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Somatotopic Studies on Cerebellar Fastigial Cells

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Summary. The somatotopic inputs into fastigial cells have been studied in relation to cutaneous mechanoreceptors of forelimb and hindlimb. Some fastigial cells were very discriminative, not only in respect of the limb, but also to restricted areas of hairy skin and related toe pads. Others were much less so, forelimb and hindlimb cutaneous receptors evoking similar excitatory-inhibitory responses. In addition, from the contralateral hindlimb, responses were evoked which were comparable with those from the ipsilateral limb.

Somatotopic diagrams have been constructed which show in four experiments the sites of fastigial cells in the parasagittal plane of the microelectrode tracks. For each experiment four separate plottings give a comparison of the sizes of responses evoked for forelimb and hindlimb: excitation from nerve volleys; inhibition from nerve volleys; excitation from pad taps; inhibition from pad taps. In this way it is shown that fastigial cells with similar somatotopic relations often occur in clusters, particularly when assessed by their inhibitory responses.

Since fastigial inhibition is largely due to Purkyně cells, there is an attempt to correlate the somatotopic relations of Purkyně cells with the somatotopy of fastigial cell inhibition. The excitation of fastigial cells exhibits less somatotopic discrimination, which conforms with the poor somatotopic discrimination of cells of the lateral reticular nucleus.

In a final discussion there is consideration of two principal projections from the vermis of the anterior lobe: Purkyně cells inhibiting Deiters neurones directly; Purkyně cells inhibiting fastigial cells which in turn monosynaptically excite Deiters neurones, the inhibition of Deiters neurones being then by disfacilitation. The degree of forelimb-hindlimb convergence in these pathways is reconsidered and is diagrammatically illustrated.

Key words: Cerebellar nuclei — Fastigial neurones — Somatotopy — Cerebellar function

In the two preceding papers (Eccles, Sabah and Táboříková, 1974a, 1974b) there has been an account firstly of the responses of fastigial cells under a wide variety of inputs from cutaneous nerves or cutaneous mechanoreceptors and secondly an experimental investigation into the pathways involved in the production of these excitatory and inhibitory responses. Finally a summarizing diagram was constructed. However, in these accounts there has been a concentration on analyses of responses of individual units without reference to the func-

tional operation of the fastigial nucleus as a main relay station for the cerebellar output. This paper is concerned with an attempt to discover how far the Purkyně cell projection is channelled so that the discriminative functions of the Purkyně cells (cf. Eccles, Faber, Murphy, Sabah and Táboříková, 1971a, 1971b; Eccles, Sabah, Schmidt and Táboříková, 1972a, 1972b, 1972c) are preserved or reorganized at this first stage of their relay along the pathways to the motor machinery of the spinal cord. We are concerned with the attempt to see how far the connectivities onto the fastigial nucleus can be recognized as having a meaning in the control of posture and movement. Since the excitatory input to fastigial cells is largely via the poorly discriminative LRN pathway (Rosén and Scheid, 1973a, 1973b, 1973c), it has been postulated that the excitatory input to fastigial cells provides an amorphous background of excitation on which the discriminative Purkyně cell output is expressed (cf. Eccles, 1973). Usually this is by an inhibitory sculpturing, but it could also be by a disinhibitory addition to the background excitation.

This paper describes an experimental investigation in which the somatotopic relations of fastigial cells are studied, and in which an attempt is made to discover if there is a somatotopic pattern of Purkyně projection to the fastigial nucleus corresponding to that revealed by anatomical studies (Walberg, Pompeiano, Brodal and Jansen, 1962; Walberg and Jansen, 1964; Pompeiano, 1967).

Methods

The experimental methods have been described in the first paper of this series (Eccles, Sabah and Táboříková, 1974a) and in the earlier papers quoted there.

Results

A) Somatotopic Discrimination by Fastigial Cells

1. Inputs from Ipsilateral Limbs

In Fig. 1 there is a display of discriminative responses by the same fastigial cell that was used in a preliminary illustration (Fig. 2, Eccles, Sabah and Táboříková, 1974a). That illustration showed a powerful excitatory-inhibitory response to inputs from the ipsilateral hindlimb — peroneal nerve stimulation or taps to toe 5. In Fig. 1A there are two specimen records of the effects of a tap to toe 2 of the hindfoot and the averaged responses for 64 traces, the PSTH and the CFD. There is a clear excitatory-inhibitory response. In B the PSTHs and CFDs show that with the other toe pads the inhibition was much larger for HT4 and HT5, and somewhat larger for HT3. HCP closely resembled HT2 in its moderate effectiveness. Figure 1 also illustrates the usual finding that for a particular fastigial cell the receptive field for hair receptors is related to the receptive field for pad receptors, which has also been reported for Purkyně cell responses (Eccles, Sabah, Schmidt and Táboříková, 1972b). In C the largest E-I response was evoked from hairy skin lying just proximal to the pads of T4 and T5 and taps to these pads were the most effective. The shading indicates two grades of effectiveness for the receptive field for hair receptors.

Somatotopically the fastigial cell of Fig. 1 is of significance because its receptive field is virtually restricted to the hindfoot, both for the pad and the hair

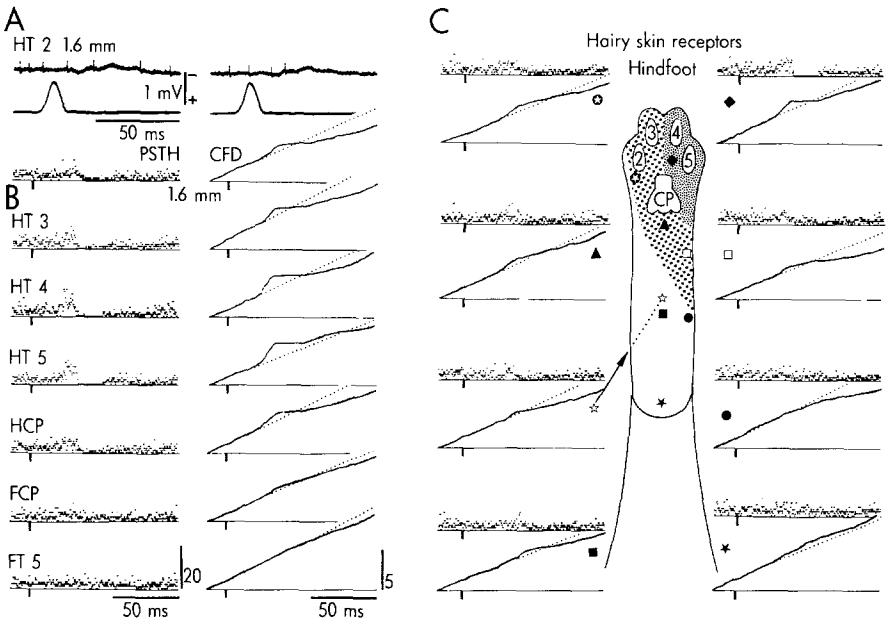

Fig. 1. *Somatotopic relations of a fastigial cell to cutaneous mechanoreceptors.* A gives specimen records of responses to a 1.6 mm tap to toe 2 of the ipsilateral hindfoot and the PSTH and CFD for addition of 64 such responses in 256 bins of 0.5 msec each. In B are the PSTHs and CFDs of responses to taps to the other hindfoot pads and also to two forefoot pads, FCP and FT5, as indicated. In C are the PSTHs and CFDs for responses evoked by brief air jets to the spots indicated by corresponding symbols on the hairy skin of the ipsilateral hindfoot. Note that the open star denotes a spot on the ventral surface of the foot. All PSTHs and CFDs are formed by the addition of 64 responses in 256 bins of 0.5 msec. Same time and count scales throughout. Fastigial cell 3 mm from midline in an unanesthetized decerebrate preparation

