*J. Physiol.* (1961), **158**, *pp.* 544–559
*With 1 plate and 5 text-figures*
*Printed in Great Britain*

# THE FUNCTIONAL CHARACTERISTICS OF SINGLE CELLS IN THE CAUDAL PART OF THE SPINAL NUCLEUS OF THE TRIGEMINAL NERVE OF THE CAT

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

(*Received* 28 *April* 1961)

The primary sensory nuclei of the trigeminal nerve are more closely grouped than those serving the skin of the trunk and limbs; and the spinal nucleus in particular is more accessible to investigation than the diffuse spinothalamic system with which it is held to be analogous. It stretches from the rostral medulla to the second cervical segment; and its afferent supply is made up of primary fibres of the trigeminal nerve which run caudally through the medulla and enter the nucleus along its lateral side. Sjöqvist (1938) showed that section of these afferent fibres in the caudal medulla, in man, caused facial analgesia with loss of thermal sense but preservation of tactile sense. The spinal nucleus might therefore be expected to have interesting properties, differing from those of the dorsal-column-lemniscal system, which have been much more extensively studied.

Our investigation was almost entirely limited to the caudal part of the spinal nucleus, which constitutes, in length, only about a third of the whole. A brief description of our results has been given earlier (Gordon, Landgren & Seed, 1960).

## METHODS

All experiments were done with cats, anaesthetized with pentobarbitone sodium in an initial intraperitoneal dose of 38 mg/kg and subsequent intravenous doses of 5–10 mg. The animals were kept deep enough to prevent spontaneous movements or movements in response to stimulation. In the course of some experiments in which anaesthesia was steadily maintained for some hours, 8 mg of gallamine triethiodide was given intravenously to produce a neuromuscular block. The block lasted for 15 min or so, and artificial ventilation was used during this period.

The operation for exposing the caudal medulla and first cervical segment is described, with a photograph of this region, by Gordon & Paine (1960). The caudal part of the spinal trigeminal nucleus is partly overlaid by the cuneate nucleus, whose clear-cut surface markings were a useful guide in inserting electrodes. The cat's head was clamped in a frame attached to an animal-holding stand, using the internal auditory meatus, lower margins of the orbits, and hard palate as fixation points. The rod pressing upwards on the palate was

* Present address: Department of Physiology, Kungl. Veterinärhögskolan, Stockholm 51, Sweden.
† M.R.C. Scholar.

small and slightly away from the mid line, so that as much of the mouth cavity as possible was free for applying stimuli. The neck was held by a clamp attached to the sides of one of the lower cervical vertebrae.

*Recording.* External records from single cells and fibres were made with glass micropipettes, filled with 3 M-KCl, and with a resistance at 50 c/s of 3·5–7 MΩ. Other details of recording technique are given by Gordon & Paine (1960).

*Orthodromic stimulation.* The receptive fields of all units responding to mechanical stimuli were explored in as much detail as possible, and those responding to movements of whiskers were always tested for directional sensitivity. A number of mechanoreceptive units were tested for thermal sensitivity, using a device by which a slowly-running jet of air at room temperature could be switched, without significant change of flow, to a jet of air at other temperatures ranging from about 0° to 60° C. These temperatures were measured thermoelectrically. Warm or cool water was sometimes introduced into the mouth cavity for the same purpose. A number of spontaneously discharging cells which did not respond to mechanical stimulation were also tested for thermal sensitivity. Some cells responded to steady pressure, and the thresholds of some of these were determined with a simple device consisting of a Perspex disk of known area acting against a spring calibrated in grams weight. Pressures were expressed in dyn/cm².

Pairs of electrically controlled mechanical stimulators (Gordon & Paine, 1960) were sometimes used to study interaction when precise timing of the stimuli was important. Measurements of minimum latency of response in some units were made by stimulating the skin electrically through pairs of steel needles with the points 1–2 mm apart.

*Antidromic stimulation.* In a number of experiments attempts were made to excite cells in the spinal trigeminal nucleus antidromically by stimulating through electrodes inserted in the region of the contralateral medial lemniscus in the caudal thalamus (Horsley–Clarke frontal plane 4–5). The technique for inserting the transverse row of five electrodes is described in detail by Gordon & Seed (1961).

*Histological reconstruction.* Records were kept of the rostro-caudal position (measured from the obex) and the transverse positions (measured from the mid line) of each electrode track, and measurements were made of the depth of each responding unit from the surface of the cord. In 6 of the 18 experiments attempts were made to locate the electrode tracks histologically and to reconstruct the positions at which responses had been found.

