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TERMINATION AND FUNCTIONAL ORGANIZATION OF THE DORSAL SPINO-OLIVOCEREBELLAR PATH

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SUMMARY

1. The spino-olivocerebellar path ascending through the dorsal funiculus (DF-SOCP) was investigated in decerebrate cats with the cord transected in the third cervical segment except for the dorsal funiculi. The climbing fibre responses evoked in Purkinje cells were studied by recording the mass activity at the cerebellar surface and by recording from single cells.

2. The DF-SOCP forms a disynaptic path from the spinal cord to the cerebellar cortex as shown by latency measurements. Anatomical studies have recently demonstrated that the relays are in the rostral part of the dorsal funiculus nuclei and in the dorsal accessory olive.

3. The DF-SOCP projects to sagittal zones in the pars intermedia and vermis of the anterior lobe. The somatotopical organization is predominantly transverse in the pars intermedia and predominantly longitudinal in the vermis.

4. The olivary neurones in the DF-SOCP are activated by the flexor reflex afferents from wide receptive fields. The fields are restricted to one ipsilateral limb and the majority of the olivary neurones could be activated from all the nerves tested in this limb.

5. Natural stimulation of receptors evoked excitation in about half of the olivary neurones investigated. This excitation was elicited by pressure against deep structures. Inhibitory effects were rarely observed.

6. The dorsal and ventral spino-olivocerebellar paths are compared.

INTRODUCTION

During an investigation of the classical spino-olivocerebellar path ascending through the ventral funiculus (VF-SOCP, Oscarsson & Uddenberg, 1966; Oscarsson, 1968) it was discovered that the anterior lobe of the cerebellum is effectively activated also by a spino-olivocerebellar path

ascending through the dorsal funiculus (DF-SOCP, Oscarsson, 1967*a*, 1968*b*). The first relay of the DF-SOCP is in the dorsal funiculus nuclei and has been identified anatomically. Lesions in these nuclei result in terminal degeneration in the contralateral inferior olive: the origin of the fibres is mainly or exclusively in the rostral parts of the nuclei (Hand & Liu, 1966; P. Hand, personal communication) and the main termination is in the dorsal accessory olive (Gerebtzoff, 1939; Hand & Liu, 1966; Morest, 1967; Ebbeson, 1968).

The present paper describes the projection of the DF-SOCP to the anterior lobe and the behaviour of the olivocerebellar neurones on stimulation of limb nerves and on natural stimulation of receptors. The large responses evoked in the intermediate and vermal parts of the anterior lobe suggest that the DF-SOCP is as important as the VF-SOCP in forwarding information from the cord to the cerebellum. The climbing fibre responses recorded in the intermediate part of the anterior lobe by several authors (Eccles, Provini, Strata & Taborikova, 1967; Provini, Redman & Strata, 1967) were presumably largely mediated by the DF-SOCP, though spino-olivocerebellar paths ascending in the ventral and lateral funiculi might have contributed (Larson, Miller & Oscarsson, 1968; Miller & Oscarsson, 1968; Oscarsson, 1968). Some of the results have been described in a preliminary report (Oscarsson, 1967*a*).

METHODS

The experiments were performed on cats decerebrated at a precollicular level. The dissection was made under pentobarbitone anaesthesia and no additional anaesthetic was added after the decerebration. The recording was performed 3–14 hr after the last dose of anaesthetic. The preparations were paralysed with gallamine triethiodide in order to prevent reflexes, and artificially ventilated. The blood pressure was continuously recorded and prevented, when necessary, from falling below 90 mm Hg by intravenous infusion of a glucose–dextran solution containing aramine. The body temperature was kept between 36 and 38° C.

The anterior cerebellar lobe was exposed from the primary fissure to the inferior colliculi. In three experiments part of lobule III and the hidden part of lobule IV were exposed by sucking out the colliculi. The exposed cortex was covered with warm mineral oil. A laminectomy was performed at the second cervical vertebra and the spinal cord transected in the third cervical segment except for the dorsal funiculi. Under a binocular dissection microscope the cord tissue ventral to the fibrous septum between the dorsal and lateral funiculi was carefully split with the aid of two sharp forceps. The dissection resulted in a millimetre wide gap between the cord ends. The cord was afterwards fixed in formalin and the completeness of the transection was assessed. The following nerves were dissected and mounted for stimulation bilaterally: in the hind limbs the hamstring and sural nerves and in the forelimbs the superficial and deep radial nerves. In some experiments the muscular component of the suprascapular nerve, the axillary nerve and the nerve to the long head of the triceps were also taken. The superficial radial nerve was often left in continuity with the periphery in order to allow natural stimulation of receptors.

Conventional stimulating and recording techniques were used. When recording, the nerves were usually stimulated at a frequency of 0·8 per second. The incoming volleys were monitored by triphasic recording from the exposed dorsal funiculi in the lumbar region (hind limb nerves) and in the third cervical segment (forelimb nerves). The stimulation strength is expressed in multiples of the strength needed for evoking a barely visible ingoing volley (threshold strength, *T*). The cerebellar surface potentials were recorded with a silver ball electrode, the indifferent electrode being in the temporal muscles. In many experiments the surface potentials were recorded after averaging with a digital computer (CAT 1000). Field potentials and unitary potentials in the cerebellar cortex were recorded with capillary micro-electrodes filled with a potassium citrate solution. The tips of the electrodes were broken to give a diameter of 1·5–2·0 μ and a resistance of 5–7 MΩ. To improve mechanical stability for recording, the electrodes were passed through a hole of a glass plate and a bilateral pneumothorax was performed.

The cerebellar lobules were identified after fixation in formalin using the criteria described by Larsell (1953). In some cases the micro-electrodes were broken and left in the cerebellum which facilitated identification of the electrode tracks.

RESULTS

Recording from cerebellar surface

The experiments were performed on cats with the cord transected in the third cervical segment except for the dorsal funiculi. The potentials recorded from the cerebellar surface in these preparations can be attributed to the cuneocerebellar tract which terminates as mossy fibres (Grant 1962; Holmqvist, Oscarsson & Rosén, 1963) and the DF-SOCP which terminates as climbing fibres. The cuneocerebellar tract is activated exclusively from forelimb nerves, whereas the DF-SOCP is activated from both forelimb and hind limb nerves. The surface responses evoked by the two pathways are readily distinguished (see Miller & Oscarsson, 1968). The climbing fibre responses have a longer latency and, in the projection areas, a much larger amplitude than the mossy fibre responses evoked from the same nerve. Furthermore, the climbing fibre responses are immediately recognized by their highly characteristic variations in amplitude which occur especially at stimulus frequencies above one per second. The potentials wax and wane in irregular cycles with durations of up to half a minute (Miller & Oscarsson, 1968).

