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The Ventral Spino-Olivocerebellar System in the Cat. I. Identification of Five Paths and their Termination in the Cerebellar Anterior Lobe

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Summary. 1. The spino-olivocerebellar paths ascending through the ventral funiculus (VF-SOCPs) and projecting to the cerebellar anterior lobe were investigated in cats with the spinal cord transected in the third cervical segment sparing only the ventral funiculus on one side. The climbing fibre responses evoked in Purkinje cells by limb nerve stimulation were studied by recording the mass activity at the cerebellar surface or in the molecular layer.

2. Five VF-SOCPs were distinguished on the basis of their receptive fields, response latencies, and projection areas.

3. The projection areas consist of narrow sagittal zones. Three zones (a, b_1 and b_2) lie in the vermis and extend throughout lobules II–V. Two zones (c_1 and c_3) lie in the pars intermedia and are restricted to the classical hindlimb area, lobules II–IV. The VF-SOCPs are labelled according to their termination zones: a-VF-SOCP, b_1-VF-SOCP, etc.

4. The a-, c_1- and c_3-paths are activated from the ipsilateral hindlimb, whereas the b_1- and b_2-paths are activated bilaterally from the forelimbs and hindlimbs, respectively. The latencies of the responses evoked from the ipsilateral hindlimb are relatively short for the c_1-path and successively longer for the c_3-, b_2- and a-paths.

5. The olivary transmission showed fluctuations in efficacy independent for the different VF-SOCPs. The effect of anaesthetics on this transmission also differed between the paths.

6. It is concluded that the five VF-SOCPs relay in different compartments of the inferior olive which are tentatively identified.

Key words: Ventral spino-olivocerebellar paths – Climbing fibres – Inferior olive – Cerebellum – Sagittal organization

Introduction

The projection areas of the many spino-olivocerebellar paths (SOCPs) form narrow sagittal zones in the cerebellar anterior lobe as demonstrated by the distribution of evoked cortical potentials (Oscarsson 1969b, 1973, 1976). These

zones are indicated in the diagrams of Figure 6A–C and identified by letters and indices using a nomenclature modified after Voogd (1969) who described similar zones on the basis of observations on the fibre compartments in the cerebellar white matter and the corticonuclear connections. Each zone is innervated by climbing fibres originating from a separate compartment of the inferior olive represented by a small circumscribed region of that nucleus (Armstrong, Harvey and Schild, 1974; Groenewegen and Voogd, 1976a; Brodal and Walberg, 1977). Each olivary compartment receives a unique input from two or three spinal paths and from the motor cortex (Miller, Nezlina and Oscarsson, 1969; Oscarsson, 1976). The SOCPs are divided into groups ascending through the different spinal funiculi (DF-SOCPs through the dorsal funiculus, VF-SOCPs through the ventral funiculus, etc.). The SOCPs in each group are defined by their projection zones in the cerebellar cortex using the letters and indices shown in Figure 6A (Oscarsson, 1976).

It has been suggested that each sagittal zone represents a functional unit controlling a special motor mechanism (Oscarsson, 1969b, 1973, 1976). The climbing fibre path originating from a certain olivary compartment usually reaches only one sagittal zone and presumably carries information closely related to the particular motor function of that zone. The observations made by Voogd (1969) suggest that each zone has its own efferent path through which it may exert its motor control.

Knowledge of the functional orgaization and termination of the SOCPs is a pre-requisite for understanding the function of the sagittal zones in the cerebellar cortex and we have now made a systematic study of the SOCPs ascending through the ventral funiculus of the spinal cord (VF-SOCPs). These paths are unique among the SOCPs in that the spinal afferents make monosynaptic contacts with the olivary neurones (Brodal, Walberg and Blackstad, 1950; Oscarsson, 1968, 1973). The paths cross the midline twice: at the segmental level and after the olivary relay. It will be demonstrated that the organization and termination of the VF-SOCPs are much more complex than assumed in an earlier, preliminary study (Oscarsson, 1968). Five VF-SOCPs can be distinguished on the basis of their receptive fields, segmental organization and termination zones in the cerebellar cortex. Collectively these paths will be denoted the ventral spino-olivocerebellar system.

The first two papers in this series will be devoted to the identification of the different VF-SOCPs and their termination zones in the anterior (this paper) and posterior lobes (Oscarsson and Sjölund, 1977a). In the following papers the segmental organization and supraspinal control will be described, leading to a hypothesis of the information carried by the paths (Oscarsson and Sjölund, 1977b; Andersson and Sjölund, 1977; Sjölund 1977). Some of the findings were described in a preliminary paper (Oscarsson and Sjölund, 1974).

Methods

The experiments were performed on 31 cats, 2–3 kg of weight. Three types of preparations were used for the present experiments: a) intact animals anaesthetized with sodium pentobarbital

(Nembutal, Abbot), 40 mg/kg i.p., followed by 2–5 mg/kg i.v. at intervals, b) intact animals anaesthetized with alpha-chloralose (BDH), 80 mg/kg i.v. and c) unanaesthetized decerebrate preparations. The last group of animals was given an initial dose of sodium pentobarbital or inhalation anaesthesia with ether and after craniotomy decerebrated by suction at the precollicular level. The preparations were paralyzed with gallamine triethiodide (Flaxedil, Rhodia) and were artificially ventilated. The endexpiratory CO_2-concentration was continuously monitored and kept between 3.5 and 4.5%. The mean blood pressure was maintained above 90 mm Hg, when necessary by the i.v. infusion of a Ringer-dextran solution containing Aramine (MSD). The rectal temperature was recorded and kept between 37.5 and 38.5° C.

The cerebellar anterior lobe was exposed on the left side from the colliculi to beyond the primary fissure by removing the bony tentorium to the midline after ablation of the left occipital lobe. In some experiments both sides of the anterior lobe were exposed. A photograph was taken and the cortex was covered with warm mineral oil to prevent drying. Laminectomies were performed in the rostral cervical and lumbar regions to stimulate and record from the spinal cord. The medulla was covered with a high density, isolating carbonfluor liquid (FC 40, 3M Company) to prevent drying and shunting of currents. Before or during the recordings (cf. Results) the spinal cord was transected in the third cervical segment except for the right ventral funiculus (cf. Oscarsson, 1968). The sciatic (except hamstring) nerves and the ulnar or common radial nerves were dissected bilaterally and mounted for stimulation.