The technique of reconstruction was as follows. At the end of the experiments tracks were made on each side of the cord, caudal to the recording site, with a fine hypodermic needle loaded with Indian ink and inserted parallel to the plane of the electrode tracks. These ink tracks were a known distance apart; and measurement of this distance after fixation gave an indication of the shrinkage produced. In some experiments the last glass electrode used was broken off and its tip left *in situ*; and another similar electrode was inserted, at a known transverse distance, on the other side of the cord, and also broken off. These electrodes were removed after fixation and were found to have left clear tracks in the sections, which were easier to use than the ink tracks in estimating shrinkage: the position of the last recording site of the experiment was also very positively determined. The head and neck were then perfused, first with 0·85 % sodium chloride and then with 5 % formaldehyde-saline. Fixation was completed by immersion. The relevant tissue was removed, and the caudal surface trimmed until it was flush with the ink tracks. Serial paraffin sections, 25 μ thick, were then cut, parallel to the trimmed surface, through the relevant region. The sections were stained with thionine.

An attempt was then made to identify in the section some part of each electrode track (see Plate 1); and if any boubt existed about the identity of a track, that one was eliminated from the reconstruction. Tracings were then made from the sections showing the visible parts of each track, through which lines were then drawn along the presumed course of the rest of the track. A correction for shrinkage was then applied to the depth measurements

made during the experiments, and the calculated positions of the recorded responses were drawn in along the track line. Two alternative conventions were used in calculating these positions. In one, the surface reading made during the experiment was assumed to give the true surface: this assumption is not always justified, because of possible indentation of the surface by the electrode, obscuring of the surface by fibrin, and a variety of other local causes. In the other, the depth readings at the point where forelimb responses disappeared during entry of the electrode were assumed to correspond with the lower border of the cuneate nucleus. This second convention gave reconstructions in which the evidence from adjacent tracks fitted together much more consistently. Examples of the use of both conventions are given in Text-fig. 5.

## RESULTS

Our results are derived from a study of 250 single neural units which responded to stimulating the facial hairs, or soft tissues, usually skin or mucous membrane, of the face and mouth cavity. Almost all of these were found in a region whose rostral limit lay 3 mm rostral, and caudal limit 11 mm caudal, to the obex. Fifty-five of these units we classify as fibres, on account of their monophasic positive spikes and negligible resting or injury discharge: there was good reason to believe that most of these were found in afferent tracts of primary trigeminal fibres (see e.g. Text-fig. 5(*c*)). The remaining units we classify as cells on account of their spikes being either diphasic or monophasic negative, with a resting discharge in the absence of stimulation, and high-frequency discharge upon injury by the electrode. When histological reconstructions were made, these latter units were found to be confined to nuclear regions. 'Fibre-type' and 'cell-type' action potentials are shown in Text-fig. 1 (*a'*) and (*c'*) respectively.

The cells could be divided into two main classes with strikingly different properties; and it is with this difference that we are mainly concerned in this paper. For immediate convenience we have called these two classes '*A*' and '*B*'.

### '*A*' *cells*

These cells responded to ipsilateral 'tactile' stimuli; and it will be seen from our account of them that in general they closely resemble 'tactile' cells in other sensory nuclei. The vibrissal receptors of the face are known to be specialized, however (Fitzgerald, 1940); and we give a separate account of the cells responding to vibrissal stimulation, while including them in the '*A*' class.

*General properties of 'A' cells.* These cells always responded at very low threshold to mechanical stimuli like bending hairs or touching the skin or mucous membrane lightly with a glass rod. Apart from vibrissal responses (see below), the discharge was almost always of a rapidly adapting kind. Seventeen out of the total of 140 '*A*' cells were tested with thermal stimuli, using streams of warm or cold air between the extreme limits of $-2$ and $+60°$ C: no evidence of thermal sensitivity was seen in any of these.

The majority of the '*A*' cells responded only to stimulation of the hairs

of the face. Their receptive areas were always well defined, ranging between 0·1 and 26 cm², with a mean at 3·7 cm². Two-thirds of these were of 1 cm² or less, and most of the small areas lay near the mouth or nose. Some of the larger receptive areas lay in the territory of more than one division of the trigeminal nerve.

About a fifth of the '*A*' cells responded to light touch on skin or mucous membrane, but not to touching hairs. The receptive areas of these ranged between 0·04 and 12 cm², with a mean at 0·41 cm². Within this group were 11 cells with receptive areas confined to the lips; and these areas were all very small (range 0·04–0·5 cm²; mean 0·11 cm²).