It has been demonstrated that the climbing fibre responses are surface positive in the projection areas (Oscarsson & Uddenberg, 1966; Oscarsson, 1967*a*, 1968; Armstrong & Harvey, 1968; Miller & Oscarsson, 1968). Negative potentials with a similar latency are recorded from extensive areas and represent electrical spread of the climbing fibre responses generated in the projection areas (Oscarsson, 1968). The positive potentials recorded in the projection areas and evoked through the DF-SOCP had amplitudes ranging from 100 to 600 μV in the different experiments. These values are similar to those reported for the responses evoked through the VF-SOCP (Oscarsson, 1968).

Typical mossy and climbing fibre responses are shown in the averaged records of Fig. 1. The climbing fibre responses evoked by stimulation of the forelimb nerve, deep radial, was preceded by a mossy fibre response (upper traces). The mossy fibre response had a latency of 4 msec (records 2–4). The climbing fibre response was especially large in record 3 (arrow) obtained

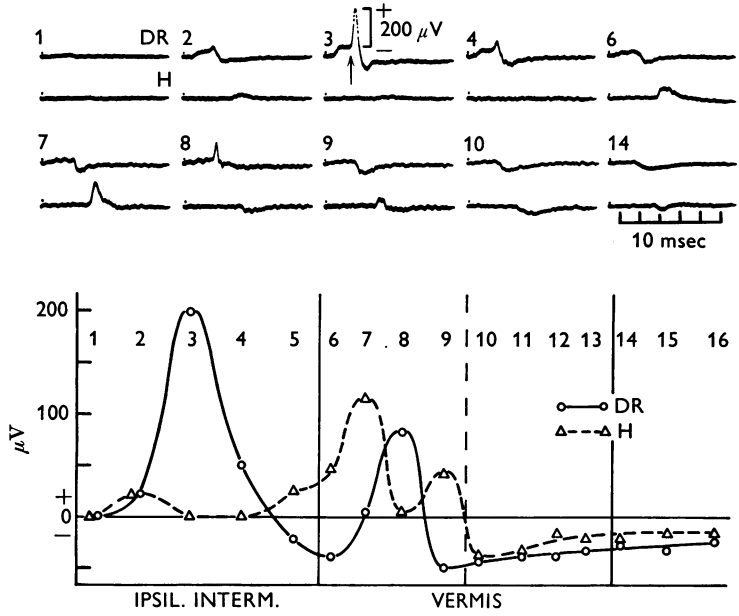

Fig. 1. Potentials recorded from surface of rostral folium in lobule V. The potentials were evoked by stimulation of the deep radial nerve (DR) and the hamstring nerve (H) at a strength of 20*T* and recorded from many points (1–16) along the folium to show characteristic distribution. The spinal cord was interrupted in the third cervical segment except for the dorsal funiculi. The sample records were obtained by averaging twelve sweeps and taken from the appropriately labelled points (see graph). Dots mark stimulus artifacts. The climbing fibre response (beginning indicated by arrow in record 3) obtained on stimulation of the deep radial nerve was preceded by a mossy fibre response evoked through the cuneocerebellar tract. The curves show amplitude of climbing fibre potentials plotted against their distribution along the folium. Continuous vertical lines indicate borders of intermediate parts of anterior lobe. Interrupted vertical line indicates mid line. Abbreviations: IPSIL., ipsilateral; INTERM., pars intermedia.

from the middle of the pars intermedia and had a latency of 13 msec. On the other hand, the climbing fibre response evoked from the hind limb nerve, hamstring, arose directly from the base line (lower traces, records 2, 6, 7, 9).

Projection areas. The projection areas of the DF-SOCP were studied in fifteen experiments by recording the distribution of the surface positive

potentials. As the projection is unilateral and the preparations in most cases were bilateral, the number of observations are almost twice as many. In the majority of the experiments the anterior lobe was exposed from the primary fissure to the inferior colliculi which corresponds to lobule V and at least the caudal part of lobule IV. In three experiments more rostral parts of the anterior lobe, including parts of lobule III, were also exposed.

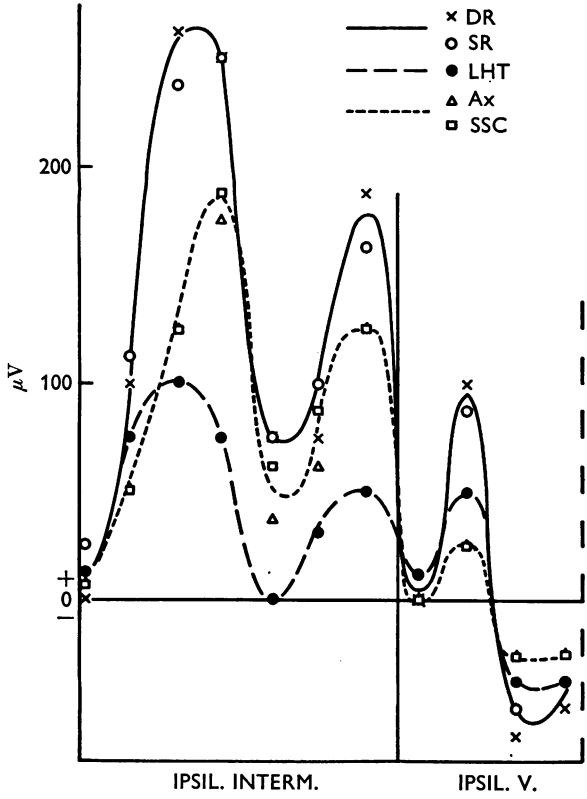

Fig. 2. Similarity in distribution of climbing fibre potentials evoked from different nerves in the forelimb. Recording from folium in lobule V. The nerves were stimulated at 20*T* and are indicated in key of graph. Abbreviations: DR, deep radial nerve; SR, superficial radial nerve; LHT, nerve to long head of triceps, Ax, axillary nerve; SSC, muscle component of suprascapular nerve; IPSIL., ipsilateral; INTERM., pars intermedia; V., vermis. Preparation and conventions as in Fig. 1.

