J. Physiol. (1961), **155**, *pp.* 589–601
With 1 *plate and* 4 *text-figures*
Printed in Great Britain

AN INVESTIGATION OF NUCLEUS GRACILIS OF THE CAT BY ANTIDROMIC STIMULATION

BY G. GORDON AND W. A. SEED*
From the University Laboratory of Physiology, Oxford

(*Received* 7 *November* 1960)

It can be assumed that the dorsal column nuclei and medial lemniscus provide an orderly system of topographical projections through which information from the whole body surface reaches the thalamus. A particular part of the body is 'represented', throughout the long axis of nucleus gracilis, by a rostral section whose cells have large receptive areas, a middle section with small receptive areas and considerable mutual inhibition, and a caudal section with intermediate receptive areas (Gordon & Paine, 1960). These sections differ functionally; and we felt that an investigation of their projections, in the lemniscus and elsewhere, would help one to understand the meaning of this arrangement. It would also help to show in what form the thalamus receives its information.

Antidromic stimulation is a useful means of studying projections (see, e.g. Lundberg & Oscarsson, 1959), and its analytical value in studying the organization of nucleus cuneatus has been shown by Amassian & de Vito (1957). In this paper we describe antidromic excitation from the medial lemniscus and cerebellum: a brief description of the results was given earlier (Gordon & Seed, 1960).

METHODS

All the experiments were done with cats anaesthetized with sodium pentobarbitone. External records were made from single cells in nucleus gracilis with glass micropipettes, filled with 3 M-KCl and with a resistance at 50 c/s of 3·5–7 MΩ. The techniques for exposing the nucleus, for holding the animals and for inserting the electrodes, have been described in detail in a previous paper (Gordon & Paine, 1960).

Orthodromic stimulation

The size and distribution of the peripheral receptive area of each cell which responded to tactile stimulation of the skin was investigated by moving hairs with a glass rod or touching bare skin (e.g. the pads of the foot) with a camel-hair brush. When accurate timing of a tactile stimulus was needed, the electro-mechanical transducers described by Gordon & Paine (1960) were used.

Antidromic stimulation

In all experiments attempts were made to activate individual cells in nucleus gracilis antidromically by stimulating electrically at sites to which their axons might project (either

* M.R.C. Scholar.

the medial lemniscus or the anterior lobe of the cerebellum). Stimuli could be applied singly, in pairs, or in brief high-frequency trains. They were square pulses of 60 μsec duration, isolated from earth by transformer coupling.

Medial lemniscus. Stimuli were applied through buried electrodes. The electrode holder consisted of five parallel stainless-steel tubes, 23 mm long and spaced 1·25 mm apart, clamped between two suitably grooved Perspex plates. The tubes, which were used as guides, had an internal bore just allowing passage of an insulated steel needle of about 0·6 mm diameter. A number of these needles were prepared before each experiment: they were adjusted by attaching 'stops' of solder near the eye, so that when the needles were pushed home into the guides some 28 mm of shaft projected beyond the lower end of the guides and their tips were level. The electrodes used for stimulation were insulated with varnish except for about 1 mm at the tip, the diameter of this terminal millimetre being about 0·15–0·2 mm.

A preliminary exploration was always made with a recording electrode inserted in the centre tube of the electrode holder. This electrode was a steel needle similar to those described above, but insulated up to its tip and more finely tapered: the resistance of such electrodes in Ringer's solution was 20–30 kΩ. The electrode was inserted by a manipulator aligned on Horsley–Clarke co-ordinates into the probable position of the medial lemniscus at the caudal end of the thalamus. Brushing sounds heard in the loudspeaker on tactile stimulation of the contralateral hind limb were a guide to the position of the lemniscus. In frontal planes 4–5 the most satisfactory responses were usually found 5–7 mm from the mid line and 17–20 mm deep to the cortical surface. When this position had been found, the recording electrode was removed, and stimulating electrodes were inserted into the guides of the electrode holder. In early experiments one stimulating electrode was placed on either side of the recording site (electrode separation 2·5 mm). In later experiments five stimulating electrodes were inserted in a transverse row, the middle one through the guide previously occupied by the recording electrode (electrode separation 1·25 mm). Some needles fitted rather loosely in the guides, so that their tips did not always have the equidistant spacing of the guides themselves: this accounts for irregularities in the spacing of the tracks in Text-fig. 3*a*, and also for electrode 3 in this figure not coinciding transversely with the position of the recording electrode. A system was available whereby stimuli could be applied between any two adjacent electrodes, with reversible polarity. The positions of the electrodes were afterwards found histologically.