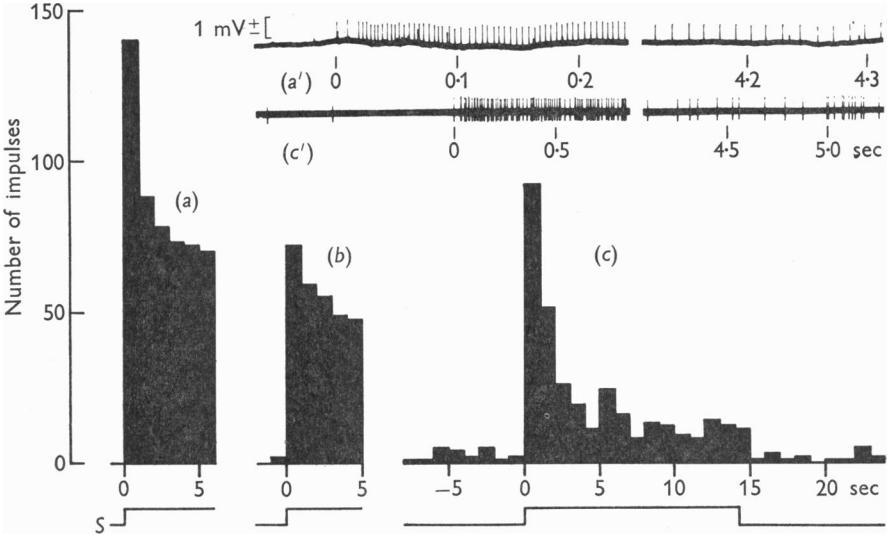
*Cells and fibres responding to stimulation of vibrissae.* The maxillary tactile hairs (or vibrissae) are thought to have a special sensory significance for the carnivores; and Fitzgerald (1940) showed that their nerve endings had the special properties of slow adaptation and directional sensitivity. We have recorded from a number of fibres, on the lateral side of the spinal nucleus, which responded only to vibrissal stimulation; and almost all of them showed these two special properties. Text-fig. 1(*a*) and (*b*) shows the first few seconds of the responses to maintained steady displacement in two vibrissal fibres, with characteristically slow adaptation. Of the 20 fibres from which we recorded, 14 responded to stimulation of single vibrissae only. We have also recorded from a few fibres responding to stimulation of supraorbital tactile hairs. These showed the same special properties, and should probably be classified functionally with the maxillary vibrissae.

In the nucleus itself we recorded from a number of cells responding to vibrissal stimulation. The slow adaptation which was so characteristic of the fibres was uncommon among the cells, most of which adapted as quickly as tactile cells normally do, a fact which might depend on the presence of a general anaesthetic. Text-fig. 1(*c*) shows a response in which adaptation was slower than in the majority of these cells. Clear-cut directional sensitivity also was much less common among cells than among fibres.

Only 10 out of 32 cells had receptive fields confined to one vibrissa alone. The number of vibrissae from which the remaining cells could be excited ranged from 2 to 12. This implies some spatial convergence of afferent fibres upon the cells; and this is borne out by our finding a small number of cells of rather large receptive area including both vibrissae and ordinary hair.

*Latency of 'A' cell responses to electrical stimulation of the receptive surface.* Latencies of the responses produced by electrical stimulation in the receptive area give an indication of the conduction time of the pathway. Latency shortens with increasing size of shock, because of temporal and

spatial summation in the nucleus; so that it is necessary to use shocks well above threshold and to find the minimum latency. Twelve '*A*' cells and 2 tactile fibres were tested in this way; and the minimum latencies, with an exception of 11 msec for one cell, lay between 1·7 and 4·2 msec. The




Text-fig. 1. Discharges in response to steadily maintained displacement of maxillary whiskers. Receptive area confined in each case to one whisker. Histograms show the number of impulses in each 1-sec period: the period of observation is shown by the length of the abscissa. The beginning and end of the stimulus are shown by upward and downward displacements respectively in line *S*.

(*a*) and (*b*) 'Fibre-type' responses in different units, recorded from a region 10 mm rostral to the obex and 6 mm from the mid line. A number of similar units were found in this region; and the electrode probably lay among afferent fibres of the Vth nerve. Part of the record from which (*a*) was drawn is shown in (*a'*), above; the spikes in both (*a*) and (*b*) were monophasic and positive.

(*c*) 'Cell-type' response, recorded from the spinal trigeminal nucleus 1·2 mm caudal to the obex and 3·75 mm lateral to the mid line (position verified histologically). Part of the record is shown in (*c'*), above: the spikes were diphasic (positive–negative).

