J. Physiol. (1975), **245**, *pp.* 409–424
With 6 text-figures
Printed in Great Britain

ORGANIZATION OF CLIMBING FIBRE PROJECTIONS TO THE CEREBELLAR CORTEX FROM TRIGEMINAL CUTANEOUS AFFERENTS AND FROM THE *SI* FACE AREA OF THE CEREBRAL CORTEX IN THE CAT

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(*Received 11 June 1974*)

SUMMARY

1. In cats anaesthetized with pentobarbitone, the projection of climbing fibres (CFs) to the cerebellar cortex from trigeminal cutaneous branches and from the face area of the sensorimotor (*SI*) cortex was mapped, using the technique of laminar field potential analysis.

2. The CF projections from both the trigeminal nerve and the *SI* face area were found to be localized to the same cerebellar folia, viz. chiefly the ipsilateral lobule *HVI*, with a small overlap on to the adjacent folia of lobule *V* and crus *Ia* of *HVIIA*. Frequently a projection from the superficial radial nerve to part or all of this area, was also found.

3. A correspondence in the distribution and amplitudes of CF potentials evoked at most points by stimulation of the trigeminal nerve and the *SI* cortex was found. This implies a convergence of afferents from these two sources at or before the inferior olive.

4. In more than half of the cats, a small area of the cerebellar hemisphere was found, in which contralateral as well as ipsilateral trigeminal stimulation would evoke CF potentials. Usually inputs from the superficial radial nerve and the *SI* cortex also converged upon this area.

5. The organization of CF projections from trigeminal and superficial radial nerve afferents to the cerebellar hemisphere was found to occur in the same 'patchy' pattern of somatotopy that has been described for spinal nerve inputs to the anterior lobe.

6. One constant factor was found in the pattern of organization of CF projections to this area from cutaneous afferent nerves. That is, only the afferents from overlapping areas of skin projected to a given recording point: no instance of CF projections from trigeminal branches innervating discontinuous skin areas was observed.

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INTRODUCTION

Most spinal nerves are represented in the cerebellar cortex by both climbing fibre (CF) and mossy fibre (MF) inputs (Eccles, Provini, Strata & Táboříková, 1968*b*). In recent years, detailed studies have elucidated the pattern of projection of these fibres on to the anterior cerebellar lobe (Eccles, Provini, Strata & Táboříková, 1968*b*; Kitai, Táboříková, Tsukahara & Eccles, 1969; Oscarsson, 1968, 1969). The general pattern of projection is established, although there is controversy over some details (Eccles *et al.* 1968*a*, *b*; Oscarsson, 1973). A similar pattern of CF and MF projection has been found to occur on to the anterior lobe, from various areas of the cerebral cortex (Provini, Redman & Strata, 1968; Miller, Nezlina & Oscarsson, 1969). This dual projection has been shown to occur in a somatotopic manner; that is, the forelimb area of the cortex projects specifically to points in the anterior lobe to which peripheral forelimb nerves project, in both the MF and CF systems. The same pattern of convergence is found for the projection of hindlimb nerves, and the hindlimb area of the *SI* cortex. The most powerful cerebral projection to the anterior lobe appears to come from the specific somatosensory projection areas (*SI*) for forelimb and hind limb (Fennell & Rowe, 1973).

Several authors have drawn attention to the presence of projections of an unspecified nature from the face to the cerebellum (Adrian, 1943; Snider & Stowell, 1944; Darian-Smith & Phillips, 1964), but no detailed study of the pattern of specific trigemino-cerebellar projections has been made. In the present study, the localization and pattern of projection of CFs from trigeminal cutaneous afferents and from the *SI* face area of the cerebral cortex to the cerebellum, has been determined by systematic field potential mapping. To support the findings of this study, further investigations have been carried out to determine the response characteristics of single Purkinje cells in the trigeminal CF projection area; these results are reported in an accompanying paper (Miles & Wiesendanger, 1975). Some of the findings reported here were presented to the January 1974 meeting of the Canadian Physiological Society, and were the subject of a short communication (Miles, Cooke & Wiesendanger, 1974).

METHODS

Preparation of animals. Twenty-seven cats weighing 2·5–3·8 kg were used in this investigation. The animals were anaesthetized with an initial intraperitoneal injection of pentobarbitone sodium (35 mg/kg). A moderate depth of anaesthesia was maintained throughout all experiments by administration of small supplementary doses, which were usually given intraperitoneally. Throughout the recording period all animals were immobilized with gallamine triethiodide, intravenously. Artificial respiration was adjusted to maintain an end-expired CO_2 of 3·5–4·0 %. Blood

pressure was continuously monitored, and maintained above 100 mmHg by slow infusion of Rheomacrodex ® when necessary. Deep body temperature was maintained at 38 ± 1 °C by a thermostatically controlled water blanket. The cat's head was secured in a stereotaxic apparatus, and the occipital pole of the right cerebral hemisphere was removed with careful attention to haemostasis. The right hemicerebellar surface and the area of the coronal and anterior suprasylvian gyri (*SI* 'face' area) of the left cerebral cortex were then widely exposed, and protected by a pool of warmed mineral oil or, occasionally, by agar 4 % in saline.

