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AN ANALYSIS OF THE REPRESENTATION OF THE FORELIMB IN THE VENTROBASAL THALAMIC COMPLEX OF THE ALBINO RAT

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SUMMARY

1. Glass micro-electrodes have been used to record from a total of 998 units situated in the ventrobasal thalamic complex in the deeply anaesthetized albino rat.

2. Of these units 889 responded to electrical stimulation of the contralateral forelimb and fifty-one to the contralateral hind limb. The remaining units consisted of those with receptive fields on the trunk, head and those which responded to stimulation of more than one limb. Only the latter group of units showed any spontaneous activity in the absence of intentional stimulation.

2. Of the units which responded to electrical stimulation of the contralateral forelimb the receptive fields, modality and latencies of response were accurately determined for 505 units. The mean latency to supramaximal stimulation at the wrist was 4·49 ($\pm$ 0·04 S.E. of mean) msec; and to mechanical stimulation (for 146 of these units) at the centre of the receptive field 6·58 ($\pm$ 0·12) msec. The modalities were distributed as follows: light pressure, 391; heavy pressure, 47; hair movement, 40; claw sensitive, 15 and joint movement, 12 units.

4. The forelimb representation within the ventrobasal thalamic complex was somatotopically organized, the over-all appearance being that of an incompletely closed fist, palmar surface uppermost, thumb medial, with the wrist caudal and the digital tips rostral and dorsal.

5. The central projection was distorted, some parts showing expanded representation, notably the tips of digits II and III and the medial wrist pad. Other parts were contracted, e.g. the wrist, forearm and shoulder.

6. Units with receptive fields consisting of the whole of a walking pad had shorter mean latencies, to tactile stimulation, than those whose field was a single spot on a pad.

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7. Units were found to show an abolute unresponsive time to the second of a pair of identical supramaximal electrical stimuli of up to 50 msec, and a relative unresponsive time which could last up to 500 msec. The absolute unresponsive and relative unresponsive times to the second of a pair of tactile stimuli was shorter being 30 and 150 msec respectively.

8. The effect of decortication was to increase the excitability of thalamic units to peripheral stimulation both in the initial and later discharges.

INTRODUCTION

It has been shown that in the ventrobasal thalamic complex of the rat there is a somatotopic array of modality specific cells responding to stimulation of predominantly the contralateral body half (Davidson, 1965; Emmers, 1965; Wall & Egger, 1971). The representation is oriented such that the part devoted to the head is located caudal and medial with more caudal parts of the body represented at successively more lateral and rostral points in the ventrobasal thalamic complex (Emmers, 1965).

Adrian (1943) observed that the area of the primary sensory cortex devoted to each part of the body surface depended upon the use and sensitivity of that part rather than on its absolute size. A similar relationship has been reported for the thalamic representation which often reflects the behavioural adaptations of the particular species studied. For example, Welker, Johnson & Pubols (1964) showed that in the raccoon, a manually dexterous animal, each digit had its own large thalamic projection enclosed in a fibrous lamina. Welker *et al.* (1964) and Welker & Johnson (1965) compared the results they obtained using evoked mass potentials as response criteria with those obtained by using unit cluster data noting that the latter gave a greater degree of differentiation of the central representation, i.e. less overlap and changes in the size of representation of the different body parts. The increased specificity they concluded was due to the volume of thalamus over which the different responses were summed and which could include both pre- and post-synaptic potentials. They also considered a single unit analysis would give an even greater degree of resolution than unit cluster responses. Most previous studies have used mass evoked responses or multi-unit recordings as the response criterion, many using metal micro-electrodes with little or no distinction being made between presynaptic (lemniscal) and post-synaptic (ventrobasal cell) origins of the responses. The present study has used glass microelectrodes to record the extracellular responses of single thalamic cells and has been reported in brief elsewhere (Angel & Clarke, 1973).

METHODS

(*a*) *Anaesthesia.* A total of 304 female albino rats (Sheffield strain) in the weight range 190–210 g were used. Each animal was anaesthetized with 1·0 ml. urethane (25 % (w/v) in 0·9 % saline) administered intraperitoneally without premedication. This dose was usually just sufficient to abolish reflex withdrawal to a firm pinch. If not, more was administered until the reflex was just abolished. Generally the total dose of urethane varied between 1·3–1·5 g/kg body weight.

(*b*) *Preparation.* After tracheal cannulation the left cerebral cortex was exposed by an extensive craniotomy and the dura mater removed. The foramen magnum was opened to drain off c.s.f. and also to reduce the possibility of cerebral oedema which grossly affects the response characteristics of the central nervous system (Angel, Berridge & Unwin, 1973). The results from animals showing any sign of cerebral oedema have not been included in this study. The animal was then mounted in a stereotaxic frame with the head held rigid at three points, by rods entering each external auditory meatus pushed in to rupture the tympanum and a bar clamped against the hard palate immediately behind the upper incisors. In this position the top of the incisor bar was 23° below the horizontal plane through the ear bars. This orientation offers two advantages: (*a*) the longitudinal axis of the forebrain is horizontal, and (*b*) in this position easy access is gained to the dorsal column nuclei. Its major disadvantage is that the orientation is different from that of existing atlases (e.g. Albe-Fessard, Stutinsky & Libouban, 1966; DeGroot, 1959; König & Klippell, 1963).

A pool was formed by clamping the reflected skin of the head and neck between an inner Perspex ring and an outer metal clip and filled with liquid paraffin B.P. at 37° C which had been equilibrated with 0·9 % saline. To reduce cerebral movement to respiration or cardiac pulsation the animal was suspended, with the body unsupported, between the ear bars and a pin placed deep to the ligaments covering the pelvic girdle, and the trunk slightly stretched by means of a screw drive. Body temperature (rectal) was maintained at 37 ± 0·5° C by circulating water at 40° C through a hollow copper block placed underneath, but not in contact with, the animal.

(*c*) *Recording.* The zero reference point chosen for the stereotaxic co-ordinates in the rostrocaudal and mediolateral planes was the point of intersection of the sagittal and lambdoideal sutures – the lambda. The zero reference point in the dorsoventral plane was the cortical surface. The micro-electrode holder could be moved in each of the three planes by means of lathe slides and the movement was measured with Mercer dial gauges. A fine control over vertical movement was achieved by using a hydraulic drive which allowed movements of 5 μm to be made with accuracy. Glass micro-electrodes filled with 3 M sodium chloride solution with tip diameters 2–5 μm were used. The activity from the micro-electrode was led via a chlorided silver wire to a FET follower and the output from this was fed into a Tektronix type 122 pre-amplifier. The output from the pre-amplifier was displayed on a Tektronix type 502A oscilloscope and recorded, together with a stimulus marker, on an unmodified cassette recorder (Akai GXC40D). Timing pulses were derived from a Devices Digitimer.

(*d*) *Stimulation.* Electrical pulses continuously variable from 0 to 90 V with a duration of 0·1 msec were applied to the limbs through lint pads soaked in 3 M saline tied securely, but not so tightly as to cause venous obstruction, one wrapped around the wrist or ankle (negative) the other around the first digit (positive).

The mechanical stimulus used was a brief tap delivered by means of a plastic tipped steel probe (1 mm diameter) attached to the moving coil of a 35 Ω general

purpose loudspeaker (RS type 2½ in. 35 Ω) from which the cone had been removed. Probe displacement was varied by means of an IC power amplifier (motorola type MC1438R) the low output impedance (10 Ω) of which effectively (and fortuitously) damped out the impedance of the loudspeaker to give a critically damped non-oscillating mechanical pulse. To a 1 msec square wave input the pulse lasted 4·4 msec with a time to peak of 1·5 msec.