Conventional stimulating and recording techniques were used. The stimuli to the peripheral nerves were square pulses of 100 μs duration. The stimulation frequency was set at the best "tuning" frequency of the inferior olivary cells of the particular preparation, usually about 1/sec for the sodium pentothal and unanaesthetized animals (Oscarsson, 1973) and 3–5/sec for the chloralose-anaesthetized animals. The incoming volleys were monitored by triphasic recording from the dorsal funiculi in the lumbar region (hindlimb nerves) and by monophasic recording from the interrupted dorsal funiculi in the third cervical segment (forelimb nerves). The stimulus strength was expressed in multiples of the strength needed to evoke a barely detectable incoming volley (threshold strength, T). The stimulus was 20 T which would activate all myelinated fibres except the most high treshold ones (Eccles and Lundberg, 1959). In most experiments the spinal cord (the right ventral funiculus and sometimes the dorsal funiculi) could be stimulated with a monopolar silver ball electrode (cathode), the indifferent electrode being in the dorsal musculature. The cerebellar surface potentials were recorded with a silver ball electrode, moved in minute steps observed in a dissection microscope. The recording positions were plotted on a large print of the photograph taken earlier. Field potentials were usually recorded with capillary microelectrodes filled with a potassium citrate solution. The tips of the electrodes were broken or ground to give a diameter of 1.5–2.0 μm and a resistance of 4–8 MΩ. In some experiments electrolytically sharpened glasscovered platinum electrodes with a tip diameter of 1 μm were used for the same purpose. To increase stability, a bilateral pneumothorax was performed.

All electrode tracks, the deepest being 9 mm, were defined during the experiments by values read on a micromanipulator and later reconstructed from histological sections. The depth of the recording positions were related to the surface of the cerebellar cortex and to the borders between the cortical layers as revealed by the changes of the field potentials (Eccles, Ito and Szentágothai, 1967). In each experiment one or two electrodes were left in the brain to facilitate later identification of the tracks. To aid further in identifying spots recorded from, electrolytic lesions were made in some tracks. At the end of the experiments the brains were fixed in situ by intra-arterial infusion of a 10% formalin solution. After about 12 hours, the cerebella were dissected out and fixed for at least 1 week in formalin. The electrodes were then removed and the cerebella embedded in celloidin. Serial sections were made at 50 or 100 μm in a transverse plane parallel to the row of electrode tracks. Staining was performed with toluidine blue. After corrections for tissue shrinkage, calculated from the distance between electrode tracks, large drawings of the cerebellar sections were made and the tracks and recording positions indicated. The cerebellar lobules were identified using the criteria described by Larsell (1953). The exact extent of the spinal lesions was checked by inspection through a dissection microscope after formaline fixation and staining of the medullary surface with methylene blue.

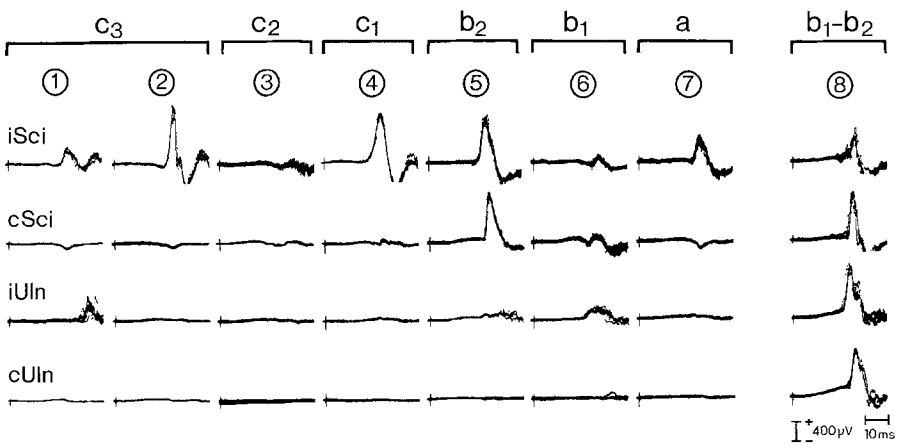

Fig. 1. Potentials recorded from surface of cerebellar anterior lobe on stimulation of ipsilateral (i) and contralateral (c) sciatic (Sci) and ulnar (Uln) nerves. The recording points are marked out by vertical bars on the inset diagram of Figure 2. Points 1–7 (in order from lateral to medial) were in a relatively rostral folium of Larsell's lobule V, and point 8 in a caudal folium. Sagittal zones (a, b_1 etc.) from which the records were obtained are indicated above each column of records. Records are formed by superposition of 4–6 traces. Calibrations for all records in lower right corner. Chloralose anaesthesia

Results

The experiments were performed on cats with the spinal cord transected except for the right ventral funiculus in the third cervical segment. The spinal lesion interrupted the known spinocerebellar paths that terminate as mossy fibres and all the spino-olivocerebellar paths except the VF-SOCPs (Oscarsson, 1973, 1976).

A. Distribution of Climbing Fibre Responses in the Anterior Lobe

The projection areas of the VF-SOCPs were demarcated by studying the distribution of the climbing fibre responses evoked in Purkinje cells on limb nerve stimulation. These responses were recorded either as characteristic, sharply rising positive potentials from the cerebellar surface or as negative fields from the molecular layer (Eccles, Ito and Szentágothai, 1967; Armstrong and Harvey, 1968; Oscarsson, 1968).

In 31 experiments we mapped the distribution of the positive surface potentials in lobules IV and V of the anterior lobe which were evoked by stimulation of the left and right hindlimb (sciatic) and forelimb (ulnar or common radial) nerves. The responses were evoked on the left side, contralateral to the ascending spinal tract (Oscarsson, 1968) as would be expected since the neurones in the inferior olive are innervated by spino-olivary fibres ascending on the ipsilateral side and send their axons to the contralateral