Cerebellum. In this preliminary investigation the only region explored by stimulation was a small area of the cortex of the anterior lobe. This area corresponded to the region in which Adrian (1943) and Snider & Stowell (1944) found responses to tactile stimulation of the hind limbs.

The occipital pole of the cerebral hemisphere was removed by suction, and the anterior lobe of the cerebellum exposed by nibbling away part of the bony tentorium cerebelli with bone forceps. After opening the cerebellar dura it was usually possible to see the lateral part of the first seven or eight folia of the anterior lobe. The wound was then filled with warm paraffin.

The cortex was stimulated through a pair of silver-ball electrodes about 3 mm apart, placed on the surface of the 6th and 7th folia. The site from which responses could be obtained at lowest threshold was found by making small adjustments of position.

Measurement and notation. The positions of responses in the rostrocaudal dimension of nucleus gracilis are given on a scale of millimetres, zero being the rostral border of the nucleus (see Gordon & Paine, 1960).

RESULTS

All our observations from nucleus gracilis were of single neural units; and we propose, for reasons given before (Gordon & Paine, 1960), to refer

to these responding units as cells. We have confined ourselves here to cells with cutaneous receptive areas wholly or partially upon the hind foot, below the ankle. Nucleus gracilis may be divided, from the point of view of the receptive areas of its cells, into three sections; and we shall refer throughout to the following mean figures for the receptive areas of the cells in the different sections: rostral section (0–4 mm) 58·9 SE. $\pm$ 8·7 cm^2 (n = 115); middle section (4–7 mm) 4·6 $\pm$ 0·98 cm^2 (130); and caudal section (7–12 mm) 15·0 $\pm$ 3·2 cm^2 (94). The difference between these figures and those given by Gordon & Paine (1960) depends only on a different method of expression of the same data.

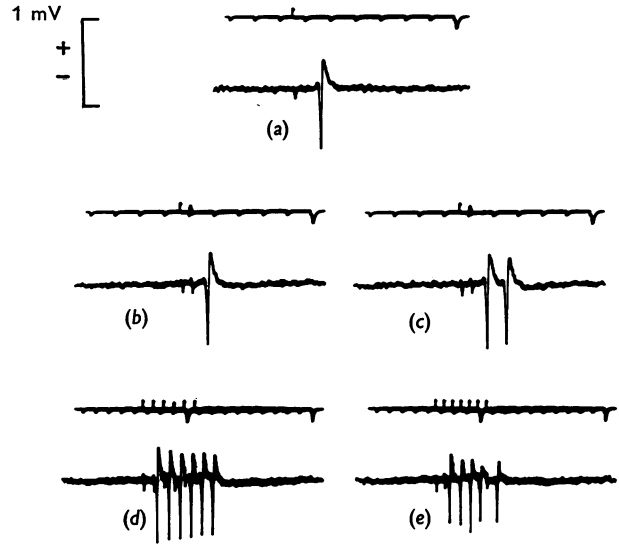
The cutaneous receptive areas of cells in nucleus gracilis are distributed over a very wide range, the ratio between the largest and the smallest being approximately 1:1000. It was convenient to classify these receptive areas into groups with limits successively doubling (0·5–1 cm^2, 1–2 cm^2, 2–4 cm^2, etc.). Areas measured during experiments are necessarily approximate, and such a method of grouping covers the range satisfactorily. The best way of presenting these data would be in the form of 12 histograms, expressing the distribution of receptive areas in each of the 12 1-mm steps along the nucleus. Text-fig. 1 of Gordon & Paine (1960) presents the data in a very compressed form, using mean figures for receptive area in each 1-mm step which are geometric means, giving less weight to individual observations of large receptive area. This figure expresses the general situation conveniently; but arithmetic means would give better values for the mean receptive areas. The figures given above are therefore derived from arithmetic means, using the convention that all areas in the group 0·5–1 cm^2 were 0·75 cm^2, all in the group 1–2 cm^2 were 1·5 cm^2, etc.

Interpretation of responses to lemniscal and cerebellar stimulation

Antidromic excitation. The great majority of responses formed a group with properties which strongly suggested that they resulted from antidromic excitation. In this case a single shock to the lemniscus or cerebellum evoked a response consisting of only one spike (Text-fig. 1*a*). The threshold for this spike was constant; and its latency varied by no more than 3 %, without any relation to the strength of the shock. In the population fired in this way by lemniscal stimulation, the latencies were distributed between 0·86 and 2·85 msec, 75 % lying between 1 and 2 msec. In the population fired by cerebellar stimulation, latencies lay between 1·0 and 1·9 msec.

