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TERMINATION AND FUNCTIONAL ORGANIZATION OF THE VENTRAL SPINO-OLIVOCEREBELLAR PATH

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SUMMARY

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

2. In the spinal cord the forelimb component of the VF-SOCP occupies a medial part and the hind limb component a lateral part of the ventral funiculus.

3. The main projection of the limb nerves through the VF-SOCP is to the lateral two thirds of the vermis of the anterior lobe. The projection area consists of three sagittally arranged bands: a lateral band receiving olivary axons activated exclusively from the ipsilateral hind limb, an intermediate band receiving olivary axons activated bilaterally from the hind limbs, and a medial band receiving olivary axons activated bilaterally from the forelimbs. Some olivary neurones are activated from all four limbs.

4. The latency of the climbing fibre responses was about 22 msec on stimulation of ipsilateral hind limb nerves and about 20 msec on stimulation of ipsilateral forelimb nerves. The responses evoked from contralateral nerves had a latency which was about 3 msec longer than the latency of the corresponding ipsilateral responses.

5. The olivary neurones were usually activated from all tested muscle and skin nerves in the limb(s) constituting the receptive field. Cutaneous afferents and groups II and III muscle afferents were responsible for the excitation elicited by single shock stimulation of the nerves. Brief repetitive stimulation revealed additional activation from mainly Ib, but also Ia, afferents in ipsilateral hind limb nerves.

6. Natural stimulation of receptors evoked responses in about half of the olivary neurones tested. The responses were elicited by strong pressure against deep structures. Inhibitory effects were seldom observed.

7. Climbing fibre responses appeared inconsistently and with a long latency in the intermediate part of the anterior lobe. Presumably the spinal tract projects to the intermediate part through an indirect path, possibly involving a number of relays in the brain stem.

8. The discussion is concerned with the differential termination of the various spino-olivocerebellar paths in the anterior lobe, and with the significance of the organization in sagittal bands. It is suggested that the VF-SOCP forwards information about the activity in segmental interneurones, only partly and indirectly related to peripheral events.

INTRODUCTION

Recent investigations have demonstrated that there are at least three spino-olivocerebellar paths (Oscarsson & Uddenberg, 1966; Oscarsson, 1967*a*; Larson, Miller & Oscarsson, 1968). In the spinal cord these paths are located in the ventral, dorsolateral, and dorsal funiculi respectively and they terminate in the anterior cerebellar lobe according to different projection patterns. The present investigation is concerned with the path which ascends through the ventral funiculus of the cord (VF-SOCP). The spinal tract of this path terminates in the ventrolateral part of the dorsal accessory olive and caudally in the ventrolateral part of the medial accessory olive (Brodal, Walberg & Blackstad, 1950; Mizuno, 1966). The axons of the olive cross the mid line and reach the cerebellum through the contralateral restiform body. That part of the olive which receives afferents from the ventral spino-olivary tract projects to the vermis of the anterior lobe (Brodal, 1940; Brodal *et al.* 1950). The termination of the olivary axons in the cerebellar cortex as climbing fibres and the responses they evoke in the Purkinje cells are described in the recent monograph by Eccles, Ito & Szentágothai (1967).

Potentials in the accessory olives presumably representing activity in the VF-SOCP were first described by Morin, Lamarche & Ostrowsky (1957). They recorded activity with a latency of 15–30 msec following stimulation of cutaneous hind limb nerves but were unable to detect any response following stimulation of muscle nerves. The responses were large when evoked from contralateral nerves and small when evoked from ipsilateral nerves and depended on a pathway ascending through the ventral quadrant of the cord, ipsilateral to the olive. More recently, the discharge in the VF-SOCP was recorded from the olivo-cerebellar axons at the level of the restiform body by Grant & Oscarsson (1966). They reported large responses with a latency of about 20 msec on stimulation of muscle as well as skin nerves and concluded that Morin and co-workers had used a stimulation of muscle nerves that was too weak to evoke activity in the VF-SOCP.

A detailed investigation was recently made of the responses evoked in the dorsal accessory olive both on antidromic stimulation from the cerebellar cortex and on electrical stimulation of hind limb nerves (Armstrong, Eccles, Harvey & Matthews, 1968; Armstrong & Harvey, 1968). Stimulation of muscle and skin nerves evoked responses in overlapping areas and there was extensive convergence of excitation from various nerves to individual neurones. A contribution from Group I afferents in some muscle nerves was demonstrated on brief repetitive stimulation.

The present investigation deals specifically with two problems: the projection pattern of the VF-SOCP in the anterior cerebellar lobe, and the responses evoked in individual climbing fibres on electrical stimulation of hind limb and forelimb nerves and on natural stimulation of deep and superficial receptors in the limbs. As described in two preliminary reports, the path terminates in somatotopically arranged, longitudinal zones in the vermis (Oscarsson & Uddenberg, 1966; Oscarsson, 1967*b*). This projection pattern contrasts with the classical somatotopic organization in transverse fields (Adrian, 1943; Snider & Stowell, 1944; Carrea & Grundfest, 1954; Combs, 1954; Grant, 1962*b*; Provini, Redman & Strata, 1967).

METHODS

The experiments were done on cats decerebrated at a pre-collicular level. The dissection was made under pentobarbitone anaesthesia and no additional anaesthetic was given 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, when necessary, prevented from falling below 90 mm Hg by intravenous infusion of a glucose-dextran solution containing aramine.

The anterior cerebellar lobe was exposed from the primary fissure to the inferior colliculi. In some experiments lobule III and the hidden part of lobule IV were exposed by sucking out the colliculi. The exposed area was covered with warm mineral oil. The spinal cord was transected in the third cervical segment except for the left ventral funiculus and sometimes a small adjacent part of the left lateral funiculus. The right hemisection of the cord was made at one level and the lesion interrupting the dorsal part of the cord on the left side about half a centimetre further rostrally. 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 right quadriceps, gastrocnemius-soleus, and plantar nerves were also available for stimulation.

Conventional stimulating and recording techniques were used. When recording, the nerves were usually stimulated at a frequency of 1/sec. The incoming volleys were monitored by triphasic recording from the dorsal funiculi in the lumbar region (hind limb nerves) and by monophasic recording from the interrupted dorsal funiculi in the third cervical segment (forelimb nerves). The stimulation strength is expressed in multiples of the strength needed for evoking a barely visible incoming 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 the hole of a glass plate pressed lightly against the cerebellar surface and a bilateral pneumothorax was performed.

The extent of the spinal lesions was determined by inspection through a binocular microscope after formalin fixation and staining of the surface with toluidine blue. 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

The experiments were performed on decerebrate cats with the spinal cord interrupted in the third cervical segment except for the left ventral funiculus. The cord lesion interrupted the known spinocerebellar paths that terminate as mossy fibres and which include the dorsal, ventral, and rostral spinocerebellar tracts, the cuneocerebellar tract, and the spinoreticulocerebellar path (Oscarsson, 1965; Grant, Oscarsson & Rosén, 1966, and unpublished). The lesion also interrupted two spinoolivocerebellar paths which ascend through the dorsal part of the lateral funiculus and through the dorsal funiculus, respectively (Oscarsson, 1967*a*; Larson *et al.* 1968).

Surface potentials

Stimulation of hind limb and forelimb nerves evoked large surface positive potentials in restricted areas of the anterior lobe. These potentials delimit the projection areas of the VF-SOCP as demonstrated by observations on climbing fibre responses evoked in individual Purkinje cells (see below). The positive potentials had an amplitude of 100–500 μV in the different experiments. They showed the characteristics described for surface potentials generated by the olivocerebellar path (Armstrong & Harvey, 1968). Negative potentials were recorded from extensive areas and presumably represent electrical spread of fields generated in the projection areas.