(*e*) *Histology.* Histological determination of the tissue explored was carried out in two ways. Either the electrode was left *in situ* at the end of the experiment and the brain fixed and a thin section containing the electrode examined after clearing in methyl salicylate (Wall, McCulloch, Lettvin & Pitts, 1955); or the stereotaxic co-ordinates were superimposed on cresyl violet stained sections of a rat brain cut in the plane of the stereotaxic frame.

(*f*) *Analysis.* It became apparent early on in the investigation that superimposing positions of units from different animals on common grids in parasagittal and coronal planes would not reveal the finer details of the somatotopic arrangement. Slight variations in brain size, angles of penetration and the spatial relationship of the lambda to the ventrobassal thalamic complex, would all tend to increase the apparent overlap in the projection. A more qualitative approach was therefore employed, a nearest neighbour analysis. The following question was posed. If a particular receptive field was chosen then what receptive field was found at a distance of 100 μm in each direction, i.e. rostral, caudal, medial, lateral, dorsal and ventral to it?

This procedure was repeated for each receptive field type in each experiment. The results from a large number of experiments could then be pooled and the percentage number of each field type encountered in each direction from the chosen receptive field calculated. The field with the highest percentage occurrence in each direction was considered to be the one actually located there. The whole projection could then be fitted together, rather like a three-dimensional jigsaw.

RESULTS

(*a*) *Cell numbers.* A total of 998 single units were isolated in the 304 animals. Of these, 899 responded to electrical stimulation of the contralateral forelimb and fifty one to stimulation of the contralateral hind limb. The remaining forty-eight units were composed of eight with receptive fields confined to the trunk, twenty-four units responding to stimulation of more than one limb and sixteen units isolated in decorticate preparations. One property common to all the units isolated, with the exception of those responding to both contralateral limbs, was their total lack of spontaneous activity in the absence of intentional stimulation. Typically the response of units activated by electrical stimulation of the periphery was a single spike, lasting for 0·5–1·5 msec predominantly positive going and frequently preceded by a small pre-potential. The above figures do not, of course, represent a true sample of the cellular population within the ventrobasal thalamic complex. There was an intentional bias towards isolating units activated by stimulation of the contralateral forelimb – which was the main purpose of this investigation. A better quantitative sample would be given by considering the numbers of units isolated in the

early experiments prior to the establishment of the stereotaxic co-ordinates for the forelimb projection to the ventrobasal thalamic complex. In the initial experiments a grid of penetrations 100 μ apart was used to explore the thalamus. For the first thirty animals this gives 184, forty-two and fifteen units for receptive fields localized to the contralateral fore- and hind limbs and for more than one limb respectively. Fig. 1 shows the outline of the distribution of stereotaxic co-ordinates, along the mediolateral and rostrocaudal axes, for these three different types of thalamic unit which shows that they were capable of spatial as well as functional separation.

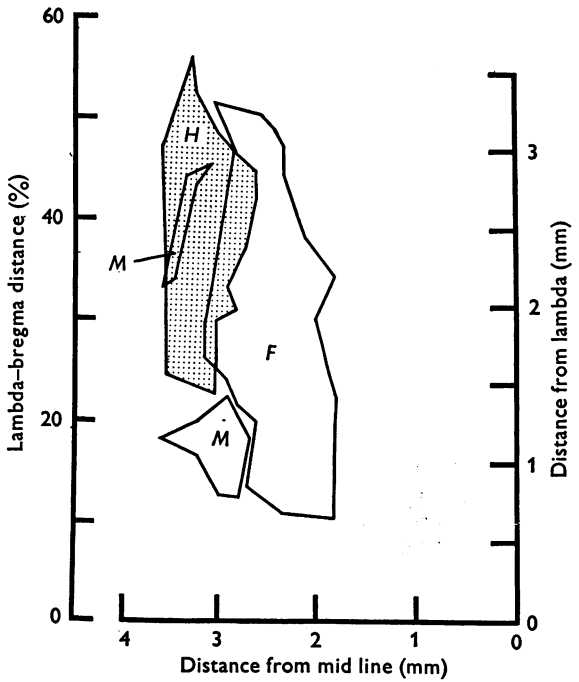

Fig. 1. An outline of the distribution of stereotaxic co-ordinates along the mediolateral and rostrocaudal axes of penetrations from which single thalamic units were obtained. *F*, units with receptive fields on contralateral forelimb. *H*, units with receptive fields on contralateral hind limb (shaded). *M*, units with receptive fields not restricted to a single limb.

Of the 899 units which responded to electrical stimulation of the contralateral forelimb accurate determinations of the latency, response modality and receptive field were obtained for 505 units. Of these 505 units 428 had small receptive fields located on the paw and seventy-seven had receptive fields on the shoulder and arm. The only units with small receptive fields

found above the wrist were four which were excited by moving the guard hairs just above the wrist.

(*b*) *Responsive thalamic volume for contralateral forelimb units.* Fig. 2*A* shows the distribution of these 505 units as a three-dimensional display along the rostrocaudal (Fig. 2*A RC*), mediolateral (Fig. 2*A ML*) and dorsoventral (Fig. 2*A DV*) axes. Their position along this latter axis was taken as the depth below the cortical surface at which the amplitude of

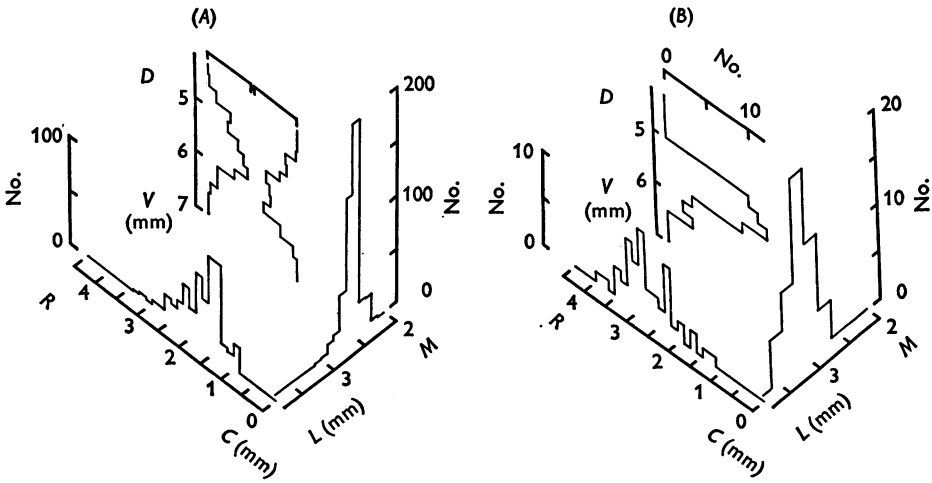

Fig. 2. The distribution in the ventrobasal thalamus of units with receptive fields on the contralateral forelimb (*A*) and hind limb (*B*) as a three-dimensional display along the rostrocaudal (*RC*), mediolateral (*ML*), and dorsoventral (*DV*) axes. The *DV* axis has been split in (*A*) to show the distribution of units in the rostral half, and in the caudal half of the ventrobasal thalamic complex.

the unit response was largest. Ninety per cent of the units were found 1·0–2·9 mm rostral to the lambda, 2·2–2·7 mm lateral to the mid line and from 5·0–6·3 mm deep to the cortical surface. The distribution along the rostrocaudal axis was markedly skew with 50 % of the units found in the caudal 0·4 mm of the projection along this axis. In addition 90 % of the units encountered in this caudal portion were found 5·0–6·3 mm below the cortical surface, whereas 90 % of the units in the rostral 0·7 mm were found between 5·0–6·1 mm below the surface. Thus the responsive thalamic volume, approximately 1·14 mm^3, resembles a truncated wedge approximately 0·5 mm wide, 1·9 mm long, 1·3 mm high in its caudal portion and 1·1 mm high in its rostral portion.