Stimulation procedures. In two preliminary experiments to determine the intensity of stimulation required to evoke CF potentials, the infraorbital nerve was dissected, cut distally, and mounted in an oil pool for bipolar stimulation with silver hook electrodes. In these instances, the afferent volley was monitored from the trigeminal sensory root, after removal of the ipsilateral cerebral hemisphere. This procedure was not routinely followed, however, since in most experiments the concurrent study of the receptive fields of individual Purkinje cells made it desirable to minimize the damage to the facial skin that was necessarily incurred during dissection of the extra-cranial trigeminal branches. In subsequent experiments, therefore, paired stainless steel needles insulated to 1 mm from the tips, were placed for permucosal electrical stimulation of each of the three major trigeminal cutaneous branches ipsilateral to the exposed cerebellum (viz. supraorbital, infraorbital and mental nerves), and for the contralateral infraorbital nerve. The position of the nerves was determined by palpation of the bony foramina through which the nerves emerged from the skull, and the accuracy of the subsequent permucosal electrode placement was checked by observing the reflex facial responses to a low intensity electrical stimulus (< 6 V, 0·05 msec). A sleeve electrode was placed for stimulation of the ipsilateral superficial radial nerve. The stimulus intensity for each trigeminal branch was adjusted to a level which was suprathreshold for reflex twitches in the facial musculature, but just subthreshold for eliciting the jaw opening reflex. Since it is known that the onset of the jaw opening reflex coincides with the activation of Aδ fibres in the trigeminal afferent volley (Thexton, 1968; Keller, Vyklický & Syková, 1972), the stimulus intensity used for each nerve presumably excited all or most of the large diameter cutaneous afferents from the face.

To locate the 'face' area of the *SI* cortex, a preliminary mapping was made of the potentials evoked in the area of the coronal sulcus of the cortical surface by trigeminal stimulation. The stimulating electrode, consisting of 2 steel needles with tip separation of 2 mm, was then thrust to a depth of 3 mm into the area of cortex where the highest amplitude, short latency trigeminal-evoked response was recorded. The cortical stimulus was a train of 4 pulses of 0·1 msec duration, at a frequency of 500 c/s. The stimulus current was monitored by measuring the potential difference across a 100 Ω resistor. For most experiments an intensity of 0·5–1·0 mA was used, although occasionally a current of up to 2·0 mA was used.

Recording procedures. The recording electrodes were glass micropipettes, filled with 4 M-NaCl, and having a tip DC resistance of 2–8 MΩ. Tracks were systematically made to a vertical depth of 5 mm throughout lobules *IV*, *V*, *VI*, *HVI* and crus Ia of *HVIIA* of the ipsilateral hemicerebellum (Larsell, 1953). By observing the sequence of changes in the peripherally evoked field potentials as the electrode was advanced through the various folial layers, it was possible to accurately determine the points at which the electrode tip lay in the ML of each folium traversed (Eccles *et al.* 1968*a*). The optimal field potentials evoked in each ML traversed by stimulation of each nerve and *SI* in turn were photographed with a kymograph camera, and the electrode depth relative to the surface was noted.

To ensure accurate identification of the folial layers in which responses were evoked, many electrodes were cut off and their shafts left *in situ*, during the course

of each experiment. The cerebellum was removed at the end of the experiment, and was fixed for several days in 10 % formalin solution. The micro-electrodes were then removed, and transverse sections of 50 μm thickness were cut using a freezing microtome: these sections were stained with the thionin technique. The reference tracks were readily identified under the microscope and, with a knowledge of the topographical relationship of all the penetrations, the histological positions of all or most tracks could be accurately determined.

RESULTS

Electrical stimulation of peripheral nerves evokes complex field potentials in the cerebellar cortex as a consequence of both MF and CF activation. A detailed investigation has shown that the MF and CF components of these complex potentials can be resolved by the technique of laminar field potential analysis (Eccles *et al.* 1968*a*). The important criteria for the identification of CF projection areas from peripheral nerve inputs are the latency and wave form of the negative potential that is evoked in the molecular layer (ML). Furthermore, the amplitude of the negative potential evoked in the ML by stimulation of any nerve can be taken as an index of the effectiveness of that nerve in exciting the CFs which synapse on to the dendritic tree of Purkinje cells nearest the electrode tip (Eccles *et al.* 1968*a*). Examples of typical, trigeminally evoked, negative CF potentials, together with illustrations of the MLs in which they were recorded, can be seen in Figs. 3 and 6. In the present experiments, the barbiturate anaesthesia was deliberately maintained at a depth which substantially depressed the amplitude of the short latency MF potentials which were evoked concurrently with CF potentials (Latham & Paul, 1971; Gordon, Rubia & Strata, 1973).