receptors. The pads of the forefoot (FCP and FT5 of B) were almost ineffective, and stimulation of the superficial radial nerve gave only a slight prolonged excitation, which contrasts with the very strong E-I response evoked in this fastigial cell by peroneal nerve stimulation (Eccles, Sabah and Táboříková, 1974a, Fig. 2B).

Figure 2 illustrates the more remarkable somatotopic relationships for another fastigial cell lying along the same microelectrode track as the cell of Fig. 1, and only 200 μm from it. This cell was even more strongly oriented to the hindlimb. Taps to the pads of the forefoot and even superficial radial nerve stimulation had little or no influence, which contrasts with the powerful inhibitory-excitatory-inhibitory response to the peroneal nerve stimulation (Fig. 2A). It should be noted in parenthesis that later in this same experiment many fastigial cells in other tracks were strongly influenced from the forelimb nerve and pads. The somatotopic exclusiveness of this cell was strongly displayed in A by responses to taps on the hindfoot pads. Toe 5 was very effective with a small initial inhibition preceding the strong E-I response, which almost matched that evoked by peroneal nerve stimulation. Toes 3 and 4 evoked weak E-I responses and the central pad was almost ineffective. Matching this high specificity of lateral over

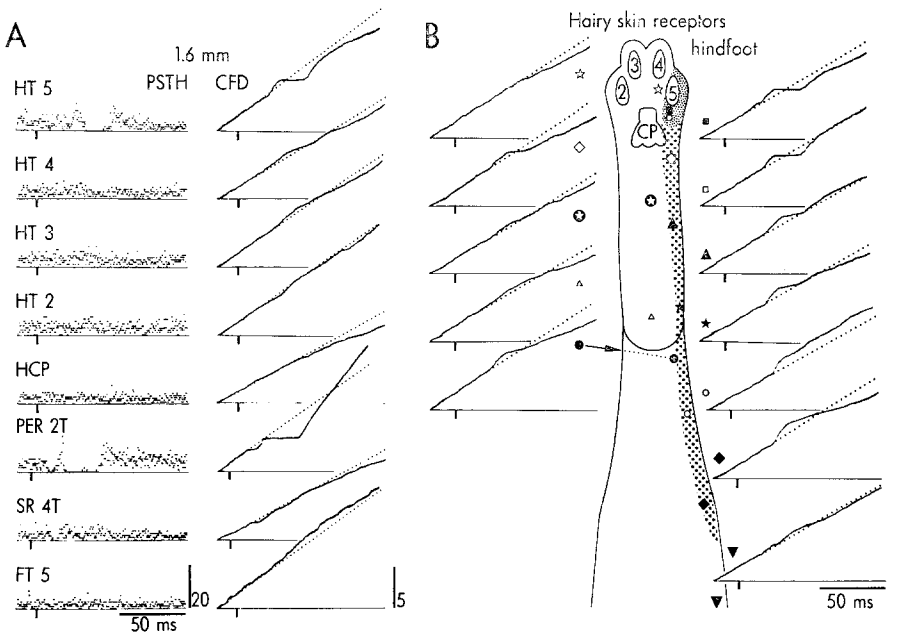

Fig. 2. *Somatotopic relations of a fastigial cell to cutaneous mechanoreceptors.* In A are PSTHs and CFDs of responses of a fastigial cell to taps of 1.6 mm to all hindfoot pads and also to forefoot T5 as indicated. There are also PSTHs and CFDs of responses evoked by stimulation of peroneal and superficial radial nerves. In B are the CFDs of responses evoked by air jet stimulation of the hairy skin at the sites indicated by corresponding symbols. The solid circle denotes the stimulated point on the ventral surface of the foot. All PSTHs and CFDs are formed by the addition of 64 responses in 256 bins of 0.5 msec. Same count and time scales throughout. This fastigial cell was in the same microelectrode track as that of Fig. 1, being 200 μm more superficial

medial foot pads there was a remarkably restricted field for hair receptors (B). Just proximal to T5 pad there was a strong E-I response almost equal to that from the T5 pad tap, and there was a strip on the lateral side of the foot and leg up to the thigh which was quite effective, particularly in excitation. On the other hand, only small responses could be evoked from the hairy skin medial to this lateral strip. One site on the ventral surface of the foot (filled circle) was also fairly effective. Again, the shaded area gives the receptive field for this fastigial cell, the hair receptor zone embracing the pad receptor zone.

The fastigial cells of Figs. 1 and 2 were exceptional in their almost exclusive orientation to a limb, both for excitatory and inhibitory responses, in these cases the hindlimb. A fastigial cell with a fairly strong orientation to the forelimb has already been illustrated (Eccles, Sabah and Táboříková, 1971, Fig. 1). All grades of selective orientation have been observed, some cells showing almost none, being influenced in the same manner and degree from both forelimb and hindlimb as in Fig. 3. Here the superficial radial (A) and peroneal (B) nerves were almost equivalent in their initial E and later prolonged I actions. Pad taps to forelimb (C) and hindlimb (D) had the same general actions — an initial E and a later

