J. Physiol. (1973), **228**, *pp.* 527–540
With 1 *plate and* 3 *text-figures*
Printed in Great Britain

SOMATOTOPIC ORGANIZATION OF VIBRISSAL RESPONSES IN THE VENTRO-BASAL COMPLEX OF THE RAT THALAMUS

BY PHIL M. E. WAITE

From the Department of Physiology, University College London, Gower Street, London, W.C. 1

(*Received 28 July 1972*)

SUMMARY

1. The region of the ventro-basal complex (VB) of the thalamus responding to movements of the whiskers has been mapped electrophysiologically in rats under either urethane or barbiturate anaesthesia.

2. Whisker responses were found in the dorso-medial part of VB throughout its rostro-caudal extent; they occupied one third to one half of the total VB region.

3. Most cells responded to movements of only one whisker and the responses were somatotopically organized. The different horizontal lines of whiskers were represented at different rostro-caudal levels within the nucleus, the most dorsal line being represented most caudally. At each level the larger, more caudal whiskers were represented more dorsally and laterally than the smaller, more rostral whiskers.

INTRODUCTION

The technique of mapping of cortical evoked potentials was first used by Marshall, Woolsey & Bard (1937, 1941) and Adrian (1941). Results from such experiments and similar ones on the thalamus led to the suggestion (Rose & Mountcastle, 1952) that the relative volume of neural tissue related to a particular skin area reflected the importance of that area for the animal. Since then, there have been numerous confirmations of this idea in many species (see, for instance, Woudenberg, 1970).

In rats, the complex structure of the whiskers (Vincent, 1913; Patrizi & Munger, 1966), the large size and number of the afferent nerve fibres supplying them (Vincent, 1913) and the large volume of cortex involved in vibrissal responses (Welker, 1968, 1971) indicated that the whiskers provide a particularly important sensory input. Recent studies on single units in the trigeminal ganglion (Zucker & Welker, 1969) and the trigeminal nucleus (Nord, 1968) have supported this idea, as have behavioural ones (Vincent, 1912; Welker, 1964).

At the thalamic level, although previous studies have indicated that a large region of the ventro-basal complex (VB) is involved in vibrissal responses (Davidson, 1965; Emmers, 1965), no studies have specifically concentrated on whisker responses. In this paper the somatotopic organization within the vibrissal region of VB, found by electrophysiological mapping experiments, is described. Later papers will describe the types of unitary responses found with controlled mechanical movements of the whiskers and with electrical stimulation of the motor nerve. Two preliminary reports of some of these results have already been published (Waite, 1969, 1972).

METHODS

The experiments were performed on thirty-two albino rats of either sex weighing 200–250 g. Most were anaesthetized with urethane (1·4 g/kg I.P.) but in a few cases Nembutal, given I.P. (initial dose, 40–50 mg/kg, followed by 2-hourly injections, 5–10 mg/kg), or a trichloroethylene-air mixture, given by inhalation, were used. A tracheal cannula was inserted and a craniotomy performed to expose about 7 mm^2 of cortex on the left side, 1–4 mm lateral and 1–4 mm behind bregma.

The animal was mounted in a stereotaxic head-holder with the vertical zero plane passing through the ear-bars and lambda; this is the same as that used by Albe-Fessard, Stutinsky & Libouban (1966). The rectal temperature was maintained at 37–38° C.

Recordings were made with glass micro-electrodes filled with an 18% solution of NaCl saturated with Fast Green dye (2 μm tip, 1–4 MΩ impedance). Signals were fed into a high-impedance input stage and then amplified and displayed on an oscilloscope (Devices, Ltd.; over-all decay time constant of the system was 0·8 msec) and monitored on a loudspeaker.

The whiskers and body surfaces were stimulated manually by light stroking with a glass probe or moving a single whisker with fine forceps. The whole extent of the vibrissal area of the ventro-basal complex was mapped by making a series of up to twenty vertical micro-electrode penetrations at 0·3 mm intervals in both the medio-lateral and rostro-caudal directions. For each penetration the micro-electrode was lowered through the brain, whilst manually stimulating the whiskers and body surface, until clearly drivable unit-cluster responses were encountered. The whisker or body area driving the cluster of units, and the depth, was noted; the track was continued, noting changes in receptive fields and depth until no more drivable responses occurred. The position of the track was then marked by the method of Thomas & Wilson (1965). In six initial experiments the positions and lengths of the whiskers on one side of the face were measured.

Histology

At the end of each mapping experiment the rat's vascular bed was perfused with saline followed by 10% formal saline, then the brain was dissected out and left in 10% formal saline for 24–48 hr. Serial frozen sections throughout VB were cut coronally at 30 or 60 μm, as parallel as possible to the original electrode tracks. The sections were stained with cresyl violet-acetate and the positions of the green spots, marking each track, measured under the microscope.

Accuracy

In each coronal section containing a spot, the position of the spot was measured as the distance from the mid line and the depth below the cortical surface; these measurements were accurate to within 0·1 mm. The rostro-caudal estimation of the position of the spot was made by a comparison of the sections with those in the atlas of Albe-Fessard *et al.* (1966) at two or three different planes throughout VB. The number of sections between these planes were counted and, since their thickness was known, the distance between them could be calculated. These distances were compared with those in the atlas and were always within $\pm 0{\cdot}1$ mm (in 5 mm, i.e. 2%).