Threshold of CF activation

In two preliminary experiments, the afferent volleys in the trigeminal sensory root were monitored, while the CF potentials evoked in the ML of the cerebellar cortex (lobule *HVI*) were simultaneously recorded. The afferent trigeminal volley was found to reach its maximum amplitude at a stimulus intensity of about 4 times threshold (T); however, no evidence of an Aδ component in the afferent volley was seen when the stimulus was increased to $5T$. This is in good agreement with other observations on the thresholds of $A\delta$ fibres in trigeminal afferents (Keller *et al.* 1972). The conduction velocity of the trigeminal nerve over this range of stimulus intensities was calculated to be 50 m/sec in one animal, and 55 m/sec in the other. The average amplitude of field response evoked by 20 successive stimuli at 0·5 c/s, was calculated on a Data Retrieval Computer (Nuclear Chicago). In Fig. 1*A*, the mean amplitudes of CF potentials evoked at seven levels of trigeminal stimulus intensity are plotted for recordings

obtained at four different electrode locations within the ML of the trigeminal CF projection zone. The maximum amplitude of the negative potentials evoked at these four sites ranged from 500 to 900 μV. In each instance, CF potentials were evoked at stimulus intensities that were barely above the threshold for the afferent volley in the peripheral nerve. Raising the trigeminal stimulus intensity to $2T$ resulted in CF potentials of maximum amplitude; no further increases in response amplitude occurred with stimulus intensities as high as $5T$. It can be concluded that, in trigeminal cutaneous afferents, stimulation of the lowest threshold, fastest-conducting fibres is effective in evoking CF responses in the cerebellar cortex. This is consistent with the finding in the accompanying study (Miles & Wiesendanger, 1975) that gentle mechanical stimulation applied to the face is effective in eliciting CF responses in single Purkinje cells within the trigeminal projection area.

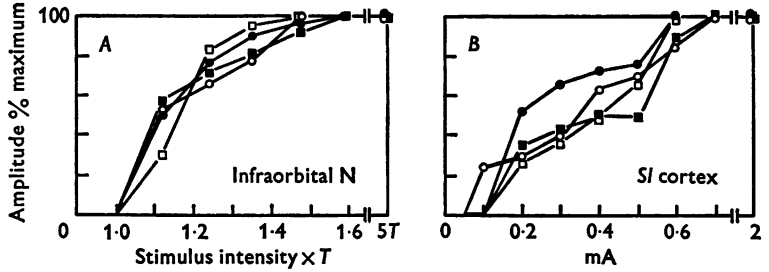

Fig. 1. Relationship of averaged amplitude of CF field potentials in ML, to stimulus intensity. *A*, the amplitudes of CF field potentials recorded at four different points in the ML, which were evoked at eight levels of intensity of stimulation of the infraorbital branch of the trigeminal nerve. Stimulus intensity is expressed in multiples of the threshold (T) of excitation of the afferent volley in the infraorbital nerve. *B*, same vertical scale as *A*; the CF response amplitude is plotted against the *SI* cortical stimulus current (mA), at eight levels of *SI* stimulus intensity, for four ML recording sites. Records from *A* and *B* taken from different animals.

For comparison, in Fig. 1*B*, the amplitude of the CF negative potential is plotted against the intensity of stimulation (mA) of the face area of the *SI* cerebral cortex, again for four electrode sites in the ML of the trigeminal CF projection zone. In this instance, too, the mean CF potential was computed from 20 successive stimuli, at 0·5 c/s. These records were obtained from two other animals having intact cerebral cortices. A cortical stimulus intensity of less than 0·2 mA was effective in eliciting low amplitude CF responses at all four recording sites. With increasing intensity of stimulation, a graded increase in the mean amplitude of the response was found, with the maximum amplitude CF potential being evoked at a stimulus

intensity of less than 1 mA in each case. An increase in cortical stimulus intensity to 2 mA did not produce further increases in the amplitude of the evoked CF response.

Localization of trigeminal and SI cortical inputs

The cerebellar folia in which trigeminally evoked CF potentials were found are illustrated in Fig. 2. This projection area, ipsilateral to the stimulating electrodes, includes most of lobule *HVI*, plus the closely