Note the greater rate of adaptation and less regular discharge in (*c*) than in (*a*) or (*b*). All three units showed directional sensitivity to whisker displacement.

combined peripheral and central paths are approximately 80 mm long, but calculations of conduction velocity on this basis are hardly justifiable because of the existence of an unknown nuclear delay. These figures are useful mainly because of the comparison which will be made below between the latencies of '*A*' and '*B*' cells.

*Inhibition of 'A' cells by stimuli outside the receptive area.* Inhibition of sensory cells by stimulation outside, but usually near, their receptive areas

is now well known. It has been shown for cutaneous tactile cells in both the dorsal column nuclei (Amassian & de Vito, 1957; Gordon & Paine, 1960) and in the sensory cortex (Mountcastle, 1957). It is easily demonstrated by using a pair of electrically operated mechanical stimulators, one inside the receptive area (testing) and one outside it (conditioning). The time interval between these stimuli is controlled electronically.

A serious artifact can be introduced if these stimuli are applied close together on the skin; because the conditioning stimulus may spread and interact physically with the test stimulus in such a way as to reduce the effectiveness of the latter. A spurious 'inhibition' would then occur. We have used a control in our experiments by which we hoped to define this artifact quantitatively. Recordings were made from a number of single vibrissal *fibres* in the afferent tract, stimulating the appropriate vibrissa with the 'test' stimulator. The 'conditioning' stimulator was then applied to hairs or vibrissae at a number of known distances from the receptive vibrissa; and this stimulus was increased in size in an attempt to produce an 'inhibition'. It was assumed that all such 'inhibitions' were due to the physical artifact and that no genuine inhibitory interaction occurs between primary fibres. We were unable to produce the artifact with our largest conditioning stimulus (1·5 mm displacement of the hair 5 mm or more from the skin) when the two stimuli were 15 mm apart or more, and interaction rarely occurred when they were only 10 mm apart. With a separation of 5 mm interaction was seen in about half the tests made, and at strengths of conditioning stimulus small enough to make any confident distinction between genuine and spurious cell inhibitions impossible. We have therefore discarded all evidence from cells at spatial separations less than 10 mm; and have allowed a factor of safety in amplitude of conditioning stimulus of at least $\times 2$ when accepting any others as genuine.

Tests for inhibitory interaction were made for only 16 '*A*' cells, with a variety of receptive areas of 5 $cm^2$ or less, and 6 of these showed an undoubted inhibitory conditioning by stimuli applied at distances of 10–40 mm from the receptive area. Inhibition may well be commoner among these cells than our results show, because the region within 10 mm of the test stimulus, which we could not confidently use, may contain the most powerful inhibitory region.

*Antidromic excitation of 'A' cells.* Antidromic excitation of cells in the spinal trigeminal nucleus was attempted in some experiments, using stimulating electrodes in the region of the medial lemniscus of the opposite side at the level of the caudal thalamus. About 40 % (34 out of 82) of the '*A*' cells tested in this way gave responses which we regard as antidromic, using the criteria given by Gordon & Seed (1961). The latencies for the antidromic spike fell in the range 0·5–2·7 msec. One cell fired repetitively in response to the lemniscal shock, and had a longer latency than the rest (3·1 msec) and this may have been excited trans-synaptically.

It is clear, therefore, that a substantial number of '*A*' cells project to the contralateral thalamus in the lemniscal system.

*Topographical arrangement of 'A' cells within the nucleus.* It was said earlier that the '*A*' cells were found in the spinal nucleus itself. The evidence for this comes from the six experiments in which histological

reconstructions were made (see Methods); but in the other experiments also it was clear that these cells lay in a circumscribed region of the cross-section of the cord, separated by a 'silent band' 100–400 $\mu$ wide from the overlying cuneate nucleus. '*A*' cells with adjacent receptive areas were grouped together within the spinal nucleus, and an orderly topographical change in the receptive fields occurred along each recording track. Ventral movement usually gave a rostral shift in receptive field.

Cells with mandibular fields were found medially. Those with maxillary fields lay lateral and ventral to these; and those with ophthalmic fields lay lateral and ventral to the maxillary group. This oblique laminar arrangement of the cells belonging to the three divisions of the trigeminal area was found at all the rostro-caudal levels investigated; and agrees with the arrangement described by Darian-Smith & Mayday (1960). The tracings in Text-fig. 5 show some examples of the reconstructed electrode tracks from which this general arrangement was established.

