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TOPOGRAPHY AND NOCICEPTIVE RECEPTIVE FIELDS OF CLIMBING FIBRES PROJECTING TO THE CEREBELLAR ANTERIOR LOBE IN THE CAT

BY C.-F. EKEROT*, M. GARWICZ AND J. SCHOUENBORG†
From the Institute of Physiology and Biophysics, University of Lund, Sölvegatan 19, 223 62 Lund, Sweden

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SUMMARY

1. The cutaneous receptive fields of 225 climbing fibres projecting to the forelimb area of the C3 zone in the cerebellar anterior lobe were mapped in the pentobarbitone-anaesthetized cat. Responses in climbing fibres were recorded as complex spikes in Purkinje cells.

2. A detailed topographical organization of the nociceptive climbing fibre input to the C3 zone was found. In the medial C3 zone climbing fibres with receptive fields covering proximal and/or lateral parts of the forelimb projected most medially. Climbing fibres with receptive fields located more medially on the forelimb projected successively more laterally. The sequence of receptive fields found in the lateral C3 zone was roughly the reverse of that in the medial C3 zone. Climbing fibres with receptive fields restricted to the digits projected preferentially to the caudal part of the forelimb area, whereas those with receptive fields covering both proximal and ventral areas of the forearm projected to more rostral parts.

3. The representation of the forelimb was uneven. Receptive fields with a focus on the digits or along the lateral side of the forearm dominated.

4. The proximal borders of the receptive fields were located close to joints. The area from which maximal responses were evoked was usually located eccentrically within the receptive field. Based on spatial characteristics the receptive fields could be divided into eight classes, which in turn were tentatively divided into subclasses. Similar subclasses of receptive fields were found in different cats. This classification was further supported by the results of a quantitative analysis of eighty-nine climbing fibres. The receptive fields of these climbing fibres were mapped with standardized noxious stimulation.

5. Climbing fibres terminating within sagittal strips (width, 100–300 μm; length, > 1 mm) had receptive fields which belonged to the same subclass. There were commonly abrupt changes in receptive fields between such microzones. Most classes of receptive fields were found in both the medial and the lateral parts of the C3 zone. However, receptive fields with a focus on the ventral side of either the metacarpals, the wrist or the forearm were found only in the medial part of the C3 zone.

* Authors' names are in alphabetical order.
† Author for correspondence.

Furthermore, the class of receptive fields restricted to the lateral side of the upper arm and shoulder was only found in the lateral part of the C3 zone.

6. In the discussion, it is proposed that climbing fibres projecting to each microzone carry information from spinal multireceptive reflex arcs acting on a single muscle or a group of synergistic muscles. It is further suggested that each microzone controls the activity of the corresponding motoneurone pool(s) via pathways through the anterior interposed nucleus and the red nucleus.

INTRODUCTION

The climbing fibre projection to the forelimb area of the C3 zone in the cerebellar anterior lobe is topographically organized (Ekerot & Larson, 1979*b*). Inputs originating from different nerves have different projection areas in the C3 zone. The medial and the lateral parts of the C3 zone have separate representations of the forelimb.

Recent studies have shown that climbing fibres projecting to the C3 zone receive a multisensory input from tactile Aβ fibres, unidentified Aδ fibres and nociceptive C fibres from the skin (Ekerot, Gustavsson, Oscarsson & Schouenborg, 1987*b*; Ekerot, Oscarsson & Schouenborg, 1987*c*). The receptive fields on the skin for tactile and nociceptive inputs are co-extensive (Ekerot *et al.* 1987*c*). On noxious stimulation of the skin prominent surface field potentials are evoked, reflecting synchronous activation of large groups of climbing fibres. These field potentials occurred in sagittal strips. It was therefore suggested that climbing fibres with the same receptive field project to restricted cortical areas thus forming sagittally oriented microzones (Ekerot, Garwicz & Schouenborg, 1987*a*).

By a systématic mapping of cutaneous receptive fields the topographical organization of the climbing fibre projection to the forelimb area of the C3 zone was determined. The hypothesis that the C3 zone is composed of microzones was evaluated. A comprehensive analysis of the spatial organization of the receptive fields was made to clarify what information these climbing fibres mediate. Preliminary results have been reported (Ekerot, Garwicz & Schouenborg, 1990*a*, *b*).

METHODS

Preparation

Twenty cats weighing 2·4–4·5 kg were anaesthetized with pentobarbitone, 40 mg kg^{-1} I.P. Supplementary doses of the anaesthetic (3–4 mg kg^{-1} I.V.) were given to maintain an anaesthetic level characterized by constricted pupils and a blood pressure that remained stable during noxious stimulation of the skin. Cannulas were inserted into the trachea, and the right femoral vein and artery. The mean arterial blood pressure was 100–140 mmHg. A continuous infusion (150 μl min^{-1} of 5% glucose in Ringer acetate) was given to compensate for water and mineral losses. The cats were paralysed with gallamine triethiodide or pancuron bromide and artificially ventilated. The end expiratory CO_2 concentration and rectal temperature were continuously monitored and maintained at physiological levels. In order to further check the anaesthesia the effect of the muscle relaxant was periodically allowed to wear off. The anaesthesia was always found to be adequate. At the conclusion of the experiment the cat was killed by an overdose of pentobarbitone and subsequently perfused with 10% formalin in saline through the femoral artery. The cerebellum was removed for verification of the recording sites.

The cats were mounted on a rigid frame by clamping the spine of two thoracic and one lumbar

vertebra and fastening the head by earpins. Local infiltration of Xylocaine was used to avoid stimulation of nociceptors by the clamps and earpins. The left cerebellar anterior lobe was exposed by a craniotomy and removal of the occipital lobe. The cerebrospinal fluid was drained through a hole in the dura mater of the caudal brain stem in order to increase the mechanical stability of the cerebellum. A bilateral pneumothorax was made to reduce respiratory movements.

At the start of the recording session the location of the sagittal zones in the anterior lobe was determined from the receptive fields and latencies of climbing fibre responses evoked on electrical stimulation of the skin (cf. Oscarsson, 1973; Ekerot & Larson, 1979*a*). Field potentials were recorded from the surface of the cerebellum using a ball-tipped electrode (tip diameter about 0·2 mm). Glass-coated tungsten microelectrodes (5–10 μm exposed tips) were used for extracellular recording of climbing fibre responses in single Purkinje cells. The recording sites were marked on a photograph of the exposed cerebellar surface.

Stimulation of the skin

The skin of the left forelimb was carefully shaved to permit localized mechanical stimulation. Intracutaneous electrical stimulation (intensity about 2 mA) with a pair of fine needles was used as a search stimulus for Purkinje cells.