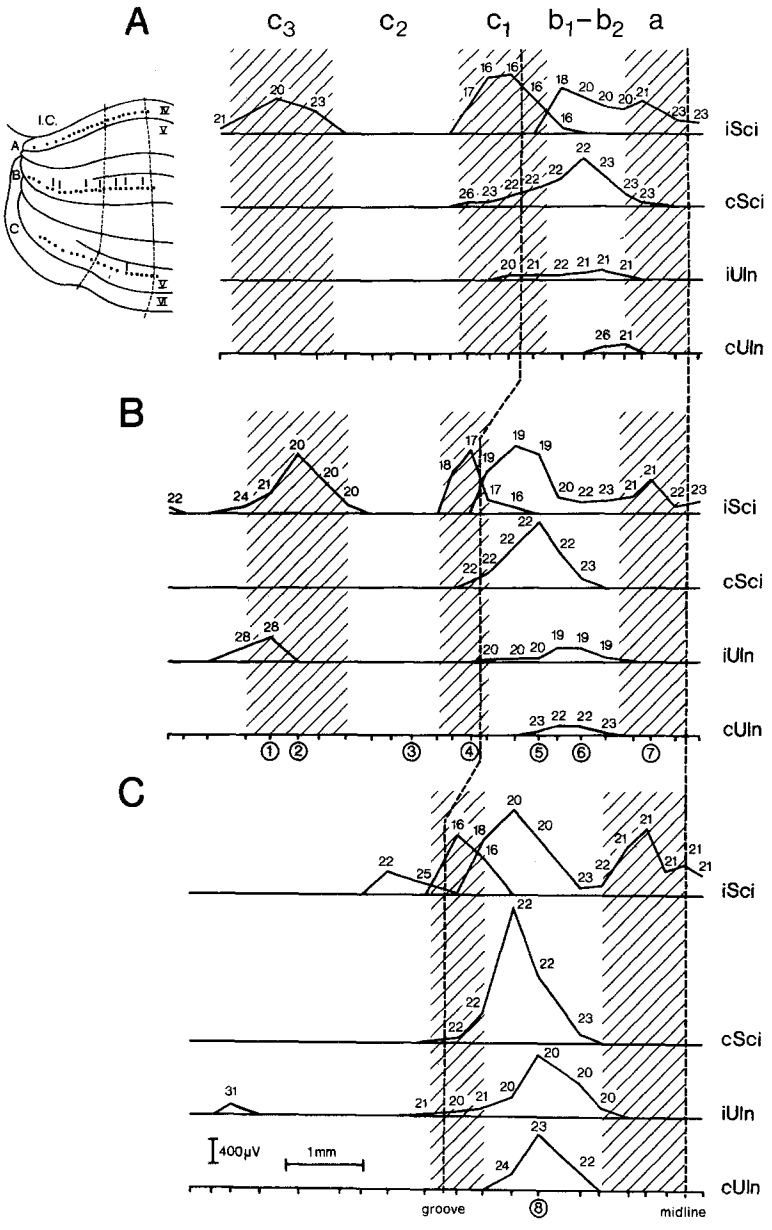

Fig. 2. Distribution of climbing fibre responses recorded as surface-positive potentials along three folia (**A**–**C**) of cerebellar anterior lobe. Recording points indicated on the inset diagram. Amplitudes of potentials (ordinates) plotted against recording positions indicated along the abscissae. Numbers above the curves indicate latencies in ms. Encircled numbers along the abscissae of diagrams B and C label recording sites (indicated by vertical bars in the inset diagram) from which the sample records in Figure 1 were obtained. Midline and paravermal groove indicated by vertical interrupted lines. Approximative extent of VF-SOCP projection areas in zones a, c_1 and c_3 indicated by hatching. Roman figures in inset diagram refer to lobules according to Larsell (1953). I.C., inferior colliculus. Other abbreviations as in Figure 1. Chloralose anaesthesia

side of the cerebellum (Brodal, 1940; Brodal et al., 1950). Typical observations from a preparation under chloralose anaesthesia are illustrated in Figures 1 and 2. Records were obtained from the points indicated along the three folia labelled A, B and C in the inset diagram of Figure 2. Figure 1 shows sample records from the points marked out by vertical bars on the inset diagram (Fig. 2). The records numbered 1–7 in Figure 1 were from folium B and the records labelled 8 from folium C. The responses changed in a characteristic way when the recording electrode was moved in small steps from a lateral point (position 1) on the pars intermedia to a medial point (position 7) on the hemivermis (Fig. 1). Laterally in the pars intermedia (position 1), climbing fibre responses were evoked on stimulation of the ipsilateral (left) hindlimb nerve and inconstantly with a small amplitude and long latency on stimulation of the ipsilateral forelimb nerve. The hindlimb response was maximal in position 2, disappeared almost completely in the middle of the pars intermedia (position 3) and increased again paravermally (position 4), where the response latency was shorter. In the lateral part of the vermis (position 5) the response was evoked from the hindlimbs bilaterally and had a relatively long latency. More medially the hindlimb responses were replaced by a bilateral input from the forelimbs (position 6). The forelimb responses were small in position 6 but much larger in position 8 in a more caudal folium (cf. Fig. 2C). The hindlimb and forelimb responses often occurred in overlapping areas as in position 8. Finally, in the medial part of the vermis (position 7) ipsilateral hindlimb responses with a relatively long latency reappeared.

The three sets of curves (A–C) in Figure 2 represent all the observations made along the three folia in the inset diagram. The amplitudes of the potentials are plotted as a function of the recording positions indicated along the abscissa. The numbers along the curves indicate the latencies of the responses and the lines connect amplitudes with similar latencies. A detailed analysis of this kind was made for several folia in many experiments. It appeared that responses with the same receptive fields (ipsilateral or bilateral, hindlimb or forelimb) and similar latencies occurred in sagittal zones which extended across many folia. Five main zones were identified and denoted by the letters and indices of the modified Voogd nomenclature (see Introduction). The three zones responding mainly to stimulation of the ipsilateral hindlimb nerve, c_3, c_1 and a, are hatched in Figure 2. The remaining two zones, b_2 and b_1, are activated bilaterally from the forelimbs and hindlimbs, respectively, and occupy the lateral part of the vermis. The b_1- and b_2-zones usually overlapped considerably and may then collectively be denoted the b_1–b_2-zone (Figs. 1 and 2).

The distribution of the climbing fibre responses was also determined in five experiments by recording the negative fields generated in the molecular layer of the superficial cortex. Figure 3 shows observations from one experiment confirming the results obtained by recording positive potentials from the cerebellar surface. However, the width of the sagittal zones was in some experiments slightly more narrow when determined by the distribution of the negative fields, as was also reported by Miller and Oscarsson (1970).