For comparison the distribution of the fifty-one hind-limb units has been plotted in the same manner as for the forelimb (Fig. 2*B*). From this

it can be seen that 90 % of these units were found 2·2–3·4 mm rostral to lambda, 2·7–3·5 mm lateral to the mid line and 5·0–6·2 mm below the cortical surface. Thus the hind-limb units were found lateral, rostral and for the most part above the location of the forelimb units.

The rostro-caudal dimensions were calculated from the mean lambda to bregma distance of 6·60 mm (± 0·38 mm S.D. of an observation). In all experiments this distance was measured by aligning a micropipette tip, filled with indian ink for easy visualization, on these two landmarks using at least two different angles of viewing and the recording electrode position

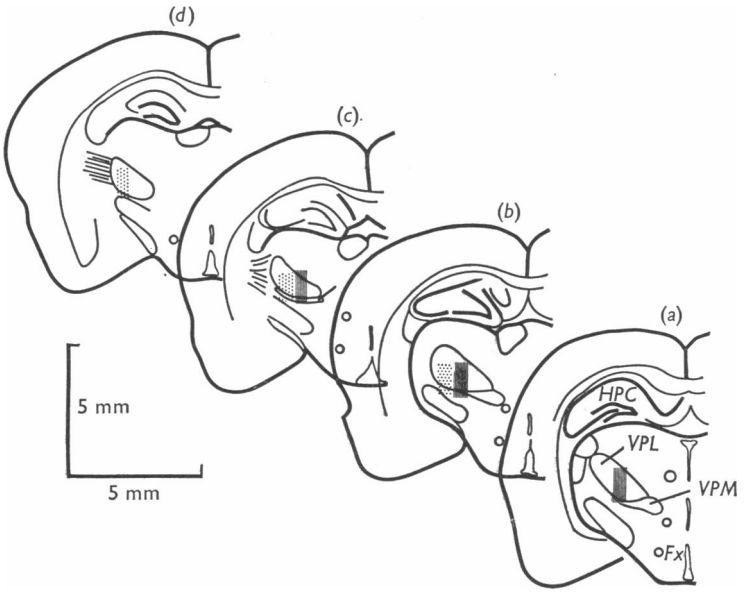

Fig. 3. The rectangular blocks of tissue containing 90 % of the co-ordinates of units with receptive fields on the forepaw (vertical bars) and the hind-paw (dots) superimposed on an atlas cut in the same plane as the stereotaxic frame, 1·5(*a*), 2·0(*b*), 2·5(*c*) and 3·0 mm(*d*) anterior to lambda. Each section represents the distribution of units in a 0·5 mm span (i.e. the distribution shown in (*a*) represents a compression of the volume from 1·25 to 1·75 mm anterior to lambda in a single plane). *L*, medial lemniscus, *HPC*, hippocampus, *VPL*, nucleus ventralis posterolateralis, *VPM*, nucleus ventralis posteromedialis, *Fx*, Fornix.

noted as the percentage of this distance anterior to the lambda. After the initial series of experiments to locate the ventrobasal thalamic complex it became apparent that one could localize the forelimb projection either by measuring the penetration as a percentage or absolute distance and that a penetration 2·0 mm rostal and 2·5 mm lateral to lambda was certain to encounter the forelimb thalamic projection area. From the responses

recorded in such a penetration a particular area could be selected with reference to these responses (see section (*e*) below).

Superimposing the above co-ordinates upon sections of an atlas cut in the same plane as the stereotaxic frame and direct examination of the position of the micro-electrode tip in methyl salicylate cleared sections, showed that these dimensions fell within the boundaries of the ventrobasal thalamic complex (see Fig. 3).

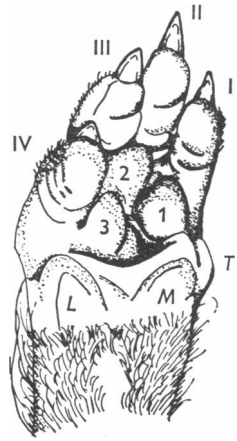

Fig. 4. A drawing of the right forepaw of the rat viewed from its ventral aspect. *T*, vestigal thumb; I–IV, digits; 1, 2 and 3, the pads between the bases of digits I and II, II and III, III and IV respectively. *M*, medial wrist pad. *L*, lateral wrist pad.

(*c*) *Modality sorting.* Determination of the adequate stimulus to which the unit would respond revealed five basic types of unit. Those responding to gentle stimulation of the skin with a wooden stylus or wisp of cotton wool, taking care not to disturb deep tissues, was the most frequently encountered type, 391 units or 77·4 % of the sample. These are termed light pressure units. Forty-seven units (9·3 % of the sample) responded to stimulation sufficiently intense to disturb deep tissues, heavy pressure units. Movement of hairs, taking care to avoid touching the underlying skin, yielded forty units (7·9 %), fifteen units (3 %) were claw sensitive and responded to light pressure to, or movement of a claw. The remaining twelve units (2·4 %) responded to movement at one or more joints; care being taken to eliminate the other types.

(*d*) *Surface anatomy of the forepaw.* Spatial terms used (medial, lateral, dorsal and ventral) describe the paw as though the animal was in its usual posture (Reighard & Jennings, 1949) with the palmer aspect in contact with the floor (ventral) the thumb medial and digit IV lateral.

Fig. 4 shows a drawing of the right forepaw of the rat viewed from its ventral surface. The paw bears four major digits, numbered I–IV from the medially placed index finger. Each of these digits bears a claw on its dorsal surface. The small thumb (*T*, Fig. 4) bears a flattened nail. The tip of each digit is expanded on its ventral surface into a glabrous pad. Digits II and III are longer and more prominent than digits I and IV. Between the bases of the digits on the ventral surface are three fleshy glabrous pads described as pads 1–2, 2–3 and 3–4 (1, 2 and 3 respectively in Fig. 4). Two other

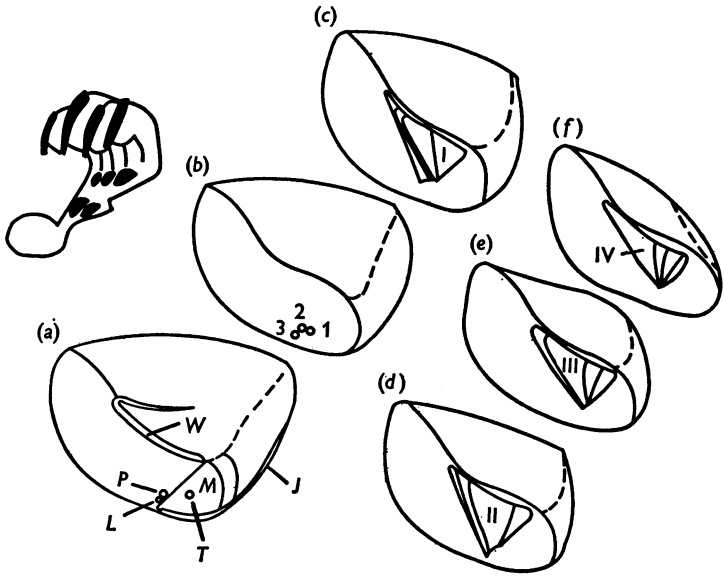

Fig. 5. The ventrobasal thalamic region shown in Fig. 3 (*VPL*) enlarged with the relative positions of the representation determined by the 'nearest neighbour analysis' superimposed on successively rostral sections (*a–f*). A figurine is also shown (upper left) to aid spatial orientation of the projection. *P*, palm; *L*, lateral wrist pad; *T*, thumb; *M*, medial wrist pad; *J*, joint rotation; *W*, wrist and arm. 1, 2 and 3, pads between bases of digits I and II, II and III, III and IV respectively. I, II, III, IV, digits.

fleshy pads are found on the ventral surface just distal to the wrist. These are described as the medial and lateral wrist pads (*M* and *L*, Fig. 4). The ventral surface of the paw, up to and including the wrist pads, is entirely glabrous. The dorsal aspect of the paw is hairy, although sparsely so when compared with the remainder of the forelimb.