Sometimes there was a discrepancy between the histological measurements, described above, and those made during the recording of responses. No tracks were used in which the histological measurements differed from those taken during recording by more than $\pm 0{\cdot}3$ mm in the rostro-caudal or medio-lateral directions, or more than $\pm 0{\cdot}5$ mm in the depth measurements. This corresponds to a maximum error, from the zero co-ordinate, of 10% for the depth and medio-lateral measurements and 6% for the rostro-caudal measurements. When the positions of responding cells in different animals were compared the maximum discrepancy was 10%. Since the discrepancy between the histological and recording measurements of positions is of the same order, it is impossible to decide whether this 10% variation is due to a true anatomical difference in the position of VB or to experimental error.

For constructing the maps the histological positions of the spots were used rather than the measurements of the electrode tracks made during the recording. This was done for four reasons:

(*a*) The spots were small and discrete (maximum diameter 50 μm) and it is unlikely that the whole spot had moved in position.

(*b*) Swelling or dimpling could give a false measurement of depth whilst recording. Where swelling of the exposed cortex had occurred, this was corrected in the histological measurement by measuring to the surface of the unexposed side.

(*c*) Shrinkage during the histology was not important; in initial control experiments in which two spots were made at different depths on the same track, no consistent differences were found between histological measurements and those made during recording.

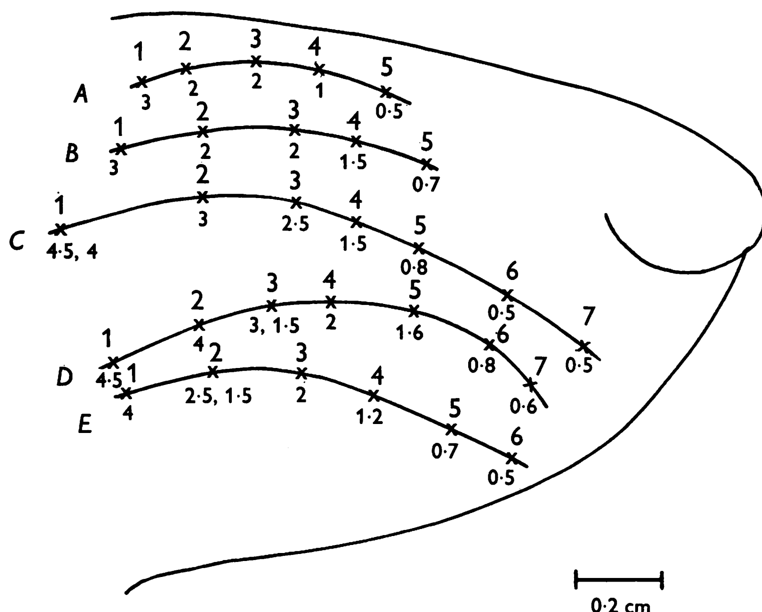
(*d*) Although a slight angling of the section would cause an under, or over, estimate of a measurement, sections were cut as parallel as possible to the plane of the electrode tracks and the deviation was never more than 5% ($\pm 0{\cdot}2$ mm in 5 mm or 4%). For the rostro-caudal measurement, an attempt was always made to estimate the plane at the position of the spot.

RESULTS

On the rat's face the whiskers lie along five horizontal lines with five to seven whiskers per line. In the early experiments, in which the position and length of all the whiskers were measured, it was found that the whisker positions were fairly constant in different rats and a typical layout is shown in Text-fig. 1. There are usually five whiskers on the two most dorsal lines and six to eight whiskers along the three lower lines. The lines were called *A* to *E* from dorsal to ventral and the whiskers along them 1 to 7 from caudal to rostral. A similar nomenclature was used by Zucker & Welker (1969) and Welker (1971). The longest whiskers are found most

caudally, lines *C* and *D* having the longest of about 4–5 cm. The whiskers get progressively shorter the more rostral their position on the line. Whiskers less than 0·5 cm long were not considered as they are hard to distinguish from the ordinary hairs. Occasionally two whiskers, usually of different lengths and thicknesses, emerge from the same orifice.

Pl. 1 is a photograph of one of the coronal sections through a rat's brain; it shows the position of the VB and also two of the green spots used for measuring the micro-electrode position.



Text-fig. 1. Plot of one side of a rat's face showing the positions of the whiskers (X) and the nomenclature used for referring to a whisker (letter, and numbers above lines). The number below each whisker indicates its length in cm. In some cases where two whiskers emerge from one orifice, the lengths of both are given.

Under urethane anaesthesia, within the vibrissal area of the ventro-basal complex, it was found that the majority of the cells were silent unless the whiskers were moved. When the whiskers were moved, clear 'driven' responses could be heard and seen. In any one part, the majority of cells were fired by movement of one whisker only and hence, by making a series of parallel electrode tracks, the extent of the whole region and the localization of different whiskers within the region could be mapped out. The maps were made from the mass response of a group of cells, not isolated single units. However, the length of track over which responses to one whisker were recorded was 50–400 μm, average 150 μm, while the change

from one whisker to the next extended over approximately 20 μm and therefore the mass response allowed quite sufficient resolution for the mapping.