In ten experiments the distribution of climbing fibre responses in cortex situated deep in lobules V–II was investigated by recording the negative fields in

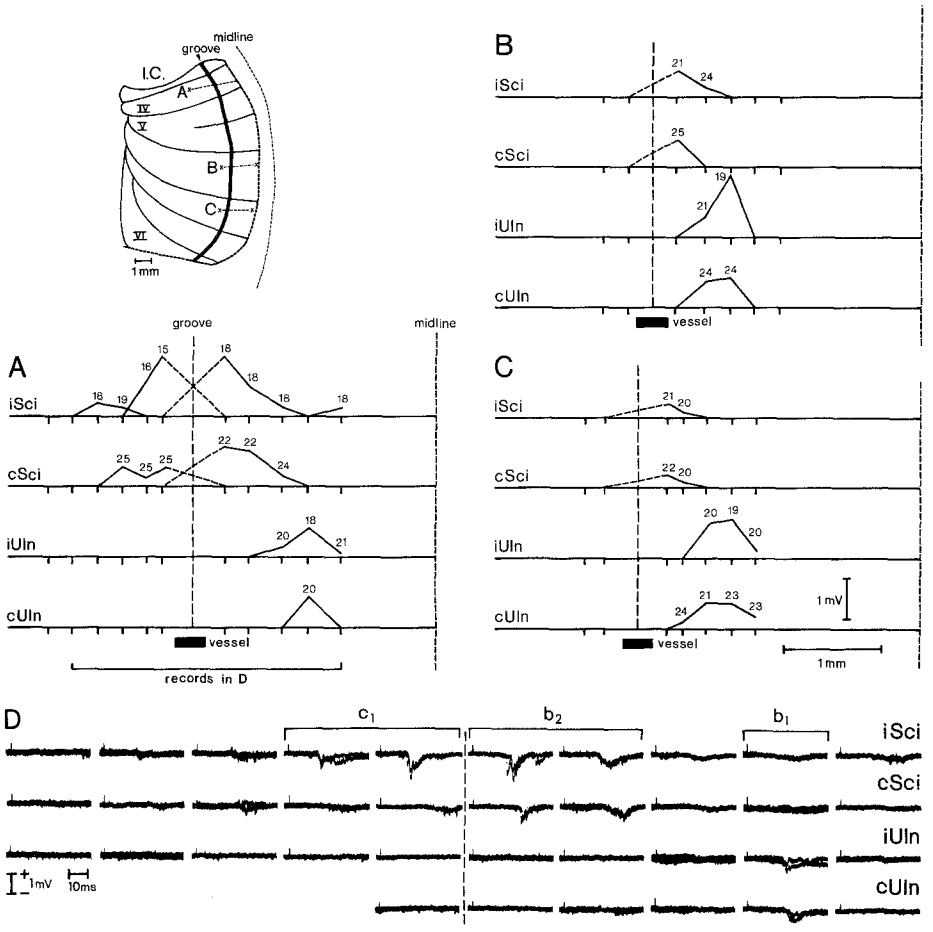

Fig. 3. Distribution of climbing fibre responses evoked by stimulation of limb nerves in vermal and paravermal areas of three folia, **A–C**. The responses were recorded as negative field potentials from the molecular layer of the superficial cortex. Diagrams **A–C** show the amplitudes of the potentials (ordinates) plotted against recording positions marked out along the abscissae. The recording points formed transverse rows which are indicated by interrupted lines (**A–C**) on the inset diagram. The lines in diagrams **A–C** connect potentials with similar latencies. Figures above the curves give the latencies. Uncertain parts of curves (long distance between recording points) indicated by interrupted lines. **D** shows sample records obtained from the recording points indicated at bottom of diagram **A**. Four to six superposed traces. The inset diagram shows the exposed part of the cerebellum. The border between the vermis and pars intermedia (groove) is represented by the black vessel. Midline indicated by interrupted line. Abbreviations as in Figure 1. Pentobarbitone anaesthesia

the molecular layers. Two experiments are shown in Figure 4 demonstrating that the c_1- and c_3-zones and the intervening unresponsive c_2-zone exist also in lobules IV and III. In Figure 4B the c_3- and c_1-zones merge ventrally in lobule III with the disappearance of the interjacent c_2-zone. In the same Figure (4B) the bilateral responses of the b_1- and b_2-zones can be followed throughout

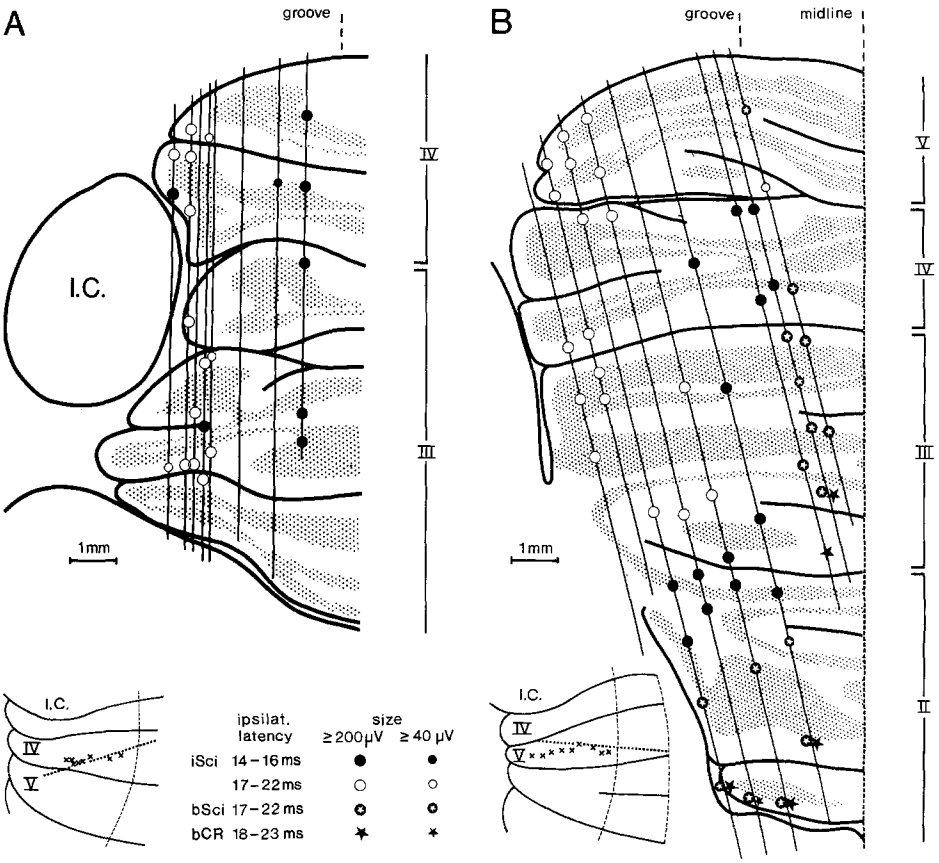

Fig. 4. Distribution of climbing fibre responses evoked by limb nerve stimulation and recorded as negative field potentials from the molecular layers in the deep part of the anterior lobe. Two experiments, **A** and **B**. Vertical lines represent microelectrode tracks. Recording sites with negative fields indicated by the different symbols explained in the key. Fields with an amplitude of 40 μV were the smallest discernible in these experiments. The responses were elicited ipsilaterally from the sciatic nerve (iSci), bilaterally from the sciatic nerves (bSci) or bilaterally from the common radial nerves (bCR). The latencies refer to ipsilateral stimulation. Insets: crosses indicate position of microelectrode tracks, interrupted lines the plane of the histological section. I.C., inferior colliculus. Roman figures indicate lobules numbered according to Larsell (1953). Pentobarbitone anaesthesia

lobules V–II laterally in the vermis. In lobule II the plane of the figure passes through the vermal part only which explains why the b_1- and b_2-responses occurred throughout the lateral part of the transection.