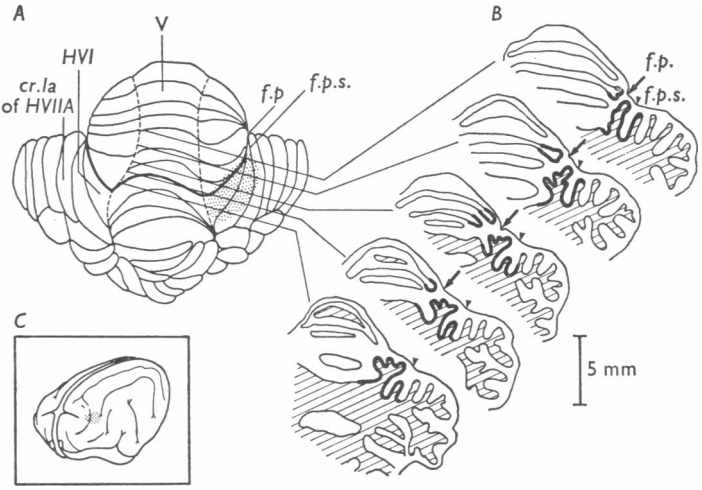

Fig. 2. Line drawings of the cerebellar surface and five transverse sections of the cerebellum, cut in the planes indicated. The general extent of the CF projection from the trigeminal nerve and the *SI* cortex is shown on the cerebellar surface by the stippled area in *A*, and in the Purkinje cell layer of the transverse sections by the thick black line in *B*. The oblique shading in the transverse sections indicates the white matter. Note that the folia of lobule *HVI* lie between *f.p.* and *f.p.s.* in *B*. The inset *C* is a sketch of the cerebral hemispheres with stippling showing the position of the *SI* face area. Abbreviations: *f.p.*, primary fissure, *f.p.s.*, posterior superior fissure; *V*, vermal lobule *V*; *HVI*, hemispheral lobule *VI*; *cr. Ia* of *HVIIA* anterior primary folium of crus *I*.

adjacent areas of both the anterior lobe and crus *Ia* of *HVIIA*. The arrangement of the subsidiary folia of *HVI* was found to be particularly inconstant; hence the large number of electrodes usually left *in situ* was useful in correlating histological sections with surface landmarks. Frequently, positive identification of the folia was only possible *post mortem*, in histological sections.

Electrode penetrations through the stippled area of Fig. 2*A* typically revealed a trigeminal projection to all parts of the ML of the *HVI* folia,

and frequently also to the ML of adjoining folia. The extent of this trigeminal projection is shown in Fig. 2*B*. The vermis and right hemisphere of the cerebellum in Fig. 2*A* was cut into transverse histological sections; five of these, cut in the planes indicated, are shown schematically in Fig. 2*B* by line drawings. The Purkinje cell layer to which trigeminal nerve branches were found to project is indicated by the heavy black line in *B*. The trigeminal projection area can be seen to include parts of the folia of lobule *V* and crus *Ia* of *HVIIA*, in addition to most of lobule *HVI*.

In the investigation of the cerebro-cerebellar projection, the optimal stimulus intensity was determined in each experiment by making several preliminary recordings in lobule *HVI*, and selecting an intensity which was high enough to evoke a CF potential about equal in amplitude to that evoked by trigeminal nerve stimulation. This intensity, usually 0·5–1·0 mA, was then kept constant throughout the experiment. In each experiment, the over-all area of the cerebellum in which CF field potentials were evoked by stimulation of the *SI* face area of the cerebral cortex coincided closely with the area in which trigeminally evoked CF field potentials were found.

The latencies of the peripherally evoked CF potentials ranged from 11 to 25 msec, when measured to the peak of the negative potential evoked in the molecular layer. A fairly consistent pattern of latency distribution was found in most animals. In the rostrolateral part of the trigeminal projection area, latencies of evoked responses were usually 11–16 msec, whereas the latency of responses evoked in the more medial and caudal part of *HVI* was often greater, usually being in the range 15–25 msec. Deviations from this general pattern of latency distributions were frequently found, however. Within a single vertical track traversing several folia, the peak latency of the trigeminally evoked CF field potential was occasionally found to vary by as much as 5 msec from the ML of one folium to the ML of the next. The *SI*-evoked potential, however, was not found to vary by more than 2 msec in such a penetration. In fact, the latency of CF potentials evoked by *SI* stimulation was subject to very little variation within each experiment, and usually lay within the range of 18 to 22 msec, measured from the first pulse of the stimulus train to the peak of the negative CF potential.

In about half of the cats, a small area was found in the caudo-medial part of the trigeminal projection area (lobule *HVI*), in which CF potentials were evoked by contralateral as well as by ipsilateral trigeminal stimulation. At recording sites within this small area, the amplitude of the CF field potential evoked by contralateral trigeminal stimulation was often found to be very similar to the amplitude of the ipsilaterally evoked CF potential. The latency to the peak of the contralaterally evoked field potential

was always 2–6 msec longer than that of the ipsilateral potential. In this area of bilaterally convergent inputs, CF potentials of very similar amplitude could frequently be evoked not only from both infraorbital nerves, but also from the ipsilateral supraorbital, mental and superficial radial nerves, and from the contralateral *SI* cortex. The field potentials evoked in one track that passed through this focus of convergence are illustrated in Fig. 3. A transverse histological section through the caudal area of lobules *VI* and *HVI* is shown schematically in Fig. 3*A*, with the position of the electrode track being indicated by the interrupted line. The three points in the ML at which CF field potentials were recorded are indicated by asterisks. The evoked potentials recorded at four depths along this track are reproduced in Fig. 3*B*. In the most superficial ML (0·460 mm),