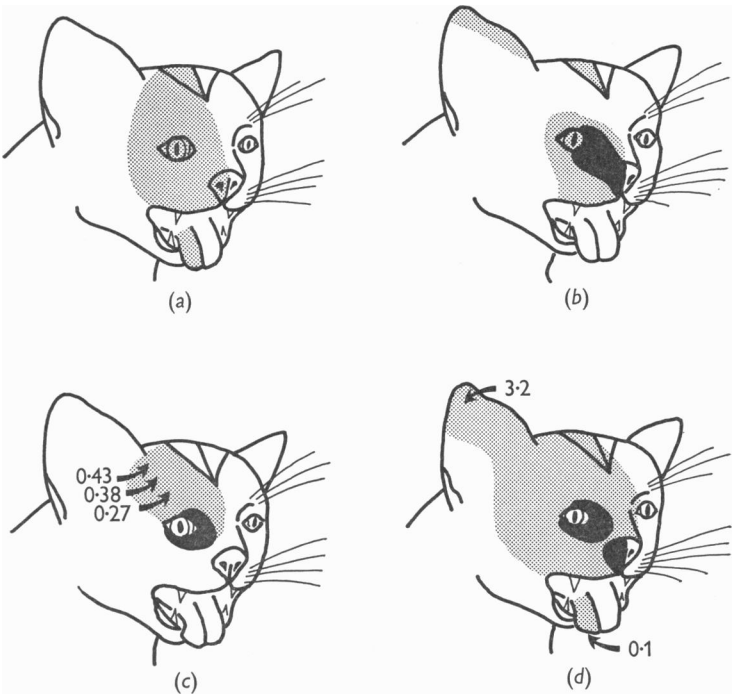
### '*B*' *cells*

Twenty-one of the cells investigated formed a group ('*B*') with very distinctive properties, differing from the more numerous '*A*' cells in threshold, receptive area, and adaptation, and also in their anatomical position.

*General properties of* '*B*' *cells.* The receptive areas of these cells were large, usually involving the territories of more than one of the divisions of the trigeminal nerve. The commonest type of receptive area occupied the maxillary and ophthalmic divisions; but some lay in the maxillary and mandibular divisions and a few included parts of all three divisions. The centre of the field usually lay in the region of the eye and side of the nose. The conjunctiva and nictitating membrane were often included, and sometimes the cornea as well. The field was not always in one continuous piece, and it was often possible to excite the cell from separate regions like the pinna or supraorbital periosteum, and sometimes from the tongue. When a cell was observed continuously for an hour or so the size of the receptive area was not always constant, but showed minor extensions or contractions. These changes were usually difficult to measure confidently, because the actual boundaries of the area could not be defined as precisely as with '*A*' cells. Four examples of the receptive areas of '*B*' cells are shown in Text-fig. 2. These areas were normally confined to the ipsilateral half of the face, but it will be seen that the example in Text-fig. 2(*d*) extends a little across the mid line.

The mechanical threshold for excitation of '*B*' cells was on the average much higher than for '*A*' cells. The contrast was particularly obvious in the peripheral parts of their receptive fields, where firm pressure with

a glass rod, light pinches or pinpricks were effective stimuli, but light touch was not. The centre of the field usually had a lower threshold (see Text-fig. 2), and here light touch, and even occasionally brushing hairs might be effective. In some experiments we tried to get estimates of the pressure thresholds in those parts of the receptive fields where pressure could be evenly applied; and it was usually found that this threshold increased