(*e*) *Somatotopic arrangement.* Fig. 3 shows the extent of ventrobasal thalamic tissue occupied by the contralateral forelimb projection obtained by superimposing the stereotaxic co-ordinates, outlined in section (*b*) above, on sections taken in the same stereotaxic plane. This responsive

volume is shown enlarged in Fig. 5 and the relative positions of the representation determined by the nearest neighbour analysis is superimposed. A figurine is also shown to aid visualization of the analysis. The shoulder, forearm and wrist is represented by a strip of tissue at the caudolateral pole of the forelimb thalamic area. The strip extends to some extent, along the dorsal edge as well. Just rostral to this strip one encounters an area from which responses to stimulation of the thumb, medial and lateral wrist pads are obtained. The area for the medial wrist pad is the largest and appears to envelop the thumb area. More rostral still are found the areas for the palm and the fleshy pads at the bases of the digits with pad 1–2 medial and pad 3–4 lateral. At the rostral pole of this projection the digital representation is found. Each digit occupies a wedge-shaped volume of tissue with a strict and orderly sequence of representation; digit I caudomedial and digit IV rostrolateral. The expanded glabrous digital tips, and dorsal aspects of the digits were found to occupy the rostrodorsal portion of these wedges. All units responding to joint rotation were found to occupy a thin ventral lamina of tissue.

The over-all appearance of the forepaw representation can be likened to an incompletely closed fist with the digital tips occupying the rostrodorsal portion and the wrist, arm and shoulder the caudolateral portion of the thalamic area. It must be emphasized that the figurine is not intended to convey accurate quantitative information about the forelimb representation; it is included to aid visualization of the spatial orientation.

Fig. 6 shows diagrammatically the various surface features of the forelimb (*A*), the relative surface areas of these features (*B*) and the percentage number of cells devoted to each part per unit surface area (*C*). The distortion in the central projection is shown by the difference in area of the different parts in Fig. 6*B* and *C*. It can be seen that some parts have undergone a relative contraction and others an expansion in their central projection. The tips of digits II and III are enormously expanded whereas the tip of digit I is contracted and that of digit IV remains about the same relative size. The rest of digits I and IV are greatly expanded, that of digit II slightly expanded and that of digit III is contracted. Other expanded parts are the fleshy pad 1–2, the palm, thumb and medial wristpad. The rest of the forelimb shows a relative contraction. It should be emphasized that the dorsal surface of the paw was poorly represented. The distorted central projection of digits II and III can be seen from Fig. 7 in which the number of units with receptive fields over the entire digital tip, the glabrous tip, the dorsum of the tip and the claw has been plotted for each digit, together with the total number of units found for each digital tip.

(*f*) *Latencies of thalamic responses.* The mean latency to electrical stimulation of the 505 forelimb units was 4·49 ($\pm$ 0·04 S.E. of mean) msec

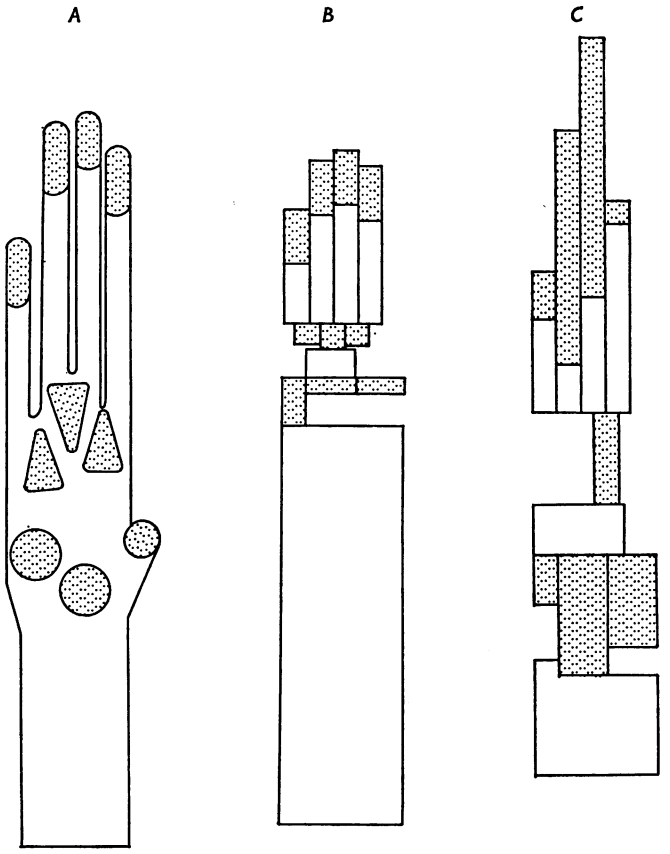

Fig. 6. Shows diagrammatically the various surface features of the forelimb (*A*), the relative surface areas of these features (*B*), and the percentage number of cells devoted to each part per unit surface area (*C*). The distortion in the central projection is shown by the difference in area of equivalent parts in *B* and *C*.

compared to 9·37 (± 0·21) msec for the fifty-one hind-limb units and 29·58 (± 14·54) msec for the seventeen units with fields comprising more than one limb. Dividing the forelimb units into five functional types gives latencies of 4·46 (± 0·04) msec for light pressure, 4·92 (± 0·11) msec for heavy pressure, 4·40 (± 0·15) msec for claw sensitive, 4·36 (± 0·11) msec for hair movement and 4·50 (± 0·15) msec for units activated by joint movement. Within this population only the units activated by heavy pressure had a latency statistically different ($P < 0·001$) from that of the light pressure units. For 146 units which responded to stimulation of the forepaw latencies to electrical and mechanical stimulation (applied at the centre of the receptive field) were compared. The mean latency to electrical

stimulation was 4·29 (± 0·06) msec and to mechanical stimulation 6·58 (± 0·12)msec. The latencies of these units have been plotted in histogram form in Fig. 8*A*, from which it can be seen that to both types of stimulation the distribution was bi-modal. (Heavy pressure units were excluded from this sample because the mechanical stimulator was ineffective in exciting this type of unit.) Again no statistically significant difference was found in comparing the latencies of the different modality types and surprisingly the latency was not related to position of the unit on the paw (see Fig. 8*C*).