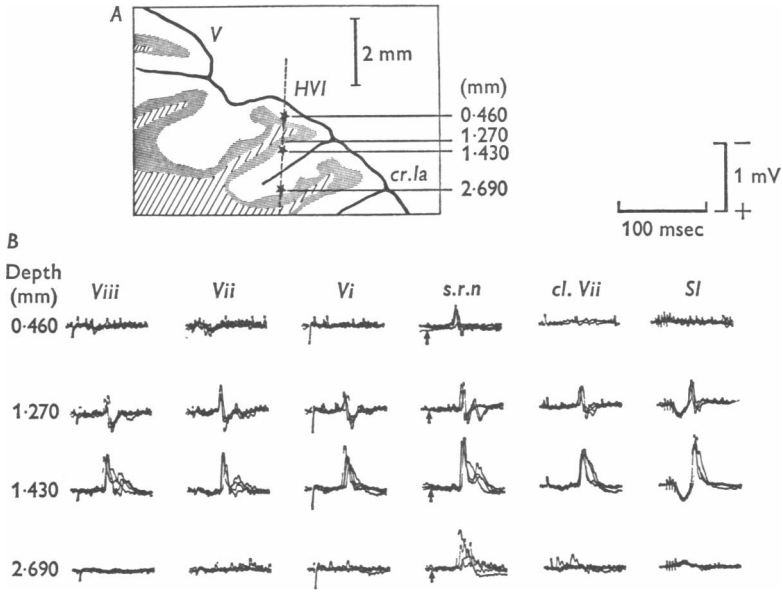

Fig. 3. CF field potentials evoked at four points along a vertical micro-electrode track which traversed the caudo-medial part of lobule *HVI* and crus *Ia*. *A*, line drawing from the histological section, with the GL indicated by stipple and the white matter by oblique shading; the path taken by the micro-electrode is shown by the interrupted vertical line. The positions of the three points in the ML through which the electrode passed are marked with asterisks. *B*, field potentials evoked by electrical stimulation at each of the depths indicated. Note that the potentials at 1·270 mm from the surface were recorded in the GL on the undersurface of *HVI*; the potentials at 0·460 mm, 1·430 mm and 2·690 mm correspond to the ML positions marked with asterisks in *B*. Abbreviations: *Viii*, mental nerve; *Vii*, infraorbital nerve; *Vi*, supraorbital nerve; *s.r.n.*, superficial radial nerve; *cl. Vii*, contralateral infraorbital nerve; *SI*, face area of *SI* cerebral cortex; others as in Fig. 2.

a CF potential was evoked only from the superficial radial nerve. As the electrode was advanced into the granular cell layer (GL) on the underside of *HVI* (1·270 mm), negative–positive potentials were evoked from all inputs. These changed to negative field potentials of about equal amplitude in the ML at 1·430 mm, signifying a convergence from these six inputs on to CFs which synapse on to Purkinje cells in this area. When the electrode was advanced further, to the ML of crus *Ia*, only superficial radial nerve stimulation was effective in eliciting CF negative field potentials.

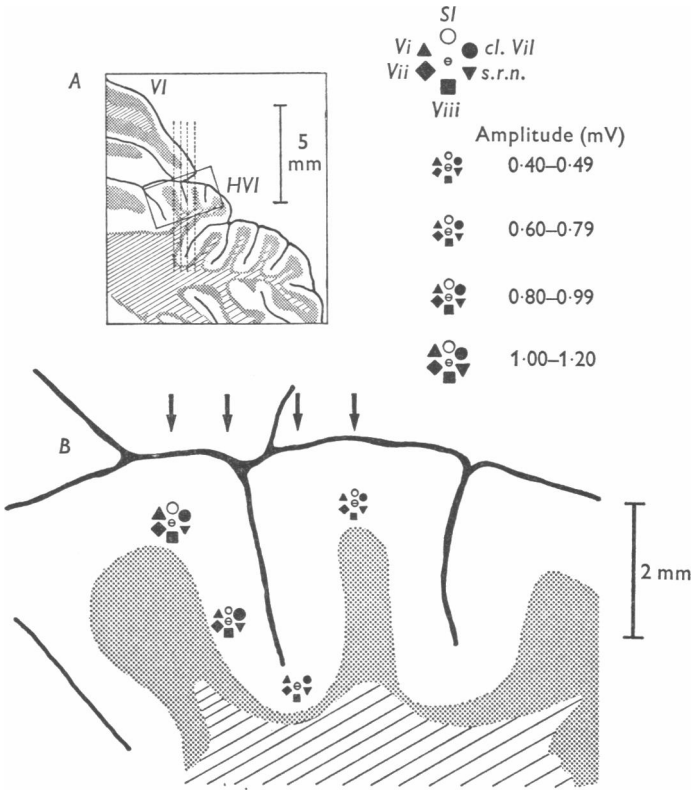

Fig. 4. Excitatory convergence of six inputs on to CFs projecting to a restricted area of cerebellar cortex. *A*, line drawing from a transverse histological section cut through the caudal part of lobules *VI* and *HVI* of the cerebellum, showing path taken by four micro-electrode penetrations. The cellular layers enclosed in the inset square of *A* are shown enlarged in *B*; the arrows indicate the position of the four micro-electrode tracks. Four recording points in the ML of *HVI* are shown as ⊖. At each recording site, the amplitude of the CF field potentials evoked from six input sources is indicated by six key symbols. The inputs and amplitudes of evoked CF field potentials are indexed by the shape and size of the key symbols. Abbreviations as in Fig. 3.