The maps were constructed by plotting a series of graphs of depth against lateral measurements for the different rostro-caudal planes. The position of the electrode tracks, measured from the histology, were drawn in on these graphs, together with the whisker, or part of the body surface, firing the cells at each point. Altogether results from seven complete mapping experiments were used, five under urethane anaesthesia and two under barbiturate. The graphs from each experiment were combined and selected tracks from four rostro-caudal levels are shown in Text-fig. 2. The schematic projections of the region, shown in Text-fig. 3, have been constructed from the combined graphs and enable the organization to be more easily visualized.

It can be seen that the total vibrissal region extends from 4·3 to 5·7 mm anterior to lambda; from 2·5 to 3·5 mm laterally and lies between 4·2 and 5·9 mm below the cortical surface. This agrees well with the position of VB seen histologically in the present study (the outlines are drawn in Text-figs. 2 and 3) and shown in the atlas of Albe-Fessard *et al.* (1966). The vibrissal region comprises approximately the whole of the dorso-medial half of VB, throughout its rostro-caudal extent.

Text-figs. 2 and 3 also show that within the vibrissal region there is a remarkable degree of somatotopic organization. No obvious differences in the total area or organization were found between animals under urethane and those under barbiturate. However, under light levels of barbiturate the localization of responses was less obvious; although the unit-cluster responses at one point were predominantly from one whisker, adjacent whiskers commonly caused some responses as well.

The most dorsal line of whiskers (line A) was found to fire cells in the most caudal part of the nucleus, and more ventral lines fired successively more rostral cells. The most caudal whiskers (numbers 1 and 2) were found to fire the most dorsal and also the most lateral cells. Therefore, as a micro-electrode was moved deeper into the thalamus, cells were fired by successively more rostral whiskers and more medial tracks also tended to give responses from more rostral whiskers. No ipsilateral responses were seen although no systematic tests for these were made.

Under both urethane and barbiturate anaesthesia, the whiskers were nearly always stationary and the thalamic region was silent, without external stimulation. An attempt was also made in two experiments to map the region when the animal was anaesthetized with Trilene, under which the whiskers usually vibrate. However, it was found that the thalamic cells had a high level of background activity which made it hard

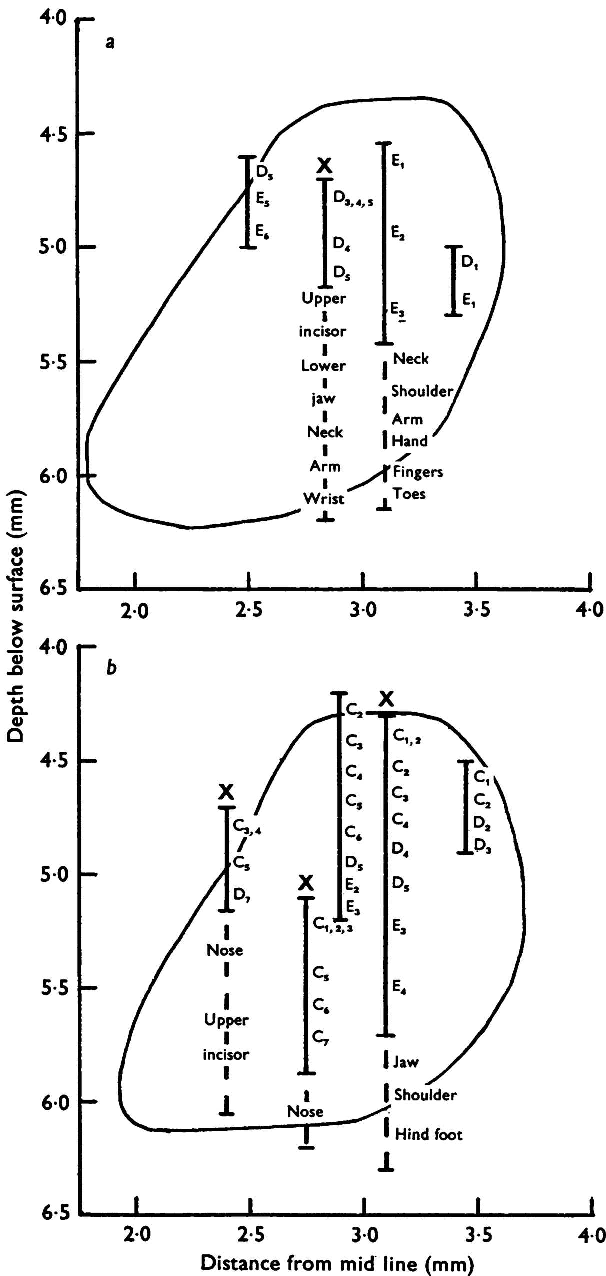


Fig. 2*a*, *b*

Text-fig. 2. Graphs of depth below the brain surface against the distance laterally from the mid line, for four rostro-caudal levels within VB: *a*, 5·2–5·6 mm rostral to lambda. *b*, 5·0–5·2 mm rostral to lambda. *c*, 4·6–4·8 mm rostral to lambda. *d*, 4·2–4·6 mm rostral to lambda. The outline of VB, averaged from coronal sections from three experiments, is shown at each level. The vertical lines show the regions from which somatic responses were