The longitudinal and transverse extent of the five VF-SOCP zones were studied in many similar experiments (Table 1). The findings will be presented separately for each zone.

The a-Zone. Climbing fibre activity in the most medial part of the vermis was generated by stimulation of the ipsilateral hindlimb nerve with a latency of 18–25 ms (see Oscarsson and Sjölund, 1977b). The potentials were mainly seen

Table 1. Number of experiments in which surface and molecular layer recordings were obtained from indicated lobules and zones

		No. of experiments				
		Zone a	Zone b_1	Zone b_2	Zone c_1	Zone c_3
Surface recordings	lob. IV	7	26	31	31	27
	lob. V	12	23	25	20	17
	lob VI	5	4	3	0	0
Molecular layer recordings	lob. II	1	1	1	1	1
	lob. III	3	6	6	6	5
	lob. IV	4	5	7	9	7
	lob. V	2	5	4	2	3

in cats under chloralose anaesthesia and occurred throughout the explored area, i.e. lobules II–V. The width of the zone in the rostral lobules was 500–700 μm, whereas caudally in lobule V it was somewhat wider, up to one mm (cf. Fig. 2). Sometimes (in six experiments out of 12), a small response with a long latency (25–30 ms) from the contralateral hindlimb nerve was found in the medial part of the zone.

The b_1-Zone. Lateral to the a-zone, climbing fibre responses were evoked from nerves in both forelimbs, the ipsilateral input being the more effective. The responses had a latency of 17–25 ms on stimulation of the ipsilateral nerve and 19–27 ms on stimulation of the contralateral nerve and occurred in all types of preparation used. The termination zone had a width of 300–500 μm and was found throughout lobules II–V (Figs. 2–4). In the rostral lobules it lay immediately adjacent to the a-zone, whereas in lobule V the distance between the a- and b_1-zones gradually increased in the caudal direction (Fig. 2; Fig. 7 in Oscarsson and Sjölund, 1977a) leaving an inactive area in between. The maximal potentials were evoked in lobule V (Figs. 2 and 3).

The b_2-Zone. The Purkinje cells of this zone were activated from both hindlimbs, from the ipsilateral sciatic nerve with a latency of 16.5–23 ms and from the contralateral nerve with a latency of 18–25 ms. The responses occurred under all experimental conditions tested and formed a zone that was 500–800 μm wide and located just medial and parallel to the paravermal groove (Figs. 2–4). In Figure 3 this zone was well separated from the b_1-zone but in most experiments there was some overlapping of the two zones. In the b_2-zone the ipsilateral hindlimb response usually had a larger amplitude than the contralateral response, except under chloralose anaesthesia when the reverse was often found (Fig. 2C). The responses evoked in lobule IV and rostrally in lobule V were usually of the same size.

The c_1-Zone. At or slightly medial to the paravermal groove in lobule IV the bilateral hindlimb input of the b_2-zone was replaced by large climbing fibre responses of short latency (14–17 ms) evoked from the ipsilateral sciatic nerve

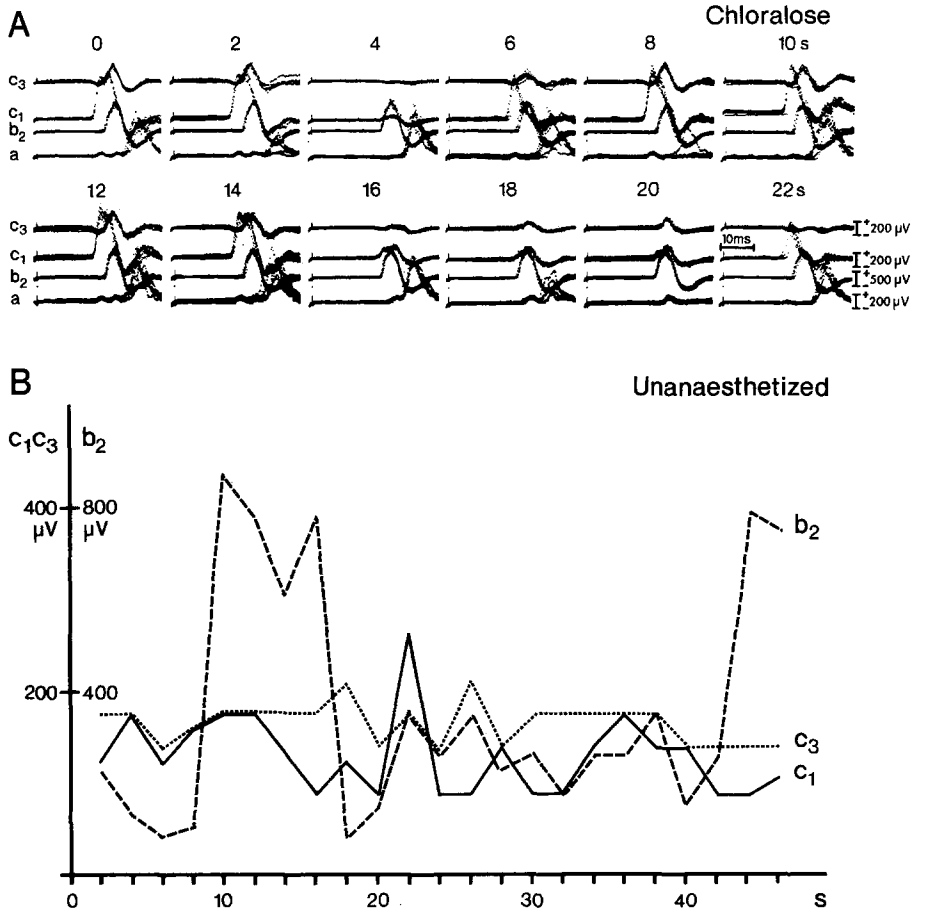

Fig. 5. Fluctuations in amplitude of climbing fibre responses evoked by stimulation of the ipsilateral sciatic nerve and recorded as positive potentials from the cortical surface in the 'hindlimb zones' of the anterior lobe. **A** Responses recorded simultaneously from the c_3-, c_1-, b_2- and a-zones in cat under chloralose anaesthesia. Stimulation rate 5/s. The records consist of 4–6 sweeps and were taken at regular time intervals as indicated by the figures. **B** Responses recorded simultaneously from the c_3, c_1- and b_2-zones in unanaesthetized decerebrate cat (responses in a-zone suppressed). The amplitudes of the potentials are plotted against time. Stimulation rate 1/s