Projection areas. The surface potentials evoked by stimulation of limb nerves were mapped in twelve experiments. In most cases the muscle nerves were stimulated at a fixed and relatively high stimulus strength (30–40 T). With this strength, the potentials evoked from the muscle nerves, the hamstring and deep radial nerves, were usually larger and less variable than the potentials evoked from the cutaneous nerves, the sural and superficial radial nerves. The area between the primary fissure and the colliculi was explored in all experiments and corresponds to lobule V and at least the caudal part of lobule IV. In three experiments lobule III and the rostral part of lobule IV were explored after removal of the dorsal part of the mesencephalon. The mapping was performed by moving the recording

electrode in small steps (0·5–1·5 mm) along the individual folia. The characteristic distribution of positive and negative potentials shown in Fig. 1–3 were found in every experiment.

The curves and sample records in Fig. 1 refer to potentials recorded from a folium in lobule V, midway between the primary fissure and the border to lobule IV. The hamstring nerves in the hind limbs and the deep radial nerves in the forelimbs were stimulated. Large positive potentials

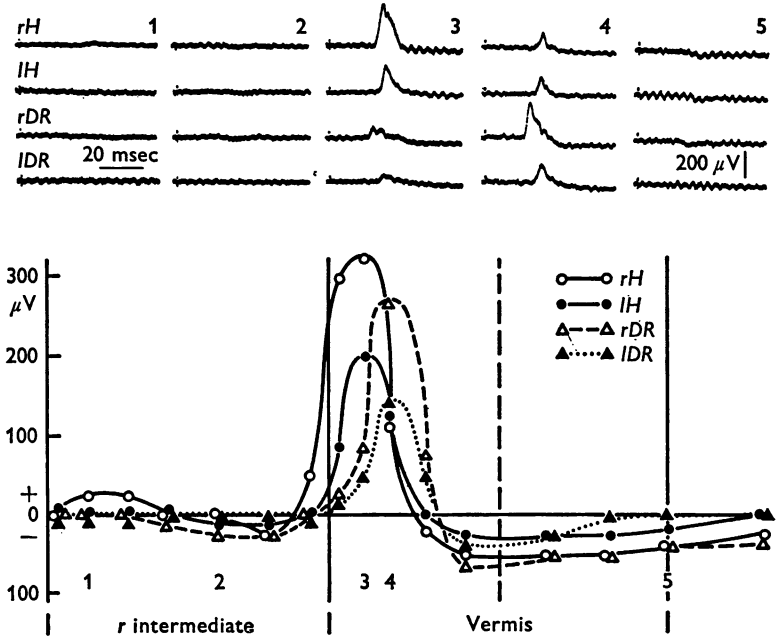


Fig. 1. Potentials recorded from surface of cerebellar folium located midway between rostral and caudal borders of lobule V. The potentials were evoked by stimulation of one muscle nerve in each limb at a strength of 40 *T* and recorded from many points along the folium to show characteristic distribution. The spinal cord was interrupted in third cervical segment except for the left ventral funiculus. The sample records were obtained by averaging 12 responses and taken from points 1–5 (see diagram). Positivity is recorded upwards. Dots mark stimulus artifacts. The curves show amplitude of 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: *r*, right; *l*, left; *H*, hamstring nerve; *DR*, deep radial nerve.

were evoked in the lateral two thirds of the right vermis. More medially in the right vermis and on the left side of the anterior lobe negative potentials were recorded. These negative potentials represent fields generated from a distance as shown by the following experiment. The left halves of lobules IV and V were sucked out and replaced by gelfoam soaked

in saline. Following the ablation the positive potentials in the right vermis were reduced by 49 % presumably because of a deteriorated blood supply. On the left side, from the surface of the gelfoam, negative potentials could still be recorded though decreased in amplitude by 46 %, that is to a similar extent as the positive potentials on the right side.

The potentials were small in the right intermediate part of lobule V. In the experiment shown in Fig. 1, the right hind limb nerve evoked a small positive potential laterally and a small negative potential medially. In other experiments the right hind limb nerves often evoked slightly larger positive potentials, and occasionally as large as in Fig. 3. These positive potentials had a longer latency than those recorded in the vermis and will be discussed below. The potentials evoked from the other limbs in the right intermediate part were usually negative and very small.

The positive potentials evoked from the different limbs in the right vermis had different maxima. Stimulation of the hind limb nerves evoked potentials lateral to those evoked from the forelimb nerves. Close inspection of the curves in Fig. 1 shows that the potentials from the left hind limb nerve had a more medial distribution than the potentials from the right hind limb nerve, whereas the potentials evoked from the left and right forelimb nerves had identical maxima. This differential distribution was a regular finding and is further elaborated by the observations on unitary recording.

The potentials evoked in the vermis of lobules IV and III had a distribution similar to those recorded in lobule V (compare Figs. 1 and 2). However, in some experiments stimulation of the right nerves evoked large positive potentials in the right intermediate part, as illustrated in Fig. 2. Large positive potentials were almost always evoked from the right hind limb nerves in lobule III and in the rostral part of lobule IV. More caudally these potentials decreased in amplitude and they were usually small or even missing in lobule V (Figs. 1 and 3). In a few experiments large potentials were evoked also from the right forelimb nerves (Fig. 2) and had then a rostro-caudal extent similar to the hind limb potentials. The potentials evoked in the intermediate part always had a longer latency than the corresponding potentials in the vermis (see next section). The long latencies suggest an indirect pathway as does the fact that the potentials in the intermediate part were small or absent in some experiments. Stimulation of the left hind limb and forelimb nerves never evoked surface positive potentials in the intermediate part.

In a few experiments, a small and inconstant positive potential appeared after a long latency (30–36 msec) in the trough formed by the negative potential recorded in the lateral part of the left vermis, in lobule IV. This potential was only evoked from the right hind limb nerves. It presumably represents a subsidiary climbing fibre projection. The latency

was longer than that of the projection to the right intermediate part and as much as 10–15 msec longer than that of the projection to the right vermis.

The distribution of the potentials evoked from different nerves in the same limb was the same and independent of stimulus strength. The curves in Fig. 3 demonstrate this fact for potentials evoked from three nerves in the right hind limb. The potentials were recorded from lobule V and the long latency responses in the intermediate cortex were unusually large. The potentials evoked from the cutaneous nerve (sural) and from the mixed plantar nerve were large already at weak stimulus strengths (Fig 3 *A*).

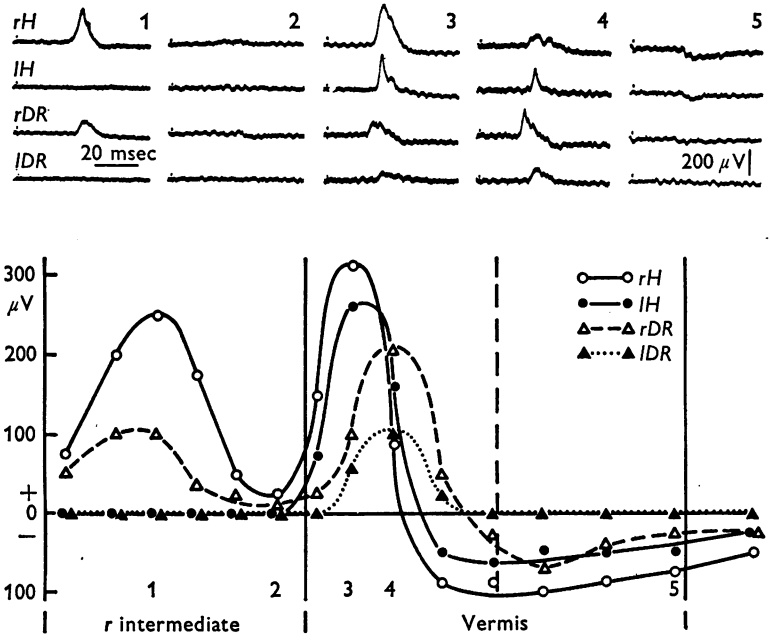


Fig. 2. Potentials recorded from surface of cerebellar folium located midway between rostral and caudal borders of lobule IV. From the experiment also shown in Fig. 1. Conventions and abbreviations as in that figure.