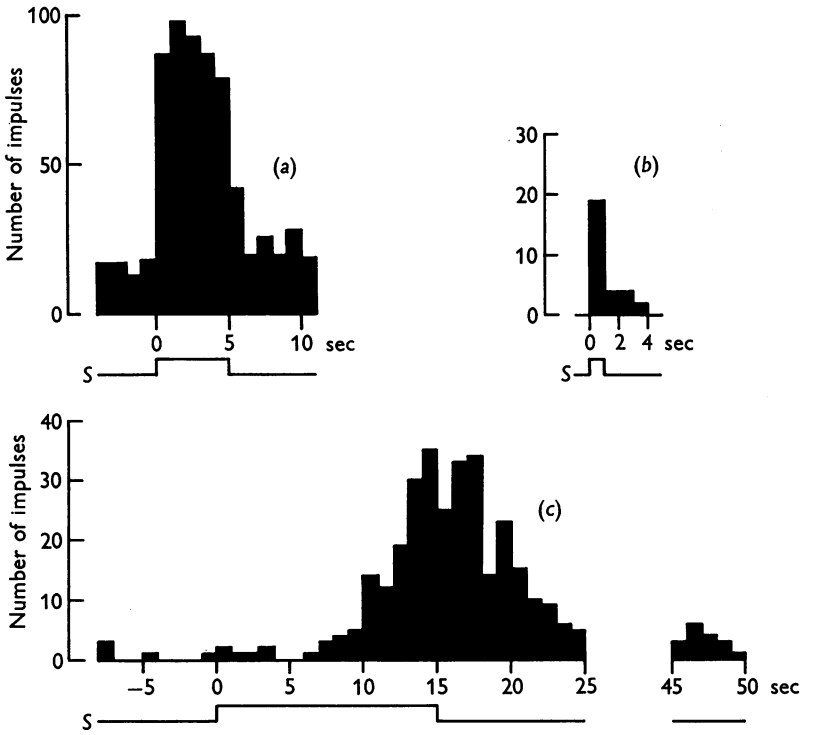

Text-fig. 2. Drawings to show the receptive areas of four '*B*' cells, in different animals. In each, the dotted area shows the extent of the receptive area, with the most sensitive part in black. The numbers in (*c*) and (*d*), multiplied by $10^6$, give the thresholds to pressure in dyn/cm$^2$, in the parts of the receptive area where such measurements could be made satisfactorily.

The triangular area on either side of the mid line on the forehead represents the front end of a sagittal incision in the scalp, exposing the periosteum.

progressively towards the periphery (Text-fig. 2(*c*)). The measured thresholds in the periphery ranged between $0{\cdot}1 \times 10^6$ and $3{\cdot}2 \times 10^6$ dyn/cm$^2$. Eight of these cells were also tested with thermal stimuli, and seven responded, but only to extreme stimuli—over 50° C or less than 5° C. Such stimuli were felt as painful on the human arm after 15–20 sec.

The pattern of discharge of a '*B*' cell in response to a mechanical stimulus was always slowly-adapting, and the response often continued

for some seconds after the stimulus was withdrawn (Text-fig. 3(*a*) and (*b*); and Text-fig. 4(*d*)). This was also true of the response to extreme thermal stimuli (Text-fig. 3(*c*)). Irregular resting discharge at a low frequency, in the absence of stimulation, was very common among these cells. We did not find any obvious inhibition of this resting discharge when mechanical stimuli were given to various parts of the face on either side.




Text-fig. 3. Discharges of '*B*' cells. Histograms show the number of impulses in each 1-sec period: the period of observation is shown by the length of the abscissa. The beginning and end of the stimulus are shown by upward and downward displacements respectively in line *S*.

(*a*) Response of a '*B*' cell to pinching the upper eyelid.

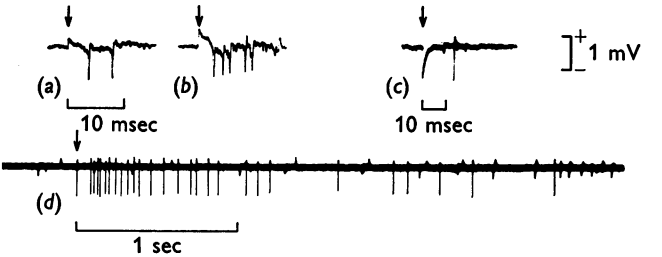
(*b*) Response of another '*B*' cell to pinching the pinna.

(*c*) Response of the same cell as in (*b*) to stimulating the medial angle of the eye with a jet of hot air at about 50° C. Part of the record between 25 and 45 sec has been omitted. Other responses of this cell are shown in Text-fig. 4, and its receptive area in Text-fig. 2(*b*). Its probable position is shown by the upper of the three crosses (×) in Text-fig. 5(*b*).

The high mechanical threshold of '*B*' cells, particularly when the stimuli were given to regions like the eye, nose and pinna, naturally raised the doubt whether the responses were secondary to reflex muscular

contraction. Seven typical '*B*' cells were tested both before and during neuromuscular block, however, without any alteration in the response being detected.

*Latency of response of 'B' cells to electrical stimulation of the receptive surface.* This latency was generally longer than that of '*A*' cells. In the cells tested the minimal latencies to stimulation in the most sensitive part of the receptive area ranged from 2·2 to 12·5 msec (6 out of 7 lying between 4·0 and 12·5 msec). When minimum values were obtained from the peripheral parts of the area they were three to six times greater (see Text-fig. 4 (*a–c*)).




Text-fig. 4. Discharges of a '*B*' cell.

(*a*) and (*b*). Two responses to single-pulse electrical stimuli to the edge of the upper eyelid near the medial angle. (*a*) Stimulus around threshold: latency 3·6 msec. (*b*) Stimulus approximately twice threshold: latency 2·2 msec. Latency did not shorten further with increase in stimulus.