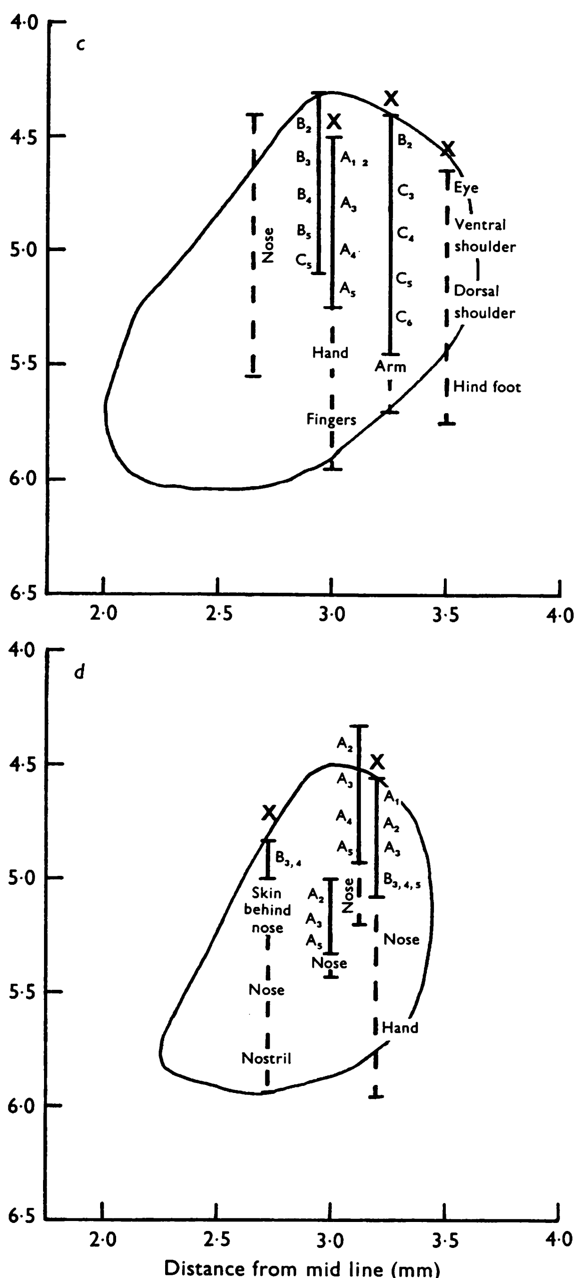


Fig. 2*c*, *d*

obtained, either from the whiskers (continuous line) or other areas (dashed line); the whisker or body area driving the cells is given at the side. The particular lines shown have been selected from ten to twenty micro-electrode tracks made at each level during seven experiments. Tracks from experiments under barbiturate anaesthesia are marked X; the others are from animals under urethane.

to distinguish evoked activity and thus prevented mapping in the way described for the other anaesthetics.

As a rather crude test of whether the larger, caudal whiskers had a relatively larger representation in the thalamus than the smaller rostral ones, a comparison was made between the lengths of the electrode tracks

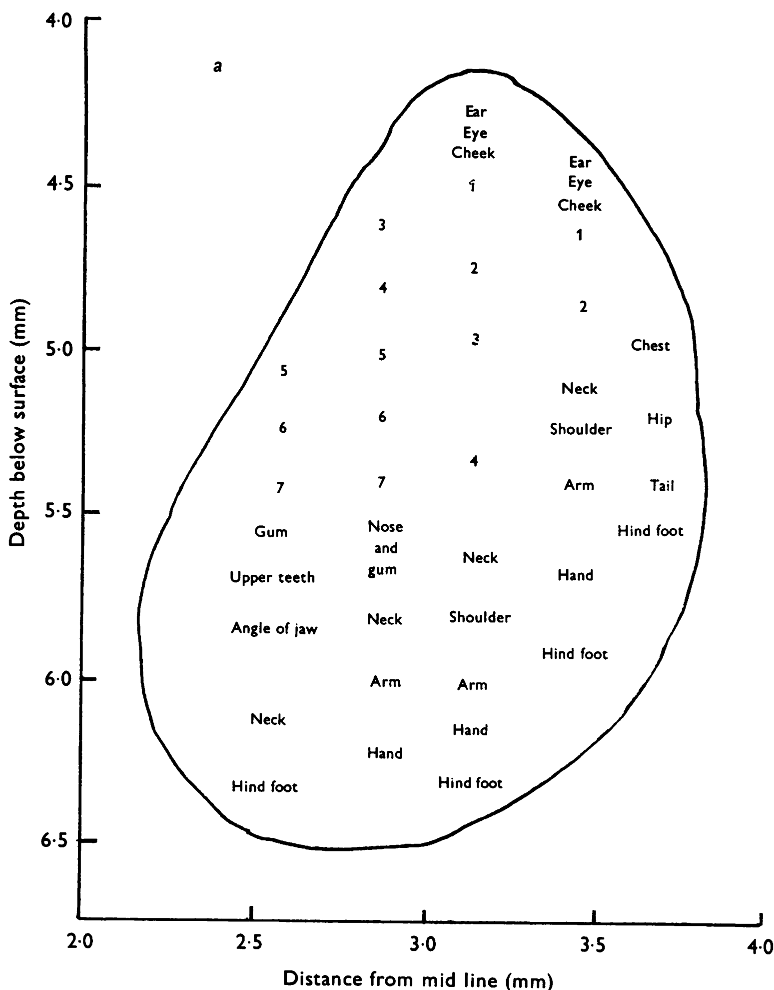


Fig. 3*a*. For legend see facing page.