Brief repetitive stimulation (four shocks at 330/sec) evoked a response also from relatively low threshold muscle afferents, as shown in Fig. 3*B*. These potentials had a distribution similar to those evoked from the sural and plantar nerves. At high strengths a single stimulus was sufficient to evoke a large response from the muscle nerve and again the distribution of the potentials was the same for the various nerves (Fig. 3*C*). Similar observations were made in other experiments with the potentials evoked from the quadriceps, gastrocnemius-soleus, hamstring, and sural nerves in the hind limbs, and with the potentials evoked from the deep and superficial radial nerves in the forelimbs.

The positive potentials evoked in the vermis from the right hind limb and forelimb nerves (hamstring, sural, deep and superficial radial) usually had an approximately equal amplitude and were always large, especially in the rostral part of lobule V and the caudal part of lobule IV. The potentials evoked from the left nerves were smaller and more variable in the

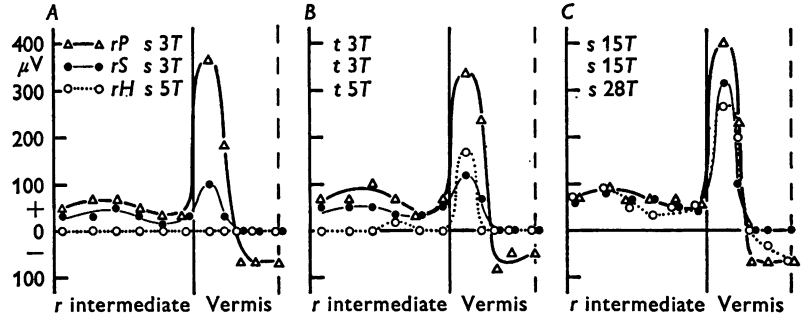


Fig. 3. Similarity in distribution of potentials evoked at different strengths and from different nerves in the same limb. Recording from folium in lobule V. The right plantar (*rP*), right sural (*rS*), and right hamstring (*rH*) nerves were stimulated either with single shocks (*s*, diagrams *A* and *C*) or with brief tetani (*t*, diagram B) at stimulus strengths indicated and expressed in multiples of nerve threshold (*T*). The brief tetani consisted of four shocks given at 330/sec. Preparation and conventions as in Fig. 1.

different experiments. The relative size of the potentials evoked from the right hind limb and forelimb nerves varied in a systematic way along the rostro-caudal extent of the vermis, as illustrated in Fig. 4*A* and *B*. The forelimb potentials were larger in lobule V and the hind limb responses larger in lobules IV and III. The responses from the left nerves varied in parallel with those from the right nerves. The variation in amplitude of the potentials evoked from the muscle nerves in the four limbs is given in Table 1, representing values from ten experiments.

Latencies. The latencies of the positive potentials evoked in the vermis on muscle nerve stimulation and shown in Table 2 represent the lowest values found in each of eleven mapping experiments. The latencies refer to potentials evoked by single stimuli but there was no significant change in latency when a brief tetanus (four shocks at 330/sec) was used except in some cases when the responses were very small on single shock stimulation. The latencies of the surface potentials evoked from the skin nerves were not recorded systematically but fell within the same range as the corresponding muscle nerve latencies.

The potentials evoked from the left nerves had a latency that was about 3 msec longer than the latency of the responses from the right nerves. This latency difference might indicate that the cell bodies of the spinal tract are

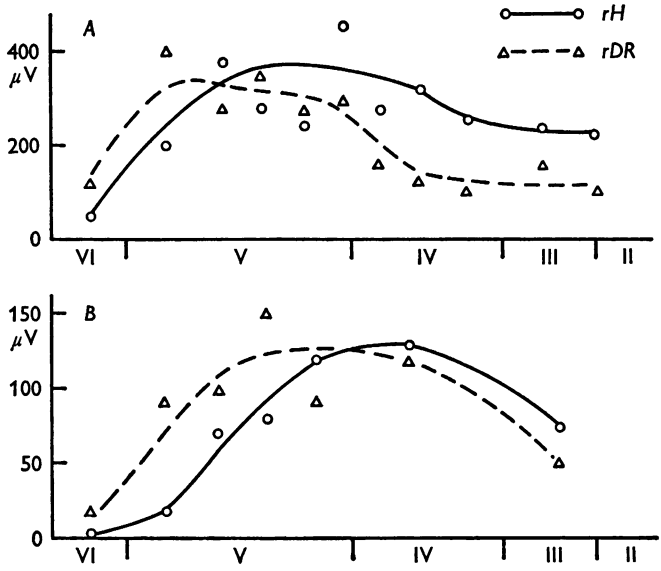


Fig. 4. Variations in amplitude of positive potentials recorded along sagittal projection bands in vermis; from two experiments (*A* and *B*). The potentials were evoked by stimulation of right hamstring (*rH*) and right deep radial (*rDR*) nerves at a strength of 40*T*. The maximal potentials recorded in each folium were plotted against their sagittal distribution in lobules II–VI. The records used for plotting were obtained by averaging twelve responses. Preparation as in Fig. 1.

TABLE 1. Amplitude of positive potentials recorded from right vermis in lobules V and IV, respectively, and evoked from right and left hamstring and deep radial nerves. The amplitude is expressed as percentage of amplitude of response from right hamstring nerve. The figures represent mean and range of values obtained in ten experiments. The measurements were made midway between rostral and caudal borders of the lobules

	Right hamstring	Right deep radial	Left hamstring	Left deep radial
Lobule V	100	115 (65–150)	64 (40–100)	35 (0–60)
Lobule IV	100	61 (25–100)	66 (17–110)	9 (0–23)

TABLE 2. Latencies of VF-SOCP responses in right vermis. Latencies of surface positive potentials represent lowest values recorded in each of eleven mapping experiments. Latencies of unitary climbing fibre responses represent lowest value recorded in any individual unit in each of six experiments. Mean and range are given in msec

	Right		Left	
	Hamstring	Deep radial	Hamstring	Deep radial
Surface potentials	22 (19–25)	20 (17–24)	25 (21–27)	23 (21–26)
Unitary potentials	21 (20–22)	20 (19–24)	24 (21–28)	22 (20–26)
	Sural	Superficial radial	Sural	Superficial radial
Unitary potentials	22 (21–25)	20 (18–23)	26 (23–30)	22 (20–25)

located on the right side of the cord in accordance with the general rule suggested by Oscarsson (1964), that tracts ascending in the ventral part of the cord are crossed at the segmental level. The activation of the spino-olivary tract from the left nerves would occur through interneurones crossing the cord at the segmental level (Oscarsson, 1964).

It is remarkable that the forelimb potentials appeared after a latency that was only 2–3 msec shorter than the latency of the hind limb potentials. According to Armstrong *et al.* (1968) the fastest fibres in the hind limb component of the spino-olivary tract conduct at 25–30 m/sec. Assuming that the hind limb and forelimb components originate from the level of the dorsal root entrance and have a similar conduction velocity there would be a latency difference of at least 8 msec between the hind limb and forelimb responses. The possibility should be considered that the forelimb component either originates from cord levels caudal to the dorsal root entrance or that it consists of more slowly conducting fibres than the hind limb component.

The responses evoked from the right nerves in the intermediate part had consistently a longer latency than the potentials evoked in the vermis. The additional latency for the hind limb responses was 3–5 msec and for the forelimb responses 6–12 msec (Fig. 2). It has already been suggested that the responses in the intermediate part are mediated by an indirect pathway.

Thresholds. The stimulus strengths needed for evoking surface positive potentials in the vermis are given in Table 3. The threshold strengths are expressed as multiples of the nerve threshold (T) determined by monitoring the incoming volleys (see Methods). The thresholds refer to responses evoked by a single stimulus and a brief tetanus.