(*c*) Responses of the same cell to single-pulse electrical stimulus to the supraorbital periosteum. Maximal stimulus: latency 13·0 msec.

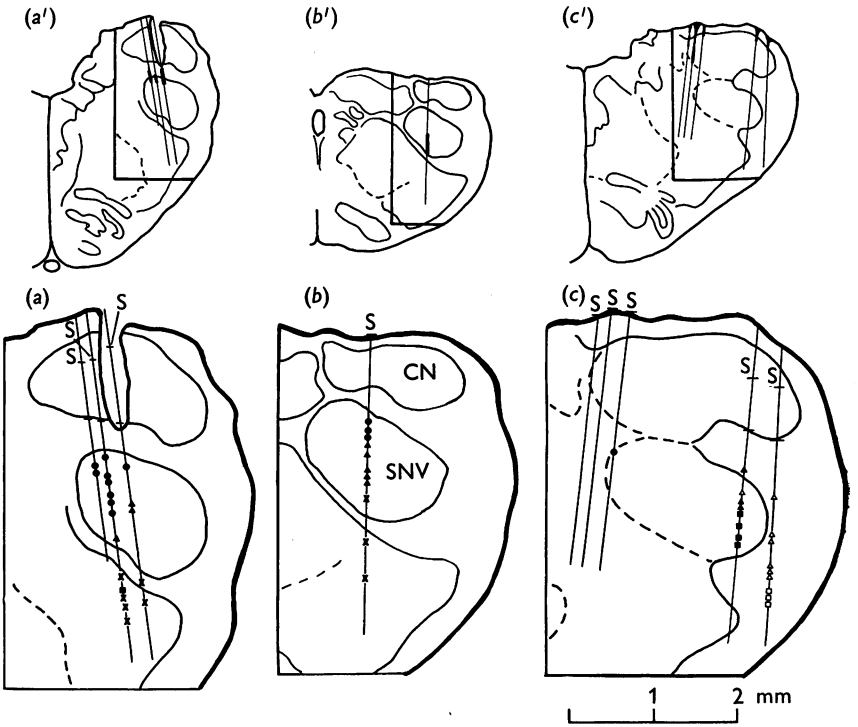
(*d*) Response of the same cell to pinching the pinna, the stimulus lasting about 1 sec. Spikes retouched. This response is also shown in Text-fig. 3(*b*). The receptive area of this cell is shown in Text-fig. 2(*b*); and its probable position by the upper of the three crosses (×) in Text-fig. 5(*b*).

*Responses of 'B' cells to lemniscal stimulation.* Of the 10 '*B*' cells tested one was fired antidromically by stimulating the region of the contralateral lemniscus; and five were fired in a way suggesting trans-synaptic excitation (see Gordon & Seed (1961) for our criteria of such excitation).

*Positions from which 'B' responses were recorded.* '*B*' cells were invariably found deep to the '*A*' cells, though it was unusual to find any 'silent band' separating the two. They were found at all the rostro-caudal levels investigated. Reconstructions of the electrode tracks show that some '*B*' cells may have been in the spinal trigeminal nucleus, very near its ventral border (Text-fig. 5(*b*)), but the errors possible in the reconstruction make a decision on this point unjustifiable. There is no doubt that a substantial number of these cells lay deep to the nucleus (Text-fig. 5(*a*)), in the region of the reticular nuclei which border the ventral and ventromedial aspects of the trigeminal nucleus at this level (see Pl. 1). Cells

responding in one or other phase of the respiratory cycle were often found deep to the '*B*' cells, and these were undoubtedly in the reticular nuclei.

*Cells with similar properties* ('*B*'-*type*). Seven cells were found which were similar in some but not in all their functional characteristics to the '*B*' cells described above. As the differences from the main group lay chiefly in the size and distribution of their receptive areas, it could be held




Text-fig. 5. Tracings of transverse sections of the spinal cord (all 1–2 mm rostral to the obex) from three animals, showing electrode tracks. (*a*), (*b*) and (*c*) are enlarged tracings of the areas framed in (*a'*), (*b'*) and (*c'*), above. The parts of each track definitely seen in the sections are shown as thickenings of the track lines in the upper tracings.

On some tracks a horizontal bar (S) is marked at the surface of the cord, indicating that in these tracks the depth positions of the recorded responses were calculated from the surface reading made during the experiment. In other tracks a bar is marked at the lower border of the cuneate nucleus, indicating that the positions were calculated from the point of disappearance of cuneate responses; the position of (S) in these tracks is likewise calculated, and does not coincide with the actual surface (see Methods).