associated with responses from all the number 1, 2 and 3 whiskers with those from whiskers 5, 6 and 7. The mean lengths for each group were 183 μm (S.E. $\pm$ 10·12 μm, $N = 82$) and 137 μm (S.E. $\pm$ 11·89 μm, $N = 45$) respectively. The difference between these two means is highly significant;

$P < 0{\cdot}01$. Although a greater length of track, on its own, is no conclusive proof that a greater volume, and hence, number of cells, is involved in the responses from the larger whiskers, it does at least suggest that this is probably the case.

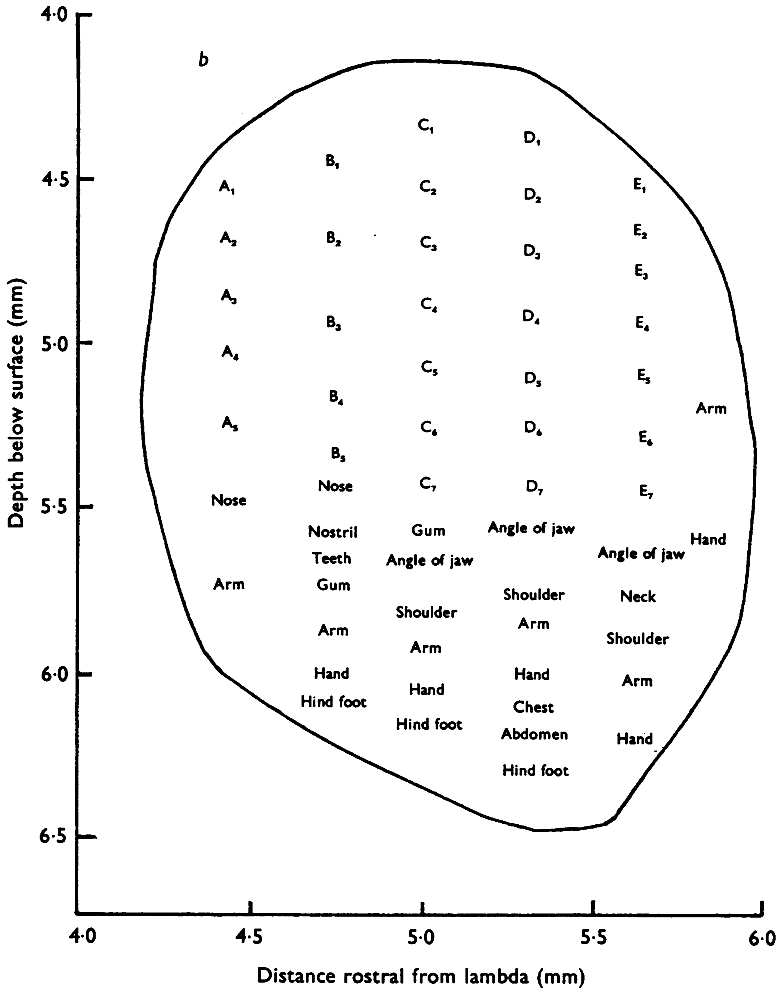


Fig. 3*b*

Text-fig. 3. Generalized layout of responses from the VB region, (*a*) for a coronal projection, plotting depth against the lateral measurement and (*b*) for a sagittal projection, plotting depth against the rostro-caudal measurement. The numbers and letters refer to the whiskers, with the nomenclature previously given. In each case the outline of VB is shown, in *a* from a section 5·1 mm rostral to lambda and in *b* calculated for 3·0 mm lateral.

DISCUSSION

The arrangement of the vibrissae on the face, found here, is similar to that reported in earlier studies in rats (Vincent, 1913; Zucker & Welker, 1969; Welker, 1971) and mice (Danforth, 1925). The region of the thalamus from which vibrissal responses were obtained agrees closely with the position of VB seen histologically, both in previous studies (Albe-Fessard *et al.* 1966) and in the present one.

Vibrissal responses have been found in the dorso-medial part of VB, throughout its rostral-caudal extent. This agrees with the general somatotopic organization of the thalamus found by other workers (e.g. Mountcastle & Henneman, 1949, 1952; Rose & Mountcastle, 1952) in which the face is represented medially (and the forelimbs and the hind limbs more laterally). It also agrees with previous maps specifically of the rat's thalamus (Davidson, 1965; Emmers, 1965). Emmers & Leeb (1963) and Emmers (1965) also reported a bilateral representation of the body, which they called S II, lying postero-laterally to S I; in the present study, the responses found on two tracks did not agree with the general somatotopic organization. Both of these tracks were dorsal and lateral and may have been from Emmer's S II area. However, ipsilateral stimuli produced no response and so it was thought more likely that the responses were from projection fibres in the internal capsule.

Vibrissal responses occupy one third to one half of the total VB complex. This disproportionately large representation occurs at other levels in rats (e.g. trigeminal nucleus, Nord, 1967; cortex, where it is 20 % of the total Sm I area, Welker, 1971). It presumably reflects the high innervation density and the importance of the vibrissae in rats.