The threshold for evoking potentials from the cutaneous nerves in the right limbs usually was approximately the same on single shock and repetitive stimulation (Fig. 5R). The response appeared with stimulation of low threshold afferents and increased with additional activation of high threshold afferents. However, in many cases the response became almost maximal at a relatively low stimulus strength as in Fig. 5R. This might be due to occlusion of excitation evoked from high threshold afferents.

Single stimuli applied to the right muscle nerves evoked surface potentials at thresholds between 2·5 and 6T except in two cases when the threshold on stimulation of the hamstring nerve was higher (9 and 15T). The response always increased when the strength was raised from 10 to 30T (Fig. 5P). These observations indicate that afferents belonging to groups II and III contributed to the excitation of the VF-SOCP (Eccles & Lundberg, 1959*a*). On repetitive stimulation hind limb and forelimb muscle nerves evoked responses at different thresholds. With the forelimb nerve, deep radial nerve, the threshold always remained above the maxi-

TABLE 3. Thresholds for evoking positive potentials in right vermis. Figures give stimulus strengths, expressed in multiples of nerve thresholds, needed for evoking barely visible cerebellar potentials on single shock and brief repetitive (4 shocks at 330/sec) stimulation. Data from eight (right hind limb) and four (right forelimb and left hind limb and forelimb) experiments. Abbreviations: *r*, right; *l*, left; *H*, hamstring nerve; *DR*, deep radial nerve; *S*, sural nerve; *SR*, superficial radial nerve

	rH	*rS*	*rDR*	*rSR*	*lH*	*lDR*
Single	2·5–15	1·3–2·5	3–6	1·8–2·2	8–13	13–40
Repetitive	1·3–2·2	1·3–2·5	2–3·5	1·7–2·2	4–8	4–8

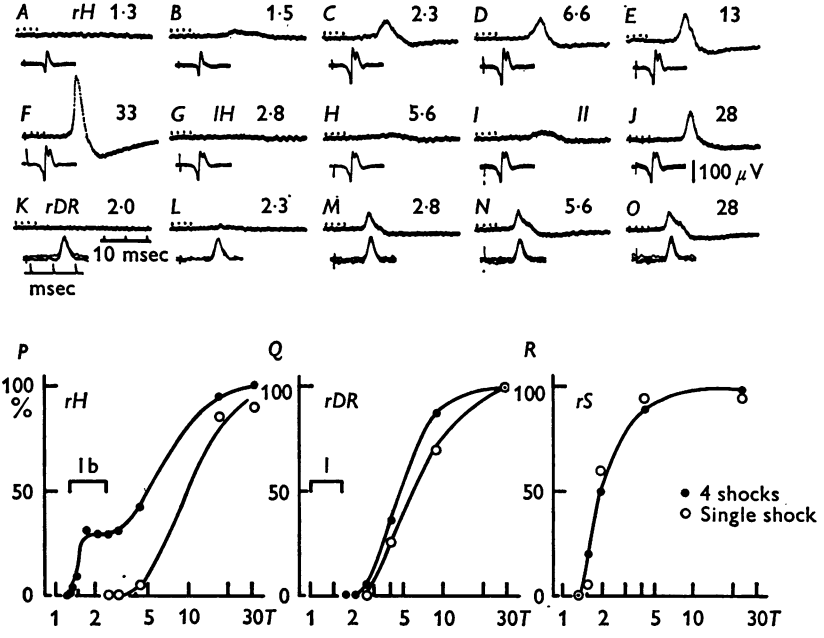


Fig. 5. Contribution from different groups of afferents to evoked cerebellar potentials. *A–F*, stimulation of right hamstring nerve (*rH*); *G–J*, stimulation of left hamstring nerve (*lH*); and *K–O*, stimulation of right deep radial nerve (*rDR*). The nerves were stimulated with four shocks (dots mark stimulus artifacts) at the strengths indicated in multiples of nerve threshold (*T*). Upper traces show surface potentials (positivity upwards) obtained by averaging of twelve responses. Lower traces show incoming volleys recorded triphasically from dorsal funiculus in lumbar cord (*A–J*) and monophasically from cut end of dorsal funiculus in third cervical segment (*K–O*). The lower traces were obtained with a fast sweep speed and by photographic superposition of several responses. *P–R*, curves obtained from a different experiment. The amplitude of the positive potentials in the right vermis, in per cent of their maximal amplitude, is plotted against stimulus strength. The potentials were evoked by single shocks and by brief tetani (four shocks at 330/sec) as indicated. Threshold and maximum for Ib afferents indicated in diagram *P*, and for group I afferents in diagram *Q*. Additional abbreviation: *rS*, right sural nerve. Preparation as in Fig. 1.

mum for the group I volley (Fig. 5*K–O*, *Q*). With the hind limb nerves the threshold was almost always below the group I maximum. Observations made in two experiments on stimulation of the hamstring nerve are shown in Fig. 5. In *A* a maximal group Ia volley (Bradley & Eccles, 1953; Eccles, Eccles & Lundberg, 1957) produced no response, whereas increase of stimulus strength to activate a small part of the Ib volley evoked a response (*B*), which increased further with activation of more Ib afferents (*B–C*). There was only a small increase of the surface potential with activation of low threshold group II afferents (*C–D*) but a marked increase on additional stimulation of group III afferents (*E–F*). The curve in Fig. 5*P* is from a different experiment and shows the appearance and growth of the cerebellar response concomitantly with the Ib volley. The plateau of the curve before the increase in amplitude occurring at higher strengths indicates that the initial response cannot be due to a 'contamination' of the Ib volley with impulses in group II afferents. Similar observations were made in seven out of eight experiments with stimulation of the hamstring nerve and strongly suggest a contribution from tendon organ afferents to the evoked potential. In the remaining case a response appeared only when the hamstring nerve was stimulated at a strength slightly suprathreshold for group I afferents.

Repetitive stimulation of the right quadriceps and gastrocnemius-soleus nerves also demonstrated effects from group I afferents in most cases. The threshold on stimulation of the quadriceps nerve was determined in four experiments as 1·1, 1·3, 1·5 and 1·6*T* respectively. Unfortunately, the threshold separation of the Ia and Ib volleys was not clear in any of these experiments. In two of the cases the low threshold suggests that Ia afferents might be effective, whereas in the two remaining cases the threshold might be taken to indicate a contribution mainly from Ib afferents. The gastrocnemius-soleus nerve was stimulated in three experiments and the response appeared at 1·2, 1·5 and 2·5*T*. In the first two cases a Ib contribution is suggested, in the third case the threshold was clearly above the group I maximum.

The thresholds for evoking potentials from the left nerves were usually higher than those determined for the right nerves (Table 3). Repetitive stimulation of group I afferents in the left hamstring and deep radial nerves was never observed to evoke cerebellar potentials (Fig. 5*G–J*).

Unitary potentials

Purkinje cells were recognized by their climbing fibre responses which occurred spontaneously at an irregular rate of usually 0·5–3/sec and, in the projection areas, were evoked by limb nerve stimulation. The recording was extracellular or intracellular and the responses had the characteristics

described in detail by Eccles, Llinas & Sasaki (1966). Typical records are shown in Figs. 6–9. Convergence of two or more climbing fibres to the same Purkinje cell is known to be uncommon and was not observed in the present material. Hence, the observations on the climbing fibre responses give information about the activity in individual olivocerebellar neurones.

The positive potentials recorded from the cerebellar surface were largely or exclusively produced by climbing fibre activity in the Purkinje cells (Oscarsson & Uddenberg, 1966; Armstrong & Harvey, 1968); the climbing fibre responses evoked by nerve stimulation were observed in cells located in the areas responding with positive potentials and the latencies and thresholds of these responses were similar to those of the surface potentials (Table 2, Figs. 6–9, and below).