Manual mechanical stimulation of the skin included light tapping with the tip of a pair of forceps, maintained firm innocuous pressure on the skin and noxious pinch. In the latter two cases a small flap of skin (area approximately 2 mm^2) was placed within the grip of a pair of flat forceps. The innocuous pressure employed was not painful, whereas the noxious pinch evoked moderate pain when tested on our skin. A nociceptive input to the climbing fibre was inferred if the responses increased when the stimulus intensity was increased from innocuous to noxious levels. This method has been evaluated in this laboratory (Schouenborg & Dickenson, 1988).

In order to quantify the responses to noxious pinch a clip exerting a force of about 9 N on an area of approximately 2 mm^2 was applied to the skin for 5–10 s. An average of twenty-seven sites on the skin were tested with this standardized pinch for eighty-nine Purkinje cells. Excessive stimulation of the same sites of the skin was avoided. Hence, the stimulation sites were slightly different for two subsequently recorded climbing fibres.

The extent of and the most sensitive area within the receptive fields were determined with both the manual pinch and the standardized pinch stimulation. The borders of the receptive fields were determined with an accuracy of about ± 1 mm on the paw and ± 2 mm on the forearm.

The recordings were stored on tape and analysed off-line by computer (LEO 386, software from RC Electronics, Inc., 'computerscope' program). The climbing fibre responses were quantified by counting the number of complex spikes in the Purkinje cells over the initial 5 s of stimulation.

Classification and data analysis

The receptive fields of the climbing fibres were classified according to their borders and foci of maximal responses. To quantitatively evaluate the classification the receptive fields were compared using three methods.

Method 1

In eight experiments two microelectrodes were used simultaneously. A total of twenty pairs of climbing fibres were studied. The responses of each pair of climbing fibres on stimulation of 9–57 sites on the forelimb were compared by linear regression analysis. The simultaneous recording from climbing fibres has the advantage of minimizing the effects of fluctuations of the excitability in the spino-olivary pathways.

Method 2

To permit a comparison between the receptive fields of climbing fibres which were not simultaneously recorded, the expected response values of a standard grid of points on the forelimb (about 1000 points) were calculated from the original response values using the Kriging algorithm (Golden Software, Inc., 'Grid' program, for additional information on the Kriging algorithm see Ripley, 1981, 1988) (Fig. 1*A* and *B*). Some additional points along the manually determined border of the receptive field (from which the spontaneous activity did not change on noxious pinch) were used to calculate the values of the grid points. An averaging procedure was used to avoid minor

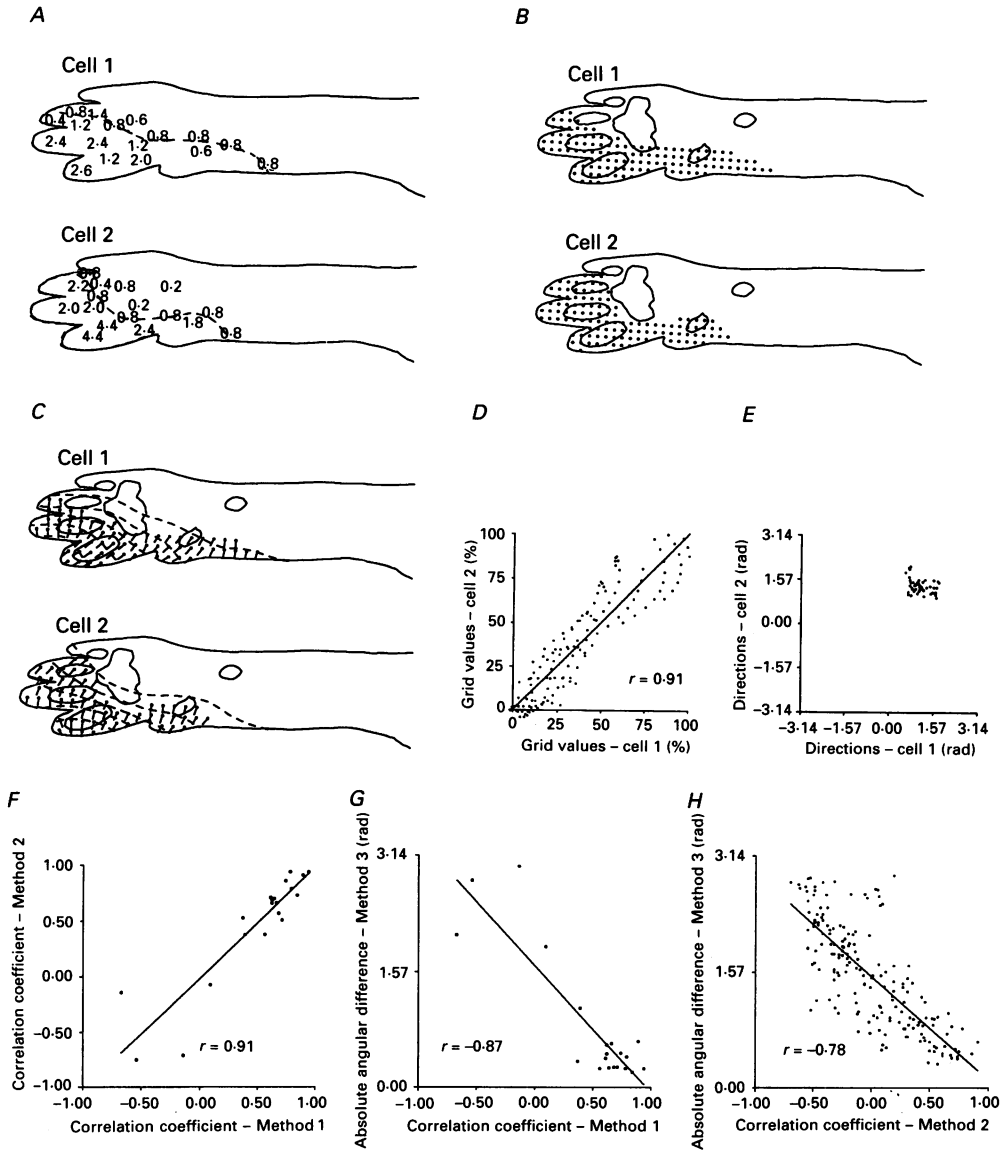


Fig. 1. Quantitative analysis of climbing fibre receptive fields of two Purkinje cells. The palmar side of the receptive fields is shown. *A*, mean frequencies of climbing fibre responses during the first 5 s of a standard noxious pinch are indicated at the corresponding stimulation sites. Dashed lines indicate receptive field borders as judged from responses evoked by manually applied pinch. *B*, dots indicate the locations of points in a standard grid in which the expected response values were calculated from the original values in *A* using the Kriging method and an additional averaging procedure (see text). *C*, dashed lines are 'isoresponse lines' as determined by the response values obtained in *B*. The small dots indicate the starting points of the vectors and the short bars show the calculated directions of the gradient of sensitivity. *D*, diagram shows the correlation between the response values obtained in *B* for the two cells. The spontaneous activity has been subtracted and the response values are expressed as the percentage of the maximal response value for each cell. Regression line is indicated; *r* is the correlation coefficient,

irregularities. Each new grid value represented the average value of the nearest forty-five grid values. The calculated 'response' values of the grid points of the receptive fields of the climbing fibres were then compared using linear regression analysis (Fig. 1*D*).