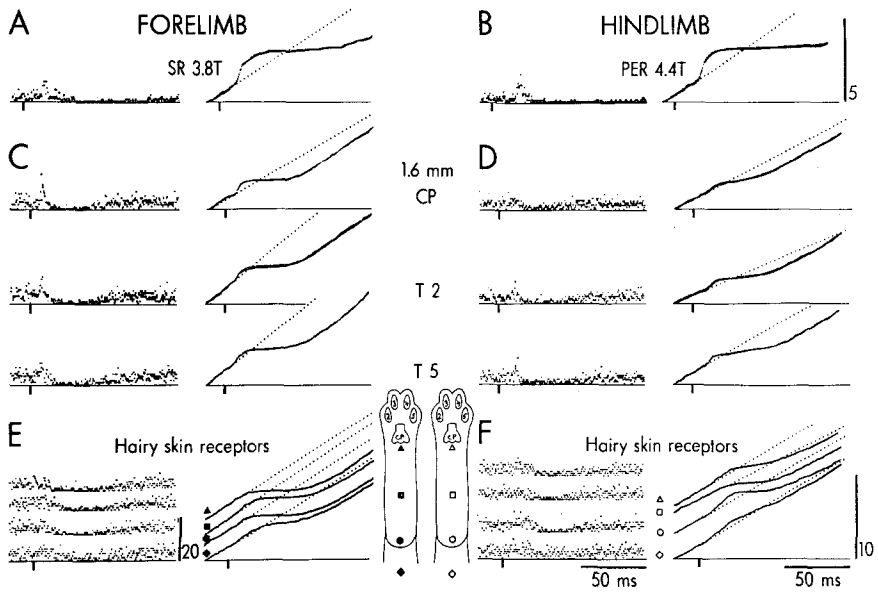

Fig. 3. *Somatotopic relations of a fastigial cell to cutaneous mechanoreceptors of forelimb and hindlimb.* In A and B are the PSTHs and CFDs evoked by stimulation of superficial radial and peroneal nerves respectively. In C and D are the PSTHs and CFDs for responses evoked by taps to the pads of forefoot and hindfoot respectively as indicated. In E and F are the PSTHs and CFDs evoked by air jet stimulation of the hairy skin at the indicated points on the forelimb and hindlimb respectively. CFDs of A and B have half the count scale of all other CFDs, otherwise all the records have the same count and time scale. Intact animal under continuous surital anesthesia

prolonged I — but the forelimb pads were more effective. Finally E and F show that hair receptors over wide areas of both forelimb and hindlimb had prolonged inhibitory actions that were very similar for corresponding skin areas on the two limbs. Not illustrated in Fig. 3 are the similar actions of pressure on the two central pads, both giving strong phasic inhibitions at "on" and "off" with no trace of tonic action. It is of special interest in Fig. 3 that it is in the prolonged inhibition that there is such similarity for forelimb and hindlimb because in general this inhibition can with assurance be ascribed to the inhibitory action of Purkyně cells. A minor alternative explanation is disfacilitation arising from inhibition of the background excitation from LRN cells (cf. Rosén and Scheid, 1973a, 1973c).

2. Inputs from Contralateral Limbs

Convergence onto fastigial cells has been found also for inputs from the contralateral limbs. Contralateral inputs were studied on 61 fastigial cells with nerve volleys from both forelimb and hindlimb nerves. It was not surprising to find that contralateral nerves were as effective as ipsilateral in exciting fastigial cells (cf. Fig. 4C, A and G, E). Contralateral input to the lateral reticular nucleus (LRN) is almost as effective in exciting as is the ipsilateral input (Rosén and Scheid,

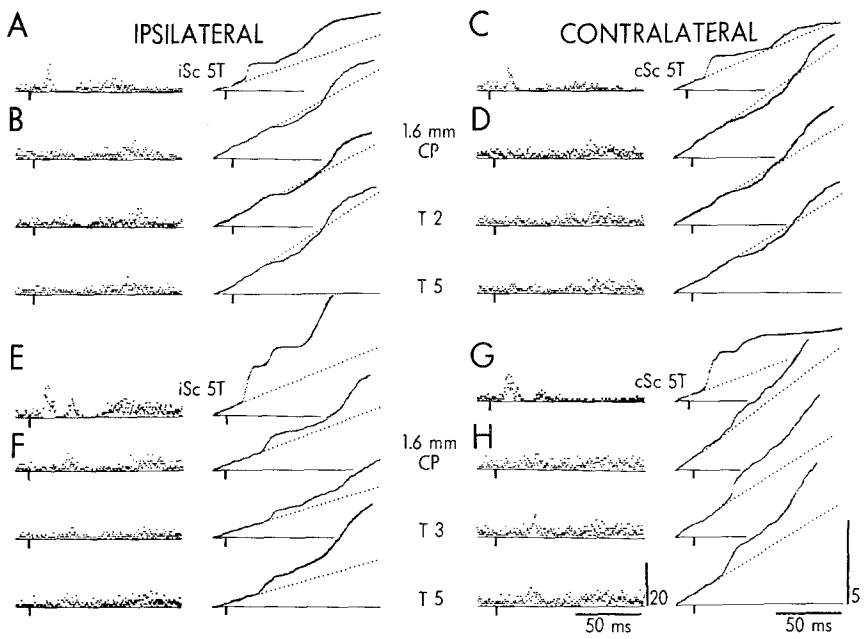

Fig. 4. *Somatotopic relations of two fastigial cells to cutaneous mechanoreceptors of ipsilateral and contralateral hindlimbs.* In A and C are the PSTHs and CFDs for responses evoked by stimulation of the ipsi- and contra-lateral sciatic nerves respectively. In B and D are similarly recorded for responses evoked by stimulation of the indicated ipsilateral and contralateral hindfoot pads. E, G and F, H are similarly recorded but from another fastigial cell 510 μm deeper along the same microelectrode track. All records are made by addition of 64 responses in 256 bins of 0.5 msec each. Same count and time scales throughout. Decerebrate, unanesthetized preparation

1973a), and the LRN provides the principal excitatory input to the fastigial cells (Eccles, Sabah and Táboříková, 1974b). However, the inputs from contralateral nerves also were effective in inhibiting fastigial cells (cf. Fig. 4C, G), and inhibitory action has in general been attributed to Purkyně cells.

We have investigated the inputs from mechanoreceptors of the contralateral hind limb with only five fastigial cells. The results of these preliminary observations were in agreement with the findings with nerve inputs. For example, comparison of the ipsilateral inputs (Fig. 4B) with the corresponding contralateral inputs (Fig. 4D) shows inhibitory responses of similar time course that were smaller on the contralateral side. The fastigial cell of Fig. 4E—H was 510 μm deeper along the same microelectrode track, but the responses to pad taps were now predominantly excitatory for both ipsilateral and contralateral pads. The time courses were similar, and in H two contralaterally evoked responses were larger than the ipsilateral in F.

Again the excitatory responses can be attributed to the LRN input to the fastigial cells, because the LRN cells are very effectively excited by mechanoreceptors of the contralateral hindfoot (Rosén and Scheid, 1973c). In agreement with the preceding section, two explanations can be offered for the inhibitory