Stimulation of limb nerves evoked climbing fibre responses in more than 140 of the investigated Purkinje cells. Of these cells 114 were encountered in the right vermis and 28 in the right intermediate part of the anterior lobe.

Responses in vermal projection area. More than 95% of the units were activated from all the nerves tested in the limb (or limbs) that constituted the receptive field. This is illustrated in Fig. 6 for a cell activated exclusively from the right hind limb. Stimulation of the hamstring, gastrocnemius-soleus, and sural nerves all evoked a climbing fibre response (*A–C*), whereas the nerves in the other limbs were ineffective (*D–F*). Convergence of excitation from nerves in the right and left limbs is shown in Figs. 7 and 8. The responses evoked from the left nerves had often a more variable latency than those from the right nerves and sometimes appeared only inconsistently.

On stimulation with single shocks the responses appeared with activation of group II and III afferents in muscle nerves and with activation of low and high threshold afferents in cutaneous nerves. Brief repetitive stimulation of group I muscle afferents in the right hind limb (but not in the other limbs) often evoked a response in agreement with the observations on surface potentials. The excitation from group I afferents was found in units that were also activated from high threshold muscle afferents and from cutaneous afferents.

The latencies of the climbing fibre responses usually varied between 20 and 30 msec. The shortest lateneies corresponded closely to the onset of the surface potential (Fig. 6) and are given in Table 2. Only occasionally were the latencies longer than 30 msec.

With respect to convergence of excitation from the various limbs nearly all the units (110 out of 114) belonged to one of four groups, as shown in Table 4. Units belonging to the various groups occurred in different sagittal bands as would be expected from the distribution of the surface

potentials (Figs. 1 and 2). Units activated exclusively from the right hind limb nerves(Fig. 6) were found in a band with a width of 0·5–1·5 mm. This band included the most lateral part of the vermis, the grove indicating the border between the vermis and the intermediate part, and sometimes also the most medial part of the intermediate cortex. Units activated bilaterally from the hind limb nerves were found in an adjacent, more medial band

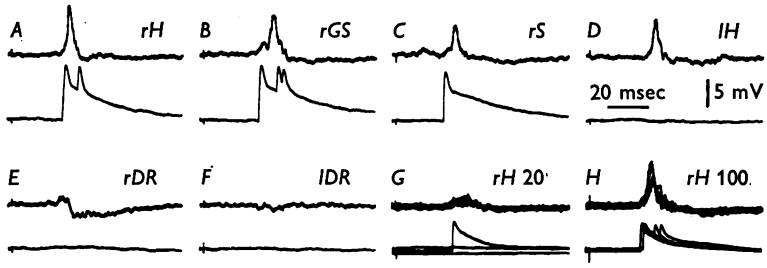


Fig. 6. Climbing fibre responses evoked from right hind limb. Upper traces record surface potentials and lower traces intracellular potentials from a Purkinje cell. Positivity upwards. Vertical calibration bar refers to lower traces. The site of recording was in the vermis close to its lateral border. Abbreviations: *r*, right; *l*, left; *H*, hamstring nerve; *GS*, gastrocnemius-soleus nerve; *S*, sural nerve; *DR*, deep radial nerve; *SR* (only in Figs. 7–9), superficial radial nerve. Nerves stimulated at 50 (*A–F*), 20 (*G*), and 100 (*H*) times nerve threshold. Note in *G* and *H* (superimposed traces) all-or-nothing nature of synaptic potential and its later component. Preparation as in Fig. 1.

TABLE 4. Convergence of excitation from various limbs to 114 climbing fibres terminating in right vermis and 28 terminating in right intermediate part. Figures show number of fibres receiving excitation from indicated limb(s)

	Vermis	Intermediate part
Right hind limb	27	16
Right forelimb	2	7
Right hind limb and forelimb	2	5
Right and left hind limbs	23	0
Right and left forelimbs	36	0
Right and left hind limbs and forelimbs	24	0

with a width of usually 0·5–1·0 mm. Further medially followed a third band with a similar width, which contained units activated bilaterally from the forelimb nerves. Typical recordings from units belonging to the last two groups are shown in Fig. 7. Some climbing fibres were activated from all four limbs, as the unit illustrated in Fig. 8. These units occurred in a transitional zone between the two medial bands and were intermingled with units activated exclusively from either the hind limbs or the forelimbs.

In the present investigation the sagittal organization was studied in the

superficial cortex of lobules V and IV both by recording climbing fibre responses from individual Purkinje cells and by recording the negative fields in the molecular layer, which are the summed responses from many of these cells (Eccles *et al.* 1966; Eccles, Provini, Strata & Taborikova, 1967). With both kinds of intracortical recording the sagittal bands activated from the right hind limb, from both hind limbs, and from both fore-

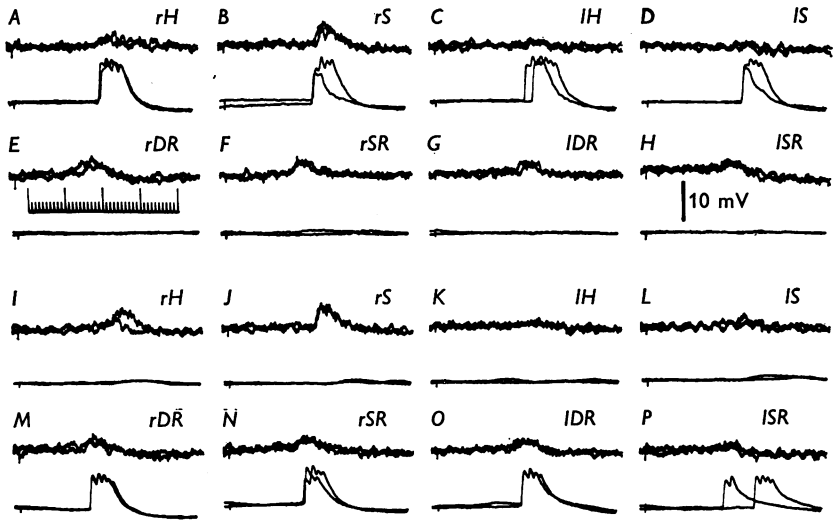


Fig. 7. *A–H*, climbing fibre responses evoked bilaterally from the hind limbs. *I–P*, climbing fibre responses evoked bilaterally from the forelimbs. The surface electrode was kept at a lateral position in the right vermis corresponding to the sagittal band activated from both hind limbs. Intracellular recording in *A–H* from a Purkinje cell located in this band, and in *I–P* from a Purkinje cell located in the more medial band activated from both forelimbs. Time marker, msec. Conventions and abbreviations as in Fig. 6.

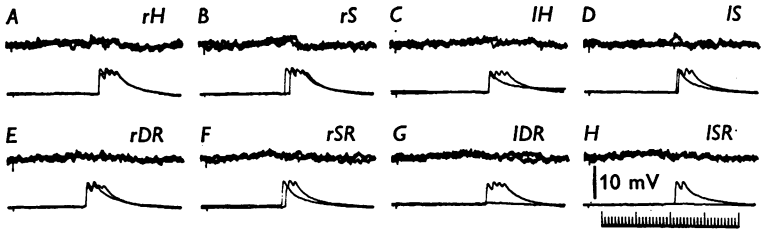


Fig. 8. Climbing fibre responses evoked from all four limbs. Intracellular recording from Purkinje cell located in transitional zone between intermediate and medial projection bands in right vermis. The surface potentials were small possibly because of a local damage of the cortex below the surface electrode, which was placed at a lateral position in the right vermis. Time marker, msec. From the experiment also shown in Fig. 7. Conventions and abbreviations as in Fig. 6.

limbs, respectively, showed little overlap, which contrasts with the marked overlap found in the distribution of the positive potentials recorded from the cerebellar surface (Figs. 1 and 2). When the exploring electrode was moved from one folium to another it was sometimes found that the location of the bands shifted up to 0·5 mm in medial or lateral direction. This indicates that corresponding sagittal points on adjacent folia are not exactly juxtaposed. Similarly, when the micro-electrode penetrated into new cortical layers beneath the superficial cortex there were often corresponding medio-lateral shifts. The sagittal organization was demonstrated at all depths of lobules IV and V. However, the borders appeared more blurred in the deep parts than at the surface possibly because of repeated medio-lateral shifts of the sagittal bands when the electrode penetrated successive cortical layers.