(Figs. 2–4). These responses occupied a zone with a width of up to one mm and located mainly in the medial part of the pars intermedia. This zone, c_1, continued rostrally into lobules III and II with the same width and presumably with the same relation to the paravermal groove, although this could not be ascertained in the present experiments. The short-latency, ipsilateral hindlimb responses were also seen in lobule V: as a rule in lamella Va and sometimes also in lamella Vb and Vc (Fig. 2C). In the caudal part of lobule V the c_1-responses occupied a very narrow zone in the lateralmost part of the vermis and in the paravermal groove (Fig. 2C).

When recording from the surface, potentials from the b_2- and c_1-zones were often picked up from the same spot (Fig. 2C), appearing as short- and long-latency components of a composite climbing fibre response. However, the two zones showed little or no overlap when studied by recording the negative field potentials from the molecular layer (Fig. 3A, D).

Small responses with a long latency (22–27 ms) were often observed in the c_1-zone on stimulation of the contralateral sciatic nerve.

The c_3-Zone. In a zone with a width of 1.1–2.0 mm located lateral to the c_1-zone in the pars intermedia of lobules III and IV no responses, or small and inconstant responses with a long latency were found on limb nerve stimulation (Fig. 1 position 3; Fig. 2). This zone presumably represents the physiological counterpart of Voogd's C_2-zone. Lateral to this zone large climbing fibre responses were evoked from the ipsilateral sciatic nerve with a latency of 16–22 ms. These responses occurred in a zone, c_3, with a width of about one mm. Rostrally this zone turned medially with the decreasing width of the pars intermedia and merged with the c_1-zone in lobule II (Fig. 4B). In lobule V the zone became more narrow by tapering from the lateral side (Fig. 6A) and was as a rule present only in lamella Va. Responses evoked from the contralateral sciatic nerve were hardly ever seen in the c_3-zone.

The responses in the c_1- and c_3-zones were large in unanaesthetized decerebrate cats and in cats under pentobarbitone anaesthesia. Under chloralose these responses fluctuated much in size (Fig. 5A), or were almost absent.

In some experiments with lightly anaesthetized cats, long latency responses evoked from the ipsilateral forelimb nerve were occasionally seen lateral and caudal to the hindlimb responses in the c_3-zone (Figs. 1 and 2), as also noted by Oscarsson (1968).

Responses Recorded from Lobule VI. Lobule VI, which by definition is part of the posterior lobe, was explored by recording from the surface in several experiments (Table 1). The positive surface-potentials of zones a, b_1 and b_2 often extended sagittally from lobule V into the adjacent one or two folia of lobule VI. In these cases the amplitude of the potentials usually decreased rapidly when the electrode was moved away from the primary fissure. Recordings were not made from the molecular layers and it is unknown if these potentials were due to electrical spread from the anterior lobe or indicated an extension of the projection zones into the posterior wall of the primary fissure.

B. Course of Spino-Olivary Tracts

Anatomical and physiological investigations of the spino-olivary tract have demonstrated that it ascends mainly through the ventral funiculus of the spinal cord contralaterally to the termination area in the cerebellum and to the main spinal input (Brodal et al., 1950; Mizuno, 1966; Armstrong et al., 1968; Oscarsson, 1968; Boesten and Voogd, 1975). The present findings indicate that there are five separate spino-olivary tracts (Oscarsson and Sjölund, 1977b) and it was considered of interest to determine if all of them were confined to the contralateral ventral funiculus. Therefore, successive small lesions with jeweller's forceps were made under the dissection microscope in the third cervical segment of four cats and in the fourth and fifth lumbar segments of five

cats. Finally, the spinal lesion spared only the contralateral ventral funiculus. The climbing fibre responses remained unchanged confirming that the spino-olivary tracts projecting to the five cortical zones all ascend in the contralateral ventral funiculus at the cervical and lumbar levels.

C. Differential Properties of Olivary Relays

The five VF-SOCPs are relayed through different compartments in the inferior olive. Differences in the synaptic organization of these compartments is suggested by observations made in the three kinds of preparation used: un-anaesthetized decerebrate, pentobarbitone, and chloralose.

The climbing fibre responses recorded as surface positive potentials or negative molecular fields show characteristic fluctuations in amplitude over periods of up to half a minute, or more, which are due to slow variations in the efficacy of the transmission through the olive (Miller and Oscarsson, 1970; Armstrong, Harvey and Schild, 1973; Oscarsson, 1973). Similar fluctuations have now been observed with the responses in the VF-SOCP zones. In Figure 5A simultaneous recordings from the four hindlimb zones are shown on stimulation of the ipsilateral sciatic nerve under chloralose anaesthesia. There were marked fluctuations in amplitude of the potentials in the a-, c_1- and c_3-zones, whereas the b_2-potentials showed little variation in size. There was some co-variation of the c_1- and c_3-potentials, while the variations of the a-potential were independent. The curves in Figure 5B were obtained from an unanaesthetized decerebrate preparation which, as was usual, lacked responses in the a-zone. The b_2-potentials fluctuated markedly, whereas the c_1- and c_3-potentials varied much less and largely independently. Similar observations were made on the responses evoked by stimulation of the spino-olivary axons at C3 indicating that the effects on the transmission were mainly exerted at the olivary relay (see Oscarsson and Sjölund, 1977b).

The observations on the three kinds of preparations can be summarized as follows. In the decerebrate cats the c_1- and c_3-respones were large and of relatively constant size, whereas the b_1- and b_2-potentials often were relatively small (but see Fig. 5B) and fluctuating. The a-responses were usually suppressed. Under pentobarbitone anaesthesia the c- and b-responses were large and of almost constant size, whereas the a-responses were suppressed. Under chloralose anaesthesia the c_1- and c_3-responses fluctuated intensely and were often completely depressed for long periods of time. On the other hand, the b_1- and b_2-responses were large and of almost constant size. The a-responses fluctuated in size but were usually well developed.