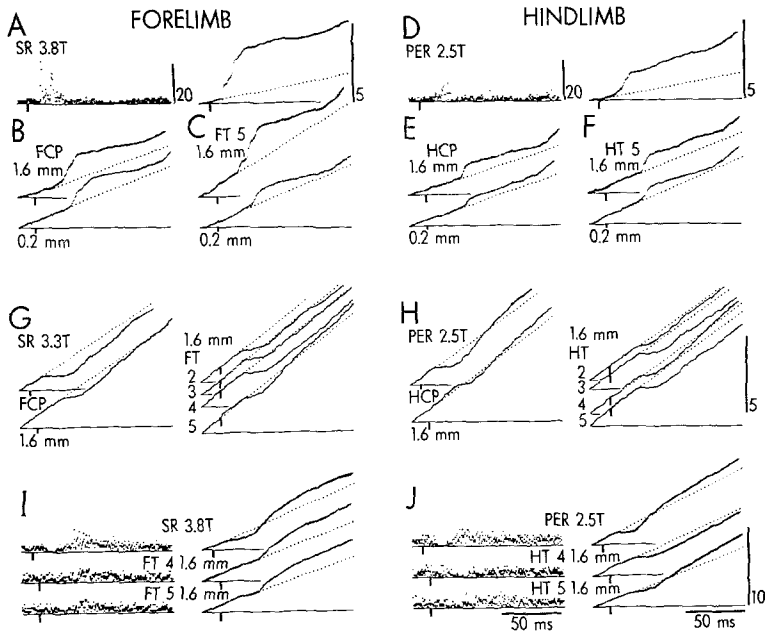

Fig. 5. *Somatotopic relations of three Purkyně cells to cutaneous mechanoreceptors of ipsilateral forelimb and hindlimb.* A and D show respectively the PSTHs and CFDs for responses evoked by forelimb and hindlimb nerve stimulation. In B and C are the CFDs for responses evoked by taps of 1.6 and 0.2 mm to the central pad and toe 5 of the forefoot. E and F are similar series for the hindfoot. G and H are from a Purkyně cell in another experiment, G being CFDs to forelimb inputs as indicated, and H for corresponding hindlimb inputs. I and J are from another Purkyně cell in the same experiment as for A—F. In I are PSTHs and CFDs for responses to forelimb inputs as indicated, and similarly for J and hindlimb inputs. Same count and time scales for A—H. With I and J there is a separate count scale for CFDs. The cell of A—F was superficial in Lobule V of lateral vermis just anterior to the fissura prima. The cells of G, H and I, J were both deep in Lobule III of the lateral vermis. Both preparations were decerebrate and unanesthetized

responses induced by inputs from contralateral nerves and pad receptors. Firstly these inputs caused inhibition of LRN cells as frequently as excitation (Rosén and Scheid, 1973a, 1973c), and this inhibition would by disfacilitation give the depressed firing of the fastigial cells such as is seen in Fig. 4A, B, C, D. Secondly the nerve and pad inputs from the contralateral side could also be effective in evoking discharges from the ipsilateral Purkyně cells with the consequent inhibition of the fastigial cells. There are reports of such action on Purkyně cells by contralateral nerve inputs (e. g., Oscarsson, 1967, 1973) and this has also been observed for inputs from cutaneous mechanoreceptors (Eccles, Sabah, Schmidt and Táboříková, unpublished observations).

B) Convergence onto Purkyně Cells from Ipsilateral Forelimb and Hindlimb

It has been a common finding that a fastigial cell is activated by cutaneous mechanoreceptors from both forefoot and hindfoot, as illustrated both in Fig. 3 and in earlier publications (Eccles, Sabah and Táboříková, 1971, Fig. 1; Eccles,

Sabah and Táboříková, 1974a, Fig. 6; Eccles, Sabah and Táboříková, 1974b, Fig. 9). No example was reported of such convergence of mechanoreceptor inputs onto Purkyně cells (Eccles, Sabah, Schmidt and Táboříková, 1972a, 1972c); yet several cases have been described for convergence of nerve volleys from forelimb and hindlimb on the same Purkyně cell (Eccles, Faber, Murphy, Sabah and Táboříková, 1971b, Figs. 3, 5A, 5B). Actually, in the previous investigation of cutaneous mechanoreceptor input to Purkyně cells, the convergence from forelimb and hindlimb receptors was not investigated. It therefore remains an open question whether inputs from forelimb and hindlimb mechanoreceptors converge onto fastigial cells via Purkyně cells that are specific for either forelimb or hindlimb or whether in the first place the convergence occurs also onto Purkyně cells. The question was settled by three decerebrate preparations in which there were altogether 19 microelectrode insertions widely dispersed in the lateral vermis of lobules V, IV and III and with recording in isolation from 97 Purkyně cells.

Since such convergence has not previously been recognized three examples are displayed in Fig. 5. The Purkyně cell of Fig. 5A—F was strongly excited by mossy fiber inputs from both forelimb (A—C) and hindlimb (D—F). Stimulation of forelimb nerve (A) and of pad receptors (B, C) was more effective than the equivalent hindlimb stimulations, but pads of forefoot and hindfoot were effective with taps of only 0.2 mm. Figure 5G and H show a similar correspondence in the responses of another Purkyně cell to forelimb and hindlimb inputs, which all evoked an inhibition. The Purkyně cell of Fig. 5I and J gave another type of response. There was an initial I and later E with both forelimb and hindlimb nerve stimulation. With taps to toe pads there was predominantly excitation with forefoot and inhibition with hindfoot. In general in Fig. 5 there was a remarkable parallel between the responses evoked from forelimb and hindlimb.

In our series there were 14 Purkyně cells clearly responding to cutaneous mechanoreceptors of both forelimb and hindlimb. Thus to a considerable extent the convergence of forelimb and hindlimb mechanoreceptors onto a fastigial cell occurs because of the prior convergence onto Purkyně cells that project to that cell. The excitatory inputs to fastigial cells largely come from LRN cells (Eccles, Sabah and Táboříková, 1974b) and there is a large convergence of forelimb and hindlimb inputs onto single LRN cells (Rosén and Scheid, 1973a, 1973c). It can therefore be presumed that the excitatory convergence onto fastigial cells from forelimb and hindlimb would occur to a considerable extent because of prior convergence onto LRN cells.

C) Somatotopic Zones in the Fastigial Nucleus

It is reasonable to assume that there is a convergence of about 200 Purkyně cells onto a fastigial cell (Szentágothai, personal communication) and that this convergence would provide the occasion for a reception by the fastigial cell of a diversity of somatotopic relations. Nevertheless, despite these two sites for somatotopic convergence, there is no randomization of input for many fastigial cells. In fact some display a remarkable somatotopic specificity, as for example the cell of Fig. 2, and to a lesser extent that of Fig. 1. It remains to enquire if cells with specific somatotopic inputs are congregated in discrete zones of the fastigial nucleus.