Forty Purkinje cells activated on nerve stimulation and encountered in the vermis were tested for excitatory and inhibitory effects on natural stimulation of receptors. The effects were judged by the increase or decrease in frequency of the background activity of climbing fibre responses. Even strong stimuli applied to superficial and deep receptors of the limbs were ineffective in twenty-two of the units. In seventeen cases there was a slight or moderate increase in the background activity. The increase was evoked from only one of the right limbs, even when electrical stimulation demonstrated convergence of excitation from several limbs. Inhibition of the resting activity was found in four units on stimulation of the left forelimb. In one of these units inhibition was obtained also from both hind limbs. Three of these four units were activated on natural stimulation of the right forelimb.

Both excitation and inhibition were evoked by moderate or strong pressure against deep structures. In many cases the effect seemed to be produced most readily by pressure against bone and tendons. No effects were seen on moderate bending of joints, vibration, or even strong stimulation of the skin (pinching). The excitatory and inhibitory effects usually adapted completely after some seconds. The receptive fields on natural stimulation were diffuse and seemed to include most of a limb, though the effects were usually stronger from its distal region.

Responses outside vermal projection area. Purkinje cells responding to limb nerve stimulation were found in the right intermediate part of the anterior lobe. They occurred mainly in its lateral part and almost exclusively in lobule IV. Almost all the positive findings were made in two experiments in which large surface positive potentials were recorded in the intermediate part. The cells responded after a relatively long latency, 25–35 msec on stimulation of hind limb nerves and 27–40 msec on stimulation of forelimb nerves. The response occurred at a relatively constant

latency as illustrated in Fig. 9. The records in the figure were obtained with brief repetitive stimulation. However, there was only a small reduction in latency (one or a few msec) and a small increase in the probability of responding, when the stimulation was changed from single shocks to brief tetani. Most of the units were activated either from the right hind limb (Fig. 9*A–E*) or the right forelimb (*F–J*), but some units were activated from both these limbs (Table 4). No responses were elicited from the left nerves except in two units of the twenty-eight tested. These units responded after a latency of 40–50 msec irregularly to repetitive stimulation of the left nerves. This weak excitation is neglected in Table 4.

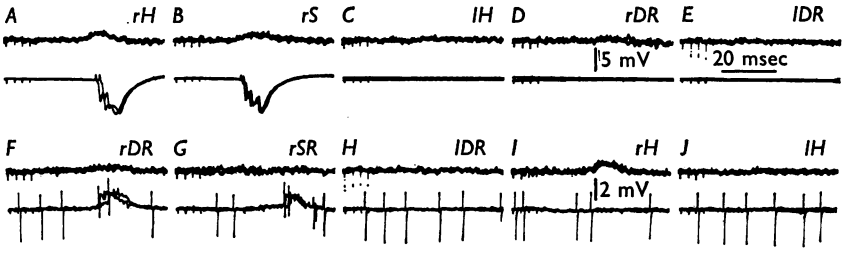


Fig. 9. Climbing fibre responses recorded laterally in right intermediate part of lobule IV. *A–E*, responses evoked from right hindlimb; *F–J*, responses evoked from right forelimb. The micro-electrode was in an extracellular position. The surface electrode was placed close to the site of the micro-electrode. Nerves stimulated with four shocks. Conventions and abbreviations as in Fig. 6.

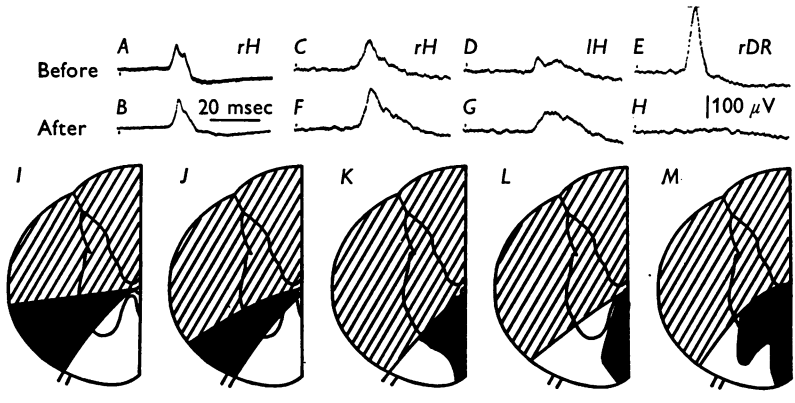
Natural stimulation was tried with ten of the twenty-eight units encountered in the intermediate part. In five of them weak acceleration of the background activity was induced by strong pressure against deep structures, in the remaining cases no effects were found. These observations are similar to those made on the vermal units.

Medial to the vermal projection area and on the left side of the anterior lobe Purkinje cells were usually uninfluenced by nerve stimulation. Occasionally, however, units were found which responded irregularly to nerve stimulation (especially a brief tetanus) after a latency of 30–50 msec.

Localization of pathway

Anatomical and physiological investigations have demonstrated that the spino-olivary tract ascends through the ventral funiculus of the cord and possibly also through the most ventral part of the lateral funiculus (Brodal *et al.* 1950; Beusekom, 1955; Grant & Oscarsson, 1966; Mizuno, 1966; Armstrong *et al.* 1968). In this investigation there was no obvious correlation between the size of the cerebellar responses and the ventral extent of the lesion in the lateral funiculus as long as it did not encroach upon the ventral funiculus.

The effect of a small lesion in the ventral part of the cervical cord was studied in five experiments. The hatched areas in the diagrams of Fig. 10 indicate the extent of the original lesion, which interrupted dorsally located pathways. The positive potentials in the right vermis were recorded before and after the addition of the lesions indicated in black. The figures given below the diagrams show the amplitude of the potentials after the lesion and are expressed in per cent of the amplitude before the



r hind leg	115	50	130	70	80
l hind leg	—	—	150	65	45
r foreleg	—	135	0	0	25
l foreleg	—	—	—	0	—

Fig. 10. Effects of ventral lesions made on the left side in the third cervical segment of the cord. Data from five experiments, *I–M*. The right half of the cord was transected (not shown). Hatched areas indicate extent of original lesion performed before recording. The positive potentials in the right vermis were recorded before (*A*, *C–E*) and after (*B*, *F–H*) the addition of the lesions indicated as black areas. Records *A* and *B* demonstrate effect of lesion in *I*, records *C–H* demonstrate effect of lesion in *K*. The figures below the diagrams show amplitude of the potentials recorded after the lesion and are expressed in per cent of the amplitude before the lesion. — indicates that the responses were not tested. Abbreviations: *r*, right; *l*, left; *H*, hamstring nerve; *DR*, deep radial nerve.

lesion. The responses were measured after averaging but long term variability of the potentials make changes of less than 10–20 % of doubtful significance. The lesion in diagram I, in the ventral third of the lateral funiculus, was without significant effect (compare records *A* and *B*). On the other hand, the lesion in *J* which encroached upon the ventral funiculus led to a marked decrease of the hind limb responses. In three experiments lesions were made in the medial part of the ventral funiculus (*K–M*). The lesion in *K* completely abolished the forelimb responses (compare *E* and *H*),

whereas the hind limb responses actually increased in size (compare *C*, *D* and *F*, *G*). The two remaining medial lesions caused a large decrease (*M*) or abolition (*L*) of the forelimb responses and a small or moderate decrease of the hind limb responses.