Discussion

The present investigation has demonstrated that the organization of the ventral spino-olivocerebellar system is much more complex than assumed before (Oscarsson, 1968). It has been established that the system consists of five paths

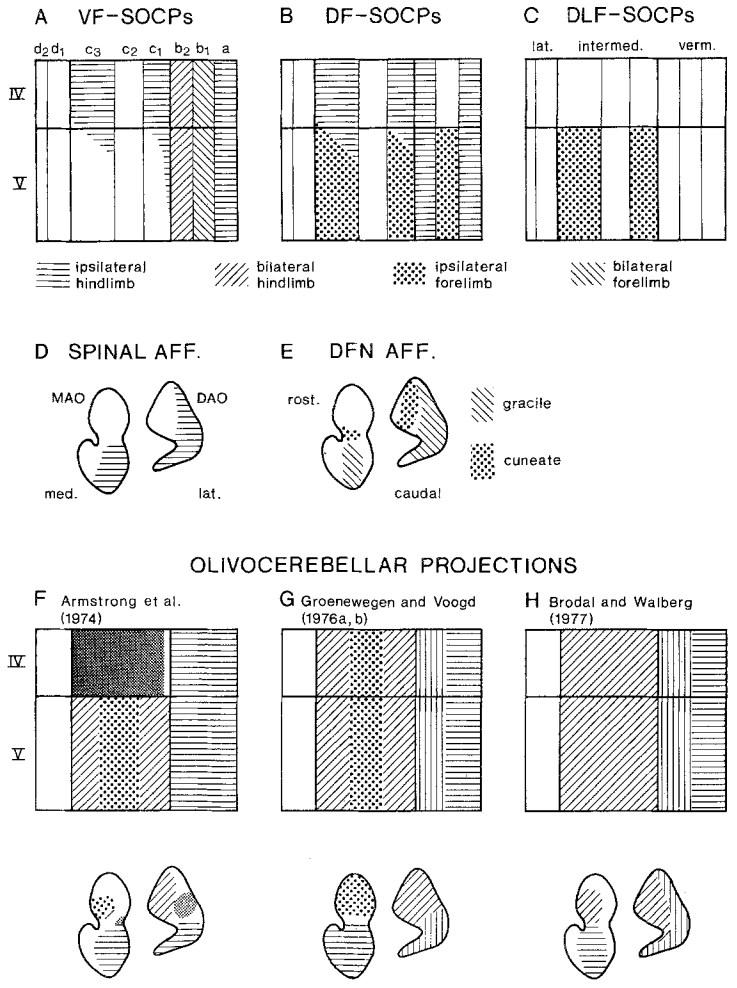

Fig. 6. Olivary projections to left side of lobules IV and V of cerebellar anterior lobe. **A–C** Projection zones of VF-, DF-, and DLF-SOCPs in the vermis and in the c_1- and c_3-zones of the pars intermedia (see text). Labelling of sagittal zones in A according to nomenclature modified after Voogd (1969). Gross division into vermal, intermediate, and lateral parts is shown in C. Somatotopical organization explained in key. (B and C after Oscarsson, 1973.) **D–E** Termination of spinal afferents (D) and afferents from the dorsal funiculus nuclei (DFN), gracile and cuneate (E), in the medial and dorsal accessory olives (MAO and DAO) on the right side. Abbreviations: aff., afferents; med., medial; lat., lateral; rost., rostral (after Boesten and Voogd, 1975). **F–H** Organization of projections from MAO and DAO to the vermis and pars intermedia according to three investigations (see text). Areas labelled in the same way are assumed to be connected

(VF-SOCPs) which terminate in the sagittal zones schematically indicated in Figure 6A (see also Fig. 7 in Oscarsson and Sjölund, 1977a). These paths are readily distinguished by their receptive fields and response latencies. The a-, c_1- and c_3-paths are activated from the ipsilateral hindlimb, whereas the b_1- and b_2-paths are activated bilaterally from the forelimbs and hindlimbs, respectively.

The latencies of the responses evoked from the ipsilateral hindlimb are relatively short for the c_1-path and successively longer for the c_3-, b_2- and a-paths. The present discussion will be devoted to the organization of the projection areas in the anterior lobe and their relation to special compartments in the inferior olive (Fig. 6).

A. Extent of VF-SOCP Projection Areas in Anterior Lobe (cf. Fig. 7 in Oscarsson and Sjölund, 1977a)

The a-VF-SOCP projects to a zone (the a-zone) which adjoins the midline and extends throughout lobules II–V (lobule I was not investigated). The a-zone is adjacent to the more lateral b_1-zone except caudally in lobule V where the two zones are separated by a gap. The transmission through the a-VF-SOCP is suppressed by pentobarbitone anaesthesia which explains why responses from this path were not observed in the previous investigation (Oscarsson, 1968).

The b_1- and b_2-VF-SOCPs project to zones (b_1- and b_2-zones) located in the lateral part of the vermis and running a course parallel to the paravermal groove. The zones extend throughout lobules II–V. The forelimb responses were maximal in lobule V, whereas the hindlimb responses were of equal amplitude in lobules IV and V or larger in lobule IV (Oscarsson, 1968, this paper). The forelimb- and hindlimb-zones overlap partly as demonstrated by the finding that many Purkinje cells are activated from all four limbs where the two zones adjoin (Oscarsson, 1968; Miller and Oscarsson, 1970). Consequently, there is no sharp border between the b_1- and b_2-zones and the division of the lateral vermis into these two parts may seem arbitrary. However, this division is justified since there are marked differences in the segmental organization of the b_1- and b_2-paths (Oscarsson and Sjölund, 1977b).

Oscarsson (1968) described a zone lateral to the b_2-zone which was activated exclusively from the ipsilateral hindlimb. This zone was reported to occupy the lateral part of the vermis, the paravermal groove, and the most medial part of the pars intermedia. This description was based on recording the small and late potentials that were evoked by stimulation of the hamstring and sural nerves (cf. Oscarsson and Sjölund, 1977b). The much larger responses evoked from the ipsilateral sciatic nerve have now permitted a more detailed investigation of this zone (c_1). In lobules II–IV it has a width of about 1 mm and occupies mainly the medial part of the pars intermedia but involves also the paravermal groove and the most lateral part of the vermis. In lobule V the c_1-zone taperes to form a narrow strip mainly located in the groove and lateralmost part of the vermis.