Method 3

The grid values were further used to calculate 'isoresponse lines' for the receptive fields of each climbing fibre (Fig. 1*C*, dashed lines). In about fifty points (Fig. 1*C*, dots) the direction of the gradient of sensitivity (Fig. 1*C*, short bars) was calculated. These directions were then compared for different climbing fibres (Fig. 1*E*). The average value of the absolute angular difference of the directions in each point (measured in radians) was calculated for each pair of climbing fibres. This comparison was based on the observation that the receptive field of a climbing fibre often shrank along the direction of the gradient of sensitivity during decreased excitability. It was therefore assumed that the direction of the gradient remains relatively stable during altered excitability in the olivary neurones. This comparison was thus made to further test the possibility that neurones with partially overlapping receptive fields in fact had the same receptive field.

In Fig. 1*F–H*, comparisons of the results of the three methods are shown. Both correlation tests (Methods 1 and 2) gave similar values (Fig. 1*F*). Furthermore, neurones with similar receptive fields, as judged from Methods 1 and 2, usually had similar directions of their gradients of sensitivity (Fig. 1*G* and *H*).

RESULTS

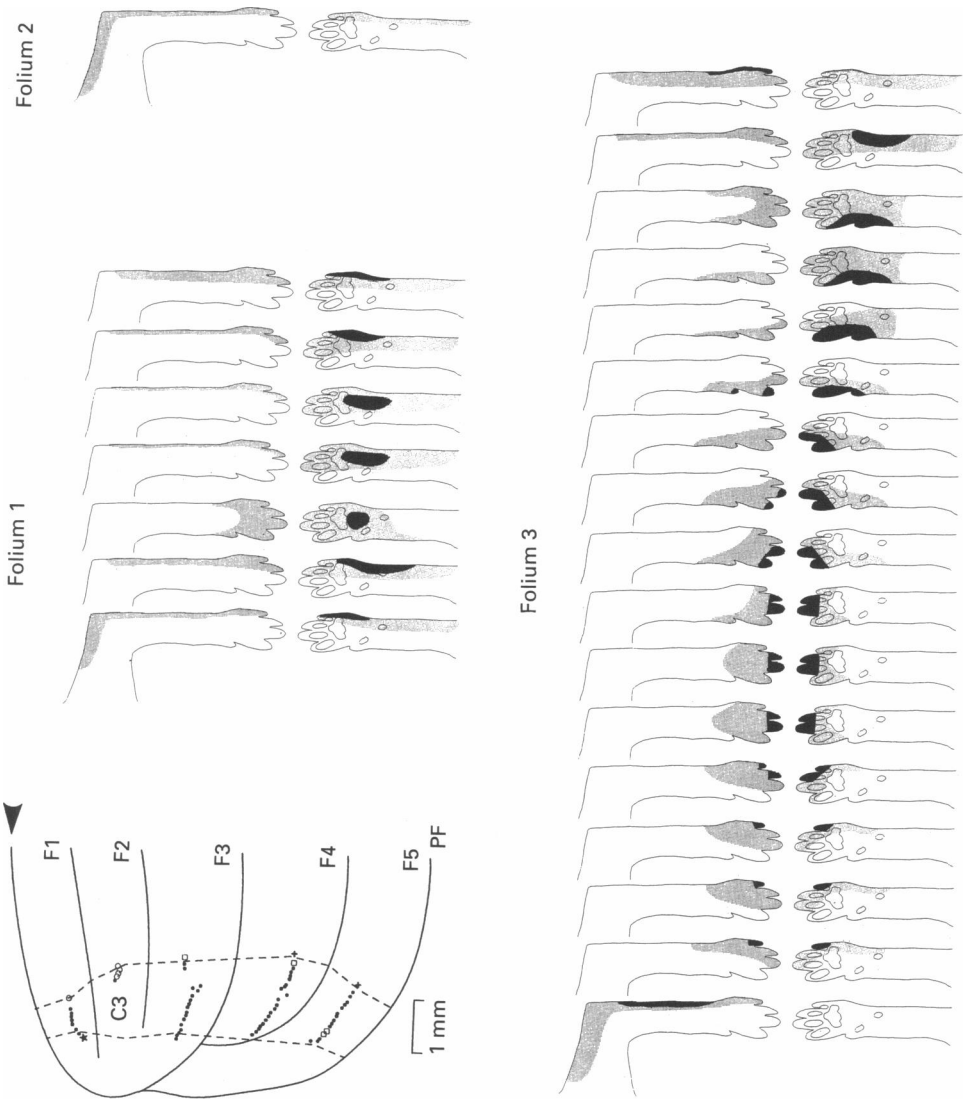
A total of 225 climbing fibres projecting to the forelimb area of the C3 zone, lobules IV and V, were included in this study. These neurones had distinct receptive fields on the ipsilateral forelimb. Twelve additional climbing fibres, exhibited considerable fluctuations of the 'spontaneous' activity and/or very weak responses on cutaneous stimulation, which prevented accurate mapping of the receptive fields. These latter climbing fibres have been excluded from the present material. The border of the receptive field and the area from which the maximal responses were evoked were determined for each climbing fibre using manual noxious pinch. In addition, climbing fibre responses evoked by a standard noxious pinch were quantified in eighty-nine Purkinje cells.

An overview

To obtain an overview, the receptive fields of climbing fibres were mapped in four to five consecutive folia with manually applied pinch in two cats. The distances between the Purkinje cells recorded from in each folium were 100–200 μm.

The results from one of these cats are shown in Fig. 2 (see legend for symbols). There were separate representations of the forelimb in the medial and the lateral parts of the C3 zone (cf. Ekerot & Larson, 1979*b*, 1982). In the medial C3 zone, climbing fibres with receptive fields covering proximal and/or lateral parts of the forelimb terminated medially, whereas units with receptive fields on the medial side of the forelimb terminated laterally. The sequence of receptive fields in the lateral C3 zone can roughly be described as the mirror image of that in the medial C3 zone. Furthermore, climbing fibres with receptive fields restricted to the digits projected preferentially to caudal folia and climbing fibres with receptive fields including both

linear regression analysis. *E*, a plot of the directions of the gradients of sensitivity, expressed in radians (rad), for the common receptive field area of the two cells. Mean difference, 0·44 rad. *F–H*, comparisons between correlation values obtained using simultaneous recordings (Method 1) and grid values obtained from the Kriging algorithm (Method 2) and the average values of the absolute angular difference of the directions of sensitivity (Method 3).