A rough estimate of the volume of thalamus involved in responses from one of the larger whiskers can be obtained if one considers that the responses occupy a cylinder 300 μm in diameter and 183 μm long (which are the average figures from the mapping experiments). This gives a volume of 0·013 mm^3, which would enclose approximately 21,000 cells of 10 μm diameter. This compares with the value of 150 primary afferents per whisker given by Vincent (1913) and a volume of 0·9 mm^3 at the cortex, calculated from Welker's estimate of an area of 0·6 mm^2 per whisker on the cortical surface (1971).

The organization within the vibrissal region is remarkable. The overall arrangement is consistent with other areas of the body in that distal (most rostal) whiskers drive more ventral cells, as do distal parts of the limbs (Mountcastle & Henneman, 1949). No histological evidence of the lamellae seen in the thalamus of certain other mammals, e.g. cat, dog, raccoon and spider monkey (Welker & Johnson, 1965; Pubols, 1968) was found

here; nor have previous studies reported lamellae in the rat thalamus. The lamellae in the raccoon and spider monkey separated different body areas (e.g. forepaw digits in the raccoon; arm, hind foot and tail in the spider monkey) and during one micro-electrode penetration there were sometimes disjunctive shifts in the position of the receptive fields of the cells, to a different body area. These were attributed to the micro-electrode crossing a lamella. In the present study there was usually a continuous shift in receptive field, from one whisker to an adjacent one, either on the same line or just above or below on an adjacent line; there were seldom 'jumps' to a non-adjacent whisker. However, in the cortex in the rat (Welker, 1971) and mouse (Woolsey & Van der Loos, 1970) each whisker does seem to be related to an anatomically distinct group of cells.

Most cells studied here were found to respond to movement of only one whisker. A similar localization to a single whisker is found in the afferent nerve fibres from rats' whiskers (Zucker & Welker, 1969) as well as those from cats' whiskers (Darian-Smith, Rowe & Sessle, 1968; Kerr & Lysak, 1964; Hahn, 1971) and from the anatomically similar carpal sinus hairs (Nilsson, 1969). At the trigeminal level, the only study in rats (Nord, 1968) states that receptive fields of vibrissal cells varied from one to eighteen whiskers but gives no figure for the relative proportions of cells with different size fields. In cats, some reports indicate that convergence occurs at the trigeminal level. For instance, Gordon, Landgren & Seed (1961) reported that only ten out of thirty-two cells were localized to one whisker; Eisenman, Landgren & Novin (1963) found 48% of the cells in principalis went to one or two whiskers, but in oralis half the cells had fields extending over all the whiskers; Darian-Smith, Rowe & Sessle (1968) found receptive fields of trigeminal cells to be 3 to 30 times larger than those of the afferent nerve fibres. However, other workers state that most cells responded to movement of only one whisker (Kruger & Michel, 1962).

The situation in rats may well differ from that in cats. The localization may also be dependent on the anaesthetic used and its depth. For the cat studies mentioned above, Gordon *et al.* and Eisenman *et al.* used barbiturate, Kruger & Michel used decerebrate animals, and Darian-Smith *et al.* used implanted electrodes in unanaesthetized animals. The reported effects of barbiturate on receptive field sizes are also conflicting. Towe & Kennedy (1961) and Ohye & Narabayashi (1971) reported a decrease in receptive field sizes in the presence of barbiturate (compared with the sizes without any anaesthetic present), while Poggio & Mountcastle (1963) found the sizes were unaltered by barbiturate. Lastly, the localization may well vary with the rostro-caudal position within the trigeminal nucleus. However, this does not seem a likely explanation for the differences reported above since Kruger & Michel looked at all levels and Darian-Smith *et al.* (1968)

recorded in caudalis (as did Gordon *et al.* 1961) and oralis (as did Eisenman *et al.* 1963).

Although the situation in the trigeminal nucleus, regarding localization, is unclear, in VB it is certainly very precise. This, again, may be an artifact of anaesthesia and this is supported by the fact that localization was rather less clear with light levels of barbiturate. However, in monkeys under either chloralose (Albe-Fessard & Bowsher, 1965) or unanaesthetized (Poggio & Mountcastle, 1963) the somatotopy within the thalamus is reported to be very clear. Also, the anatomical as well as the functional subdivisions of cells responding to each vibrissa reported in the cortex (Welker, 1971) suggests that localization may well be maintained at lower levels.

No surround inhibition or modification of a response by stimulation of adjacent down hairs or whiskers was noted but no careful testing for this was carried out. Kruger & Michel (1962) failed to find any surround inhibition for vibrissae at the trigeminal nucleus in cats, although it is present for ordinary hair responses at the dorsal column nuclei (Perl, Whitlock & Gentry, 1962; Gordon & Paine, 1960). Surround inhibition is usually considered to be a mechanism for localization and may not occur in the vibrissal sensory path because the large number of cells involved, and the lack of marked convergence, maintain the localization (to single whiskers) found in the affrent nerve fibres.

I should like to thank the Medical Research Council for the grant under which this work was done and also Professor D. G. Dawson for his invaluable advice.

REFERENCES

ADRIAN, E. D. (1941). Afferent discharges to the cerebral cortex from peripheral sense organs. *J. Physiol.* **100**, 159–191.