The period of unresponsiveness following a spike was tested by pairs of shocks, the second following the first at progressively shorter intervals, with both shocks at twice threshold strength (Text-fig. 1*b* and *c*). The earliest response to a second shock occurred with shock intervals ranging between 0·4 and 0·9 msec in the population studied. In the response to a brief high-frequency train of shocks (Text-fig. 1*d* and *e*) the stimulus frequency was followed accurately, for the first five shocks, up to maxima between 670 and 1320 shocks/sec, with a mean maximum frequency for

the population of about 900/sec. It is unlikely that responses with properties of this kind are mediated synaptically. There is no definite upper limit to the frequency which can be followed in a synaptic system; but the highest we have seen recorded was 640/sec, in a spinal interneurone excited monosynaptically (Eccles, Fatt & Landgren, 1956). All our maxima are higher than this; and Amassian & de Vito (1957) give 380/sec as the maximum frequency followed by comparable cells in nucleus cuneatus in response to synaptic excitation through the dorsal columns.



Text-fig. 1. Antidromic responses of a cell in the rostral section of nucleus gracilis to lemniscal stimulation. Threshold was 0·6 V, and all records were made with twice-threshold shocks. (*a*) response to a single shock, latency 1·0 msec; (*b*) and (*c*) responses to pairs of shocks set at a critical interval giving two responses in approx. 50 % of observations, interval 0·4 msec; (*d*) and (*e*) responses to trains of shocks at 1220/sec and 1490/sec respectively. Time markers at 1 and 10 msec intervals appear on the upper trace of each record, projecting downwards: the upward-projecting marks on the same traces signal the stimuli.

Trans-synaptic excitation. A minority of our responses failed to satisfy any of the criteria of antidromic conduction which have just been given, and we have assumed that these responses were mediated synaptically. The responses were of longer latency, falling between 3·3 and 22 msec; and latency usually shortened with increasing strength of shock. The response to a single shock was sometimes repetitive. The period of unresponsiveness after a single shock, measured in the same way as before, was 1·5–4·5 msec; and frequency-following was poor, the highest recorded being 540/sec, with the rest considerably lower than this. Trans-synaptic responses were

seen with lemniscal but not with cerebellar stimulation, and their thresholds were comparable with those of antidromic responses from the lemniscus in the same experiment.

Evidence establishing that responses can be attributed to stimulation of the medial lemniscus

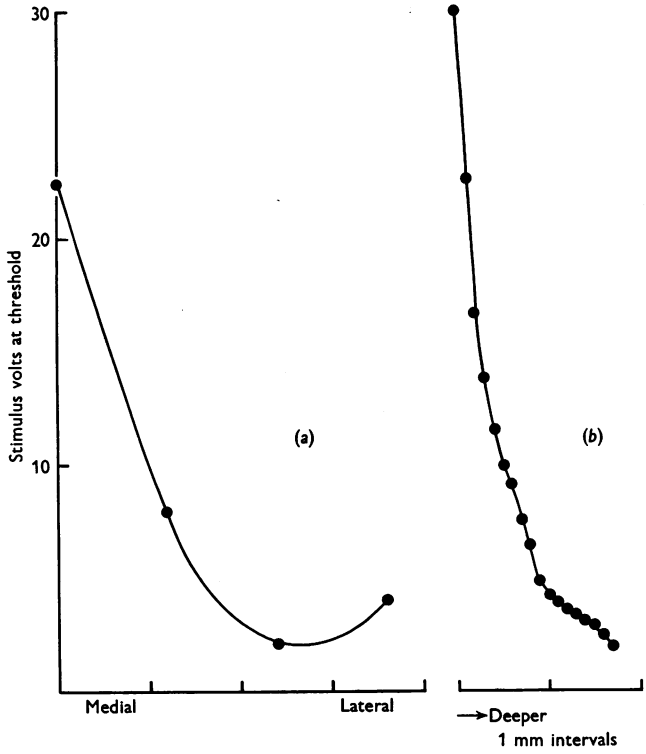
The anatomical complexities of the thalamus and mid-brain make it specially important to identify both the position occupied by stimulating electrodes inserted here and also if possible the particular structures whose stimulation gave rise to the responses that were seen. In this case we were able to show that the points from which responses were elicited at lowest threshold were grouped together in a circumscribed region corresponding closely to the known position of the medial lemniscus.