The distribution of the positive potentials was studied by recording from many points along the individual folia as shown in Fig. 1. The graph in that figure demonstrates that the positive potentials occurred in the pars intermedia as well as in the vermis. The potentials evoked from forelimb and hind limb nerves had a different distribution. In most experiments extensive mapping was made only on stimulation of one or two nerves in

each limb at the relatively high stimulus strength of 20–30 T. This strength activates an appreciable part of the high threshold afferents in the group III range and was necessary in order to evoke potentials of maximal amplitude (see below). However, the potentials evoked from different nerves in the same limb had a similar distribution which was independent of stimulus strength. Figure 2 shows the distribution of the surface potentials evoked from five nerves in the ipsilateral forelimb. Positive potentials occurred in

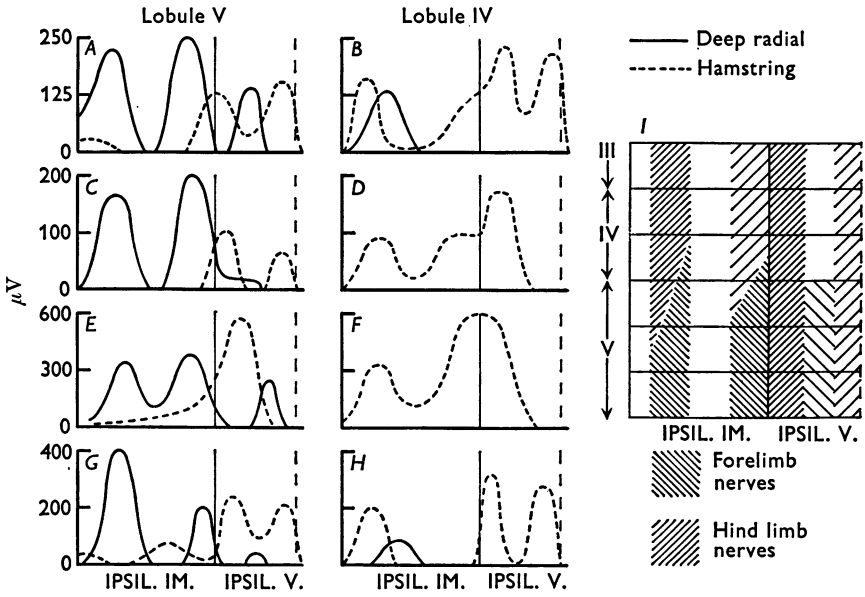

Fig. 3. Distribution of positive surface potentials evoked through the DF-SOCP from the deep radial and hamstring nerves in lobules III–V. *A–H* show the distribution in representative folia of lobules V (left graphs) and IV (right graphs) as found in four different experiments. Diagram I shows interpretation of observations made in fifteen experiments. Positive potentials were found in the sagittal zones indicated by hatching (see key). Sparse hatching indicates that the zones were found in some experiments only. Note somatotopical organization of sagittal projection zones, which is predominantly transverse in the pars intermedia and predominantly longitudinal in the vermis. Abbreviations as in Fig. 2.

three zones with similar maxima for the different nerves. It is uncertain if the slight medial shift of the maxima of the potentials evoked from the proximal nerves (axillary and suprascapular) in the lateral zone is significant.

The distribution of the positive potentials varied from experiment to experiment but some features appeared throughout or often. The curves in *A–H* of Fig. 3 show the distribution in four experiments. The pattern was characteristically different in lobule V (left graphs) and lobules IV and III (right graphs). The diagram to the right in Fig. 3 shows a tentative interpretation based on the observations made in all the fifteen experiments.

The forelimb nerves consistently evoked positive potentials in two sagittal zones in the pars intermedia. In about half of the experiments positive potentials were also evoked in one vermal zone (Figs. 1, 2, Fig. 3*A*, *E*, *G*). The three zones were restricted to the caudal part of the anterior lobe, approximately corresponding to lobule V. In the pars intermedia, the lateral zone often extended into lobule IV (Fig. 3*B* and *H*) where the potentials gradually grew smaller, whereas the medial zone often did not reach the border between lobules IV and V (as in the experiment of Fig. 1). The vermal zone was always restricted to lobule V, or part of it.

TABLE 1. Latencies of DF-SOCP responses. Latencies of surface positive potentials represent lowest values recorded in each of thirteen mapping experiments. Latencies of unitary potentials represent lowest values recorded in any individual unit in each of eight experiments. Mean and range ( ) are given in msec

	Deep radial	Superficial radial	Hamstring	Sural
Surface potentials	14 (12–16)	10 (9–12)	22 (19–25)	18 (16–20)
Unitary potentials	15 (13–16)	12 (10–13)	23 (20–25)	23 (18–25)

The hind limb nerves evoked positive potentials in four sagittal zones. A lateral zone in the pars intermedia was observed in the three experiments with the rostral part of the anterior lobe exposed and in most of the remaining experiments. Positive potentials were always recorded from a lateral zone in the vermis and in about half of the experiments also from a medial zone in the vermis. Finally, in many experiments positive potentials were recorded in the medial part of the pars intermedia. These latter potentials were sometimes seen as a broadening of the sagittal zone in the lateral part of the vermis (Fig. 3*F*) but were sometimes set off from the vermal responses (Fig. 3*B*, *D*). In the pars intermedia the hind limb zones were restricted to the rostral part of the anterior lobe, approximately corresponding to lobules III and IV. However, the zones sometimes extended into lobule V (Fig. 1, Fig. 3*A* and *G*) where the potentials gradually grew smaller. In the vermis the hind limb zones were continuous throughout the exposed part of the anterior lobe. The vermal hind limb responses were usually larger in the rostral region as can be seen from a comparison of the left and right graphs in Fig. 3.

The forelimb and hind limb zones alternated not only in the vermis (Fig. 1, Fig. 3*A*, *E*, *G*) but also in the pars intermedia when they occurred in the same folium (Fig. 1, Fig. 3*A*, *B*, *G*, *H*).

Latencies. The latencies of the climbing fibre responses evoked on stimulation of the deep and superficial radial nerves, the hamstring nerve, and the sural nerve, were studied in thirteen experiments. The values in

Table 1 represent the shortest latencies found in each experiment. The latencies in the medial zones were often slightly longer than those in the lateral zones. The latency difference ranged from 0 to 2 msec (average 0·7 msec) for the forelimb zones and from 0 to 4 msec (average 1·8 msec) for the hind limb zones. The latency increased also slightly from rostral to caudal recording sites (range 0–3 msec; average 1·1 msec). The longer latencies in the medial and caudal recording sites are presumably explained by longer intracerebellar conduction distances.

The average latency on stimulation of the superficial radial nerve, 10 msec (Table 1), should be compared with the average latency of the climbing fibre responses evoked by stimulation of the dorsal funiculus in the third cervical segment, 8·4 msec (S. Miller & O. Oscarsson, unpublished observations). The latency difference of 1·6 msec is identical with the time for conduction of the fastest fibres from the periphery to the third cervical segment and demonstrates that the path in the dorsal funiculus consists of primary afferents. This could not be taken for granted, since Uddenberg (1968) has demonstrated that the dorsal funiculus contains a large ascending pathway consisting of second-order neurones.