ALBE-FESSARD, D. & BOWSHER, D. (1965). Responses of monkey thalamus to somatic stimuli under chloralose anaesthesia. *Electroen. Neurophysiol.* **19**, 1–15.

ALBE-FESSARD, D., STUTINSKY, F. & LIBOUBAN, S. (1966). *Atlas Stéréotaxique du Diencéphale du Rat Blanc.* Paris: Editions du Centre National de la Recherche Scientifique.

DANFORTH, C. H. (1925). Hair in its relation to questions of homology and phylogeny. *Am. J. Anat.* **36**, 47–68.

DARIAN-SMITH, I., ROWE, M. J. & SESSLE, B. J. (1968). 'Tactile' stimulus intensity: information transmission by relay neurons in different trigeminal nuclei. *Science N.Y.* **160**, 791–794.

DAVIDSON, N. (1965). The projection of afferent pathways on the thalamus of the rat. *J. comp. Neurol.* **124**, 377–390.

EISENMAN, J., LANDGREN, S. & NOVIN, N. (1963). Functional organization in the main sensory trigeminal nucleus and in the rostral subdivision of the nucleus of the spinal trigeminal tract in the cat. *Acta physiol. scand.* **59**, suppl. 214.

EMMERS, R. (1965). Organization of the first and second somesthetic regions (S I and SII) in the rat thalamus. *J. comp. Neurol.* **124**, 215–228.

EMMERS, R. & LEEB, I. J. (1963). Patterns of somesthetic representation in S I and S II in rat thalamus. *Fedn Proc.* **22**, 394.

GORDON, G., LANDGREN, S. & SEED, W. A. (1961). The functional characteristics of single cells in the caudal part of the spinal nucleus of the trigeminal nerve of the cat. *J. Physiol.* **158**, 544–559.

GORDON, G. & PAINE, C. H. (1960). Functional organization in nucleus gracilis of the cat. *J. Physiol.* **153**, 331–349.

HAHN, J. F. (1971). Stimulus-response relationships in first-order sensory fibres from cat vibrissae. *J. Physiol.* **213**, 215–226.

KERR, F. W. L. & LYSAK, W. R. (1964). Somatotopic organization of trigeminal ganglion neurones. *Archs Neurol. Psychiat., Chicago* **11**, 593–602.

KRUGER, L. & MICHEL, F. (1962). Reinterpretation of the representation of pain based on physiological excitation of single neurons in the trigeminal sensory complex. *Expl Neurol.* **5**, 157–178.

MARSHALL, W. H., WOOLSEY, C. N. & BARD, P. (1937). Representation of tactile sensibility in the monkey's cortex as indicated by cortical potentials. *Am. J. Physiol.* **119**, 372–373.

MARSHALL, W. H., WOOLSEY, C. N. & BARD, P. (1941). Observations on cortical somatic sensory mechanisms of the cat and monkey. *J. Neurophysiol.* **4**, 1–25.

MOUNTCASTLE, V. B. & HENNEMAN, E. (1949). Pattern of tactile representation in the thalamus of the cat. *J. Neurophysiol.* **12**, 85–100.

MOUNTCASTLE, V. B. & HENNEMAN, E. (1952). Representation of tactile sensibility in the thalamus of the monkey. *J. comp. Neurol.* **97**, 409–441.

NILSSON, B. Y. (1969). Structure and function of tactile hair receptors on the cat's foreleg. *Acta physiol. scand.* **77**, 396–416.

NORD, S. G. (1967). Somatotopic organization in the spinal trigeminal nucleus and the dorsal column nuclei and related structures in the rat. *J. comp. Neurol.* **130**, 343–356.

NORD, S. G. (1968). Receptor field characteristics of single cells in the rat spinal trigeminal complex. *Expl Neurol.* **21**, 236–243.

OHYE, C. & NARABAYASHI, H. (1971). Sensory transmission in the human thalamus. *Proc. Int. Union Physiol. Sci.* **9**, 428.

PATRIZI, G. & MUNGER, B. L. (1966). The ultrastructure and innervation of rat vibrissae. *J. comp. Neurol.* **126**, 423–436.

PERL, E. R., WHITLOCK, D. G. & GENTRY, J. R. (1962). Cutaneous projection to second-order neurones of the dorsal column system. *J. Neurophysiol.* **25**, 337–358.

POGGIO, G. F. & MOUNTCASTLE, V. B. (1963). The functional properties of ventrobasal thalamic neurons studied in unanaesthetized monkeys. *J. Neurophysiol.* **25**, 775–806.

PUBOLS, L. M. (1968). Somatic sensory representation in the thalamic ventrobasal complex of the spider monkey (Ateles). *Brain Behav. Evol.* **1**, 305–323.

ROSE, J. & MOUNTCASTLE, V. B. (1952). The thalamic tactile region in the rabbit and cat. *J. comp. Neurol.* **97**, 441–490.

THOMAS, R. C. & WILSON, V. J. (1965). Precise localization of Renshaw cells with a new marking technique. *Nature, Lond.* **206**, 211–213.