In experiments conducted specially for this purpose a transverse row of five stimulating electrodes was inserted in the caudal thalamus. It was reasonable to suppose that the lemniscus lay at about the centre of this row and at about the same depth as the tips of the electrodes (see Methods). For each cell which responded antidromically in the contralateral nucleus gracilis, the threshold for stimulation was found between each adjacent pair of electrodes in turn, giving a set of four readings from which a graph was constructed (see Text-fig. 2*a*). Reversal of the polarity of the stimulus allowed another set of four readings to be made, giving another curve with its minimum slightly displaced to one side following the slightly changed distribution of cathodal currents. All the complete curves were strikingly uniform, threshold rising approximately exponentially from its minimum with distance, and being rather more than doubled 1 mm away. A similar relationship probably exists when the spatial co-ordinate is vertical; but in our case such measurements could only be made by moving the electrodes more deeply or superficially through the brain, with some consequent drag on the whole tissue. The curve in Text-fig. 2*b* was obtained by withdrawing the electrodes in measured steps, using the pairs of electrodes giving the lowest threshold in the transverse plane.

The sets of threshold readings from one such experiment, with a transverse row of electrodes, are given in Table 1. The reading representing the lowest measured threshold in each set is marked with an asterisk, and it will be seen that most of these minimum readings are related to electrode 3, and the remainder to electrode 4, as cathode. Plate 1 shows a photomicrograph of a section of the brain of this animal, cut in the plane of the stimulating electrodes; and Text-fig. 3*a* is a tracing of this photograph showing the positions of the electrodes, numbered as they are in Table 1. Text-fig. 3*b* is a figure re-drawn from Ranson & Ingram (1932), showing the position and size of the degenerated medial lemniscus at this level. It

is clear from these figures that the area of tissue which lies between the two minimum-threshold electrodes must include, and is probably identical with, the medial lemniscus.

This localization and grouping of minimal-threshold points was found in all our later experiments in which a transverse grid of electrodes was used,



Text-fig. 2. Graphs showing the change in threshold for the antidromic response of a single cell in nucleus gracilis, occurring with change of stimulus position in the caudal thalamus.

(*a*) Threshold changes with alterations of transverse position. The abscissal positions of the four points give the transverse spacing of the four electrodes used successively as cathodes.

(*b*) Threshold changes for another cell with alteration of vertical position. The electrodes were withdrawn in steps from the lowest-threshold point.

and from these experiments some 35 % of our experimental results were obtained. Histological evidence from almost all the earlier experiments in which responses resulted from stimulating this region showed that the single pair of electrodes embraced the probable position of the lemniscus with much the same precision. In one experiment where the thresholds were of the order of 15–20 V, the electrode tips were afterwards found to

have been about 1 mm too superficial. As we developed experience of this technique and learned to adjust the depth of the electrodes to a position giving uniformly low thresholds, the proportion of cells in nucleus gracilis which could be fired antidromically increased slightly but significantly. It is of some interest that such small adjustments of depth, combined with selection of the appropriate electrodes when a row of these had been inserted, always lowered the threshold for an individual cell to values between 0·6 and 1·0 V with the stimulating pulses and conditions described.

TABLE 1. Thresholds (V) for antidromic excitation of cells in nucleus gracilis by lemniscal stimulation, related to the transverse position of the stimulating cathode

Cell no.	No. of electrode used as cathode					Anode medial (*M*) or lateral (*L*) to cathode
	1	2	3	4	5	
1	—	9·2	3·9*	5·2	33·6	*M*
	24·9	5·5	2·2*	20·0	—	*L*
2	—	14·0	2·1*	2·7	7·2	*M*
	33·9	6·4	1·1*	2·3	—	*L*
3	—	32·9	6·4*	8·9	15·6	*M*
	46·7	24·4	3·2*	8·7	—	*L*
4	—	14·0	4·4	3·0*	4·8	*M*
	—	—	—	—	—	—
5	—	8·2	1·8†	1·8†	—	*M*
	31·4	3·8	0·7	—	—	*L*
6	—	19·3	4·8	2·7†	—	*M*
	45·0	15·0	2·3†	—	—	*L*