Folium 2
Folium 1
Folium 3
F1
F2
F3
F4
F5
PF
C3
1 mm

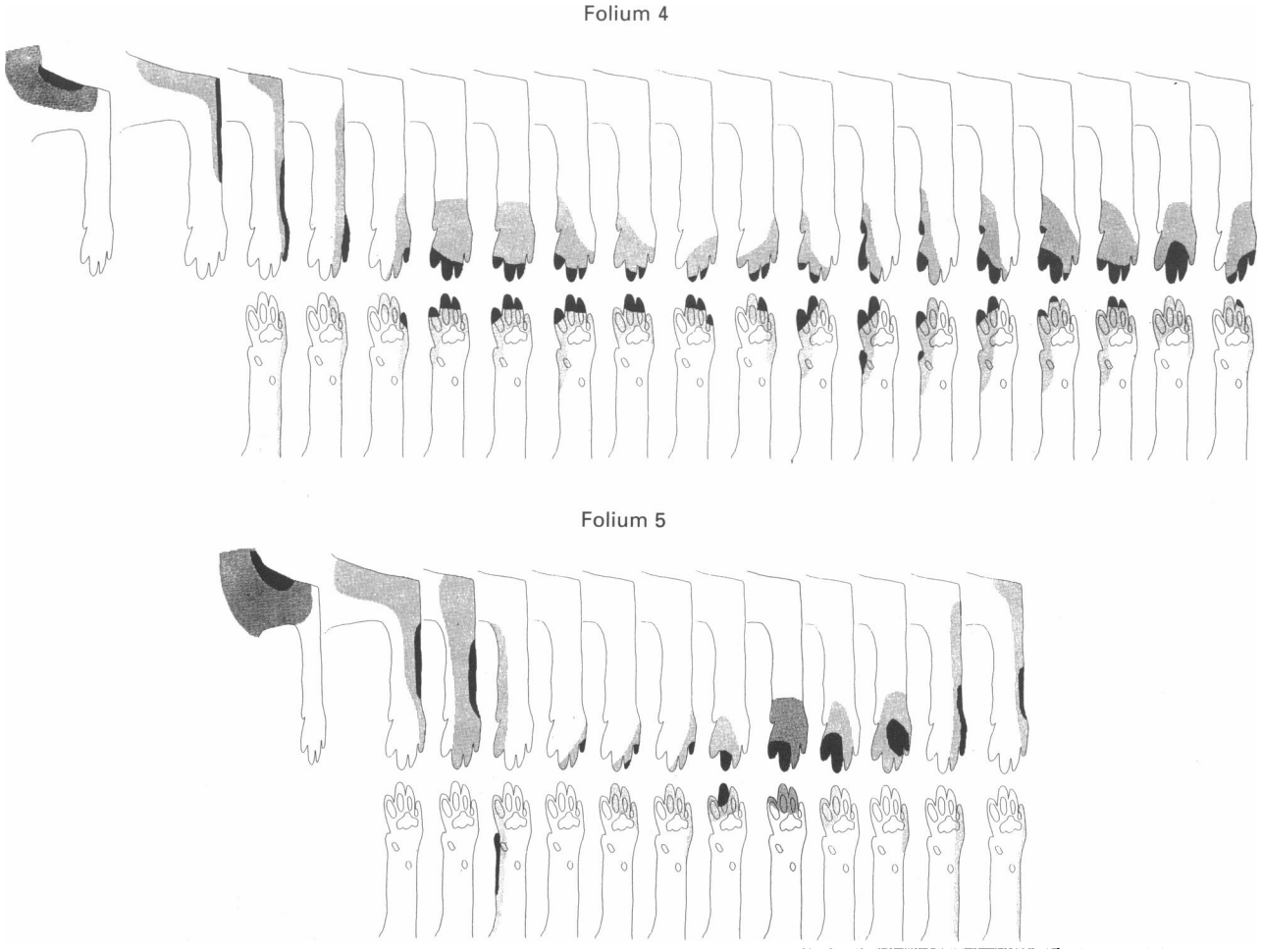


Fig. 2. Overview of the topographical organization of the cutaneous nociceptive climbing fibre input to the forelimb area of the C3 zone. Top left, recordings were made in the five most caudal folia (F1–F5) of the left anterior lobe. Dashed lines indicate approximate borders of the C3 zone. Location of Purkinje cells recorded from are indicated by: dot, receptive field on the forelimb; ★, receptive field on the thorax; ○, receptive field on the hindlimb; □, not activated; +, cell belonging to the C2 zone. PF, primary fissure. Arrow-head indicates border between lobules IV and V. The receptive fields of the climbing fibres were determined using manual noxious pinch. Only receptive fields on the forelimb are shown (shaded areas). Blackened areas indicate the area from which the strongest responses were elicited.

proximal and ventral areas on the forearm were located in the rostral folia (See also Fig. 5*A*).

Similar, although not identical, sequences of receptive fields in the medio-lateral axis were found in all cats. It is conceivable that this variability is a reflection of the rostro-caudal shifts of the position of the forelimb area of the C3 zone with respect to the fissures between different cats (Ekerot & Larson, 1979*a*). Since recordings along the medio-lateral axis were made mainly from Purkinje cells located in the exposed parts of the cortex variability in the sequences of receptive fields would be expected.

In caudal folia the sequence of receptive fields was often more complex than in middle and rostral folia. For example in Fig. 2, Folium 4, there is an additional sequence of receptive fields going from the medial to the lateral side of the paw which is inserted into the middle of the C3 zone.

Microzones

In previous studies it was suggested that climbing fibres with the same receptive field terminate within narrow sagittally oriented microzones (Ekerot *et al.* 1987*a*, *c*). In order to evaluate this hypothesis the receptive fields of climbing fibres projecting to restricted areas in the C3 zone (medio-lateral interval between recording tracks, 10–100 μm) were analysed quantitatively in nine experiments. Figure 3 shows the results from one of these experiments. It can be seen that the receptive fields of climbing fibres terminating within sagittal strips (width, 100–300 μm; length, > 1 mm), i.e. units within groups A–H, I–L, M–N and O–P, have practically the same extent and spatial distribution of sensitivity. There are abrupt changes in receptive fields between adjacent areas of uniform receptive fields. The correlation values between the responses of simultaneously recorded climbing fibres are indicated in Fig. 3*B*. The correlation values from comparisons of original response values (Method 1) were similar to those found using grid values (Method 2).

Longitudinal extent of the microzones

Similar, or apparently identical, receptive fields were sometimes found in 2–4 adjacent folia (Fig. 2). Hence, it is conceivable that the microzones can comprise up to four folia, approximately in a sagittal plane. It should be kept in mind, though, that recordings were usually not made from Purkinje cells deep in the fissures. Thus, whether or not the microzones are continuous in the fissures cannot be determined from the present study. However, previous studies, using nerve stimulation, suggest a similar organization throughout the fissures (Ekerot & Larson, 1979*a*).

Classification of the nociceptive receptive fields

Since similar receptive fields were present in different cats and there seemed to be a small number of different receptive fields it was possible to classify them. The proximal border of the receptive fields was typically close to joints and thus the fields showed stepwise changes in extent (e.g. Figs 2 and 3). On this basis eight classes of receptive fields were delineated (Fig. 4). Climbing fibres belonging to different classes had different locations in the C3 zone (Fig. 5*B*).