Stimulation of the VF-SOCP in the ventral funiculus of the third cervical segment evoked a climbing fibre response after 6·8–7·5 msec, whereas the corresponding latencies on stimulation of the dorsal funiculus varied between 7·7 and 9·0 msec (S. Miller & O. Oscarsson, unpublished observations). The shortest latency difference was less than one msec and indicates that the DF-SOCP in the brain stem is interrupted by one synapse more than is the VF-SOCP. This synapse can be assigned to the dorsal funiculus nuclei (see Introduction).

It is concluded that the most direct path in the DF-SOCP is disynaptic but the possibility of more complex paths is not excluded.

Thresholds. Stimulation of the muscle nerves, deep radial and hamstring, evoked climbing fibre responses only when the strength was supramaximal for the group I afferents. The threshold varied between 2·2 and 5·0*T* on single shock stimulation and was only slightly reduced on brief repetitive stimulation (Fig. 4*A–E*, *K–O*; Table 2). In some cases the response grew to a maximum at relatively low stimulus strengths exciting mainly groups I and II afferents but usually afferents in the group III range made a definite contribution. Stimulation of the skin nerves, superficial radial and sural, evoked responses when the strength was raised to about 1·5*T* (Fig. 4*F–J*; Table 2) and there was hardly any reduction in threshold on brief repetitive stimulation. The thresholds were similar in the various projection zones.

Recording from Purkinje cells

Purkinje cells were recognized by their climbing fibre responses which occurred spontaneously at an irregular rate of usually 0·5–3 discharges per second and, in the projection areas, were evoked by limb nerve stimulation (Eccles, Llinas & Sasaki, 1966; Oscarsson, 1968). Convergence of

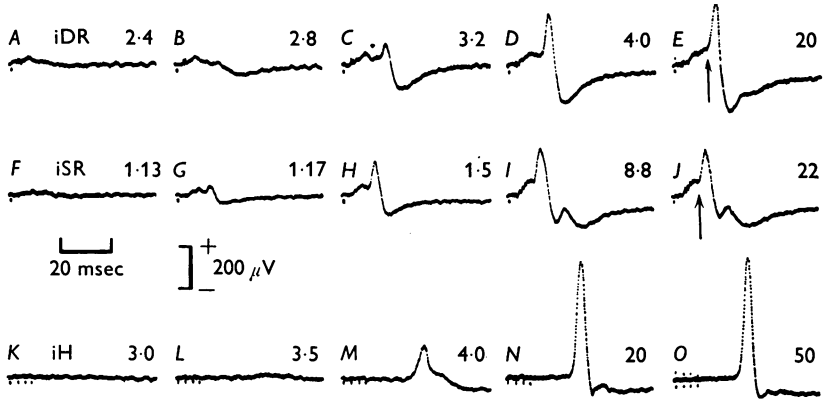

Fig. 4. Contribution from different groups of afferents to DF-SOCP responses. *A–E*, stimulation of ipsilateral deep radial nerve (iDR); *F–J*, stimulation of ipsilateral superficial radial nerve (iSR); *K–O*, stimulation of ipsilateral hamstring nerve (iH). The nerves were stimulated with one (*A–J*) and four shocks (*K–O*), respectively, at the strengths indicated in multiples of nerve thresholds. The forelimb responses were recorded from lateral zone in pars intermedia, lobule V, and the hind limb responses from lateral zone in vermis, lobule IV. The traces were obtained by averaging twelve sweeps. Dots mark shock artifacts. DF-SOCP responses evoked from forelimb nerves (beginnings indicated by arrows in *E* and *J*) were preceded by mossy fibre responses evoked through cuneocerebellar tract. Preparation as in Fig. 1.

TABLE 2. Thresholds for evoking DF-SOCP responses. Figures give stimulus strengths, expressed in multiples of nerve thresholds, needed for evoking barely visible surface responses on single shock and brief repetitive (four shocks at about 300/sec) stimulation. Data from six (deep radial and hamstring), five (superficial radial), and three (sural) experiments

		Deep radial	Hamstring	Superficial radial	Sural
Single:	Range	2·2–4·5	2·2–5·0	1·1–2·0	1·2–1·8
	Mean	3·0	3·9	1·5	1·4
Repetitive:	Range	2·1–3·5	2·2–3·5	—	—
	Mean	2·6	3·3	—	—

two or more climbing fibres to the same Purkinje cell is known to be rare and was not observed in the present experiments. Hence, the observations on the climbing fibre responses evoked in individual Purkinje cells give information about the activity in individual olivocerebellar neurones.

Nerve stimulation. Stimulation of limb nerves evoked climbing fibre responses in 135 Purkinje cells investigated (ten experiments). Table 3 shows the distribution of these cells according to main receptive field (forelimb or hind limb) and localization in the pars intermedia or vermis. The cells activated from forelimb and hind limb nerves, respectively, were encountered in the appropriate sagittal zones delimited by the surface positive potentials. Outside the projection zones the Purkinje cells were usually uninfluenced by nerve stimulation, though a few cells responded irregularly and after long latencies. The latter cells are not included in

TABLE 3. Distribution of 135 Purkinje cells investigated according to main receptive field and localization

	Pars intermedia	Vermis	Total
Forelimb	78	14	92
Hind limb	12	31	43
Total	90	45	135

Table 3. Most of the Purkinje cells were recorded in micro-electrode penetrations not deeper than 3–4 mm. In a few penetrations in the pars intermedia the electrode passed from lobule V into lobule IV. In these cases the cells encountered in the beginning of the track were activated from forelimb nerves and those in the deeper part from hind limb nerves. The change in receptive fields occurred approximately at the border between lobules IV and V.

The vast majority of the units responded only to stimulation of the nerves in one limb. For example, the unit in Fig. 5 was activated from all the nerves tested in the ipsilateral forelimb (*A–E*) but not from the nerves in the other limbs (*F–H*). However, eight cells responded irregularly and after a long latency to stimulation of nerves in the ipsilateral limb that was not the main receptive field. Further, in six cells of 110 investigated there was a weak excitation from contralateral nerves, as in the unit shown in Fig. 6. The latencies of the contralateral responses were 5–20 msec longer than those of the ipsilateral responses.

Most units were activated from both the muscle nerve (deep radial or hamstring) and the skin nerve (superficial radial or sural). The responses evoked from the cutaneous nerves often appeared less regularly than the responses from the muscle nerve, and were occasionally missing. Fifty-seven units found in four experiments had forelimb receptive fields and were tested on stimulation of the following nerves: the deep and superficial radial, triceps, suprascapular, and axillary nerves. Thirty-four of these units (60 %) responded to all the five nerves. Of the remaining units all except two responded to stimulation of four nerves. In the majority of

the cases the responses were evoked by a single stimulus, but in some units brief repetitive stimulation was needed for evoking a response from some of the nerves.