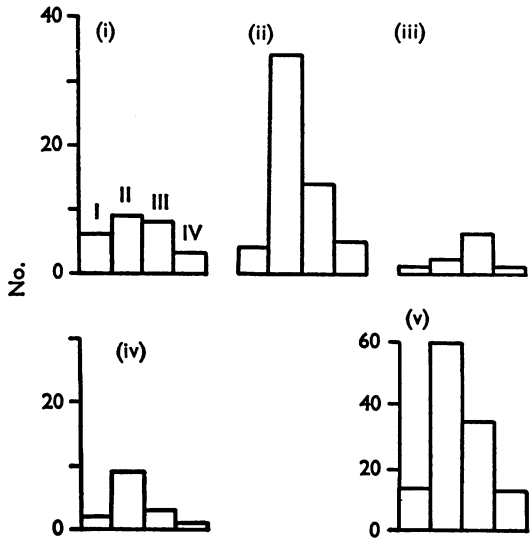

Fig. 7. Shows the number of units of various receptive field types found for each of the four digits represented by the vertical blocks I, II, III and IV. (i) receptive field consisting of the whole of the digital tip; (ii) receptive field consisting of the glabrous aspect of the digital tip; (iii) receptive field located around the claw of the dorsum of the digital tip; (iv) claw sensitive units; (v) the sum of the previous four types.

One consistent observation which was striking was the longer latency of small compared to large receptive field units. For example, three field sizes were found on the pads, spot fields, whole pad fields and half pad fields. This latter was a convenient rather than accurate delineation, their sizes fall between spot and whole pad fields. To electrical stimulation their latencies were 4·65 (± 0·22; $n = 20$), 4·31 (± 0·09; $n = 59$) and 4·55 (± 0·18; $n = 28$) msec respectively. These showed no statistically significant difference. When the latencies to mechanical stimulation were compared, however, a statistically significant difference was found ($P < 0·02$) between the latencies of the spot (7·50 ± 0·59 msec; $n = 8$) and whole (6·10 ± 0·26 msec; $n = 20$) but not half pad fields (6·65 ± 0·36 msec;

$n = 17$). The mean areas of receptive fields located on different parts of the forelimb are shown in Fig. 8*B*, which also shows for comparison the mean receptive field areas on the forelimb for the cuneate nucleus and the primary somatosensory cortex. It can be seen that the smallest receptive fields are found at the distal extremity of the limb and that the mean receptive field area progressively increases towards the proximal end of the limb.

(*g*) *Responses to paired stimuli.* In fourteen units it was possible to compare the responses to paired electrical and mechanical pulses, with separations from 10–1000 msec. Stimulus pairs were presented at a rate of one

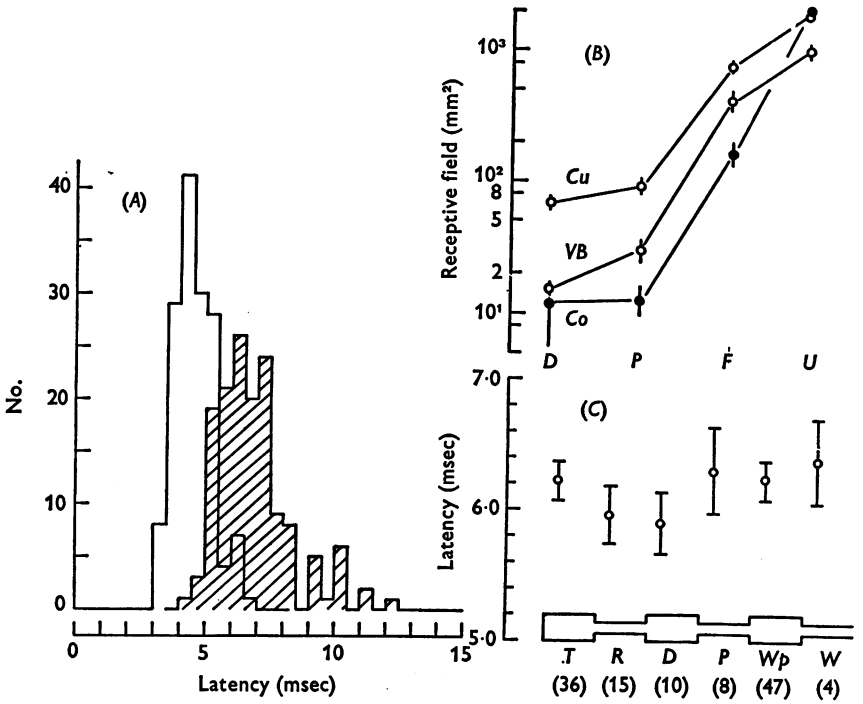

Fig. 8. (*A*) Histograms of the latency distribution of a sample of 146 units to electrical (open columns) and mechanical (shaded columns) stimulation.

(*B*) Receptive field sizes (mm² ± S.E. of mean) of units located in the primary somatosensory cortex (*Co*), ventrobasal thalamus (*VB*) and cuneate nucleus (*Cu*) which had their receptive fields centred on the digits (*D*, 138, 72 and 26 units for *Cu*, *VB* and *Co* respectively), paw (*P*, 157, 154 and 20 units), forearm (*F*, 17, 32 and 8 units), or upper arm and trunk (*U*, 22, 16 and 4 units).

(*C*) Shows the mean latencies (msec ± S.E. of mean) to mechanical stimulation at the receptive field centre of units with receptive fields located on different parts of the forepaw. Digital tips (*T*), rest of digits (*R*), pads at digital bases (*D*), palm (*P*), wrist pads (*Wp*) and wrist (*W*). The numbers in parentheses indicate the number of units of each type.

per two seconds and sixty consecutive responses were recorded to the second of each pair of the various separations. This meant that a stable recording which lasted for at least 65 min for each unit had to be made. If the unit responded to each of sixty consecutive stimuli its probability of firing was taken as unity. The stimulus strength was adjusted, in all cases, to be supramaximal for unit probability of firing to the first stimulus of the pair. A pre-requisite of this part of the investigation was that the unit should fire with unit probability to allow pooling of the results. The mean responses are shown in Fig. 9*A* and *B*. With electrical stimulation there

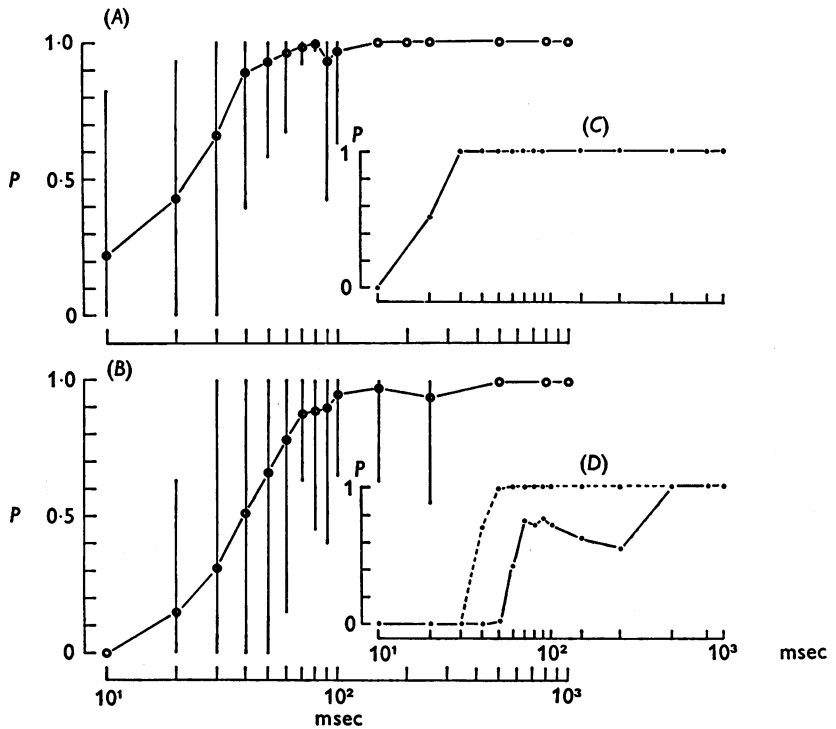

Fig. 9. The mean discharge probability P (circles) ± absolute scatter (vertical lines) of a sample of fourteen units to the second of a pair of mechanical (*A*) or electrical stimuli (*B*) at the stimulus separations shown (note log scale). (*C*) shows the discharge probability of a typical single unit to mechanical stimulation and (*D*) the discharge probability of the same unit to supramaximal electrical stimulation (dashed line) and maximal electrical stimulation.

