motor cortex. — It is postulated that the motor cortex controls activities within the "motor" thalamus through two sets of projections, a direct and a relayed projection. With regard to the former corticothalamic projection onto the VL region, it is generally considered that this direct pathway is topographically arranged in the same way as the reciprocal thalamocortical pathway. However, if this pathway has been examined in detail in several mammalian species (see review of the literature in 12), it has not yet been described in the rat. With regard to the latter corticothalamic projection, it is synaptically articulated at the level of the rostral pole of the RT. The rostral portion of the RT, which is massively supplied from the motor cortex (32), sends off its efferents onto the "motor" thalamus (as first shown by the Scheibels, 50). To our knowledge, no detailed analysis of this relayed corticothalamic pathway has been thus far published.

Anterograde terminal labelling has been mapped in the "motor" thalamus in the 14 cases of cortical injections with WGA-HRP. Moderately dense anterograde labelling was found through the same regions as those presenting retrograde cellular labelling, and the two types of labelling appeared to be topographically distributed in the same way. The complex arrangement of the projections from the cortical areas of the proximal and distal segments of the limbs respectively upon the VL is a remarkable feature of these direct corticothalamic projections (Fig. 2A). The cortical sites controlling activities in the proximal part of the limbs project to the medial regions of VL that massively project back onto them, whereas the cortical sites that control the distal segments of the limbs not only project to the lateral regions of the VL that project back onto them but also to the medial regions of the VL mentioned above. It is noteworthy that this "open" type of projection narrowly mirrors the arrangement of the VL projection onto the motor areas of the distal limbs. Therefore, in their broad lines, these direct corticonuclear projections reciprocate the thalamocortical projections to the motor cortex.

In the same cases, terminal anterograde labelling was also examined within the RT. This was restricted to a rostral region of the RT, where it disclosed a complex topographical arrangement (Fig. 2B). Cortical sites controlling movements of head, rostral and caudal limb were respectively found to project onto the RT ventrally, centrally and dorsally. Furthermore, a slight caudorostral shift was observed between the projection zones of the head, forelimb and hindlimb, successively. Other features of the motor cortical projections upon the RT, such as regarding their

differential laminar distribution, are of no concern here. Further details may be found in 12.

In 16 other rats, restricted regions of the VL and/or VM were injected with WGA-HRP. Retrograde labelling was mapped within the motor cortex and the RT. At the cortical level, the distribution of the labelling confirmed the observations summarized above regarding the direct corticothalamic projections. Within the RT, both retrograde and anterograde labelling was found, in a limited rostral region, and the two types of labelling topographically overlapped. The zone at the origin of the RT-VL projection rather strictly corresponds to the target zone of the motor cortex-RT projection. Topographically, cortico-RT and RT-VL links appear to be grossly arranged in register, and the final organization of the relayed corticothalamic pathway thus delineated broadly reciprocates that of the VL-cortex projection (Fig. 2B).

Our observations lead to the obvious conclusion that there is a consistency between the topographical arrangement found in each link of the dentato-thalamo-cortical pathways and the corticothalamic reverberating circuits. Functionally, this topographical arrangement is related to that of the motor cortex, whose somatotopical pattern is determined by its efferent, the pyramidal tract. As a consequence, particular regions of the "motor" thalamus, but also of the NL, would be specifically connected, through the corticospinal tract, to particular territories of the body musculature. This suggests a complex somatotopical arrangement of NL (Fig. 3). First, a broad differentiation may be drawn between rostral and caudal parts of the nucleus, which would be respectively involved in motor activities of the hind- and the fore-part of the body musculature. Second, a more refined somatotopical organization could be distinguished within each of the three cytoarchitectonic subdivisions of NL. NLI would be engaged in movements of the main segments of the skeletal musculature (head, trunk or legs). DIh would be related to oral or peri-oral motricity preferentially. SIp would be involved in movements of the smallest muscular masses (extrinsic muscles of the eye, vibrissae, and distal segments of the limbs).

2. Motor effects of the dentate stimulation. Participation of the motor cortex.

The stimulation of NL in normal animals. — Under our experimental conditions (light ethanolic anaesthesia, see 11), microstimulation applied to the NL induced activity in discrete sets of skeletal muscles, only in the contralateral half of the body. The intensity thresholds were in the range of 40 μ A. The fact that the peripheral effects drastically change for as minute displacements of the stimulating electrode as 200 μ m assessed the specificity of these effects. However, it has been ensured that none of the recorded movements could be due to the involvement of the neighbouring NI or to that of the surrounding white matter (for technical details and discussion, see 11).

Most of the motor effects of dentate stimulation were *simple movements*, i.e.