No distinguishing features were found between the response patterns of cells encountered in the different sagittal zones. However, it should not be overlooked that a more detailed investigation might reveal differences in patterns even within a single zone. This possibility is supported by the

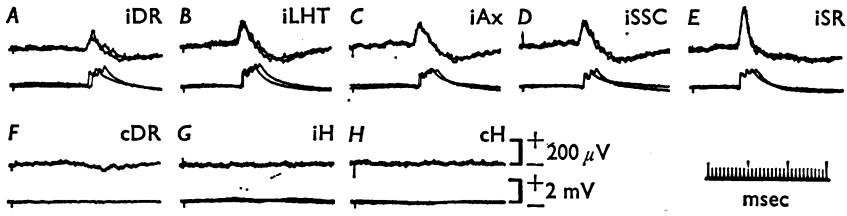

Fig. 5. Climbing fibre responses evoked from ipsilateral forelimb nerves. The stimulus strength was 15–20 times nerve threshold. Upper traces record surface potentials, and lower traces intracellular potentials from a Purkinje cell. The site of recording was in the lateral projection zone of pars intermedia, lobule V. Two superimposed traces (except in *F*). Preparation as in Fig. 1. Abbreviations (also used in Figs. 6 and 7): i, ipsilateral; c, contralateral; DR, deep radial nerve; SR, superficial radial nerve; LHT, nerve to long head of triceps; Ax, axillary nerve; SSC, muscle component of suprascapular nerve; H, hamstring nerve; S, sural nerve.

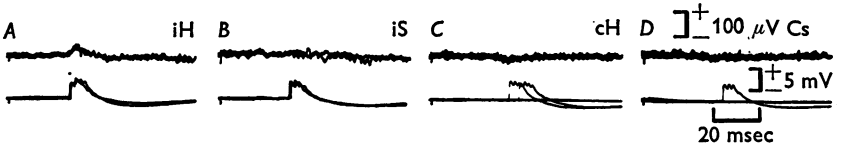

Fig. 6. Climbing fibre responses evoked from ipsilateral and contralateral hind limb nerves. The recording site was in the lateral zone of the vermis, lobule V. Conventions and abbreviations as in Fig. 5. Preparation as in Fig. 1.

observations in one experiment. Two groups of neurones with different response patterns were found in the lateral zone of the pars intermedia. In the lateral and superficial part of this zone nine cells were encountered which were characterized by short latency responses from the majority of the nerves and only weak excitation from the deep radial nerve. One of these cells is shown in Fig. 5. In the medial and deep part (from 1·5 down to 3·8 mm) of the zone ten cells were found which had a longer latency and were only weakly activated from the superficial radial nerve, as shown in Fig. 7. The latencies of the unitary potentials correspond to the latencies of a late hump in the surface response. A small late hump was observed in several experiments and occurred in all the projection zones. It might

suggest that the DF-SOCP contains a more complex path than the disynaptic one described above.

The shortest latencies of the unitary climbing fibre responses are given in Table 1 and correspond to the latencies of the surface potentials. The temporal scatter of the responses in the Purkinje cell population is shown in Fig. 8. The histograms represent the latencies of the responses evoked

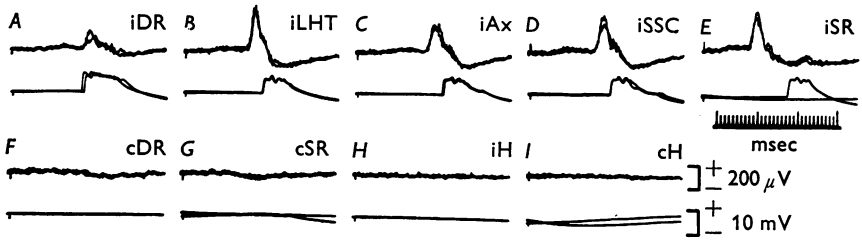

Fig. 7. Climbing fibre responses with long latencies evoked from ipsilateral forelimb nerves. Note that the unitary potentials (except in *A*) have a latency which corresponds to a late hump in the surface records. Same experiment as in Fig. 5. Conventions and abbreviations as in that figure.

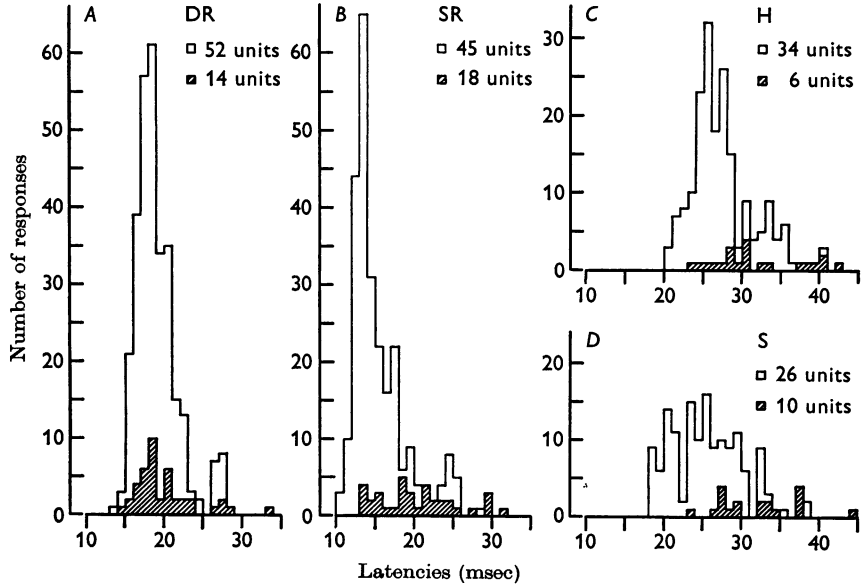

Fig. 8. Latencies of climbing fibre responses recorded fromi ndividual Purkinje cells. The histograms represent the latencies of responses to the first five stimuli (single shocks) applied to the nerve at a frequency of 0·8/sec. Most of the cells responded to each stimulus at this frequency (empty areas) but some responded only intermittently (hatched areas). Number of units recorded from is indicated on each histogram. The ipsilateral deep radial (DR), superficial radial (SR), hamstring (H), and sural (S) nerves were stimulated at 20–30*T*. Preparation as in Fig. 1.

by the first five stimuli applied to the nerve. Most of the units responded to each stimulus at the low frequency usually used (0·8 stimuli per second) and the latencies of consecutive responses varied less than 1–2 msec. However, some units were only weakly activated (hatched squares) and in these only some of the stimuli evoked a response which had a varying and relatively long latency. Brief repetitive stimulation (four shocks at 300 stimuli per second) sometimes reduced the longer latencies but it did not change appreciably the shortest latencies.