was a period of absolute unresponsiveness lasting for 10–50 msec; the number of units showing no responses to the second of the pair of stimuli being fourteen, eight, six, five and one for intervals of 10, 20, 30, 40 and

50 msec respectively. This was followed by a period of relative unresponsiveness which lasted for up to 500 msec. With mechanical stimulation the effect of the first stimulus upon the subsequent behaviour of the unit was seen to be less inhibitory. The individual units showed a period of absolute unresponsiveness for 10–30 msec. In this case, however, the number of units showing no responses to the second stimulus being seven, two and one for intervals of 10, 20 and 30 msec respectively. The period of relative unresponsiveness only lasted for 150 msec. With both types of stimulus the recovery of responsiveness was not smooth but showed a period of increased unresponsiveness between 80 and 100 msec.

That the differences seen in the recovery of the units to electrical or mechanical stimuli was not merely a reflexion of the size or synchrony of the afferent volley can be seen from the responses of one unit shown in Fig. 9*C* and *D* in which the recovery to mechanical and maximal (i.e. probability of response just unity) and supramaximal electrical stimuli were determined. It can be seen clearly that the total inhibitory effect of a supramaximal electrical stimulus is much less than that to the maximal stimulus.

(*h*) *Responses in the decorticate preparation.* In four animals a bilateral craniotomy was performed and the exposed cerebral mantle on the left hand side destroyed. A total of sixteen thalamic units were isolated from these preparations, fourteen on the decorticate side and two on the side with cortex intact, from an equal number of electrode penetrations at equivalent points passing through both ventrobasal thalami. That this probably represents an increase in the probability that the ventrobasal units would respond to a peripheral stimulus was shown by further experiments in which the animals were decorticated whilst recording from single thalamic units. Such an experiment is illustrated in Fig. 10*B* in which a single unit followed by a small mass response was recorded. After decortication the unit showed a decreased latency of discharge and the mass response an increase in amplitude. Apart from the greater ease of finding thalamic units on the decorticate side units isolated from this side showed two major differences from units isolated in the intact preparation. First, although the mean latency of discharge of the fourteen units (4·50 ± 0·23 S.E. of mean msec) did not differ significantly from those isolated in the intact animal the scatter in the latency of discharge tended to be less. For example, in another preparation a unit isolated before decortication responded between 4·6–8·9 compared to 4·6–5·0 msec after decortication (Fig. 10*A*). Secondly, the units tended to show a clear-cut pattern of after-discharge following the initial single discharge to the peripheral stimulus. These after discharges (which were only rarely seen in units isolated in the intact preparation) consisted of a constant number of impulses for any

one unit, one to six in number, and tended to occur in one of the following latency spans; 80–100, 150–200 or 250–270 msec after the stimulus.

As far as could be determined, with this very small sample, there was no change in the somatotopy as a result of the decortication in the acute preparation; i.e. the units were encountered where one would expect to find them from their receptive fields.

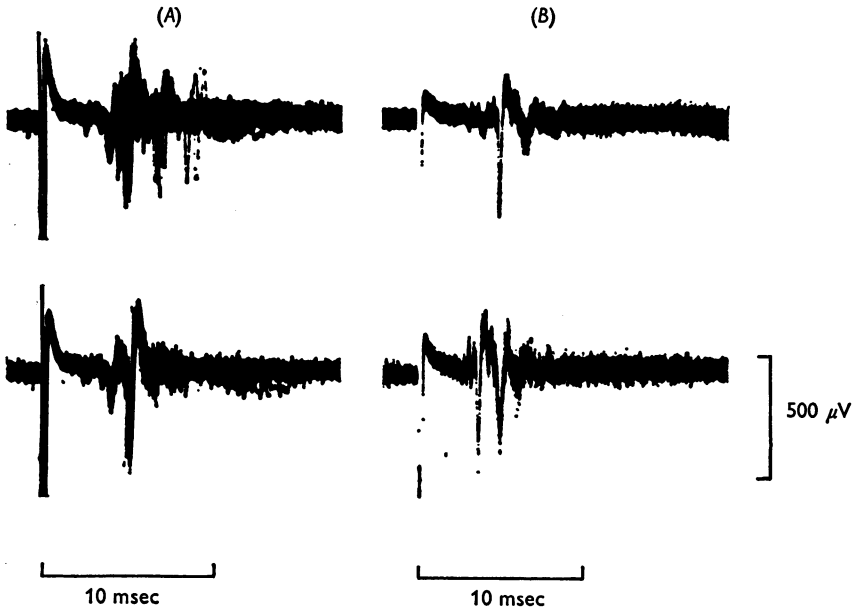

Fig. 10. The effect of decortication on the responses of two units *A* and *B* to a single peripheral electrical stimulus. Each trace consists of twenty superimposed sweeps before (upper pair) and after (lower pair) decortication.

DISCUSSION

For this study we have employed glass micro-electrodes. With this type of electrode we have never isolated, convincingly, single unit responses in tissue devoid of perikarya, e.g. in the dorsal columns or pyramidal decussations and, since the amplitude of the tract response in the thalamic mass never exceeds twice the noise level it was highly unlikely that any of the single unit, relatively high voltage responses recorded in this investigation could have been from medial lemniscal fibres. Further support for this was the frequent observation of a pre-potential preceding the spike response. Thus we can assume that the responses recorded were from a population of neurones, a population that was, moreover, confined to the ventrobasal complex of the thalamus as determined by both super-

imposition of the cell co-ordinates on the stereotaxic atlas and by visual observation of the micro-electrode tip position in methyl salicylate cleared sections.

Comparison of the distribution of cells responding to stimulating either the contralateral fore- or hind limb obtained in this study with that of Lund & Webster (1967*a*) for degeneration in the ventrobasal thalamus after lesions in the dorsal column nuclei shows a high degree of agreement. Both this and their study show the representation for the forelimb displaced medially and caudally compared with that of the hind limb (see Figs. 1 and 2). The relative paucity of degeneration at the rostral pole of the forelimb projection they observed is coupled with the observation that fewer cells were isolated from this region in the present experiments (see Fig. 2). The region of the ventrobasal complex from which cells respond to stimulation of more than one limb also corresponds in position to that shown by Lund & Webster (1967*b*) for sites of terminal degeneration after lesions of the spinal cord; the area lateral to the caudal pole of the forelimb projection (Fig. 1) occupying a region shown by these authors to receive fibres from the first two cervical segments. They postulated that this was the area of projection of the lateral cervical nucleus. This postulate is, however, uncertain since Rexed (1951) found that this nucleus was either non-existent or existed in a form different from that described in the cat. Gwyn & Waldron (1968) have described a group of cells in the dorsolateral funiculus extending the whole length of the spinal cord which they suggest may be the murine equivalent of the feline lateral cervical nucleus. The peculiar structure of the expanded apical portion of the dorsal horn has been equated by Mikhail (1972) with the feline lateral cervical nucleus. The area that overlies the hind-leg projection, near the rostral pole of the ventrobasal thalamic complex (see Fig. 1) corresponds to the projection area found by Lund & Webster (1967*b*) after lesions at all levels of the spinal cord. Units isolated from these two regions all required a natural stimulus of heavy pressure to excite them, had extensive receptive fields and responded with long and variable latencies to peripheral stimulation. They, therefore, displayed characteristics similar to those units reported by Poggio & Mountcastle (1960) located in the posterior nuclear group of the dorsal thalamus in the cat (i.e. that site defined by Rose & Woolsey, 1958). Since in the cat this area lies posterior and dorsal to the ventrobasal thalamic complex the organization of this part of the thalamic centripetal path is significantly different from the rat in which the projection is on to two areas, one at the posterolateral border, and the other in the rostrolateral portion of the ventrobasal complex. The portion at the posterolateral border corresponds very roughly with that reported by Emmers (1965) in the rat thalamus and labelled by him as the SII