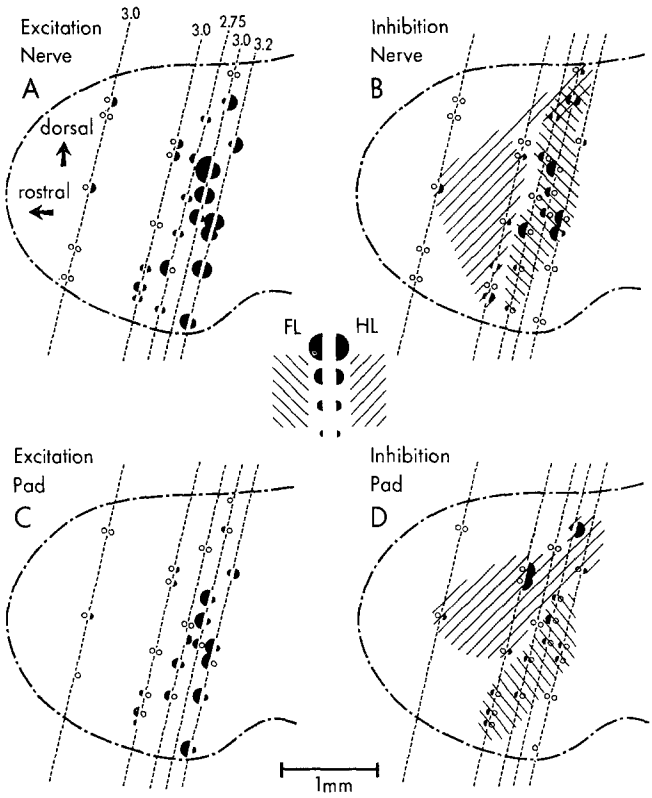

Fig. 6. *Somatotopic plots of fastigial cell responses.* Five microelectrode tracks through the fastigial nucleus have located along them symbolic representations of fastigial cells at the sites of their recordings. Each cell has a double symbol (rostral-caudal) signifying the sizes of its responses to inputs generated by nerve stimulation or pad tap to forelimb and hindlimb respectively. Note the size and symbol identification in central area. The four frames are respectively A. excitation by nerve, B. inhibition by nerve, C. excitation by pad tap, D. inhibition by pad tap. In B and D the areas of forelimb and hindlimb inhibitory influence are shaded by oblique lines, the key for identification also being in the central area. Surital anesthesia in intact preparation. Tracks were at laterality of 2.75 to 3.2 mm as indicated in A, but are projected on to the same section at 3.0 mm laterality

The intensive investigation by the Oslo school over several decades (Jansen and Brodal, 1940; Jansen, 1954; Walberg, Pompeiano, Brodal and Jansen, 1962; Walberg and Jansen, 1964) has resulted in a clear topographic picture of the projection from the cerebellar vermis to the fastigial nucleus. It is strictly ipsilateral. There tends to be a limited fanning in this projection; nevertheless a parasagittal relationship is preserved, medial and lateral areas of the vermis projecting to medial and lateral zones, respectively, of the fastigial nucleus. Also the anterior vermis projects to the anterior two thirds of the fastigial nucleus with again some fanning in the rostro-caudal direction. Despite this fanning, the hindlimb cortical zone (lobules 3 and 4) is described as projecting to the fastigial nucleus rostrally to the forelimb cortical zone (lobule 5) (Fig. 10A). Our somatotopic

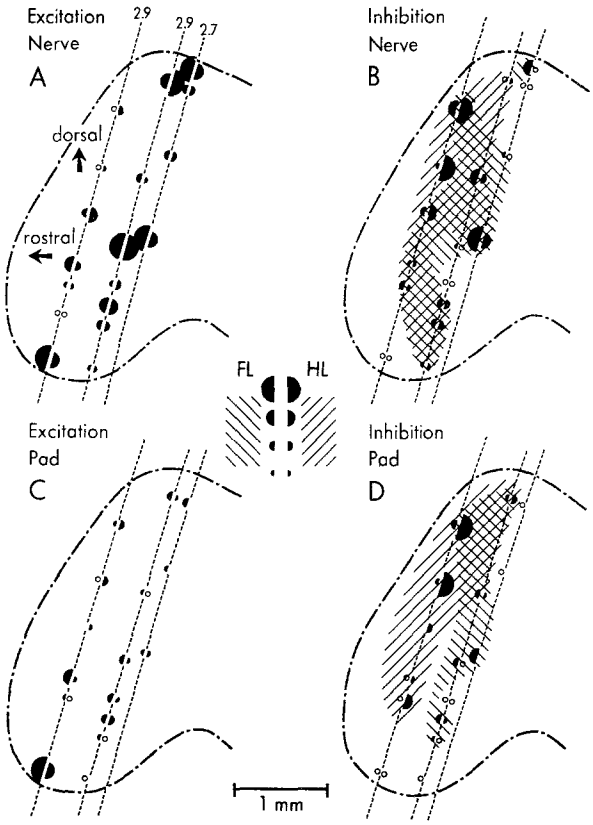

Fig. 7. *Somatotopic plots of fastigial cell responses.* As for Fig. 6 but preparation was under chloralose anesthesia in intact preparation. Tracks at laterality of 2.7 to 2.9 mm

investigations on the fastigial nucleus will be considered in relation to these precise anatomical studies as well as to our earlier somatotopic investigations on the cerebellar cortex (Eccles, Provini, Strata and Táboříková, 1968; Kitai, Táboříková, Tsukahara and Eccles, 1969; Eccles, Faber, Murphy, Sabah and Táboříková, 1971b, 1971b; Eccles, Sabah, Schmidt and Táboříková, 1972c).

Corresponding to the location of the limb somatotopic fields in the lateral part of the vermis of the anterior lobe (Eccles *et al.*, 1968; Kitai *et al.*, 1969; Eccles *et al.*, 1971a, 1971b), we have found in a few initial explorations that the limbs do not project to the medial zone of the fastigial nucleus. In fact the preferred zone is extremely lateral in that nucleus. Consequently in all later experiments the microelectrode was inserted at sites between 2.5 and 3.2 mm from the midline and in a strictly parasagittal plane so that the explored region of the fastigial nucleus would have approximately this laterality.

Though remarkable somatotopic specificity has been observed for some fastigial cells in their receptive fields within a single limb (cf. Figs. 1, 2), the somatotopic survey documented in Figs. 6—9 has been more general in its orientation. It has been concerned only with the topographic relations obtaining between the projec-

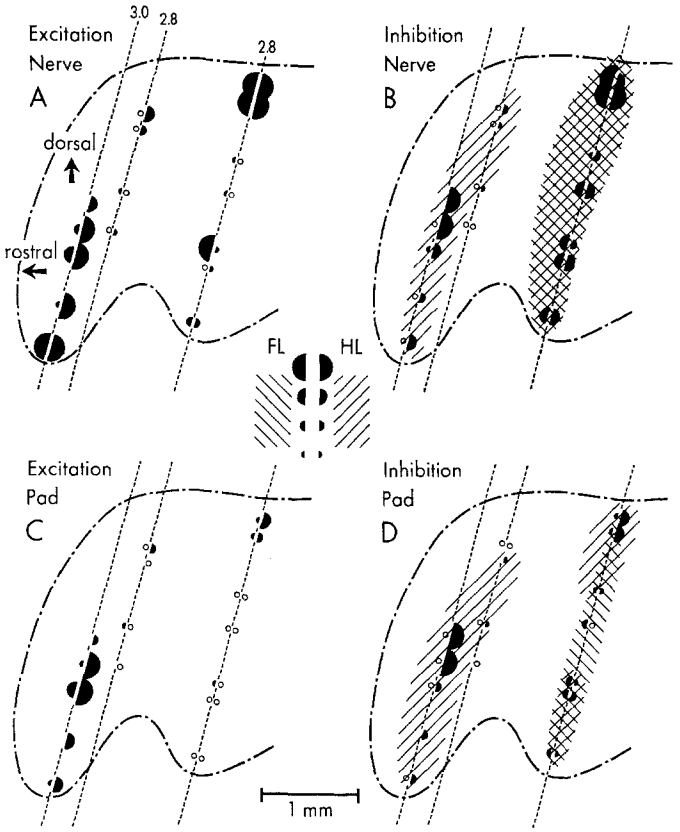

Fig. 8. *Somatotopic plots of fastigial cell responses.* As for Fig. 6 but decerebrate unanesthetized preparation. Tracks at laterality of 2.8 to 3.0 mm