The threshold for evoking a climbing fibre response on muscle nerve stimulation was suprathreshold for group I efferents even on brief repetitive stimulation. It varied from about $2T$ to more than $20T$. The threshold on skin nerve stimulation was often close to the nerve threshold but sometimes as high as $20T$.

Receptor stimulation. Fifty-eight Purkinje cells activated on nerve stimulation were tested for excitatory and inhibitory effects on natural stimulation of receptors. These effects were judged by the increase or decrease of the background activity of the climbing fibres. In these experiments the innervation of the limbs was intact except for the hamstring and sural nerves in the hind limbs and the deep radial nerve in the forelimbs. The superficial radial nerve was mounted for electrical stimulation but left in continuity with the periphery.

Even strong stimuli applied to superficial or deep receptors were ineffective in 47 % of the units. A weak increase in activity was observed in the remaining units. This increase was evoked by pressure against deep structures and sometimes by tapping against the paw. The activity usually returned to the resting level after a few seconds but the increased activity sometimes remained relatively constant as long as the pressure was maintained. In a few units release of the pressure was followed by a depression of the background activity. Touch and even strong pinching of the skin was ineffective and so was vibration and movements at the joints.

The receptive field was always limited to one ipsilateral limb and usually consisted of the entire limb or approximately half of it. In a few cases the field was limited to the lateral or medial part of the distal region of the limb.

Inhibition was observed in only two units. It was caused by pressure against deep structures. One unit was excited from the medial part of the forepaw and inhibited from its lateral part. The other unit was excited from the ipsilateral hind paw and inhibited from the contralateral hind limb.

Recording from restiform body

Grant & Oscarsson (1966) demonstrated that the mass discharge evoked by nerve stimulation in the VF-SOCP can be recorded from the olivocerebellar tract in the restiform body which has been dissected and mounted on electrodes as described by Holmqvist *et al.* (1963). In four experiments

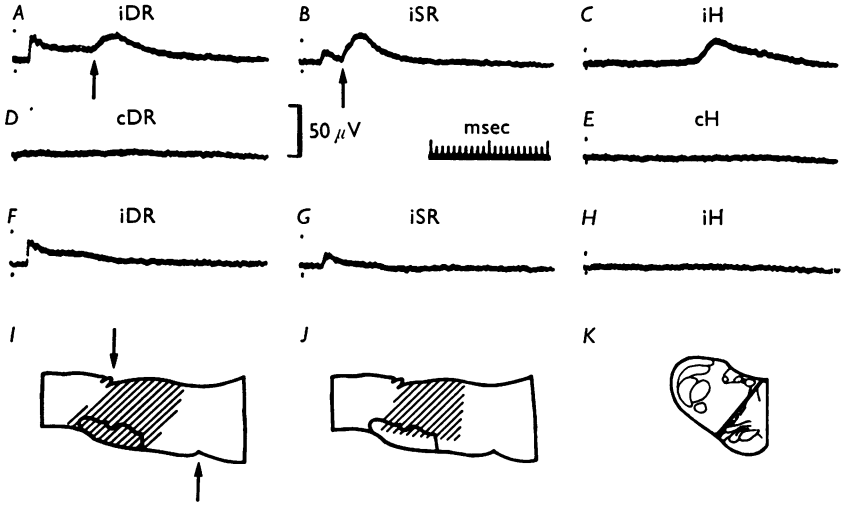

Fig. 9. Mass discharge in DF-SOCP recorded from dissected restiform body on stimulation of forelimb and hind limb nerves. The spinal cord was transected in the third cervical segment except for the dorsal funiculi. The restiform body was dissected and mounted for recording as described by Holmqvist *et al.* (1963). The forelimb DF-SOCP responses (beginnings indicated by arrows in *A* and *B*) were preceded by responses evoked in the cuneocerebellar tract. Records formed by averaging of twenty sweeps. Dots mark stimulus artifacts. Abbreviations as in Fig. 5.

Selective abolition of DF-SOCP responses after lesions in lower brain stem. *A–E* were obtained before and *F–H*, after the mid line incision which is indicated by hatching in diagram *I*. Note that the cuneocerebellar responses remained virtually unchanged (*F* and *G*). Diagrams *J* and *K* are from a different experiment in which the lesion also resulted in complete abolition of the DF-SOCP responses with no appreciable decrease of the cuneocerebellar responses. This lesion was made between the ipsilateral inferior olive and restiform body (thick line in *K*) and had the extension shown in *J* projected on the mid sagittal plane. The projection of the inferior olive on the mid sagittal plane is shown in diagrams *I* and *J*. Arrows in *I* indicate obex and caudal border of pons, respectively.

the mass discharge in the DF-SOCP was recorded from the dissected restiform body.

Records *A–E* in Fig. 9 were obtained with the lower brain stem intact. The initial part of the forelimb responses (*A*, *B*) is due to activity in the cuneocerebellar tract as described by Holmqvist *et al.* (1963). The hind limb response (*C*) and the late component of the forelimb responses

(arrows in *A* and *B*) are due to activity in the DF-SOCP. Stimulation of contralateral nerves evoked no responses (*D*, *E*). Records *F–H* were obtained after a mid line incision at the level of the inferior olive as shown by the hatched area in diagram. This lesion abolished completely the DF-SOCP responses, whereas the cuneocerebellar responses remained unchanged. A complete abolition of the DF-SOCP responses with no appreciable change in the cuneocerebellar responses was also found in a second

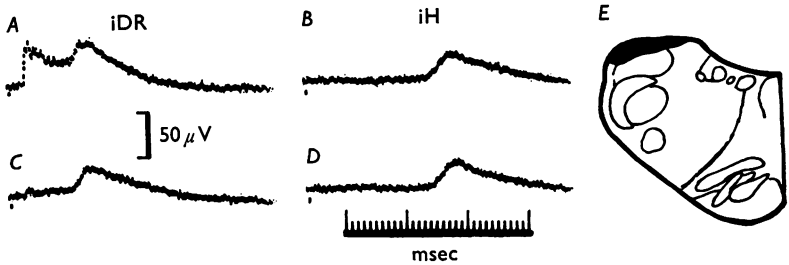

Fig. 10. Isolation of DF-SOCP responses by dorsolateral lesion in restiform body. Preparation and conventions as in Fig. 9. *A* and *B* obtained before and *C* and *D*, after the lesion made 3·5 mm rostral to the obex and indicated in diagram *E* (black). Note that the DF-SOCP responses remained unchanged, whereas the cuneocerebellar response evoked from the deep radial nerve was largely abolished.

experiment following the lesion illustrated by diagrams *J* and *K* in Fig. 9. This lesion was made ipsilaterally between the inferior olive and the restiform body (*K*).