region of the thalamic projection. The responses from cells located in these two portions of the ventrobasal thalamus were quite distinct from those atypical thalamic units which responded to stimuli of a potentially noxious character applied anywhere on the body surface found around the lateral border of, and dorsal to the ventrobasal thalamic complex by Angel (1964). These units were rarely fired by a single high intensity stimulus applied to the body surface and responded by changing their frequency of discharge to iterative electrical stimulation showing a peak change in frequency of discharge some 300–500 msec after the start of a train of stimuli.

There were two discrepancies between the physiological and anatomical descriptions of the ventrobasal thalamic complex. First, we did not find any evidence of the rostromedial curvature of the complex as shown by Lund & Webster (1967*b*, see for example their Fig. 5) and secondly, the presumed spinothalamic input found by these authors at the rostral pole of the complex appeared to be somatotopically organized. No evidence was found in the present study to corroborate this.

Although we specifically searched for, we did not find any evidence for a differential projection within the ventrobasal complex similar to the rostrocaudal differential organization seen, physiologically, in the dorsal column nuclei by Gordon & Paine (1960), Gordon & Jukes (1964), McComas (1963), Perl, Whitlock & Gentry (1962) and Winter (1965) as well as anatomically (Kuypers & Tuerk, 1964; Hand, 1966). That a similar thalamic organization to that seen in the dorsal column nuclei was unlikely had been suggested by the findings of Gordon & Seed (1961) and Gordon & Jukes (1964) who showed that a smaller fraction of cells in the rostral and caudral thirds of the gracile nucleus were fired antidromically by stimulation of the medial lemniscus than cells in the middle third in which cells with small receptive fields are located. The observations of Kuypers & Tuerk (1964) that after medial lemniscal section few cells in the rostral third showed retrograde degenerative changes would support this. In the present study it was found that the receptive fields of the cells in the forelimb thalamus resembled those found in the middle third of the dorsal column nuclei; that is with the exception of fields found above the wrist, they were small and restricted to a single digit, digital tip or walking pad. This observation is in agreement with that of Poggio & Mountcastle (1963) for the simian thalamus. Unfortunately the investigation of surround inhibition was not pursued in the present study for the reason that few cells in the dorsal column projection system showed spontaneous activity so that this phenomenon could not be demonstrated with rapidity or ease. The possibility that the cells showing large receptive fields over both contralateral limbs represent neurones with converging inputs from the rostral and caudal thirds of the dorsal column nuclei is unlikely in

that (*a*) their position corresponded to the presumed spinothalamic input of Lund & Webster (1967*b*) and (*b*) they were intermixed with cells showing receptive fields covering ipsilateral as well as contralateral limbs.

If the distribution of types of natural stimuli needed to excite the ventrobasal thalamic cells is compared to that for the cat then a striking difference is seen. For the feline gracile nucleus the proportions of cells excited by hair movement, touch or stimuli applied to the claws are 45·4%, 16·7% and 3·3% respectively (Gordon & Jukes, 1964) and for cat medial lemniscal fibres 57·6%, 15·4% and 7·7% respectively (Brown, Gordon & Kay, 1974). The proportions found in the rat were 7·9% hair sensitive, 77·4% touch sensitive and 3% claw sensitive cells. The preponderance of touch sensitive cells in the rat is probably an expression of the completely different structure and covering of the rat forepaw compared with the cat's hirsute paw. Another major difference seen in the rat was the relative absence of cells which were influenced by more than one type of peripheral stimulus. Approximately half of the 'best categorized' axons of Brown *et al.* (1974) with relatively small receptive fields on the paw showed varying degrees of excitatory convergence from two or more receptor types. In the rat only five units (excluded from the preceding analysis) with relatively small receptive fields were positively identified as having an excitatory input from more than one receptor type. Four units discharged to both hair movement and light touch and one to stimulation of a claw and light touch.

One property of the ventrobasal thalamic cells isolated in this study which requires special comment was the almost total absence of spontaneous activity in the absence of intentional peripheral stimulation. Only a few cells displayed a spontaneous discharge. Most of the cells with very large receptive fields not confined to one limb showed a spontaneous discharge. The absence of such activity in cells with small receptive fields confined to one contralateral limb is in marked contrast to the situation found in the unanaesthetized monkey (see, for example, Poggio & Viernstein, 1964) or the anaesthetized cat (see, for example, McCance, Phillis & Westerman, 1968), but agrees with the observations of Waite (1973) for the rat under deep barbiturate or urethane anaesthesia.

Of the two comprehensive investigations of the peripheral responses in the rat thalamus, one, that reported by Davidson (1965), we would discount on our criteria since he reported that 'the exposed cortex becomes edematous during the course of an experiment'. The reason why we rejected any experimental material, from the present analysis, from animals showing signs of cerebral oedema was that in such a preparation, the thalamus behaves as though the cortex had been removed (A. Angel, unpublished observations). Thus any tonic cortico-thalamic inhibition

would be removed and the responsiveness of the thalamic cells increased (see Fig. 10 and Angel *et al.* 1973). In addition both he and Emmers (1965) used metal micro-electrodes, recorded multi-unit activity and failed to adequately distinguish between presynaptic and post-synaptic responses, thus mapping dorsal-columno-thalamic termination sites as well as sites of transfer of the thalamic inflow. That this could be an important factor is shown by the more extensive volume of ventrobasal thalamus within which cuneo thalamic afferents terminate compared to that from which cellular responses can be recorded (compare Fig. 3 with Figs. 1 and 2 of Lund & Webster, 1967*a*). Davidson (1965), Emmers (1965), Wall & Egger (1971) and Waite (1973) all found, as did we, that the foreleg area is located medial to that for the hind leg. However, all previous authors have described the foreleg as being oriented perpendicular with the arm dorsal to the paw. The organization we found and the relative volumes devoted to the paw and limb differ completely from all previous work. The paw represented as a partially closed 'fist' with the vestigial thumb medial and the digital tips rostral and dorsal compares favourably with, and is a mirror image of, the organization found in the rat cuneate nucleus by Berridge (1973) and resembles that found for the raccoon in the ventrobasal thalamus (Welker & Johnson, 1965). This disparity is, in all probability, a reflexion of the different response criterion we have employed, i.e. the all-or-nothing discharge of a single thalamic cell and the careful delineation of the peripheral receptive field to discharge that cell and that cell only. Previous workers have used their electrodes to record from a volume of thalamus; a technique, it would appear to us, designed to obfuscate fine details of representation within a cellular mass.