tions to single fastigial cells of the cutaneous receptors of ipsilateral forelimb and hindlimb respectively. On the one hand there has been a comparison of the responses evoked by stimulation of cutaneous nerves, forelimb (superficial radial) and hindlimb (superficial peroneal). On the other hand, we have compared cutaneous mechanoreceptor inputs to single fastigial cells by assessing the average results of taps to forefoot and hindfoot pads respectively. A further discrimination is required in making the comparison, namely between the excitatory and the inhibitory responses of the fastigial cells, because these are for the most part produced by quite different pathways, the former via collaterals from the reticulo- and olivo-cerebellar pathways, the latter by axons of the Purkyně cells (Eccles, Sabah and Táboříková, 1974b). Experiments have been chosen for illustration in the four figures (Figs. 6—9) because each included a sufficient number of fastigial cells (17—26) in several (3—5) tracks that were approximately in the same parasagittal plane so that they could be shown without undue distortion projected onto the single sectional drawing.

In each figure there are plotted measurements from the responses of all the fastigial cells investigated. In Figs. 6—9 the responses evoked from the forelimb

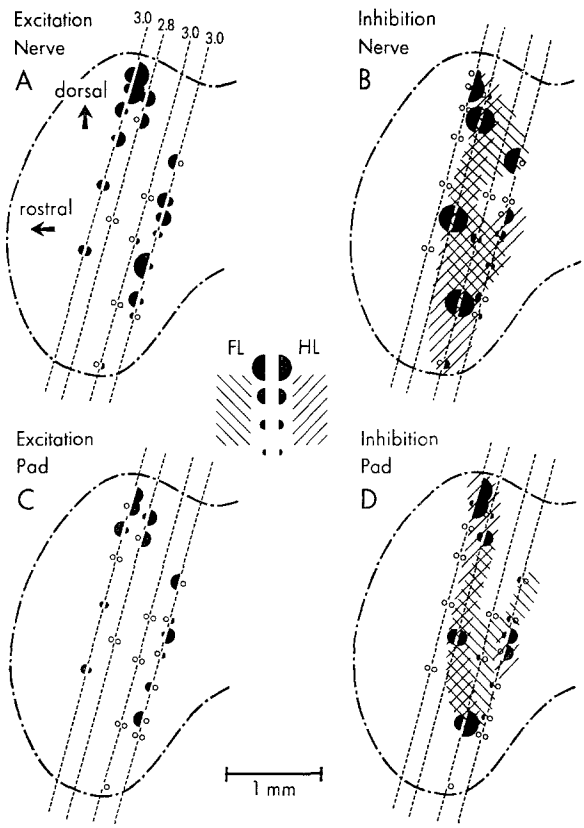

Fig. 9. *Somatotopic plots of fastigial cell responses.* As for Fig. 6 in decerebrate unanesthetized preparation. Tracks at laterality of 2.8 to 3.0 mm

and hindlimb inputs have been compared in the four plottings of A, B, C and D. In assessing the inhibitory responses, the disturbing effect of superimposed excitatory responses has been largely avoided by making the evaluation after the excitation has passed off. For example in the most favorable responses of Figs. 1 and 2 the inhibition is given the maximum assessment because after the initial excitation it caused a complete silencing of the cell for at least 10 msec (cf. Figs. 1B, HT4, HT5; 2A, HT5 and Per). The assessments were made only on those responses with latencies qualifying for plotting in the histograms of the previous paper (Fig. 4, Eccles, Sabah and Táboříková, 1974b). The plotted values in Figs. 6—9 thus would very largely be due to the pathways depicted in Fig. 11 of that paper, i. e., excitation by collaterals of the reticulo-cerebellar and the olivo-cerebellar fibers and inhibition by Purkyně cells excited to discharge by mossy fibers, both the fast and the more delayed inputs, and by climbing fibers. But in addition inhibition could be due to disfacilitation of the LRN pathway and excitation could be due to disinhibition of the Purkyně cell discharge, as already described (Eccles, Sabah and Táboříková, 1974a, 1974b).

In Figs. 6—9 there are plotted the forelimb and hindlimb values for the following sets of measurements: A, excitation by nerve volleys; B. inhibition by nerve volleys; C, excitation by pad taps; D, inhibition by pad taps.

Since there is relatively little limb discrimination in the responses of LRN cells to inputs from nerve volleys or cutaneous mechanoreceptors (Rosén and Scheid, 1973a, 1973c), it would be expected that there would also be little limb discrimination in the excitatory responses of fastigial cells. In general this is seen to be the case with the nerve stimuli (Figs. 6A, 7A, 8A, 9A). The excitatory responses from pad taps (Figs. 6C, 7C, 8C, 9C) tend to be smaller and to show more limb discrimination. For example there is a large area of forelimb dominance in Fig. 6C, and there are small irregular zones of hindlimb and forelimb dominance in Figs. 7C, 8C and 9C.

The principal interest of Figs. 6—9 is however in the inhibitory responses, because there is much more limb discrimination in Purkyně cell responses than in LRN responses (cf. Eccles, Faber, Murphy, Sabah and Táboříková 1971a, b; Eccles, Sabah, Schmidt and Táboříková, 1972b, c; Rosén and Scheid, 1973a, c). It is of crucial importance to see if this discrimination is conserved in the projections of Purkyně cells to fastigial cells, and this enquiry is of special functional interest in connection with the responses to adequate stimulation, i. e., in Figs. 6D, 7D, 8D and 9D. The responses of Fig. 6D are small because of the surital anesthesia, and as a consequence there is a good limb discrimination, cells in the dorso-rostral zone being hindlimb oriented, while those lying ventro-caudally are forelimb oriented. The inhibitory responses of the chloralose (Fig. 7D) and decerebrate preparations (Figs. 8D, 9D) tend to be larger. Figures 7D, 8D and 9D resemble Fig. 6D in that the areas of hindlimb dominance mostly lie dorso-rostrally to the forelimb zone, but there are zones of effective convergence. In general the somatotopic relationships of the fastigial cells are in agreement with the anatomical evidence that the projection from the hindlimb area of the vermis (lobules III and IV) is rostral to the projection of the forelimb area (lobule V) (Walberg, Pompeiano, Brodal and Jansen, 1962; Walberg and Jansen, 1964), but there is more overlap than was observed anatomically.