Class 1

Proximal border close to the phalangeal–metacarpal joints. Units of this class ($n = 27$) were preferentially located in the caudalmost folia of the forelimb area. The receptive fields of these units typically covered both the palmar and dorsal side of the digits.

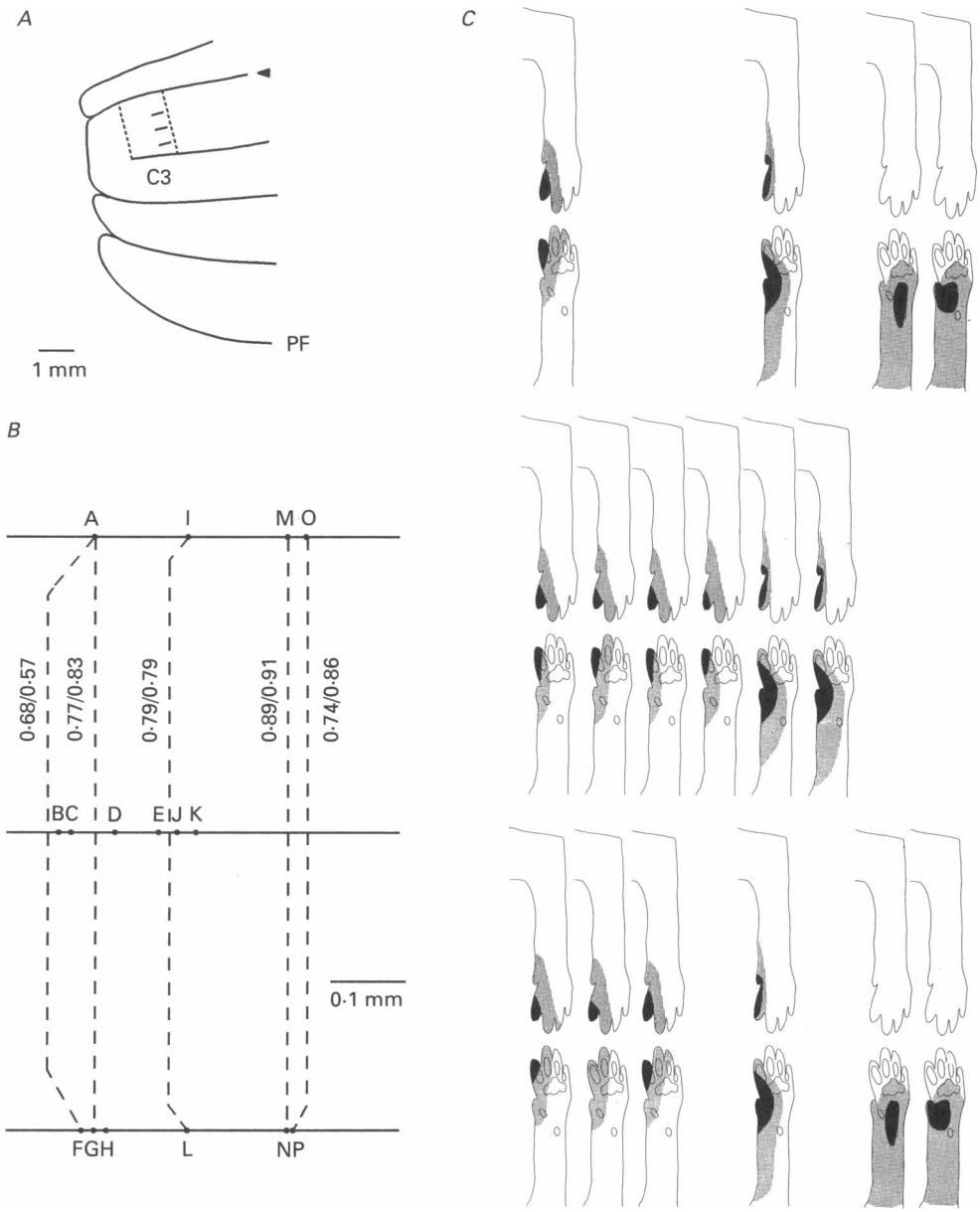


Fig. 3. Microzonal organization of the cutaneous nociceptive climbing fibre input to the C3 zone. Recordings were made in a rostral folium of the forelimb area. *A*, location of recording sites (bars) relative to the borders of the C3 zone (dashed lines). PF, primary fissure. Arrow-head indicates border between lobules IV and V. The cortical area is shown enlarged in *B*. *B*, tracking was made at three rostrocaudal levels and receptive fields were quantified using a standard noxious pinch. Dashed lines connect cells recorded simultaneously. The two figures adjacent to the lines represent correlation values obtained by quantitative comparison according to Methods 1 and 2 (see Methods) respectively. *C*, receptive fields of the cells in *B* are indicated by the shaded areas. Blackened areas indicate the area from which the responses were higher than 70% of the maximal responses.

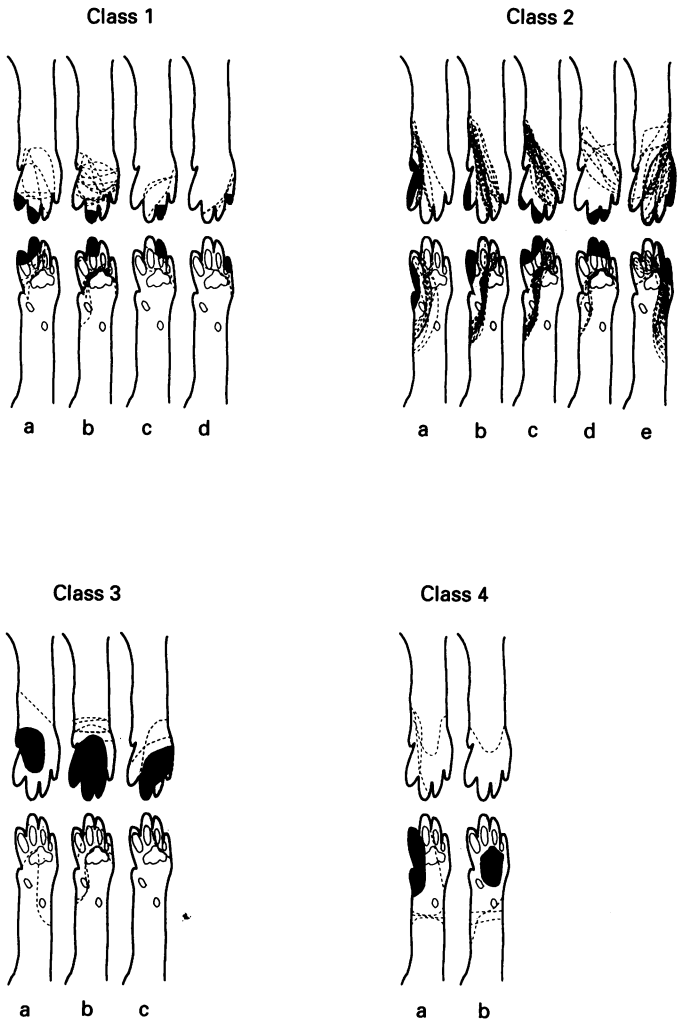


Fig. 4. For legend see facing page.