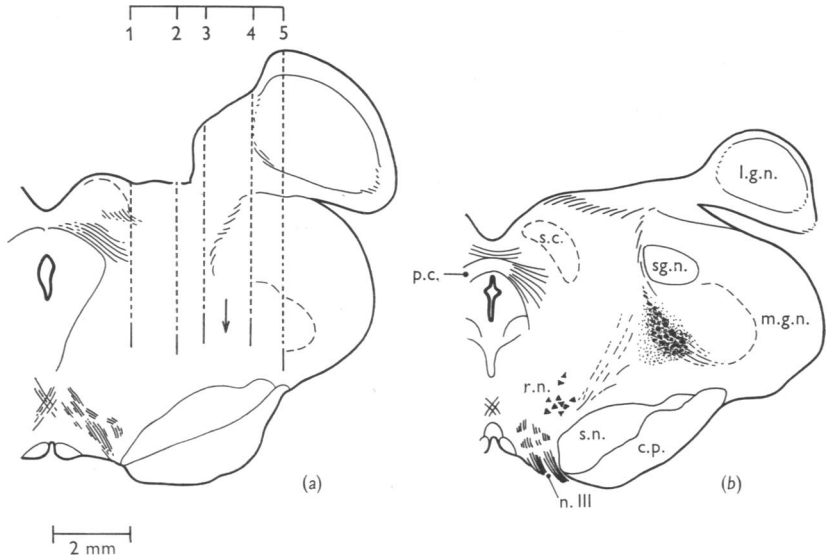
The numbers given to the electrodes (1–5) correspond to those in Text-fig. 3(*a*), which deals with the same experiment. All cells for which such data were obtained in this experiment are included. Incomplete or missing series are due to the loss of the cell through damage. * indicates the lowest-threshold point in series where a minimum was established. † indicates the lowest-threshold point in incomplete series: these values are so low that they must be at or very near the true minimum.

Distribution of antidromic and trans-synaptic responses in nucleus gracilis

We have tried as far as possible to examine the responses of cells over the whole of the rostral 12 mm of nucleus gracilis, within which functional differentiation has been shown by Gordon & Paine (1960). Particular attention was given to antidromic excitation from the contralateral medial lemniscus. The results of this investigation are summarized in Text-fig. 4.

Antidromic lemniscal responses. It was found that cells in all parts of nucleus gracilis could be fired antidromically from the contralateral lemniscus. No such responses were seen in a limited search in the nucleus of the other side (i.e. ipsilateral with respect to the lemniscal electrodes), and it may be assumed that ipsilateral projections are sparse or absent. The great majority of cells in the *middle* section of the nucleus (between 4 and

7 mm from the rostral end) were fired. Of all the cells studied here, 83% were fired (see Text-fig. 4*a*); but with the slightly improved technique of the later experiments this figure increased to 93% (of 45 cells). The percentage from these later experiments is stressed here and elsewhere because of this improved technique. The cells in this part of the nucleus



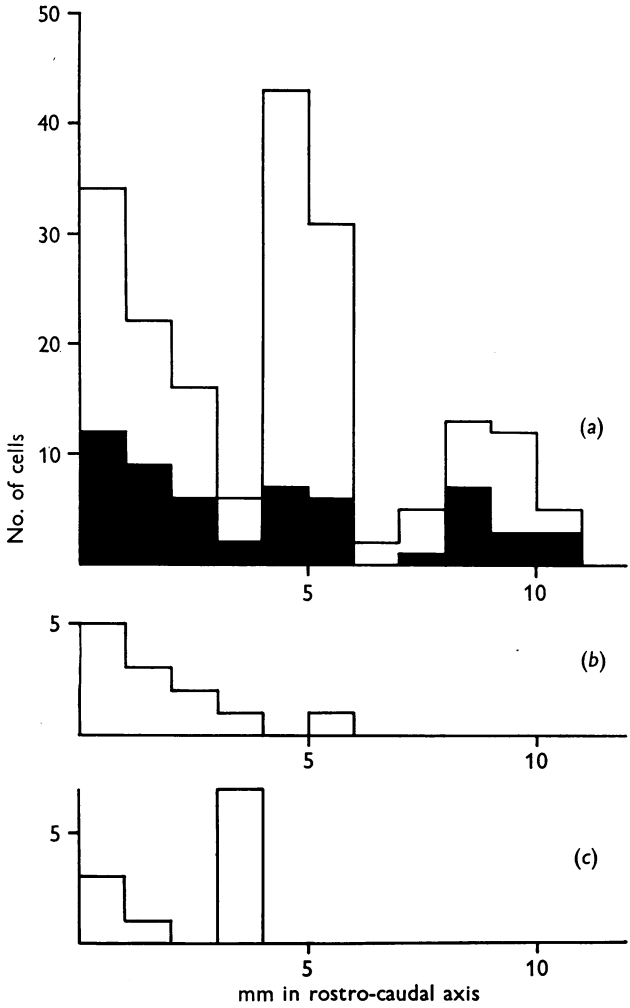
Text-fig. 3. (*a*) Diagrammatic tracing of a transverse section of brain, showing the positions occupied by the stimulating electrodes in the experiment illustrated by Text-fig. 2, Plate 1 and Table 1, and discussed in the text. The electrodes are shown as interrupted lines, with a solid line at the tip of each showing the position and length of the non-insulated part. The tip of the arrow shows the position from which lemniscal responses were recorded in this experiment. Evidence from adjacent serial sections was taken into account in establishing the position of the electrode tips. (*b*) Figure showing the position of the degenerated medial lemniscus (the densely dotted region in the centre of the figure) at about the same antero posterior position as in (*a*). Redrawn from Fig. 1 (Plate 1), Ranson & Ingram (1932), with permission. c.p., cerebral peduncle; l.g.n., lateral geniculate nucleus; m.g.n., medial geniculate nucleus; n.III, oculomotor nerve; p.c., posterior commissure; r.n., red nucleus; s.c., superior colliculus; sg.n., suprageniculate nucleus; s.n., substantia nigra.