The results of another experiment in which convergence of CF inputs on to this area was found, is illustrated in Fig. 4. In this case, the positions of four tracks through *HVI* are shown schematically in Fig. 4*A*. An enlargement of the folial area in which the convergence occurred is depicted in Fig. 4*B*, with the position of each track being indicated by an arrow. The convention used by other authors (Eccles *et al.* 1968*b*) for illustration of the projection pattern to points in the cerebellum from several inputs has been adopted here. The positions of four recording sites in the ML are indicated by small bisected circles (⊖), around which are a number of symbols. Each symbol represents the CF potential evoked at that point by stimulation of a particular nerve, the size of each symbol

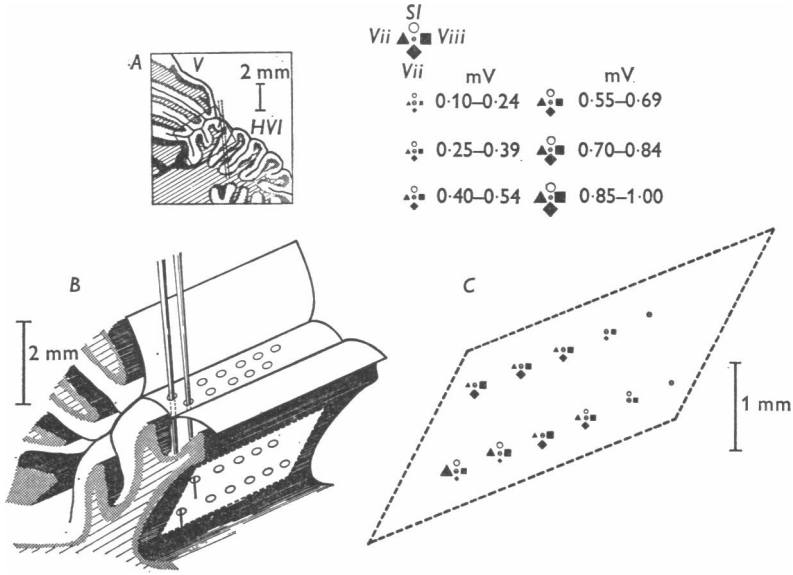

Fig. 5. Patchy organization of CF projections from three trigeminal branches and *SI* to the ML on the lateral surface of a folium of *HVI*. *A*, transverse histological section through the cerebellar vermis and hemisphere. The positions of two micro-electrode tracks traversing *HVI* are shown by interrupted lines. *B*, a rostro-caudal segment of parts of lobules *V* and *HVI* reconstructed from serial histological sections (see inset square in *A*). Eleven parallel micro-electrode penetrations were made through this segment of *HVI*. The two caudalmost electrodes are shown *in situ*; these micro-electrodes entered the surface of *HVI*, traversed its cellular layers, and emerged into the ML on its lateral surface. The entry and emergence points of the other nine tracks are also shown. An enlargement of part of the ML area on the lateral surface of *HVI* is shown in *C*, with the positions of the eleven micro-electrode tracks indicated by ⊖. The amplitudes of the CF potentials evoked from three trigeminal branches and *SI* at each of these points in the ML are represented by symbols. The index of the inputs and amplitudes is given above. Abbreviations as in Fig. 3.

being an index of the amplitude of the potential. An examination of the potentials evoked in this restricted area shows that all six inputs studied project to three of the four recording sites. Furthermore, at each point, the CF potentials evoked by stimulation of each input are of about equal amplitude. Hence, these six inputs must converge on to the CFs which project to the ML of this small area in the medial part of the trigeminal projection zone.

Pattern of trigemino-CF projection

Although the general area of cerebellar cortex to which the trigeminal nerve and the face area of *SI* cortex projected was quite well defined within each experiment, the arrangement of the CF projections from individual trigeminal branches within most of this area occurred in the same 'patchy' pattern that has been described for spinal nerve inputs to the anterior cerebellar lobe (Eccles *et al.* 1968*b*; Kitai *et al.* 1969). The anatomy of the folia in the cerebellar hemisphere presents a unique opportunity to demonstrate this patchy organization. In Fig. 5, for example, the CF projections from three ipsilateral trigeminal branches and the contralateral *SI* cortex to the ML on the lateral surface of lobule *HVI* are symbolically illustrated. Fig. 5*A* is a line drawing from a transverse histological section of the right hemicerebellum. The positions of two micro-electrode tracks are shown by the parallel interrupted lines. A parasagittal segment of part of the hemisphere is schematically represented in Fig. 5*B*. The points at which eleven micro-electrode tracks enter the surface of lobule *HVI* and then penetrate the GL to emerge into the ML of the lateral surface are shown with the two caudalmost electrodes being depicted *in situ*. Recordings were obtained of the CF potentials evoked in the ML on the lateral surface of this folium, in each of the eleven tracks. As in Fig. 4, the position of each recording site in the ML is indicated by a small bisected circle (⊖) in Fig. 5*C*, and the symbols surrounding each recording point represent the CF field potentials of various amplitudes which were evoked from different inputs. No CF potentials were elicited by trigeminal stimulation in the two most rostral recording points, as these lay outside of the trigeminal projection area in this experiment. However, considerable variation can be seen in the intensity of CF projection from each of the four inputs from one point to the next in the ML (and therefore, of course, in the Purkinje cell layer) at the other recording sites. In fact, each point within this small area of the ML is unique in the specific pattern of its CF responses to the inputs that converge upon it from four sources. One unexplained observation in this experiment was the absence of *SI*-evoked potentials in the upper row of electrode tracks illustrated here, since high amplitude potentials were evoked by *SI* in the lower row of recording points. This pattern