Classes 2, 3 and 4

Proximal border close to the wrist. There were three distinct classes with respect to the location of maximal sensitivity. Class 2 ($n = 92$) had a distally located focus mainly on the distal phalanges. Usually the palmar and dorsal sides of the digits were about equally sensitive. These units were found preferentially in the middle folia. Class 3 ($n = 8$) had maximal sensitivity on the dorsal skin mainly overlying the metacarpals. Responses from the palmar side of the paw were very weak. These units were found preferentially in the caudal folia. Class 4 ($n = 6$) had a maximal sensitivity on the palmar skin mainly overlying the metacarpals. The responses from the dorsal side of the paw were very weak. These units were found in the rostral folia.

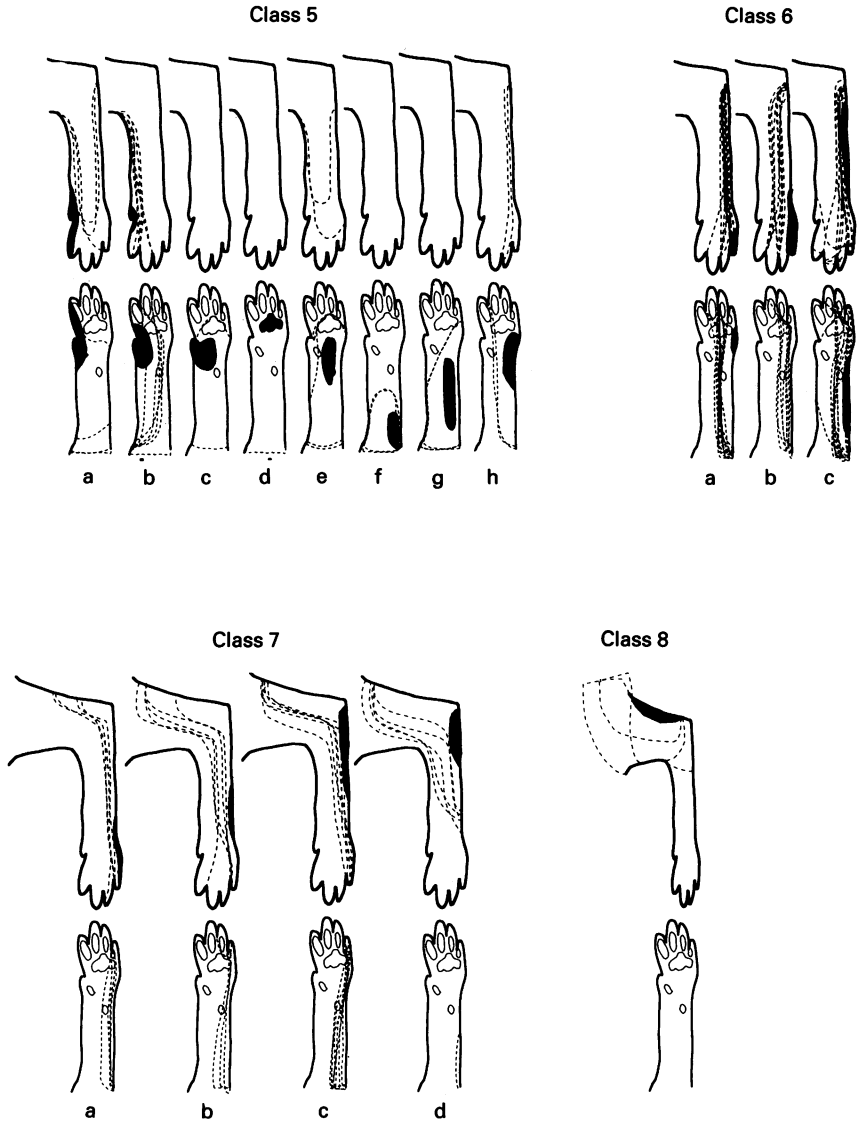


Fig. 4. Classification of cutaneous nociceptive receptive fields of climbing fibres projecting to the C3 zone. A total of 222 receptive fields from twenty experiments were classified and are shown superimposed. Dashed lines indicate borders of single receptive fields while the blackened areas indicate the most sensitive areas (corresponds roughly to the area from which the responses on standardized pinch were higher than 70% of the maximal response).

Classes 5 and 6

Proximal border close to the elbow. Class 5 ($n = 26$) had a focus on the palmar side of the metacarpals, the wrist or the forearm. With the exception of Subclass 5a these units were only located in the rostralmost folia of the medial C3 zone. Class 5a was also found laterally in the caudal folia. Class 6 ($n = 40$) had a lateral focus on the

forearm. The receptive fields were found medially in the medial C3 zone and laterally in the lateral C3 zone.

Class 7

Proximal border on the skin overlying humerus. Units of this class ($n = 20$) were located medial to Class 6 in the medial C3 zone and lateral to Class 6 in the lateral C3 zone.