have uniformly small skin receptive areas (mean 4·5 cm^2), and the mean receptive area for the cells fired antidromically did not differ significantly from this value. Our present evidence shows that almost all of them project rostrally in the contralateral lemniscal system.

In the part of the *caudal* section of the nucleus which was investigated only 60% of cells were fired antidromically (see Text-fig. 4*a*). This figure is derived from a sample of only 36 cells and is clearly not as valuable as

that for the middle section. The receptive area for these cells did not differ significantly from the mean figure of 14·3 cm² for cells in this section.

In the *rostral* 4 mm of the nucleus 63 % (of the whole population of 78 cells) were fired antidromically from the lemniscus (see Text-fig. 4*a*). The mean receptive area of these cells did not differ significantly from the mean figure of 51·1 cm² for the rostral section. This part of the nucleus was extensively investigated with the better technique of the later experiments,



Text-fig. 4. Histograms showing the distribution of different classes of cell in 1 mm limits along the rostrocaudal axis of nucleus gracilis. (*a*) Comparison between cells fired antidromically from the medial lemniscus (□) and those not so fired (■). (*b*) Cells fired trans-synaptically from the medial lemniscus. (*c*) Cells fired antidromically from the anterior lobe of the cerebellum.

in which again only 63% (of 41) cells were fired, and we are therefore inclined to accept that a substantial group of these cells is not accessible to this form of stimulation. Presumably these cells either project in paths other than the lemniscus, or have axons ending in the nucleus itself. This conclusion gets some support from the remaining evidence given below.

Trans-synaptic lemniscal responses. Responses to lemniscal stimulation which did not have the characteristics of antidromic excitation (see above) were studied intensively in a small number of experiments. The striking fact about these responses was that of the 12 cells that were satisfactorily investigated all but one were confined to the rostral section of the nucleus (see Text-fig. 4*b*); and in these experiments we were at particular pains to examine the rest of the nucleus under conditions in which these responses would have been found if they were present. There was no evidence of true antidromic excitation of any of the cells in addition to the trans-synaptic effect. The mean receptive area for the 12 cells in this group did not differ significantly from the mean for the whole population in this rostral section. The responses differed from the majority of the population, however, in the rather small size of their action potentials, which were always less than 1 mV, compared with the usual range of 1–3 mV.

We have already given reasons for believing that stimulation was in fact confined to the immediate neighbourhood of the medial lemniscus; and it seems very likely that trans-synaptic responses to such stimulation are brought about by collateral branches of lemniscal axons, within the nucleus, ending directly or through an interneurone on the cell observed. This view has already been expressed by Amassian & de Vito (1957) and by Gordon & Paine (1960).

Antidromic cerebellar responses. Our attempts to excite cells in nucleus gracilis antidromically from the cerebellum were prompted by finding a substantial number of cells which could not be excited from the medial lemniscus. Responses to cutaneous stimulation have been recorded in various parts of the cerebellar cortex. Snider & Stowell (1944) found tactile responses to stimulating the ipsilateral hind foot on the anterior lobe, and from both hind feet on the paramedian lobule. No histological evidence seems to exist, however, for a direct pathway between nucleus gracilis and any part of the cerebellum.

Our stimulation was confined to the anterior lobe; and antidromic responses were found in 11 cells of nucleus gracilis in the small number of these experiments which we carried out. These responses were all recorded from the rostral 4 mm of the nucleus (Text-fig. 4*c*); and we could find no sign of cerebellar antidromic excitation in other parts of the nucleus in spite of intensive search. Ten of these cells were in the nucleus of the same side as the cerebellar stimulus, and one on the opposite side. Their mean

receptive area (110 cm^2) was considerably higher than the mean for the whole population in this section (51 cm^2); but the number of cells involved is too small to establish a significant difference.