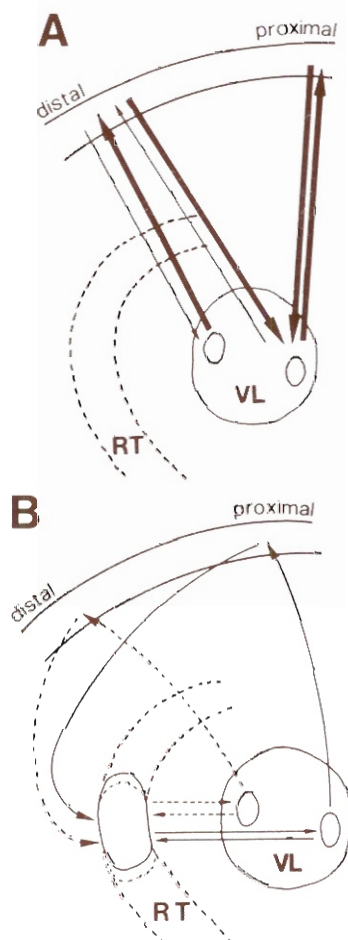


Fig. 2. — Schematic representation of the arrangement of the thalamocortical and corticothalamic reverberating circuits.

A: direct relations of the VL with the motor cortical regions of the proximal and distal segments of limbs. B: organization of the pathways including a relay to VL in the RT. For abbreviations, see Fig. 1.

affecting one single joint. More seldom, *complex movements*, i.e. concerning two or three joints, were obtained. The temporal organization of the effects showed that activation of muscles proximal and distal to a mobilized joint were almost synchronous. Intensity thresholds were very similar for simple and complex movements. The stereotyped nature of the complex movements and the practical impossibility to spatially or temporally dissociate the sets of activations elicited by single stimulations of NL confirmed the specificity of these complex movements.

Myographic records strongly suggest that the muscular activations recorded were of synergistic nature: single dentate stimulations affected agonist and antagonist muscles at a mobilized joint, as well as muscles located proximal to it. The latter

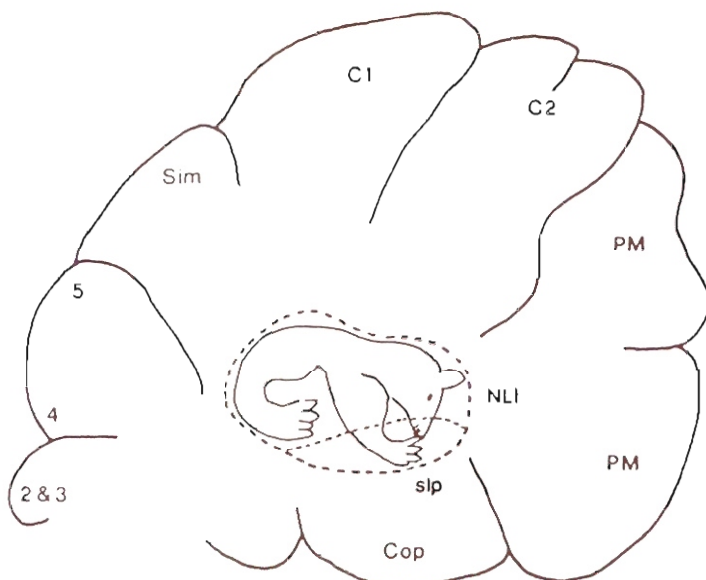


Fig. 3. - Somatotopic arrangement of the NL in the rat, as deduced from our anatomical analysis.

For abbreviations, see Fig. 1.

proximal effects might be interpreted as ensuring the dynamic fixation of the segment proximal to the mobilized joint (which realizes the mechanical support of purposeful movements).

A clear somatotopy existed in the motor effects of dentate stimulations (Fig. 4A). Most of the effects concerned the musculature of the head and/or forelimb. These effects were obtained from the central and caudal parts of the NLI, respectively. Mobilization of the hindlimb was very seldom obtained, and only from the rostral aspect of NLI. A finer somatotopical arrangement was related to the various cytoarchitectonic subdivisions. Thus, stimulations of the *NLI* mostly induced movements in both limbs, stimulations of the *dlh* induced movements of the lips, and those of *slp* induced movements of the vibrissae, of the neck, and in the intermediodistal segments of the forelimb (wrist and fingers). On the other hand, there was no apparent segregation between the sites inducing simple and those inducing complex movements. In most instances, complex movements corresponded to a combination of head and forelimb activity.