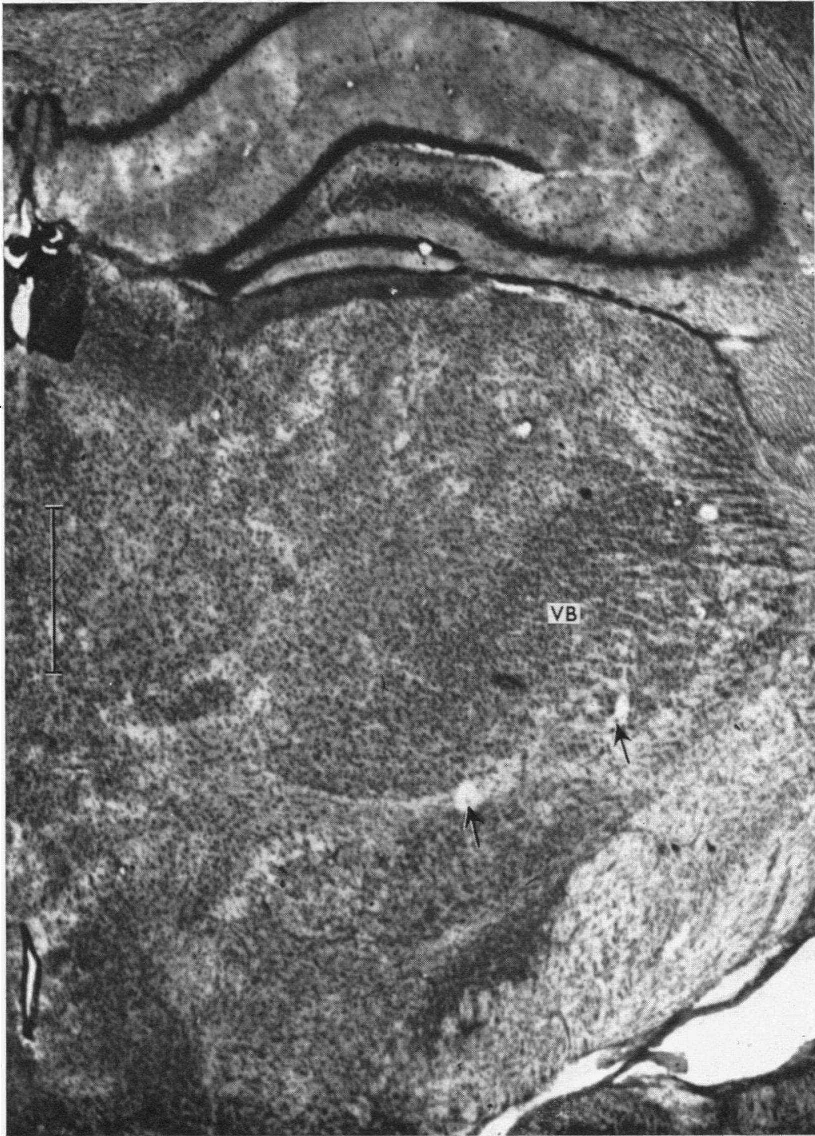
TOWE, A. L. & KENNEDY, T. (1961). Response of cortical neurones to variations of stimulus intensity and locus. *Expl Neurol.* **3**, 570–587.

VINCENT, S. B. (1912). The function of the vibrissae in the behavior of the white rat. *Behav. Monogr.* **1**, no. 5, 1–85.

VINCENT, S. B. (1913). The tactile hair of the white rat. *J. comp. Neurol.* **23**, 1–38.
WAITE, P. M. E. (1969). Organization of whisker responses in the rat thalamus. *J. Physiol.* **202**, 51–53*P*.
WAITE, P. M. E. (1972). Unitary responses in the rat's ventro-basal complex to ramp-shaped movements of the whiskers. *J. Physiol.* **222**, 59–60*P*.
WELKER, W. I. (1964). Analysis of sniffing of the albino rat. *Behaviour* **22**, 223–244.
WELKER, C. (1968). Microelectrode delineation of fine grain somatotopic organization of SmI cerebral neocortex in albino rat. *Anat. Rec.* **160**, 449.
WELKER, C. (1971). Microelectrode delineation of fine grain somatotopic organization of SmI cerebral neocortex in albino rat. *Brain Res.* **26**, 259–275.
WELKER, W. I. & JOHNSON, Jr. J. I. (1965). Correlation between nuclear morphology and somatotopic organization in the ventro-basal complex of the raccoon's thalamus. *J. Anat.* **99**, 761–790.
WOOLSEY, T. A. & VAN DER LOOS, H. (1970). The structural organization of layer IV in the somatosensory region (SI) of mouse cerebral cortex. *Brain Res.* **17**, 205–242.
WOUDENBERG, R. (1970). Projections of mechanoreceptive fields to cuneate-gracile and spinal trigeminal nuclear regions in sheep. *Brain Res.* **17**, 417–437.
ZUCKER, E. & WELKER, W. I. (1969). Coding of somatic sensory input by vibrissae neurons in the rat's trigeminal ganglion. *Brain Res.* **12**, 138–156.

EXPLANATION OF PLATE

Photograph of part of a coronal section through a rat's brain at 7·45 mm rostral to lambda. The section was stained with cresyl violet-acetate. The position of the ventro-basal complex (VB) can be seen. The arrows mark two green spots which were used for measuring the micro-electrode position on two tracks. The bar indicates 1 mm.


VB