It is interesting that three of the cells fired antidromically from the ipsilateral cerebellum were also fired antidromically from the contralateral medial lemniscus. The only conclusion to be drawn from this is that some axons leaving the nucleus send branches to both these destinations.

Cells responding to movement of joints. Gordon & Paine (1960) found that some 10% of cells in nucleus gracilis responded to stimuli such as movement of joints or deep pressure. It may be of interest that, of all such cells found in the present investigation, none was fired antidromically from the contralateral medial lemniscus; but the number of cells was small and a more extensive investigation of this question is still necessary.

DISCUSSION

The main object of this investigation was to find whether all the three functional subdivisions of this nucleus described by Gordon & Paine (1960) project uniformly to the thalamus in the lemniscal system. Our results show clearly that they do not. The almost complete projection from the middle section establishes clearly that the information contained in a large population of cells with small receptive areas is made available to the thalamus. These cells, in common with the cells of other spatially discriminating systems, are subject to a process of mutual inhibition.

In both rostral and caudal sections there were some 40% of cells for which there was no evidence of thalamic projection. The number of cells observed in the caudal section was small and the percentage figure therefore tentative: we have no evidence suggesting the destination of the axons which did not project in the lemniscus. In the rostral section, however, there was definite evidence that some of the cells not projecting in the lemniscus did project to the ipsilateral anterior lobe of the cerebellum.

We have interpreted the trans-synaptic responses to lemniscal stimulation which were seen in the rostral section as the result of excitation of cells by lemniscal axon collaterals. This is a reasonable interpretation in view of our own evidence and that of Amassian & de Vito (1957), and also the fact that Cajal (1909) described such collaterals in lemniscal fibres as they leave the cuneate nucleus. Cajal's account of them is as follows: '(Le cylindre-axe)...émet quelques collatérales destinées aux cellules-sœurs de celle qui lui a donné naissance et se porte en direction antéro-externe;... enfin, il s'unit à d'autres de ses congénères pour entrer dans la voie sensitive ou ruban de Reil médian'. If the cells on which these collaterals ended had projected in the lemniscus we should have seen an early antidromic response succeeded after several milliseconds by the trans-synaptic response.

The fact that this did not happen suggests that these cells either projected by some other path, or that their axons ended in the nucleus itself. Beyond this point any argument about their connexions must be purely tentative, but interesting possibilities exist which deserve further investigation. If these cells were intrinsic (or 'internuncial') cells, and had excitatory endings on other cells in the nucleus, we might expect to record from some of the latter, which if they projected outside the nucleus should show both antidromic and trans-synaptic firing. Amassian & de Vito (1957) describe this dual response in cells of nucleus cuneatus, and one might equally expect to see it in nucleus gracilis. Such a system of excitatory intrinsic cells might provide the basis for the extensive convergence which is needed to explain the large receptive areas of many of the cells in the rostral section. The possibility remains that some proportion of cells fired trans-synaptically are inhibitory in function, isolated examples of inhibition of cells in nucleus gracilis by lemniscal stimulation having been described (Gordon & Paine, 1960).

SUMMARY

1. Cells in nucleus gracilis which responded to tactile stimulation of the hind foot were investigated by giving electrical stimuli to the contralateral medial lemniscus and to the ipsilateral side of the anterior lobe of the cerebellum. The technique for lemniscal stimulation and its anatomical control are described in some detail.