Nerve volleys usually evoked larger inhibitory responses than the pad taps, but there tended to be similar somatotopic relationships, except that there was more overlap of the forelimb and hindlimb zones. The cells of Figs. 6—9 that received conjoint forelimb and hindlimb nerve inhibitions were almost twice as numerous as those with conjoint pad-induced inhibitions. Figures 7B and 9B are instructive in that, between the fairly selective hindlimb and forelimb cells, there was an area of very effective forelimb and hindlimb convergence. In Fig. 8B there was a rostral hindlimb zone and caudally a strong convergent zone. A remarkable example of this convergence has been illustrated in Fig. 3.

Discussion

No simple picture emerges from our studies of the somatotopic relations of fastigial cells with respect to cutaneous mechanoreceptors. On the one hand there are cells such as those of Figs. 1 and 2 of this paper and Fig. 1 of a previous paper

(Eccles, Sabah and Táboříková, 1971) that are orientated to the ipsilateral hindlimb or forelimb. On the other hand some cells are very effectively excited and inhibited by cutaneous mechanoreceptors of both forelimb and hindlimb (Fig. 3) or of both hindlimbs (Fig. 4). It has been generally recognized that the cerebellar vermis is specially concerned with the integration of movements and postures concerned with standing and locomotion and other generalized body performances (Chambers and Sprague, 1955a, b; Dow and Moruzzi, 1958; Batini and Pompeiano, 1957, 1958). Since the principal output pathway from the cerebellar vermis is via fastigial cells (Jansen and Brodal, 1940; Walberg and Jansen, 1964; Eager, 1963), it would be expected that fastigial cells are integrating stations for information from receptors widely dispersed over the body surface. Integration of forelimb and hindlimb inputs would be particularly important in a wide variety of quadripedal movements, as also would be the integration of ipsilateral and contralateral hindlimbs. Due to technical difficulties we have not studied the possible convergence of ipsilateral and contralateral inputs from forelimb mechanoreceptors.

Figure 2 illustrates the responses of the most specifically orientated fastigial cell in our series. Figure 1 provides an example of the usual mild specificity between toe pads on the one foot, and between the related areas of hairy skin. We have regularly observed that the somatotopic relation of the hairy skin corresponds to that of the toe pads as shown in Figs. 1 and 2. Responses to pressure are difficult to fit into any simple generalization. For example in the first paper of this series two fastigial cells gave good responses to pad taps and to air jets to the hairy skin but zero response to pressure (Eccles, Sabah and Táboříková, 1974a, Figs. 1 and 3), and in Figs. 2 and 3 above there were also good responses to air jets, but no tonic responses to pressure. However the fastigial cell of Fig. 1 gave good excitatory-inhibitory responses to air jets and was very effectively inhibited by pressures of 200, 500 and 1000 g to the central pad, as shown in Fig. 2D of a previous paper (Eccles, Sabah and Táboříková, 1974a). There have also been examples of excitatory correlation. The cell exhibiting the largest tonic excitations (Fig. 7A of Eccles, Sabah and Táboříková, 1974a) responded to air jets to adjacent hairy skin by a small but definite excitation, and there have been three other examples of fastigial cells strongly excited both by air jets to hairy skin and responding tonically to pad pressure. Doubtless we would have observed many more examples of convergence of tonic receptors and hair receptors onto a fastigial cell if this had been systematically tested for in our experiments. We would estimate that this convergence occurs in at least 10% of fastigial cells, but it is certainly less common than the convergence of phasic pad receptors and hair receptors, or of phasic and tonic pad responses.

The locations of fastigial cells in the nucleus can be correlated with their functions in several ways. Firstly, because of their different modes of generation, it is important to consider the excitatory and inhibitory responses separately (cf. Eccles, Sabah and Táboříková, 1974b). As already pointed out for Figs. 6—9, more specificity with respect to forelimb-hindlimb orientation is exhibited for the inhibitory responses, particularly for those evoked by adequate stimulation — the D series in these figures. When attempting to correlate this specificity with that exhibited by Purkyně cells, it would seem that the latter has more forelimb-

hindlimb specificity, though on some Purkyně cells there has been convergence of inputs from forelimb and hindlimb mechanoreceptors (cf. Fig. 5). The differential effectiveness of pads on the same foot has been documented for responses of Purkyně cells to both climbing fiber inputs (Eccles, Sabah, Schmidt and Táboříková, 1972b, Figs. 1—5) and mossy fiber inputs (Eccles, Sabah, Schmidt and Táboříková, 1972c, Figs. 8—10), but many Purkyně cells are not so selective. In our experiments a few fastigial cells exhibit this level of specificity (cf. Fig. 2), but in our experience it is more unusual than for Purkyně cells. It would appear that, in the projection of Purkyně cells to the fastigial cells, there is some randomizing of connection. Purkyně cells that are similar somatotopically do not project in some rigidly channelled manner to fastigial cells. Yet the responses of fastigial cells such as those of Figs. 1, 2 show that the randomizing of Purkyně cell connections is only partial.

Since the Purkyně cells of the vermis of the anterior lobe project to Deiters nucleus as well as to the fastigial nucleus (Ito, Kawai and Udo, 1968; Ito, Udo, Mano and Kawai, 1970), it would be expected that there would be similar somatotopy in these two recipient sites. In so far as it is possible to compare the present results with those of Allen, Sabah and Toyama (1972a, 1972b), there seems to be about the same level of specificity for the mossy fiber input. They studied the inhibitory and excitatory inputs from forelimb and hindlimb nerves and report that the response spectrum to a mossy fiber input usually spreads over several nerves and usually involved nerves in both the fore- and hind-limbs. There is thus general agreement with the A and B frames of Figs. 6, 7, 8, 9. They observed much more specificity in the climbing fiber system studied in animals anesthetized by Nembutal. Cells of the inferior olive project to cerebellum via climbing fibers (cf. Eccles *et al.*, 1967). Allen *et al.* (1972a) have shown that the climbing fiber system acts on Deiters cells by the excitatory action of axon collaterals and inhibition via Purkyně cell relay. Apparently inputs from forelimb nerves never inhibited Deiters cells orientated to hindlimb, and reciprocally for inputs from hindlimb nerves, which is in contrast with the plotted responses in the B frames of Figs. 6, 7, 8, 9. There was some cross innervation for excitatory actions via the axon collaterals, but it was much less than for the A frames of Figs. 6, 7, 8 and 9. Unfortunately, responses evoked by climbing fibers were not identified in our responses, so no valid comparison can be made.