of *SI* projection was not consistently found however; in fact, as noted earlier, a CF projection from *SI* was almost always found at points to which one or more trigeminal branches projected.

One constant factor in the organization of the peripheral nerve inputs to each patch was that, in every instance, all projections to a given ML recording site (i.e. patch) came only from trigeminal branches which innervate overlapping areas of skin, e.g. Figs. 5, 6. Consequently, at points where CF potentials were evoked from only two of the three ipsilateral trigeminal branches the only combinations of inputs found were the supraorbital and infraorbital nerves, and the mental and supraorbital nerves.

Superficial radial nerve projection

At many points in and around the trigeminal CF projection zone, stimulation of the superficial radial nerve was also effective in evoking CF potentials. The extent of the superficial radial nerve projection was quite variable between animals. The most consistent projection was to the area of the medial margin of lobule *HVI*. This is part of the zone of broad convergence from the contralateral as well as from the ipsilateral trigeminal branches, and from the *SI* cortical face area, that was described earlier (Figs. 3, 4). Another area where overlap of forelimb and face afferent projections was found was along the folia of lobules *V* and *HVI* that lie adjacent to the primary fissure. In addition to these fairly consistent projection areas, superficial radial nerve-evoked CF potentials were found in other parts of the trigeminal zone, to an extent that varied markedly from one animal to the next. In some animals, CF potentials evoked by stimulation of the superficial radial nerve were found widely over the trigeminal projection area, occasionally extending laterally even beyond the trigeminal area and into crus *I*. In other instances, the forelimb projected only to scattered islets of the ML in several regions within *HVI*; these areas also received CF inputs from one or more trigeminal branches and the *SI* cortex. Field potentials recorded in a track through an area of *HVI* which was responsive to superficial radial nerve stimulation are shown in Fig. 6. At four different points in the ML, stimulation of the mental and infraorbital nerves and of the *SI* cortex were effective in evoking CF negative potentials of varying amplitudes. In the same way, CF potentials of varying amplitudes were evoked from the superficial radial nerve at these points. The latencies of the CF fields evoked by stimulation of the superficial radial nerve ranged from 16 to 32 msec, measured to the peak of the negative potential. Shorter latency potentials were recorded in lobule *VI* and the pars intermedia of *V*, but only in areas which lay outside of the trigeminal projection zone.

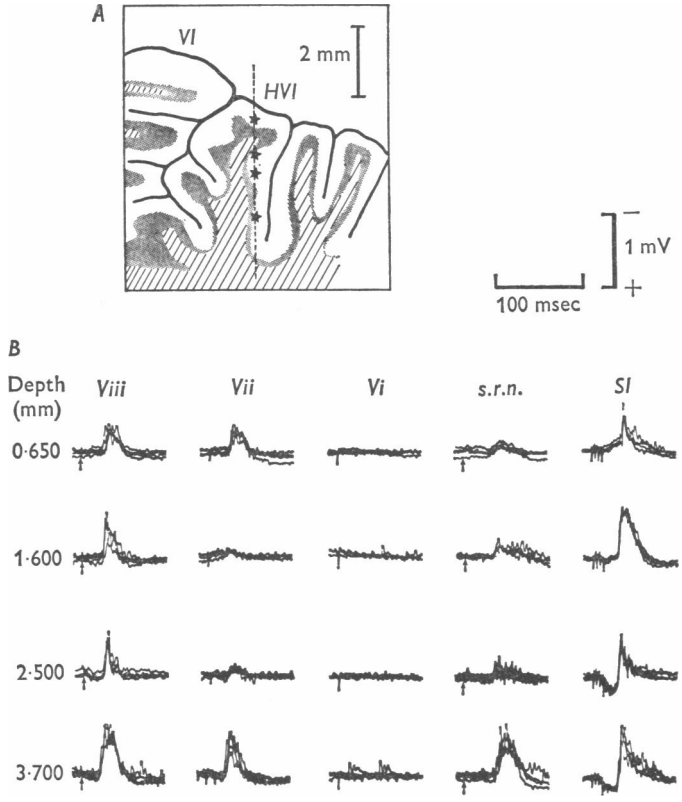

Fig. 6. Convergence of CF projections from trigeminal branches, the superficial radial nerve and the *SI* cortex. *A*, line drawing from transverse histological section through lobules *V* and *HVI*. Interrupted line shows path of micro-electrode track, with four recording sites in ML shown by asterisks. *B*, CF field potentials evoked at the four depths shown by cutaneous afferents from the face and forelimb, and from *SI*. Note the different amplitudes of CF potential evoked particularly by the superficial radial nerve and the infraorbital nerve at different points in the ML. This is an illustration of the 'patchy' projection from trigeminal and forelimb inputs. A correspondence between the amplitudes of CF field potential from the mental nerve and *SI* can also be seen.