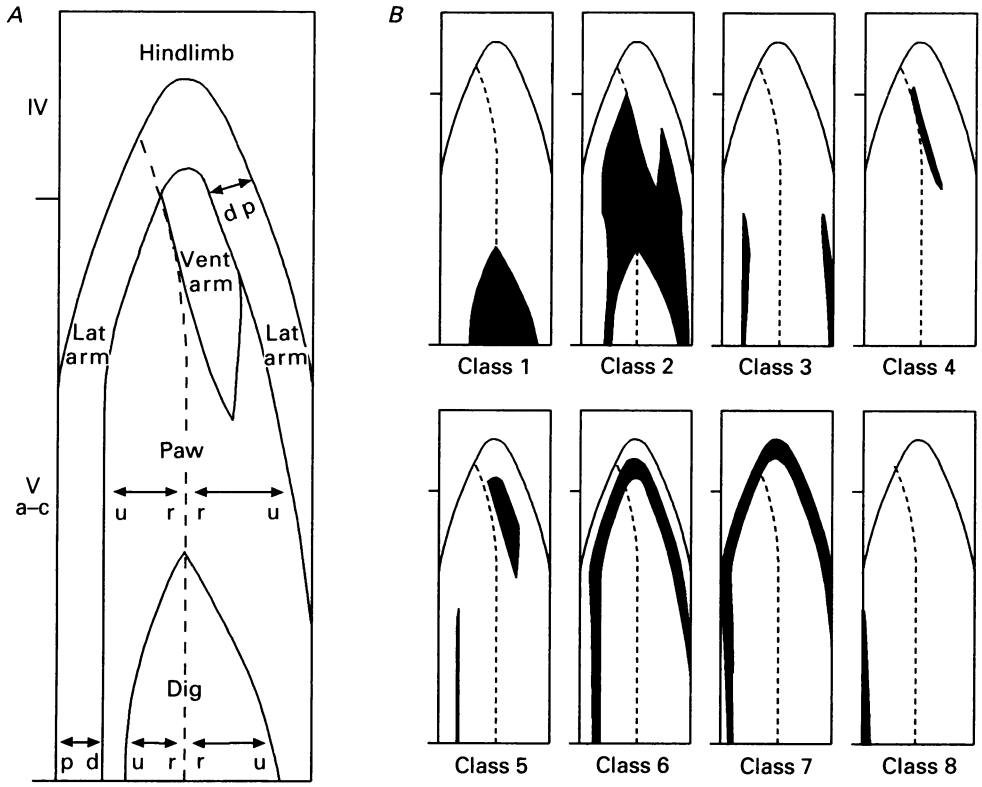


Fig. 5. Topographical organization of the climbing fibre projection from the skin of the forelimb to the C3 zone. *A*, representation of the forelimb. Cerebellar lobules are indicated to the left. Note that the schematic refers to the organization on the cerebellar surface only. Dashed line indicates border between medial and lateral C3 zone as described by Ekerot & Larson, 1982. Dig, digits; Lat, lateral; Vent, ventral; d, distal; p, proximal; r, radial; u, ulnar. *B*, projection of nociceptive receptive classes. The termination area of each class of climbing fibres is indicated by the blackened area.

Class 8

Proximal border close to the shoulder. Units of this class ($n = 3$) were located laterally in the caudalmost folia in the lateral C3 zone.

Each of the classes were further tentatively divided into subclasses on the basis of the location of the area exhibiting maximal sensitivity. In Fig. 4 the receptive fields of each subclass have been superimposed. Each blackened area roughly corresponds

to the area from which the responses were higher than 70% of maximal responses. It can be seen that the receptive fields of most units within each subclass have a similar extent. It should be kept in mind that the results from all cats were pooled in Fig. 4 demonstrating that similar receptive fields were found in different cats.

A few receptive fields ($n = 3$) did not fit into the above classification and may represent infrequent separate classes/subclasses of climbing fibres.

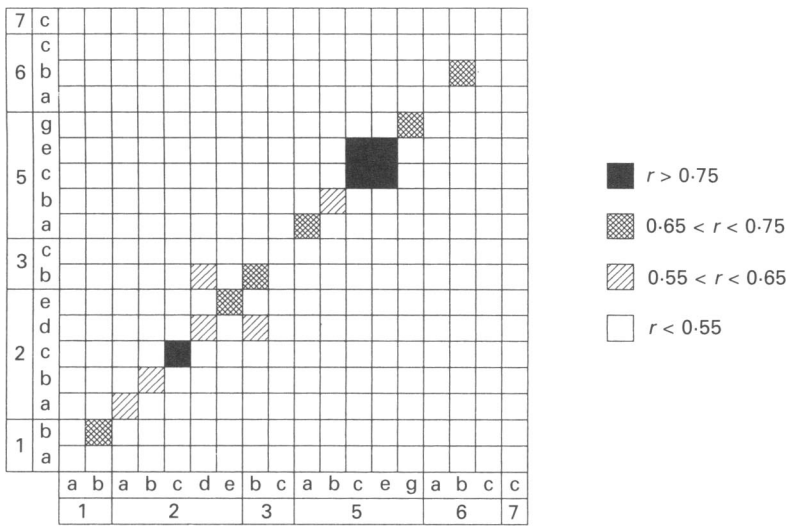


Fig. 6. Correlation values obtained using Method 2 for eighteen quantified subclasses of receptive fields. Mean correlation values (r) are divided into four different groups.

Validity of receptive field classification

In order to further evaluate the validity of the classification system receptive fields were compared using the three quantitative methods described in the Methods. Quantitative data were available in eighty-nine climbing fibres belonging to eighteen of the thirty subclasses.

In Fig. 6 the mean correlation values within and between different subclasses of receptive fields have been divided into four different groups. The correlation values were usually clearly higher within than between the subclasses. Hence, the classification system seems to be valid.

Uneven representation of the forelimb

From the overview (Fig. 2) and the classification scheme (Fig. 4) it is clear that climbing fibres with receptive fields covering the lateral parts of the forearm (i.e. Classes 6 and 7) outnumber those with receptive fields on the medial side (some subclasses of Class 5). In addition, the medial side of the upper forelimb has no representation. Also, within Classes 1–4 (receptive fields restricted to the paw), climbing fibres responding maximally on stimulation of the distal phalanges were far more common than those with a focus overlying the metacarpals. These findings suggest an uneven representation of the forelimb in C3 zone.

DISCUSSION

Characteristics and functional significance of the receptive fields

The present study demonstrates that the cutaneous receptive fields of the climbing fibres projecting to the C3 zone have a detailed spatial organization. The proximal borders of the receptive fields are typically located close to joints. Furthermore, the focus is usually eccentrically located and there is a gradual decrease of sensitivity toward the border of the receptive field. Since there appears to be a limited set of different receptive fields (about thirty subclasses) it is conceivable that the organization of each receptive field (and thus subclass) is related to a specific motor function. Since the proximal borders of the receptive fields are located close to joints their activity may be related to movements caused by contraction in single muscles or small groups of muscles acting on the same proximal joint.

It should be noted that these receptive fields are distinctly different from those of 'sensory' pathways (here defined as pathways informing specifically about activity in peripheral receptors). For example tactile excitatory receptive fields in pathways to the primary somatosensory (SI) cortex, involving the dorsal column and the spinocervical tract, have an oval or circular shape and a central focus of maximal sensitivity (Brown, Fyffe, Noble, Rose & Snow, 1980; Mountcastle, 1984). The location of the 'sensory' receptive fields appears to be independent of joints. Furthermore, the 'sensory' pathways receive a modality-specific input in contrast to the multimodal input to climbing fibres (Ekerot *et al.* 1987*b*, *c*).

The spatial organization of the receptive fields of the C3 climbing fibres is reminiscent of that of the nociceptive withdrawal reflexes (Schouenborg & Kalliomäki, 1990). In this reflex system most hindlimb muscles have unique receptive fields on the skin. Each excitatory receptive field corresponds to the area which is withdrawn during contraction of the muscle itself. The area of maximal sensitivity for each of the muscles corresponds to the area of the skin which is most effectively withdrawn by the muscle itself. Thus, the receptive fields of the withdrawal reflexes exhibit eccentrically located foci of maximal sensitivity and their distal and/or proximal borders are located close to joints.