The effects of a ventral lesion on the responses in the right intermediate part of the anterior lobe was only studied in the experiment of Fig. 10*L*. The forelimb responses were completely abolished and the hind limb responses reduced by 25 %. Presumably the path projecting to the intermediate part is contiguous with that projecting to the vermis.

These observations demonstrate that the spino-olivary tract ascends exclusively, or almost exclusively, in the ventral funiculus with the hind limb component laterally and the forelimb component medially. The finding in the experiment of Fig. 10*J* that the responses from the forelimb increased concomitantly with the decrease of the responses from the hind limb, and the opposite effect in the experiment of Fig. 10*K*, might possibly indicate a release either from supraspinal inhibition exerted at the spinal level or a release from a mutual inhibition between the hind limb and forelimb components exerted at the olivary level.

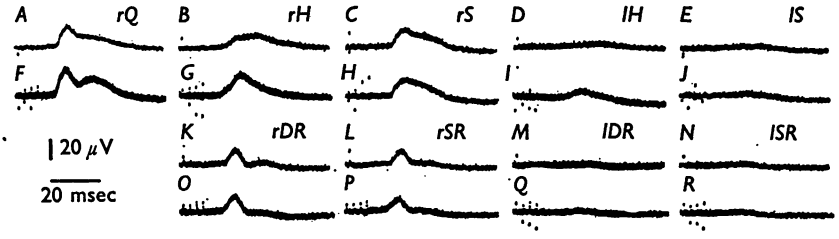


Fig. 11. Mass discharge in VF–SOCP recorded from right dissected restiform body on stimulation of hind limb and forelimb nerves. The spinal cord was transected in third cervical segment except for left ventral funiculus. The restiform body was dissected and mounted for recording as described by Holmqvist, Oscarsson & Rosén (1963). Stimulation at 30*T* with single shocks (*A–E*, *K–N*) and with four shocks (*F–J*, *O–R*). Dots mark stimulus artifacts. Abbreviations: *r*, right; *l*, left; *Q*, quadriceps nerve; *H*, hamstring nerve; *S*, sural nerve; *DR*, deep radial nerve; *SR*, superficial radial nerve.

The fact that the forelimb path ascends in the medial part of the ventral funiculus presumably explains why Grant & Oscarsson (1966) failed to find any forelimb responses in the VF-SOCP when they recorded from the pathway at the level of the restiform body. In their experiments the right ventral funiculus was dissected free for a distance of 2 cm in the cervical cord. This dissection almost certainly interrupted the ventral spinal artery and damaged the blood supply to the medial part of the intact, ventral funiculus on the left side. This presumably resulted in a conduction block

of the forelimb component in the VF-SOCP. In the present investigation the cord lesions were made with special care in order to keep the blood supply intact in the left ventral funiculus. Under these conditions, stimulation of forelimb nerves evoked a mass discharge in the VF-SOCP, which could be recorded from the dissected restiform body. This is demonstrated in Fig. 11. The responses from the right hind limb and forelimb nerves had a latency of 16·5–18 msec, which is 3–5 msec shorter than the average latency of the corresponding potentials recorded from the vermal surface. Increasing the number of stimuli from one to four resulted in a small or moderate increase in amplitude and in practically no change in latency (compare *A–C* with *F–H* and *K–L* with *O–P*). The responses from the left nerves were small in this experiment as in some of the experiments with recording from the cerebellar surface.

DISCUSSION

Activity in the cerebellar cortex evoked through the ventral spino-olivocerebellar path (VF-SOCP) was recorded in decerebrate cats with the upper cervical cord transected except for the left ventral funiculus. This permits the pathway to be studied in isolation from other spino-olivocerebellar paths, which ascend through the dorsal funiculus (DF-SOCP) and the dorsal part of the lateral funiculus (DLF-SOCP), respectively (Oscarsson, 1967*a*; Larson *et al.* 1968). The discussion will be centred around the two main findings which concern the organization of the projection areas in the anterior cerebellar lobe and the activation of individual olivocerebellar neurones from nerves and receptors in the limbs.

Projection areas

The VF-SOCP projects to the anterior lobe of that side which is contralateral to the activated inferior olive, in agreement with anatomical data (Brodal, 1940). Two projections can be distinguished, one to the vermis and one to the intermediate part. The projection to the vermis is direct as shown by the relatively short latencies of the cerebellar responses. These latencies are in agreement with those reported previously for the VF-SOCP (Morin *et al.* 1957; Grant & Oscarsson, 1966; Armstrong *et al.* 1968; Armstrong & Harvey, 1968). On the other hand, the projection to the intermediate part is characterized by inconsistent responses with a long latency. This projection is presumably indirect and possibly involves a number of relays in the brain stem, which would explain why it was not demonstrated in anatomical studies using degeneration methods (Brodal *et al.* 1950). The projection to the intermediate part is mainly limited to the rostral region of the anterior lobe (stippled area in Fig. 12, left diagram) and did not display any obvious somatotopic arrangement.

Projection to vermis. Information from the limbs reaches the lateral two thirds of the vermis through the VF-SOCP. The projection area is organized in longitudinal bands as illustrated in Fig. 12 (left diagram). The lateral band receives olivary axons activated exclusively from the ipsilateral hind limb. Olivary neurones activated bilaterally from the hind limbs terminate in an intermediate band, and olivary axons activated

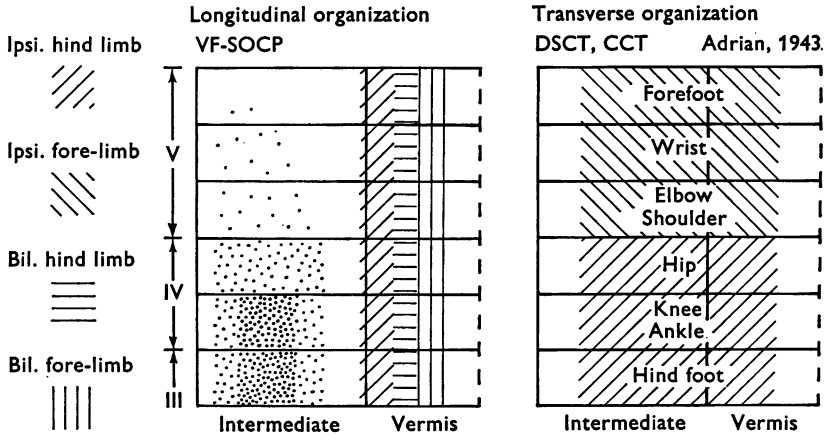


Fig. 12. Longitudinal versus transverse somatotopic organization in anterior lobe. The diagrams represent right halves of lobules V and IV and part of lobule III. Horizontal lines indicate commonly occurring sulci. Continuous, thick vertical lines indicate borders of intermediate part. Interrupted vertical line indicates mid line. Left diagram shows projection areas of VF-SOCP. The projection to the vermis in sagittal bands is indicated by hatching (see key) and the long-latency, presumably indirect, projection to the intermediate part is indicated by stippling. Density of dots shows the usual amplitude distribution of the positive potentials, which are evoked exclusively from ipsilateral nerves. Right diagram shows transverse organization as given by the termination areas of the dorsal spinocerebellar tract (DSCT) and its forelimb equivalent, the cuneocerebellar tract (CCT). The detailed transverse organization described by Adrian (1943) is tentatively indicated. Abbreviations: ipsi., ipsilateral; bil., bilateral.

bilaterally from the forelimbs, in a medial band. This organization contrasts with the classical somatotopic organization in transverse fields (Fig. 12, right diagram) first described by Adrian (1943) and by Snider & Stowell (1944).

The present observations on the vermal projection of the VF-SOCP are in agreement with the observations of Brodal *et al.* (1950). They concluded from degeneration studies that the path terminates in the vermis of the anterior lobe with forelimb and hind limb components represented to an approximately equal degree in caudal and rostral parts of the vermis. The authors stressed that the pathway did not show any obvious somatotopic organization in transverse fields.