In two experiments a lesion in the dorsolateral part of the restiform body, 3·5–3·9 mm rostral to the obex, resulted in an almost complete abolition of the cuneocerebellar responses with little or no reduction of the DF-SOCP responses (Fig. 10).

The effects of the lesions are consistent with the course of the DF-SOCP according to anatomical studies. The pathway crosses twice, before and after the relay in the contralateral olive (Brodal, 1940; Hand & Liu, 1966; Morest, 1967; Ebbesson, 1968). The lesions shown in Fig. 9 interrupted the olivocerebellar fibres and, in one of the cases (Fig. 9*I*), presumably also part of the fibres connecting the dorsal funiculus nuclei with the contralateral olive. The sparing of the DF-SOCP after dorsolateral lesions in the restiform body is consistent with the ventromedial position of the olivocerebellar fibres in this structure (Busch, 1961).

In all four experiments the climbing fibre responses evoked in the anterior lobe were recorded before ablation of the cerebellum and dissection of the restiform body. The latencies of the responses recorded from the restiform body were 3–4 msec shorter than the responses recorded from the cerebellar surface. A similar latency difference was found in the

previous investigation of the VF-SOCP (Oscarsson, 1968) and is consistent with the delay expected for the intracerebellar conduction and the synaptic delay in the cortex (Eccles, Ito & Szentágothai, 1967; Armstrong & Harvey, 1968). The rapid increase to a maximum in 3–4 msec and the slower decline of the mass discharge in the restiform body compare well with the temporal scatter of the Purkinje cell activation shown in the histograms of Fig. 8.

The mass discharge in the DF-SOCP was recorded by Holmqvist *et al.* (1963) and shown in their Figs. 1 and 4. The response was misinterpreted as due to activity in cuneocerebellar and gracilocerebellar fibres. Though a few gracilocerebellar fibres seem to exist (Hand, 1966; Gordon & Horrobin, 1967) they are evidently too few to evoke any appreciable mass discharge in the dissected restiform body as seen after lesions which abolished the DF-SOCP responses (Fig. 9*H*).

DISCUSSION

The present paper has given a detailed account of the functional organization of the DF-SOCP, similar to that previously given for the VF-SOCP (Oscarsson & Uddenberg, 1966; Miller & Oscarsson, 1968; Oscarsson, 1968). These two paths evoke large surface potentials in the anterior lobe and are presumably mainly responsible for the climbing fibre responses evoked there in animals with the spinal cord intact, although other spino-olivocerebellar paths also contribute (Larson *et al.* 1968; Miller & Oscarsson, 1968). The potentials evoked through the DF-SOCP were as large as those evoked through the VF-SOCP and occurred in more extensive areas. Presumably the dorsal path activates a larger number of olivary neurones than does the classical, ventral path.

The DF-SOCP and the VF-SOCP share certain general features: the sagittal cerebellar projection zones, excitation from the flexor reflex afferents, and weak effects on natural stimulation. However, such broad similarities, common to all the spino-olivocerebellar paths so far investigated (Larson *et al.* 1968; Miller & Oscarsson, 1968), should not obscure the differences between the pathways with respect to synaptic organization and zones of termination in the cerebellum. Some of these aspects will be discussed in the following sections.

Course and projection areas. Figure 11 shows the course and termination areas of the two paths. The DF-SOCP forms a disynaptic path from the cord to the cerebellar cortex, whereas the VF-SOCP is interrupted by at least three synapses. The dorsal path terminates in the pars intermedia as well as in the vermis of the anterior lobe (hatched zones in *B*). The VF-SOCP consists of one direct and one indirect path. The former (diagram *C*) corresponds to the classical, ventral pathway described by Brodal,

Walberg & Blackstad in 1950. It terminates exclusively in the vermis (hatched zones in *D*). The indirect path was demonstrated in physiological studies and is interrupted by interneurones in the brain stem before relaying in the inferior olive (Miller & Oscarsson, 1968; Oscarsson, 1968). It forwards information mainly from the hind limbs and terminates in the pars intermedia (stippled area in *D*).

The DF-SOCP projects to sagittal zones organized in a somatotopical pattern which is predominantly transverse in the pars intermedia and predominantly longitudinal in the vermis. In this respect the DF-SOCP

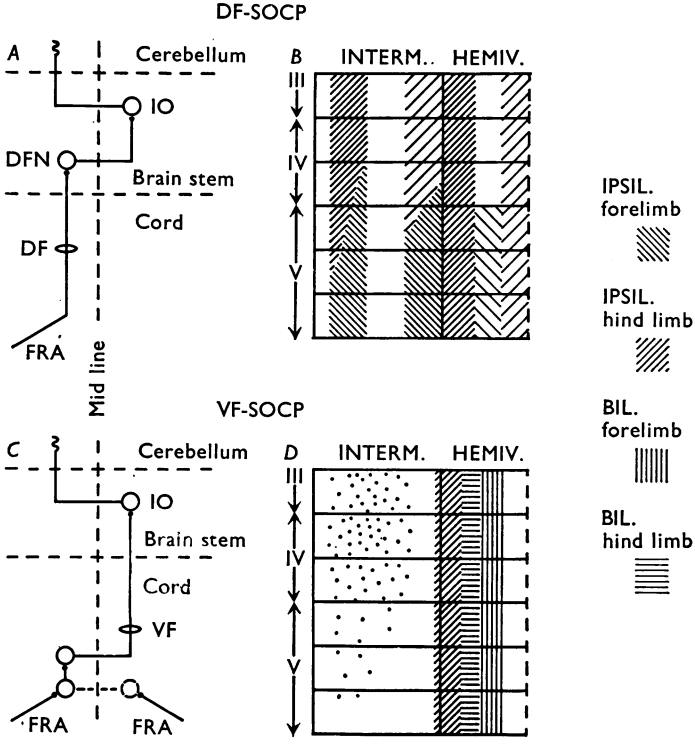

Fig. 11. Course and projection areas of DF-SOCP and VF-SOCP. Left diagrams show course and relays of DF-SOCP (*A*) and direct VF-SOCP (*C*). Interneurone drawn with interrupted lines in *C* indicates contralateral connexions to some of the components of the direct VF-SOCP. Right diagrams show projection areas (hatched) of DF-SOCP (*B*) and direct VF-SOCP (*D*) in lobules III-V of anterior lobe. Sparse hatching in *B* indicates projection areas that were found in some experiments only. The indirect VF-SOCP (not shown) is interrupted by interneurones in the brain stem before relaying in the inferior olive. It is mainly activated from hind limb nerves and projects to the stippled area in *D*. Abbreviations: IO, inferior olive; DFN, dorsal funiculus nuclei; DF, dorsal funiculus; VF, ventral funiculus; FRA, flexor reflex afferents; IPSIL., ipsilateral; BIL., bilateral; INTERM., pars intermedia; HEMIV., hemivermis.