The stimulation of NL after motor cortical ablation. — Movements of the distalmost segments of the forelimb could no more be evoked following motor decortication. However, stimulations were equally effective in intact and decorticated animals regarding other body regions (Fig. 4B). Both the topography of the effects and intensity thresholds for evoking these effects were essentially unmodified after decortication.

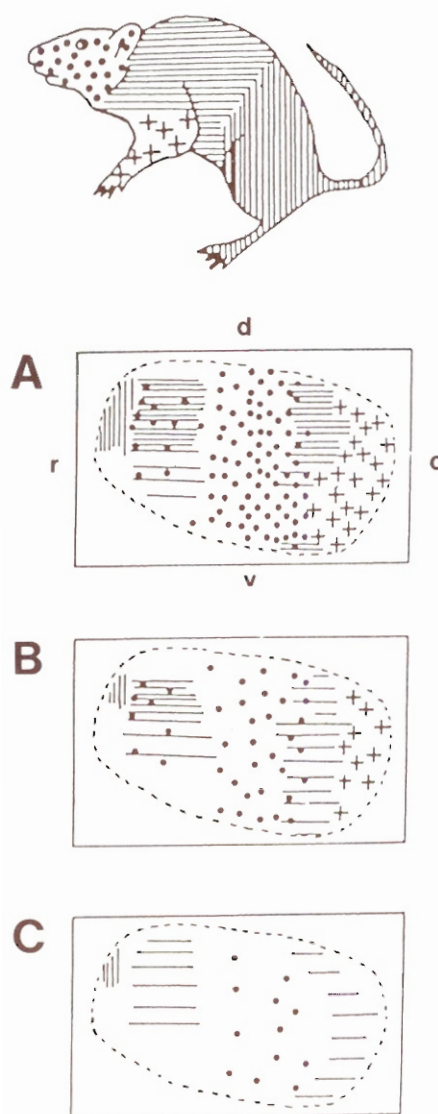


Fig. 4. — Somatotopic organization of the NL, as shown by our physiological investigation.

A: intact animal; B: following motor cortical ablation; C: following lesion of the red nucleus region. Orientation: c: caudal; d: dorsal; r: rostral; v: ventral.

The stimulation of NL after electrolytic destruction of the red nucleus. — Obviously, the electrolytic coagulations of the rubral region employed here interrupted the bulk of the cerebellothalamic fibres. Thus, not only the dentatorubral influences but also the dentato-thalamocortical influences were functionally affected by this strategy. However, we have just seen that cortical influences were only determinant

upon distal forelimb musculature. After the mesencephalic lesions, movements of the axio-proximal aspects of the body musculature were the most effectively obtained, whereas movements of the intermedial and distal limb segments disappeared. Head movements, only related to neck displacements, appeared less frequently than in intact brain rats. (Fig. 4C). The broad topography of the effects was not changed, but a dramatic increase of the intensity thresholds (more than twofold) was observed.

DISCUSSION

Three issues will be considered in this discussion. First, the main findings of our anatomical study concern the complex somatotopy existing within the nucleus lateralis of the rat cerebellum. Conclusions may be attempted on how these anatomical features relate to motor behaviours. Second, our physiological analysis revealed the functional organization of the dentate control pathways to motor cortex. Our results support the opinion that these pathways are arranged in terms of movements rather than in terms of activities in individual muscles. This will be briefly commented on. Third, the functional consequences of our lesion experiments permit to draw conclusions on the respective roles in motricity of the dentato-thalamocortical circuit and of dentato-infracortical circuits.

Two levels of organization are found in the NL. The first level concerns the existence of a rostrocaudal arrangement, which is related to a "posterior limb-anterior limb" crude somatotopy. It is worth noting that a large prevalence of the anterior limb representation upon that of the posterior limb has been found. More importantly, the second level corresponds to the presence of a multiple representation of the body in NL, in close relation to the cytoarchitectonic partition of the nucleus: each of the three cytoarchitectonic subdivisions of NL appears to be functionally connected to a specific sphere of motor behaviour. As a consequence, a single peripheral territory might be differently implicated in motor strategies, according which dentate subdivision it is triggered from and therefore in relation to the functional modality of the intentional movement concerned. *NLI* would be involved in the activation of muscular masses of all body territories, in relation to "voluntary" displacements. The specific involvement of *dli* in motor activities of the oral region (lips, tongue, vibrissae) may be taken as indicative of a linkage with highly integrated feeding mechanisms. On the contrary, *slp* would be engaged in selective activations of vibrissae, wrist and individual fingers and, to a lesser degree, moving of the eyes. These sets of activities are likely to underlie diverse procedure of exploration of the immediate surround. Thus is drawn a functional partition of the NL of the rat. This shows the relevance to the neocerebellum of the more general statement by Brooks and Thach (6) that... "one body part might be influenced by several areas in the cerebellum, each part exerting its own unique kind of control". We believe that the relative minuteness and

simplicity of the neocerebellum in the rat eased this functional dissection without biasing its basic results.