The transverse organization described by previous authors depends on several pathways. Anatomical studies have demonstrated that the dorsal spinocerebellar tract (DSCT) and its forelimb equivalent, the cunocerebellar tract (CCT), terminate rostrally and caudally, respectively, in the anterior lobe (Grant, 1962*a*, *b*). The border between the hind limb and forelimb areas corresponds approximately to the fissure between lobules IV and V. It seems likely that the detailed transverse organization described by Adrian (1943) and tentatively indicated on the diagram in Fig. 12 depends on the DSCT and CCT. The transverse organization described by Carrea & Grundfest (1954) is in good agreement with the termination areas of these two tracts. Their observations were based on recording short latency cerebellar potentials evoked by stimulation of muscle and skin nerves. These potentials can now be attributed to the proprioceptive and exteroceptive components of the DSCT and CCT (Oscarsson, 1965). On the other hand, the similar transverse organization in the intermediate part described by Snider & Stowell (1944) and by Combs (1954) was based on recording evoked potentials with a long latency. These potentials can now be interpreted as climbing fibre responses (Eccles, Ito & Szentágothai 1967) and related to the termination in the intermediate part of the two dorsally located spino-olivocerebellar paths, DF-SOCP and DLF-SOCP (Oscarsson, 1967*a*; Larson *et al.* 1968).

The somatotopic organization in longitudinal bands in the vermis was recently confirmed by Provini *et al.* (1967). They studied the distribution of climbing fibre responses in the anterior lobe on activation of cerebrocerebellar and spinocerebellar paths. With both pathways a similar somatotopic organization was established, in the intermediate part conforming to the classical transverse pattern, and in the vermis, to the longitudinal pattern first described by Oscarsson & Uddenberg (1966). The transverse pattern, demonstrated on activation of spinocerebellar paths, can be related to the termination of the DF-SOCP and DLF-SOCP in the intermediate cortex (Oscarsson, 1967*a*; Larson *et al.* 1968). The longitudinal pattern in the vermis can be explained by the vermal termination of the VF-SOCP and DF-SOCP (Oscarsson, 1967*a*). The longitudinal bands in the vermis were less sharply delimited in the experiments of Provini *et al.* (1967) than in the present investigation. There are at least two reasons for this discrepancy. Provini and his collaborators worked on cats with intact spinal cords. The longitudinal organization would be less distinct because of the simultaneous activation of two spino-olivocerebellar paths (VF-SOCP and DF-SOCP) which terminate in partly overlapping bands in the vermis. In the experiments of Provini *et al.* (1967) the climbing fibre responses were mapped with electrodes penetrating the anterior lobe in sagittal direction. This method is not well suited for demonstrating

narrow longitudinal bands. The electrode may pass obliquely through the bands. Furthermore, the small shifts of the bands in medial or lateral direction, which sometimes occur when the electrode passes from one folium to another (see Results), would tend to blur the apparent borders between the longitudinal bands.

Significance of longitudinal bands

The projection of VF-SOCP in longitudinal bands is a feature common to the three spino-olivocerebellar paths (Oscarsson, 1967*a*; Larson *et al.* 1968). With the vermal projections of the VF-SOCP and DF-SOCP the longitudinal organization represents a somatotopic pattern. With the projections of the DF-SOCP and DLF-SOCP to the intermediate part, the longitudinal organization has a different, at present obscure, significance. The termination of the spino-olivocerebellar paths in narrow, longitudinal strips should be considered in relation to the connexions made between mossy fibres and Purkinje cells. The mossy fibres activate granule cells, which in their turn activate Purkinje cells through the parallel fibres which extend along the folia for distances of up to 3 mm. As discussed by Eccles, Ito & Szentágothai (1967) a circumscribed mossy fibre input would activate a row of Purkinje cells extending for this distance along a folium. A row of similarly activated Purkinje cells is divided into segments receiving different inputs by the sagittal organization of the climbing fibre system. The transverse organization of the mossy fibre input and the longitudinal organization of the climbing fibre input permits cross-correlation of information from the two systems.

Unitary responses

The individual olivocerebellar neurones receive excitatory action from large receptive fields which include one or several limbs (Table 4). The excitation was almost always provided from all the nerves tested in the limb (or limbs) which constituted the receptive field. The excitation was evoked by stimulation of the flexor reflex afferents, that is groups II and III muscle afferents and cutaneous afferents (Eccles & Lundberg, 1959*a*, *b*; Holmqvist, Lundberg & Oscarsson, 1960). Excitation was also elicited, on repetitive stimulation, from Ib afferents in the ipsilateral (relative to investigated cortex) hind limb nerves. This indicates that tendon organ afferents contribute excitation. Some findings suggest additional excitation from Ia afferents in the ipsilateral quadriceps nerve, supporting the observations of Armstrong *et al.* (1968). The convergence from the different types of afferents is at present difficult to interpret but it should be mentioned that the same combination of afferents (flexor reflex afferents and Ib afferents in various nerves and Ia afferents in the quadriceps nerve)

give inhibition to the ventral spinocerebellar tract (Eccles, Hubbard & Oscarsson, 1961). It is remarkable that the excitation of VF-SOCP from group I afferents was found only from the ipsilateral hind limb.

The responses evoked by limb nerve stimulation appeared constantly and with little variation in latency. In contrast, the responses evoked by natural stimulation of receptors were either weak or absent. When observed, these responses were elicited by strong pressure against deep structures and excessive bending of joints. The receptive area usually included most of an ipsilateral limb. These observations are similar to those made by Thach (1967) on the 'complex spikes' in Purkinje cells which presumably represent climbing fibre responses. The complex spikes were usually evoked only by pinching or squeezing skin and deeper tissues and the receptive fields were large and ipsilateral. These observations suggest that the appropriate conditions for evoking activity in the olivocerebellar neurones on natural stimulation have yet to be defined (see next section). In the present investigation the partial transection of the spinal cord might have interrupted descending paths which facilitate the transmission from primary afferents to the spino-olivary tract but this cannot explain the weak effects on natural stimulation in the experiments of Thach (1967), which were performed on cats with intact cord.

Information forwarded by the VF-SOCP

The observations on nerve and receptor stimulation demonstrate an apparent lack of specificity with regard to both modality and space in the information forwarded by the VF-SOCP. In this respect the olivary path is similar to the spinoreticulocerebellar path (SRCP) (Grant *et al.* 1966; Oscarsson & Rosén, 1966; Crichlow & Kennedy, 1967). The reticulocerebellar neurones receive excitatory and inhibitory actions from the flexor reflex afferents of receptive fields which include several limbs, or even the whole body. The effects on natural stimulation are weak and they are most effectively evoked by strong pressure and pinching. The transmission from primary afferents to the spinoreticular neurones is polysynaptic and very effectively controlled by the pyramidal tract and several reticulospinal paths. It was recently suggested that the SRCP monitors activity in interneurones located in segmental reflex arcs (Oscarsson, 1967*b*). These interneurones would be controlled by impulses in descending paths as well as segmental afferents and utilized as a common path for descending motor control and segmental reflexes. It was hypothesized that the SRPC would give information about the effectiveness of higher centres in setting the interneuronal activity at a given level when this activity is modulated by the segmental input.

A similar hypothesis might be advanced for the information forwarded

by the VF-SOCP. Grant & Oscarsson (1966) found that stimulation of descending paths in the dorsolateral funiculus of the cord evoked a discharge in the VF-SOCP. In this respect the olivary path is similar to the SRCP and several ascending spinal tracts activated from the flexor reflex afferents (Magni & Oscarsson, 1961; Lundberg & Oscarsson 1962; Lundberg, Norrsell & Voorhoeve, 1963). This suggests that the organization at the segmental level is similar. Presumably the spino-olivary tract is activated from primary afferents through interneurones which are also strongly excited by descending paths. The VF-SOCP would give information about interneuronal activity determined by descending paths as well as segmental afferents, that is, information only partly and indirectly related to peripheral events.

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