DISCUSSION

Localization of trigeminal CF projections

The CF projection area reported in the present study is very similar to that described by Adrian (1943), although, at that time, the electrophysiological distinction between MF and CF inputs to the cerebellum was not drawn. It is interesting that cerebellar responses to natural stimulation of the face were detected in only two-thirds of the cat experiments, and

one-third of the monkey experiments, in that report. A possible explanation for this, at least in the cat experiments, is the variability in the anatomy of the folia in the cat cerebellar hemispheres.

A consistent observation in most experiments was the close topographical coincidence of the CF projections from the peripheral cutaneous afferents innervating the face, and from the *SI* face area of the cerebral cortex. Not only were the boundaries of these two projections found to coincide, but usually a positive relationship between the amplitudes of CF field potentials evoked by trigeminal and *SI* stimulation was found throughout the projection area in the cerebellar cortex. Similar observations have been made for the coincidence in the localization of CF projections to the anterior lobe from limb nerves and corresponding *SI* projection areas (Provini *et al.* 1968), although in that report the correlation of the amplitudes of peripherally and cortically evoked fields appears to be less clear. This may be partially accounted for by the slightly different method of cortical stimulation; the present study employed needles thrust into the cortical white matter, whereas Provini *et al.* stimulated the cortical surface at unspecified intensities, which may have resulted in stimulus current leakage.

In the caudo-medial part of the trigeminal projection area, the CF potentials evoked from all three ipsilateral trigeminal branches, the ipsilateral superficial radial nerve, the *SI* face area of cerebral cortex, as well as from the contralateral infraorbital nerve, were often found to be of equal or nearly equal amplitude. Furthermore, the depth profile of evoked CF potentials from the six inputs followed the same sequence of changes as the electrode was advanced. This implies that the CFs which are excited by inputs from the five nerves and *SI* not only terminate in this area of the cerebellum, but that individual Purkinje cells are probably excited by these six inputs. This was verified in the accompanying study of CF responses in single Purkinje cells (Miles & Wiesendanger, 1975). This convergence must, of course, take place at or before the level of the inferior olive, since, in almost all cases, each Purkinje cell has only one CF synapsing on to it (Eccles, Llinás & Sasaki, 1966).

Pattern of projection

The cytoarchitecture of the cerebellar cortex is unique, in that all Purkinje cells are arranged in a sheet one cell thick. All projections to the Purkinje layer, therefore, terminate in what may be conveniently regarded as a two-dimensional plane. Eccles *et al.* (1968*b*) found that projection from limb nerves to this sheet of Purkinje cells occurred in a patchy or mosaic-like pattern. In this mosaic, each unit is a group of cells which is distinguished from nearby groups of cells by the unique combination of

afferents which project to each group. The CFs which do converge on each group are usually projections from afferents innervating spatially related skin areas, or functionally related muscles. It has been theorized that the functional significance of this patchwork somatotopy is that it permits a complex comparison and integration of diverse sensory and motor information in a manner which has not yet been determined (Marr, 1969; Eccles, 1973). The findings reported here for the projection of *SI* cortex, facial and forelimb afferents to the cortex of the cerebellar hemisphere, support and extend the anterior lobe findings.

In the same way that the CF projection from the forelimb dominates the pars intermedia of lobule *V* (Eccles *et al.* 1968*b*; Provini *et al.* 1968; Oscarsson, 1968; Leicht, Rowe & Schmidt, 1973), the trigeminal CF projection was found to predominate in *HVI*. The separation of the two areas, however, is not complete, and there is overlap of the forelimb projection on to *HVI*, and of the trigeminal projection on to the lateral margin of the pars intermedia. If the hypothesis regarding the functional significance of the patchwork pattern of somatotopy is extended, then much of the pars intermedia of lobule *V* would be concerned only with information related to the forelimb and corresponding *SI* cortex. Similarly, much of *HVI*, receiving CF projections only from face and *SI* cortex, would somehow process information related to the face. The limited area of overlap of these two projections may therefore be important in somehow correlating the sensory and motor information related to the face and the forelimb, since these must work in coordination at the behavioural level in such activities as feeding and grooming.

This investigation was supported by the Medical Research Council of Canada, grant number MA3638. The authors wish to thank Dr J. D. Cooke for his helpful suggestions and criticisms of the manuscript. The technical assistance of Mrs P. Dhanarajan and Mr V. Nicol is gratefully acknowledged.

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