In an accompanying paper (Ekerot, Garwicz & Schouenborg, 1991) it is demonstrated that the postsynaptic dorsal column (PSDC) pathway (Uddenberg, 1968; Angaut-Petit, 1975; Brown & Fyffe, 1981; Brown, Brown, Fyffe & Pubols, 1983; Lu, Bennett, Nishikawa, Hoffert & Dubner, 1983) is part of the nociceptive spino-olivocerebellar pathway to the C3 zone. Since at least some of the PSDC neurones are known to issue axon collaterals to ventral areas of the spinal cord (Bennett, Nishikawa, Lu, Hoffert & Dubner, 1984) it is conceivable that these PSDC neurones are intercalated in spinal reflex paths and also signal information about their activity via the dorsal column nuclei to the inferior olive.

If the climbing fibres projecting to the C3 zone transmit information about activity in spinal reflex paths, which have an organization similar to the withdrawal reflex paths, the limited number of classes and subclasses of receptive fields within the C3 zone would correspond to a limited set of reflex circuits. For example, receptive fields with a proximal border close to the elbow (Classes 5 and 6) would correspond to the receptive fields of reflexes acting on muscles originating on the brachium and inserting on the forearm while receptive fields with a proximal border close to the wrist (Classes 2–4) would correspond to the receptive fields of reflexes acting on muscles originating on the forearm and inserting on the paw, etc.

Topographical organization

Location of classes in the C3 zone

The demonstrated orderly sequence of cutaneous receptive fields of climbing fibres projecting to the C3 zone is consistent with and extends previous findings on the topographical organization of the forelimb area of this zone (Ekerot & Larson, 1979*b*). The topographical organization is summarized in Fig. 5. Climbing fibres belonging to the same class terminate in bands which may encompass several folia. In general, receptive fields of climbing fibres projecting to bands along the medial and lateral borders of the forelimb area are located on the lateral side of the arm (medial C3 zone, Classes 6 and 7; lateral C3 zone, Classes 6–8). When moving centrally into the zone there is a shift from proximal to distal parts of the forelimb (Classes 1–5) and from lateral to medial parts of the forelimb.

It should be remembered that the medial part of the C3 zone is innervated by olivary neurones also projecting to the C1 zone, whereas the lateral part receives its innervation from olivary neurones also projecting to the Y zone (Ekerot & Larson, 1982). Hence, the classification of climbing fibre receptive fields also applies to the C1 and Y zones. However, the location of these classes in the latter two zones is not known.

Microzonal organization

There was an orderly sequence of subclasses within the projection area of each class of climbing fibres. Climbing fibres belonging to the same subclass terminated within narrow sagittally oriented cortical areas (Fig. 3). Hence, the proposed microzonal organization of the C3 zone was confirmed. The sequences of subclasses shown in Fig. 4 were arranged according to a similarity but these sequences resemble the actual sequences of subclasses found in the C3 zone.

A microzonal organization of the climbing fibre input has previously been demonstrated in the B zone in the anterior lobe (Andersson & Oscarsson, 1978*a*, *b*). In this zone the Purkinje cells of each microzone project to a separate set of neurones in the lateral vestibular nucleus. Each set of vestibular neurones is in addition innervated by collaterals of the climbing fibres projecting to the corresponding cortical microzone. It was consequently suggested that these cerebellar complexes constitute functional units controlling specific motor functions (Oscarsson, 1979).

Efferent connections of the C3 zone

The Purkinje cells of the C3 zone project to the anterior interposed nucleus (Voogd & Bigaré, 1980; Trott & Armstrong, 1987), which is connected to the spinal cord via the red nucleus and the rubrospinal tract. It is conceivable that the proposed microzones in the C3 zone, like those in the B zone, project to their own sets of efferent neurones. It has been demonstrated that microstimulation in the anterior interposed nucleus and in the red nucleus elicits discrete movements in single muscles or small groups of synergistic muscles in the ipsilateral forelimb (Asanuma & Hunsperger, 1975; Ghez, 1975; Giuffrida, Li Volsi, Pantò, Perciavalle, Sapienza & Urbano, 1980; Rispal-Padel, Cicirata & Pons, 1982). Thus, the proposed microzones of the C3 zone may be involved in the control of single muscles or small groups of muscles in the ipsilateral forelimb. This hypothesis is further supported by the present finding that the number of different receptive fields, and thus microzones, appears to be of the same order as the number of muscles in the cat forelimb.

A hypothesis

In Fig. 7 a schematic of the proposed organization of the climbing fibres to, and efferent connections from, a C3 microzone is presented. It is postulated that the forelimb area of the C3 zone is composed of microzones, each of which receives

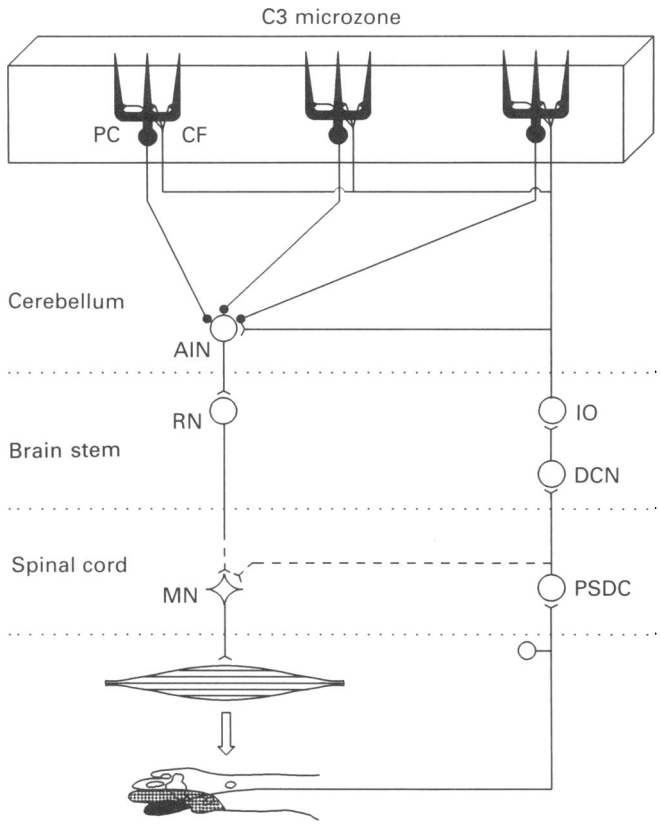


Fig. 7. Schematic diagram of the climbing fibre afferent projection to, and efferent connections from, a C3 microzone. PC, Purkinje cell; CF, climbing fibre; AIN, anterior interposed nucleus; RN, red nucleus; IO, inferior olive; DCN, dorsal column nucleus; MN, motoneurone, PSDC, postsynaptic dorsal column pathway. Dashed lines indicate indirect connections.

information via climbing fibres from spinal multimodal reflex arcs acting on a single muscle or a group of synergistic muscles. It is tentatively suggested that each of these microzones controls the excitability of the corresponding motoneurone pool(s) via pathways through the anterior interposed nucleus and red nucleus. The latter point is critically dependent on whether each microzone projects to its own set of efferent neurones in the anterior interposed nucleus. This is currently under investigation.

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