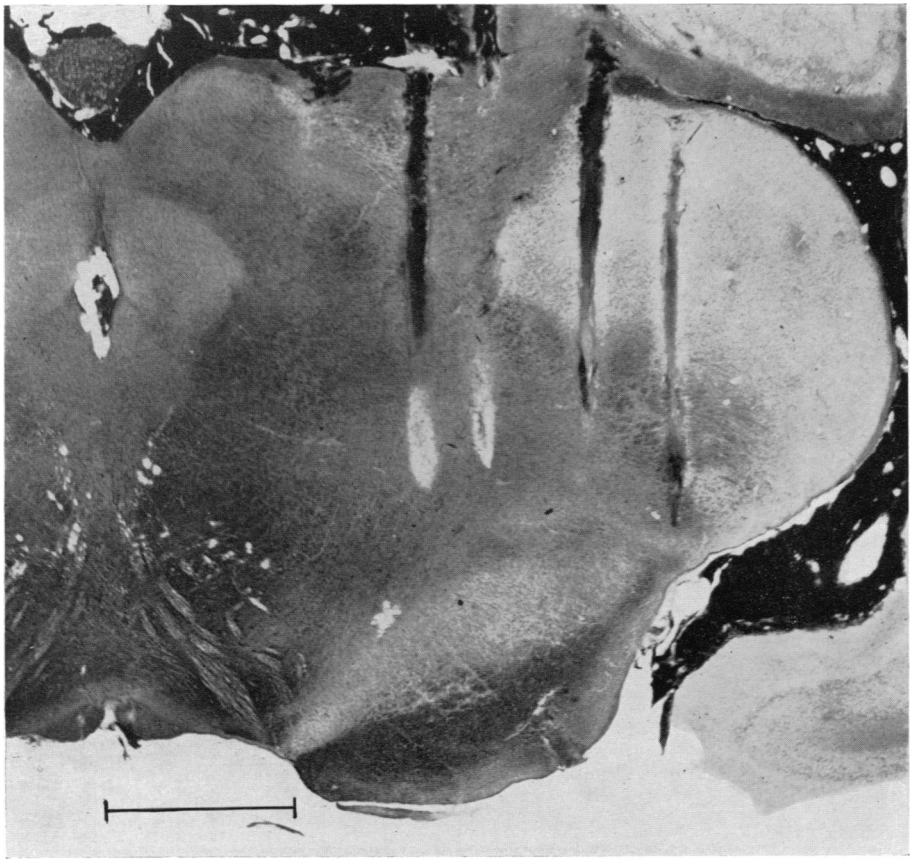
2. Cells throughout the rostrocaudal axis of the nucleus were fired antidromically from the lemniscus. A high proportion of cells were fired in the middle section, where receptive areas are small (93 % of 45 cells in the best series of experiments, and 83 % of the total cells). 60 % (of 36) cells were fired in the caudal section. In the rostral section, where receptive areas are large, 63 % of 41 cells were fired in the best series, and 63 % also of the total of 78 cells.

3. Some cells in the rostral section (but not elsewhere) were fired antidromically from the anterior lobe of the cerebellum.

4. Some cells, almost all in the rostral section, were fired trans-synaptically from the lemniscus, and the significance of these responses is discussed.

5. It was concluded that almost all the cells in the middle section project in the contralateral lemniscus; but that a significant number in the rostral section either project elsewhere (to the cerebellum, for example), or have axons ending within the nucleus (intrinsic cells). It was not possible to reach such definite conclusions about the caudal section, where the sample was rather small.

We should like to thank Mr E. H. Leach for the photomicrograph in Plate 1, and Miss Christine Court for the drawings in Fig. 3.



REFERENCES

ADRIAN, E. D. (1943). Afferent areas in the cerebellum connected with the limbs. *Brain*, **66**, 289–315.

AMASSIAN, V. E. & DE VITO, J. L. (1957). La transmission dans le noyeau de Burdach. *Colloq. int. Cent. nat. Rech. sci.* **67**, 353–393.

CAJAL, S. R. (1909). *Histologie du système nerveux de l'homme et des vertébrés*, pp. 902–903. Paris: Maloine.

ECCLES, J. C., FATT, P. & LANDREN, S. (1956). Central pathway for direct inhibitory action of impulses in largest afferent nerve fibres to muscle. *J. Neurophysiol*, **19**, 75–98.

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

GORDON, G. & SEED, W. A. (1960). Responses of single neurones in nucleus gracilis of the cat to lemniscal and cerebellar stimulation. *J. Physiol.* **152**, 63*P*.

LUNDBERG, A. & OSCARSSON, O. (1959). Identification of a third subdivision of the dorsal spino-cerebellar tract. *Experientia*, **15**, 195.

RANSON, S. W. & INGRAM, W. R. (1932). The diencephalic course and termination of the medial lemniscus and the brachium conjunctivum. *J. comp. Neurol*, **56**, 257–275.

SNIDER, R. S. & STOWELL, A. (1944). Receiving areas of the tactile, auditory and visual systems in the cerebellum. *J. Neurophysiol.* **7**, 331–357.

EXPLANATION OF PLATE

PLATE 1

Photomicrograph of the transverse section of brain from which Text-fig. 3(*a*) was traced. Four of the electrode tracks can be seen clearly. The most superficial part of the remaining one (the most medial, No. 1 of Text-fig. 3(*a*)) can just be seen: the deeper parts of this, and the track made by the recording electrode, were seen in adjacent sections. 50 μ: Heidenhain's iron-haematoxylin. Scale = 2 mm.