In attempting to give physiological meaning to the somatotopic relationships disclosed in the present investigation, account must be taken of both of the inherent limitations of our experimental procedures and of the operative principles of neuronal pathways. In this latter context the key principles are those of divergence and convergence. Possible estimates for divergence and convergence numbers for the projection of Purkyně cells to fastigial cells are 8 and 200 respectively (Szentágothai, personal communication, 1973). In any particular fastigial nucleus we have sampled only a minute fraction of the cells. However reference to Figs. 6—9 shows that, when cells were in close proximity, they often were similar in their somatotopy, forming as it were a colony or cluster (cf. Eccles, 1971). It can be assumed that similarities in inhibitory somatotopy in frames B and D result from correlated projections from Purkyně cells that are forelimb or hindlimb orientated. Likewise similarities in excitatory somatotopy imply that there are correlated projections from

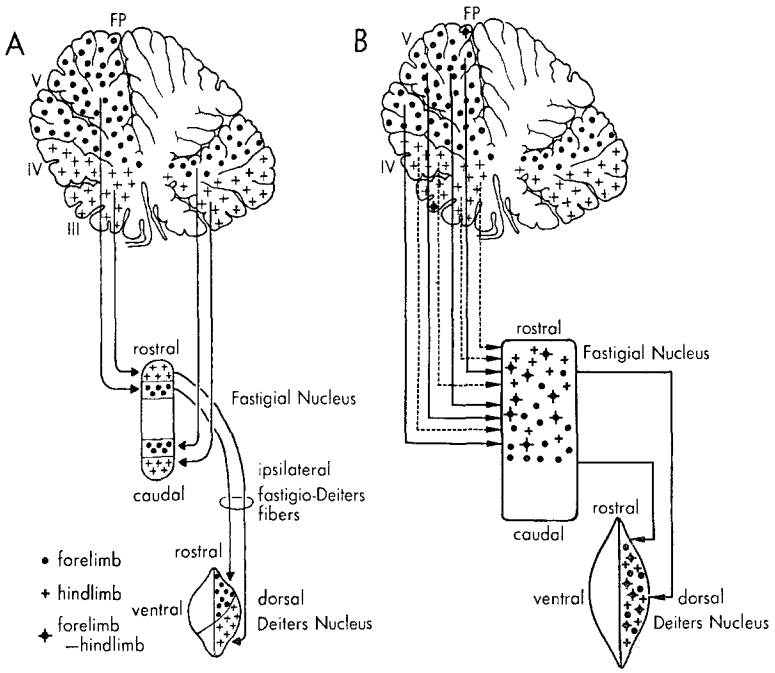

Fig. 10. *Cerebello-fastigial somatotopy. A* Diagram showing schematically patterns of localization within the cerebellar projection from the forelimb and hindlimb regions of the anterior and posterior lobes of the vermis to the fastigial nucleus and from there the Deiters nucleus. The patterns of localization were reported as being less sharp than indicated in the diagram (Brodal, Pompeiano and Walberg, 1962). *B* Modification of this diagram to show the more extensive overlap of the projection from the anterior lobe, as illustrated in Figs. 6—9. Also shown are the two Purkyně cells with symbol of cross and circle indicating that they receive from both forelimb and hindlimb as in Fig. 5, and several fastigial neurones have also the double symbol corresponding to the strong convergence on to some cells in the B and D frames of Figs. 6—9

reticulo-cerebellar and olivo-cerebellar pathways with forelimb or hindlimb orientas tion. However frames A and C of Figs. 6—9 show that in general there is less-somatotopic specification for excitation than for inhibition. This finding correlates with the general concept that the excitatory input provides an amorphous background excitation that is given somatotopic form by the sculpturing action of the more specifically organized Purkyně cell discharges.

Figures 6—9 suffer from the disability that they depict only crude somatotopic relations — ipsilateral forelimb versus hindlimb. The more selective relationships between areas of the same foot displayed in Fig. 2 and to a lesser extent in Fig. 1, are too uncommon for topographic presentation. More specificity would be expected for cells of the interpositus nucleus (cf. Eccles, Rosén, Scheid and Táboříková, 1972) because they receive inhibition from the Purkyně cells of the pars intermedia, which themselves exhibit more detailed somatotopic specificity (cf. Eccles, Sabah, Schmidt and Táboříková, 1972c, Figs. 8, 9, 10).

The arrangement of fastigial cells in clusters of similar somatotopy is important in the further projections of the fastigial nucleus, which have an excitatory action on the cells of Deiters nucleus, of the descending vestibular nucleus and of the ponto-medullary reticular formation (Eccles, Ito and Szentágothai, 1967, Chapter XIV; Ito, Udo, Mano and Kawai, 1970).

The complex geometrical organization of the cerebellar cortex with its patterned excitatory and inhibitory actions on Purkyně cells leads to the postulate that it is the principal site for the computer-like functions of the cerebellum (Eccles, 1973). Nevertheless an additional computer operation would occur in the fastigial nucleus and other cerebellar nuclei because with a sharply timed cerebellar input there is the clash on time of excitatory and inhibitory actions on fastigial cells. This precise design in temporal relationships is diagrammed in the previous paper (Eccles, Sabah and Táboříková, 1974b, Fig. 11). Furthermore, we can assume that this integrative function of fastigial cells achieves functional significance when there are clusters of similarly responding cells. The further projection of fastigial cells to Deiters neurones (Brodal, Pompeiano and Walberg, 1962; Pompeiano, 1967) results in a clash of Purkyně cell inhibition with fastigial cell excitation (Ito *et al.*, 1968, 1970), which would give an additional computational site. The effectiveness of this integration would again be dependent on the assemblage in clusters of cells with similar performance. In conclusion it can be stated that there is urgent need for a more extensive experimental investigation into the postulated cluster arrangements of the various species of cells in the cerebellar pathways together with the respective somatotopies.

Figure 10A is a simplified version of the pathways under discussion, as diagrammed by Brodal, Pompeiano and Walberg (1962): anterior vermis → rostral part of fastigial nucleus → dorsal part of ipsilateral Deiters nucleus → spinal cord. The diagram is over-simplified in two respects: the anterior vermis projects to a much larger segment of the fastigial nucleus — the anterior two thirds (Walberg and Jansen, 1964); there is some admixture of forelimb and hindlimb zones in the fastigial nucleus, not the clear separation of Fig. 10A (Walberg, Pompeiano, Brodal and Jansen, 1962). Our somatotopic observations are in agreement with these anatomically derived relationships, and even suggest a larger forelimb-hindlimb admixture of Purkyně cell projection to fastigial cells (the B and D frames of Figs. 7, 6, 8 and 9). In Fig. 10B we have modified the diagram of Fig. 10A in order to display in more detail the interactions of the vermis-fastigial-Deiters projections as we imagine them. We also include in the diagram two Purkyně cells that receive from both forelimb and hindlimb (cf. Fig. 5). The significant change lies in the much greater degree of convergence of forelimb and hindlimb inputs. The diagram is still deficient in that it omits the projections from contralateral limbs (cf. Fig. 4). The physiological meaning of the wide convergence becomes apparent when it is recognized that the vermal area of the cerebellum is concerned in coordinating movements of limbs and body in posture and locomotion, and not in the finer controls of exploratory movements by a single limb (cf. Dow and Moruzzi, 1958).

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