From the latency measurements of thalamic cells to mechanical stimulation of the periphery two facts become apparent. First the inflow from the paw to the thalamus is temporally homogeneous, there being no significant difference in the latency of response of cells with receptive fields restricted to the digital tips compared with those with restricted fields on the rest of the paw and wrist (Fig. 8*C*). Secondly, cells with different receptive fields on the glabrous walking pads show a significant difference in latency comparing 'spot' fields to whole pad fields of 1·4 msec. Since these two types of thalamic cell discharge with similar latencies to electrical stimulation at the wrist, one possible model of the system (Fig. 11*A*) is that the 'spot' field cells receive a direct input from the cuneo-thalamic inflow and also an input from the whole pad thalamic cells; these two inputs to be integrated to discharge the 'spot' field cell. The difference in latency to mechanical stimulation is sufficient to allow at least one synaptic delay. (In the rat spinal motoneurone the latency difference between the start of the e.p.s.p. and spike generation is 0·88 msec $\pm$ 0·26 msec S.D. of the

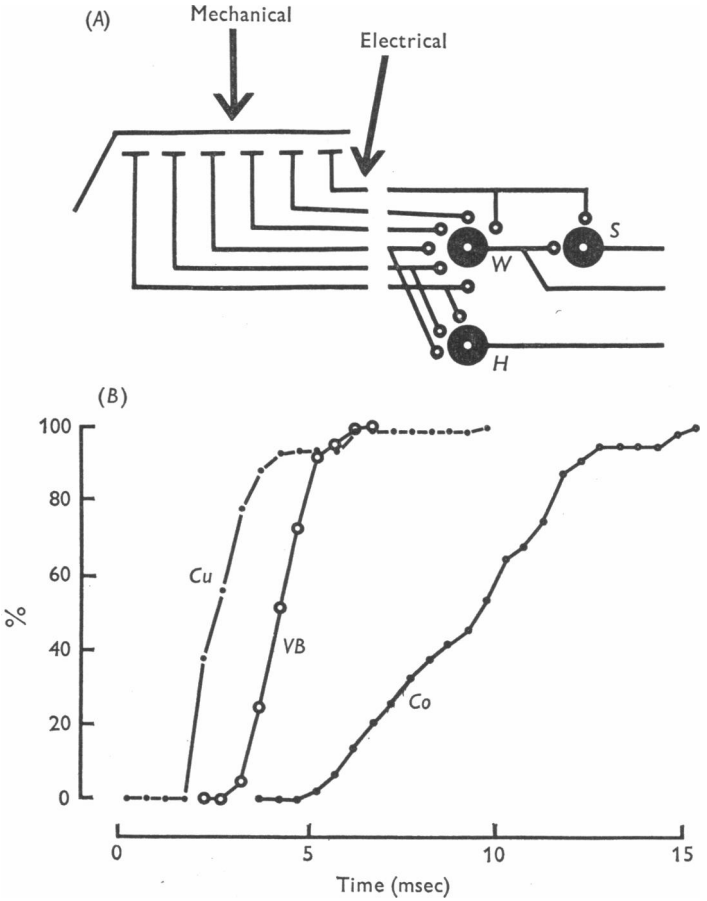

Fig. 11. *A*, Showing diagrammatically a postulated sequence of afferent input on to units whose receptive field consists of a whole pad (*W*), a half pad (*H*), or a spot on a pad (*S*). The break in the lines represents the prior processing at the cuneate nucleus. For further details see text.

B, Showing cumulative interval histograms of the latencies to peripheral electrical stimulation of populations of neurones in the cuneate nucleus (193 cells *Cu*), ventrobasal thalamic complex (147 cells *VB*) and somatosensory cortex (57 cells *Co*).

observation (Kaizawa & Takahashi, 1970); this is not the figure reported in their paper but is the result worked out from the data they present). Since there are few, if any, short axoned cells in the rat ventrobasal thalamus (Scheibel & Scheibel, 1966) the input from the whole pad cell to the 'spot' field cell is presumably via axon collaterals. If both types of cell project to the sensorimotor cortex they would give a sequential signal of pad contact followed by more precise information about the texture of that contact.

An array of such cells could possibly aid in sharpening the 'image' of the peripheral contact. Such a neuronal assembly might possibly explain why 'surround inhibition' is much less prevalent in the ventrobasal thalamus than in the dorsal column nuclei (Gordon & Manson, 1967; Poggio & Mountcastle, 1963). The 'spot' field cells, which may be described loosely, as 'showing' surround facilitation have their receptive fields located mainly on the distal edges of the wrist pads and over the glabrous digital tips. From observations of rats walking and feeding these two sites appear to be the first to come into contact with the ground, are used for holding food and would appear to form a functional palpating unit. It is not surprising that the evidence suggests that they also form a specialized sensory unit, at least in the ventrobasal thalamus.

It has been recognized for a long time that when the excitability of ventrobasal thalamic cells is tested at various times after an initial conditioning stimulus there exists a a prolonged period during which the cells are absolutely or relatively unresponsive. This lasts for as long as 100 msec in the deeply anaesthetized cat (Poggio & Mountcastle, 1963) and as long as 500 msec in the deeply anaesthetized rat (Angel, 1967). In spite of this, single cells in the ventrobasal thalamus will follow iterative electrical stimulation of the periphery at frequencies up to 75–100 per second (Rose & Mountcastle, 1959). With paired mechanical stimulation this unresponsive time is reduced and the diminution in the probability of discharge is much less marked to the second of a pair of stimuli (see Fig. 9). That this diminished unresponsiveness depends upon the manner of peripheral stimulation, rather than the size of the thalamopetal volley is clearly shown by the greater effectiveness of threshold electrical stimulation producing long-lasting inhibition than supramaximal stimulation. That this unresponsiveness is probably due to a corticothalamic inhibitory inflow as well as an intrinsic thalamic inhibition is suggested by the observation that the unresponsiveness is diminished, although not abolished, in the decorticate preparation and exacerbated by cortical hyperexcitability (Angel, 1963). That the cortex does exert a considerable tonic inhibitory influence over the ventrobasal thalamus, even in the deeply anaesthetized animal, is shown by the increased probability of discharge of thalamic cells responding either with a decreased latency or a reduction in the latency scatter, after removal of the cortex.

In the present experiments some 4000 penetrations were made passing through the ventrobasal thalamus in 304 animals; in no case did we find any cell which discharged with a high frequency comparable to those found by Andersen, Eccles & Sears (1964) in the cat thalamus. The cells they found they postulated to be either presynaptic or post-synaptic inhibitory neurones and implicated in the rhythmic phasing of discharge

of ventrobasal cells (approximately 10 Hz) after a peripheral stimulus. Since this rhythmic phasing was seen in the rat thalamus, particularly in the decorticate preparation, it either has a completely different mechanism of generation or the inhibitory neurones are not located within the confines of the ventrobasal thalamic complex, a suggestion supported by the anatomical observations of Scheibel & Scheibel (1966). We cannot, of course, be absolutely certain that the ventrobasal cells we studied were concerned solely in transmitting the cuneothalamic input to the cerebral cortex but their latencies of discharge were intermediate between those of cuneate and cortical cells with fields restricted to small areas of the contralateral forepaw (Fig. 11*b*).

Finally, we have referred throughout to the cells as being in the ventrobasal thalamic complex. Since their properties are the same as those found for the cat and monkey in the nucleus ventralis posterolateralis, *VPL* (see Rose & Mountcastle, 1959 for references) we would suggest that we can confidently call that portion of the ventrobasal thalamus from which cells with restricted peripheral fields on the contralateral limbs were found as ventralis posterolateralis. In addition it is possible on physiological grounds to find a fairly clear separation of the forepaw and hind paw projection areas and thus could split this nucleus into a lateral and medial part as ventralis posterolateralis lateral, *VPLl*, for the hind paw and ventralis posterolateralis medial, *VPLm*, for the forepaw with the coordinates given above (see Results). This would bring the nomenclature for this part of the rat thalamus into line with that suggested for the cat by Rinvik (1968).

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