is similar to the other spino-olivocerebellar paths investigated (Provini *et al.* 1967; Larson *et al.* 1968; Miller & Oscarsson, 1968). There are, however, signs of a transverse organization in the vermis and a longitudinal organization in the pars intermedia. In the vermis the potentials evoked from hind limb nerves are larger rostrally (DF-SOCP and VF-SOCP), whereas the forelimb potentials are larger caudally (VF-SOCP) or even restricted to the caudal part (DF-SOCP). In the pars intermedia a longitudinal organization is indicated at the border between the caudal forelimb area and the rostral hind limb area, where the forelimb and hind limb zones interdigitate (Figs. 1 and 3).

The DF-SOCP terminates in sagittal zones with gaps in between. These gaps are, at least partly, occupied by the sagittal projection zones of other spino-olivocerebellar paths (Larson *et al.* 1968; Miller & Oscarsson, 1968). Some of the spino-olivocerebellar paths terminate in overlapping areas, for example the DF- and VF-SOCP in the vermis. In these areas the olivary neurones are shared by the different paths demonstrating integration at the olivary level (Miller & Oscarsson, 1968). The importance of the sagittal projection zones formed by the spino-olivocerebellar paths for the integration of information from mossy and climbing fibre systems has already been discussed (Oscarsson & Uddenberg, 1966; Oscarsson, 1967*a*, 1968, Larson *et al.* 1968; Miller & Oscarsson, 1968).

Afferent activation patterns. The behaviour of the olivary neurones on nerve and receptor stimulation was, on the whole, similar in the DF-SOCP and VF-SOCP (cf. Oscarsson, 1968). In both paths excitation was evoked by the flexor reflex afferents from wide receptive fields. Additional excitation from group I muscle afferents was demonstrated on repetitive stimulation in the ventral but not in the dorsal path. However, the group I excitation in the VF-SOCP was relatively weak and, remarkably enough, evoked only from ipsilateral hind limb nerves.

The effects evoked in the two pathways on natural stimulation were very similar and no distinguishing features were observed. Even intense stimulation of superficial and deep receptors in the limbs was ineffective in about half of the neurones in both pathways. In the remaining cases weak or moderately strong excitation was evoked by pressure against deep structures. No effects were elicited by stimulation of cutaneous receptors, moderate bending at joints, or vibration. In both pathways inhibitory actions were rarely encountered.

The majority of the olivary neurones in the DF- and VF-SOCP were activated from all the nerves in the limb(s) that constituted the receptive field. This wide convergence was found when a relatively strong stimulus strength of 20–30*T* was used. Special attention was given to the results obtained with strong stimulation because, as argued in detail below, it

seems likely that the high threshold afferents constitute at least as important a part of the afferent input to the olivary paths as do the low threshold afferents. Strong activation of the DF-SOCP neurones was evoked from the nerves in one limb only. In contrast, the majority of the VF-SOCP neurones were effectively activated from two or more limbs, though the effects from one limb dominated. With both pathways the activation of the olivary neurones often occurred at different thresholds for the different nerves. These observations might explain the results of Eccles and his collaborators obtained in cats with intact spinal cord (Eccles, Provini *et al.* 1967; Eccles, 1968). They stimulated nerves at strengths not above six times threshold and found that climbing fibre responses were elicited from different combinations of nerves in different Purkinje cells. These different combinations were assumed to constitute important differences in the input to individual Purkinje cells. However, it seems likely that the differences in input would have been largely obliterated if higher stimulus strengths had been used. If so, the differences might represent variations in threshold with little functional significance. The spino-olivocerebellar paths are activated from the flexor reflex afferents, that is, cutaneous afferents, group II and III muscle afferents, and high threshold joint afferents (Oscarsson & Uddenberg, 1966; Oscarsson, 1967*b*, 1968; Miller & Oscarsson, 1968). Observations on the various paths activated or inhibited from the flexor reflex afferents have not indicated that the low threshold muscle afferents and the low threshold cutaneous afferents are of particular importance for these paths (Lundberg, 1964, 1966; Oscarsson, 1967*b*). Furthermore, the low threshold afferents stimulated by Eccles and his collaborators originate from stretch receptors in muscle, touch and pressure receptors in skin, and specific joint receptors. In all the spino-olivocerebellar paths investigated natural stimulation of these receptors has proved ineffective in evoking climbing fibre activity (Miller & Oscarsson, 1968; Oscarsson, 1968). These arguments should also be considered in the context of the hypothesis discussed below that the spino-olivocerebellar paths signal the activity in groups of interneurones at different levels in the cord and brain stem rather than modality and space specific information from peripheral receptors.

Functional significance. The information carried by the DF-SOCP seemingly lacks modality specificity and permits only crude spatial discrimination. In this respect the DF-SOCP is similar to the VF-SOCP and poses the same problems for the interpretation of the significance of this information. The high degree of topographical discreteness in the connexions between the inferior olive and the cerebellar cortex suggests that the olivary neurones forward highly specific information (Eccles, Ito *et al.* 1967; Miller & Oscarsson, 1968). The dilemma can be resolved by assuming

that the spino-olivocerebellar paths carry highly specific information concerning interneuronal activity which is determined by descending paths and only partly and indirectly by peripheral events. For example, the VF-SOCP has been suggested to monitor interneuronal activity in segmental reflex arcs which can be mobilized or inhibited by descending paths, including the pyramidal tract (Oscarsson, 1967*b*, 1968).

A detailed discussion of the possible functional significance of the DF-SOCP is unwarranted at present, but the suggestion made in connexion with the VF-SOCP should be considered. The first relay in the DF-SOCP is in the rostral parts of the dorsal funiculus nuclei which are innervated by the pyramidal tract (Walberg, 1967; Kuypers & Tuerk, 1964). Presumably the second-order neurones are activated from this tract as well as from the primary afferents. It is not certain if the axons from the rostral parts of the dorsal funiculus nuclei terminating in the inferior olive are collaterals of the thalamic projection or represent a specific reflex system. Neurones in the rostral parts of the dorsal funiculus nuclei terminate not only in the thalamus but also in a number of brain stem nuclei (Hand & Liu, 1966) some of which might have a motor function.

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