The longer latency of the responses in the c_3-zone was previously interpreted as indicating that the laterally terminating path was indirect, i.e. interrupted by interneurones in the brain stem (Oscarsson, 1968). However, it will be shown in a following paper that the long latency is due to a slow conduction velocity of the spinal tract and is compatible with a monosynaptic olivary relay (Oscarsson and Sjölund, 1977b). The c_3-zone occurs in lobules II–IV and usually also in the most rostral part of lobule V. The c_1- and c_3-zones converge rostrally to merge in lobule II where the interjacent c_2-zone disappears.

Some of the five VF-SOCP zones are not homogeneous. At least three subzones can be distinguished. The a-zone has a medial strip in which late contralateral hindlimb responses can be recorded in addition to the ipsilateral responses. A strip of Purkinje cells which are activated from all four limbs occurs where the b_1- and b_2-zones adjoin, as discussed above. Finally, a strip with ipsilateral forelimb responses having a very long latency was sometimes observed laterally to, or overlapping the caudal and lateral part of the c_3-zone. These subzones may possibly correspond to the somatotopically organized microzones reported by Ekerot and Larson (1973) to occur in the c_1- and c_3-zones formed by the DF-SOCPs (cf. Oscarsson, 1976).

B. Correlation to Projection Areas of Other SOCPs

Each sagittal zone in the anterior lobe is the termination area of two or three SOCPs (Fig. 6A–C; Oscarsson, 1976). Figure 6A–C shows diagrammatically the projection areas of the SOCPs that terminate in the vermis and in the c_1- and c_3-zones of the pars intermedia. The diagrams include only lobules IV and V which have been investigated in greater detail than the more rostral lobules. The relevant paths include, in addition to the VF-SOCPs, short-latency DF-SOCPs ascending through the dorsal funiculus and DLF-SOCPs ascending through the dorsal part of the lateral funiculus (Oscarsson, 1969a; Larson et al., 1969; Ekerot and Larson, 1973). The DF- and VF-paths project to overlapping zones in the vermis which do not receive any other SOCPs (Fig. 6A, B). More complex relations obtain in the pars intermedia which can be divided into a rostral hindlimb part (lobules IV–II) and a caudal forelimb part (lobule V) (Oscarsson, 1973). Hindlimb and forelimb activated components of the DF-paths reach respectively the rostral and caudal parts of the c_1- and c_3-zones as indicated in Figure 6B. In addition, the rostral parts of these zones receive information from the hindlimb through the VF-paths and the caudal parts, information from the forelimb through the DLF-paths, as indicated in Figure 6A and C. It is possible that the VF- and DLF-paths projecting to the c_1- and c_3-zones carry similar information. This possibility is supported by the fact that the VF- and DLF-paths projecting to the pars intermedia are unique among the SOCPs in receiving monosynaptic rather than polysynaptic excitation from primary afferents (Larson et al., 1969; Oscarsson and Sjölund, 1977b). The overlap of the projection zones demonstrated in Figure 6A–C is probably explained by the convergence of two spinal paths to the same olivary neurones (Larson et al., 1969; Miller et al., 1969; Oscarsson and Sjölund, 1977a). The two paths reaching each cortical zone have different functional organization: it is likely that they carry different but complementary information (Oscarsson, 1969b, 1973, 1976; Larson et al., 1969; Oscarsson and Sjölund, 1977b).

C. Correlation to Special Compartments in the Inferior Olive

A tentative identification of the olivary compartments projecting to the various VF-SOCP zones can be made by combining the observations illustrated in Figure 6. The diagrams of the dorsal and medial accessory olives (DAO, MAO) in D and E show the termination areas of afferents from the spinal cord and from the dorsal funiculus nuclei (gracile and cuneate) according to Boesten and

Voogd (1975). These areas should project to the zones shown in diagrams A and B, respectively. Diagrams F–H show the correlation between different parts of the olive and their projection zones in lobules IV and V of the anterior lobe according to three different investigations. Diagram F is based on the distribution of antidromic responses evoked in the olive on stimulation of the cerebellar cortex (Armstrong et al., 1974), diagram G, on the distribution in the cerebellar cortex of radioactivity and terminal degeneration following injections of radioactive leucine or small lesions in the inferior olive (Groenewegen and Voogd, 1976a, b) and diagram H, on the distribution in the olive of horseradish peroxidase following its retrograde transport from injection sites in the cerebellar cortex (Brodal and Walberg, 1977).

There is agreement that the medial part of the vermis, the a-zone, is innervated by fibres from the caudal part of the MAO (F–H). This is consistent with the finding that this part of the olive receives afferents from the spinal cord (D) and from the gracilis nucleus (E). The caudal part of the DAO, which also receives afferents from the cord and gracilis nucleus, sends its fibres to the lateral part of the vermis, the b_2-zone (F–H). Presumably this part of the olive also innervates the b_1-zone. No termination from the cuneate nucleus has been demonstrated in the caudal part of DAO which, however, might be explained by the restricted forelimb projection from the DF-SOCP to the b_1-zone (Oscarsson, 1969a).

The c_1- and c_3-zones are presumably innervated from the rostral part of the DAO as suggested by the findings of Armstrong et al. (1974) and Groenewegen and Voogd (1976a, b) (cf. Brodal and Walberg, 1977) (F–H). The hindlimb parts of the zones (lobule IV and further rostrally) would be innervated from the rostrolateral DAO (F, G) which receives afferents from the spinal cord and gracile nucleus (D, E). The forelimb parts of the c_1- and c_3-zones would be innervated from the rostromedial DAO (F) which receives afferents from the cuneate nucleus but not from the spinal cord (D, E). The c_2-zone is presumably innervated from the rostral MAO which does not receive afferents from the spinal cord or from the dorsal funiculus nuclei (D, E).

The compartments in the olive are functionally differentiated as shown by their innervation from different supraspinal structures (Walberg, 1956, 1960, 1974; Sousa-Pinto and Brodal, 1969) and different spinal paths (Oscarsson, 1973, 1976). Furthermore, the transmission through the compartments shows independent fluctuations in efficacy (Fig. 5) and is differentially influenced by various kinds of anaesthesia and by certain drugs. For example, harmaline induces rhythmic activity particularly in those compartments which receive direct spinal afferents and which are also those regions of the olive which receive the most dense innervation of serotoninergic fibres (Sjölund et al., 1977; Wiklund et al., 1977).

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