A common feature of motor activities generated by stimulations of the NL is the synergic activation of sets of agonist muscles concurring to the moving of a joint, or to the sequential moving of joints, that mimicks intentional movements. A comparison of these results with those of an analogous stimulation procedure carried out in awake monkeys (47, 48) discloses striking similarities. A same mode of operation would subserve the neocerebellar motor control in rat and primates. This suggests that the basic neuronal substrate of dentato-thalamocortical control pathways may be the same at two levels as distant as rodents and primates along the mammalian phylogenetic scale. This would be so in spite of obvious developmental differences. Thus, networks of local circuits neurones, which are thought to be the morphological substrate for precision sharpening, are much developed in the "motor" thalamus of cats as well as monkeys (21, 29, 30, 31, 45), whereas they are nearly totally absent from the thalamus of rodents (22, 43, 57). Therefore, the development along the pathways involved of such elaborate neuronal devices as networks of inhibitory local circuit neurones would not be necessary for some form of "skill" to show up.

What rat tells of the role of dentato-thalamocortical pathways in movement? We observed that, in this animal, elimination of the motor cortex was nearly uneffective upon motor responses to dentate stimulations. In agreement with Castro (9), only activations of the distal musculature, related to manipulation, were lost in rat following cortical lesions. This result is to be reconciled with observations made following sections of the pyramidal tract in primates (7, 36). In primates as in rats, the integrity of the motor cortex would only be determinant for the expression of "skill", i.e. discrete finger movements. This function would be supported by the integrity of the direct cortico-motoneuronal component of the pyramidal tract (23, 35, 37, 40, 44). Our results demonstrate the existence of a dentate control of "skilled" movements in rat as previously reported in monkey (48). "Skill" is achieved in primates through the individual usage of fingers, but also through moving of the eyes. In rat "skill" seems to be attached to the individual usage of fingers and of vibrissae. Individual displacements of the vibrissae in the rat and rotation of the eyes in monkey seem to be engaged in the same function, the exploration of surrounding space, in species preferentially active during nocturnal and diurnal part of the day respectively.

The fact that the route through the thalamus and cortex is not essential for the initiation of learned movements has been confirmed in various "higher" mammals (monkey: 39; cat: 17). Cerebellar influences on the triggering of motor activities would be carried through infracortical routes (11, 51). The present observations indicate a pivotal role in rat of the dentatorubral projection, but also of the dentoreticular projection, in triggering motor effects. On the other hand, the motor cortex which is, as emphasized by the present data, under cerebellar control, is the source of direct projections onto infracortical motor centres, specially the red nucleus (33, 38, 46, 54) and the reticular formation (49, 56). Each of these

centres is therefore under the convergent influences of NL and the motor cortex. The functions exerted by NL and motor cortex upon rubrospinal and reticulospinal systems would deserve further analysis.

S U M M A R Y

The dentato-thalamocortical projections have been studied in albino rats using anatomical and physiological approaches. The anatomical analysis reveals that the dentatothalamic input to the ventral thalamus and the thalamocortical projection from this region onto the motor cortical area have a complex topographical arrangement. The corticothalamic reverberating pathways, both direct and through a relay in the nucleus reticularis thalami, are also roughly arranged in register with the same topographical pattern. This arrangement has been reconciled with that of the motor cortex, as determined by the motor effects of intracortical microstimulations. From this is inferred a somatotopical arrangement of the cerebellar nucleus lateralis, or dentate. These observations are confirmed by the results of our physiological analysis. The movements obtained with direct microstimulations of the nucleus lateralis affect either one joint (simple movements) or, more seldom, several joints (complex movements) of the same limb. A rough rostrocaudal arrangement is found in the nucleus lateralis: the caudocentral regions of the nucleus contain the representation of the musculature of forelimb and head, whereas the hindlimb is represented in the rostralmost part of the nucleus. A more complex organization is found to be related to the three cytoarchitectonic subdivisions of the nucleus lateralis. The main, large-celled part of the nucleus is engaged in the control of the large skeletal musculature. The dorsolateral hump is involved in mouth and peri-oral activities. The ventral, parvocellular, subnucleus is involved in fine exploratory movements of vibrissae, eyes, and forelimb wrist and fingers. The implication of the dentato-thalamocortical pathways in the cortical motor activities in the rat is discussed with attention to the dentate control of the "voluntary" motricity in primates.

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