The responses are classified as follows: ●, mandibular division of face, '*A*' cell; ▲, maxillary division, '*A*' cell; ■, ophthalmic division, '*A*' cell; ○, mandibular fibre; △, maxillary fibre; □, ophthalmic fibre; ×, '*B*' cell. CN, cuneate nucleus; SN*V*, spinal trigeminal nucleus.

that the distinction we are making here is only one of degree. There is clearly an extensive spatial convergence on to all the cells we have called '*B*', and the effectiveness of this convergence would be expected to vary with general levels of excitation and inhibition, and with the effects of anaesthesia upon these levels. There was no indication, however, that the differences in these cases depended on level of anaesthesia; and we feel that the distinction is worth making for immediate descriptive purposes.

Three of these cells had the general functional properties of '*B*' cells, and lay deep to the '*A*' cells in the cord; but they had fairly well-defined receptive areas, probably no more than 1 $cm^2$ in size, one on the pinna and two on the nose. The spontaneous activity of one of the latter was consistently inhibited by pressure on the ipsilateral side of the tongue; and this was the only occasion on which inhibition was seen in a cell with these general properties.

The other four cells differed from the main '*B*' group in one striking respect—that they could be excited by strong pressure outside the trigeminal area. They all had typical receptive fields in the face, extending in one case to the contralateral side, and they all responded to squeezing either of the forepaws. Two of them also responded to squeezing the hind paws, and one to similar stimulation of the trunk. All these cells were deep-lying; and one of them was found 0·8 mm deep to other typical '*B*' cells.

*Other cells differing from 'A' cells.* A number of cells responded to moderate pressure on the skin of the face, but closer investigation often suggested that the sense organs concerned lay deep in the substance of the lip, nose or gums, making any exact definition of their properties impossible. Five cells, however, had well-defined receptive areas of 2 $cm^2$ or less, and responded, three with slowly-adapting and two with rapidly-adapting discharge, to slight sustained pressure on the skin. The resting discharge of one of them was consistently inhibited by pressure on the skin of the same side of the face, or on the tongue. They differed from the tactile ('*A*') group in their somewhat higher mechanical threshold—of the order of 0·05–0·1 ($\times 10^6$) dyn/$cm^2$, in their failure to respond antidromically to contralateral lemniscal stimulation, and in lying deeper in the cord in a region where '*B*' cells might also be found. For lack of further information they remain an ill-defined group.

## DISCUSSION

The part of the spinal nucleus which we have examined corresponds in rostro-caudal position to the part called by Meesen & Olszewski (1949), in the rabbit, 'nucleus tractus spinalis trigemini caudalis'. It also corresponds in position to the part of the spinal nucleus deafferented, in

man, by Sjöqvist's trigeminal tractotomy (Sjöqvist, 1938). The loss of pain and temperature sensation produced by this operation naturally led to the belief that there would be striking functional differences between the cells in the nucleus at this level and the cells of primary 'tactile' nuclei. Our findings suggest that in the cat, at any rate, this is not so: in their tactile responses, orderly topographical arrangement and lemniscal projection, the cells which we definitely localized to the spinal nucleus proper (our '*A*' cells) resemble those of other tactile nuclei such as the gracile and cuneate (see also Kuhn, 1949). Harrison & Corbin (1942) showed that tactile fibres run as far caudal as this in the spinal tract in the cat, and our results are a logical extension of theirs. Their paper gives a good account of the controversy which had continued for many years on this particular matter.

Our '*B*' cells form a group with remarkably consistent properties which contrast in many respects with those of the cells in typical tactile nuclei. These contrasting properties include a wide—but often discontinuous and fluctuating—receptive area, a threshold to mechanical stimulation which increases towards the periphery of the area, and a sensitivity to extreme thermal stimuli. They resemble closely the properties of the cells of the posterior group of thalamic nuclei, described by Poggio & Mountcastle (1960). They differ from the 'common carrier cells' found in the spinal dorsal horn by Wall (1960) in their larger receptive areas, and in their generally higher thresholds, particularly to thermal stimuli; though quantitative comparisons of this kind may not be justified, since our animals were anaesthetized with barbiturate, whereas Wall worked on unanaesthetized spinal animals. The nature of the convergence which gives '*B*' cells their sensitivity to different kinds of stimulus is not known. Local convergence of '*A*' cells upon them could only account for the relatively small tactile part of their sensitive range; and therefore they must receive either primary fibres with appropriately high thermal and mechanical thresholds from the spinal tract, or secondary fibres from a region unknown.

We have shown that at least a substantial number of '*B*' cells lay deep to the spinal nucleus, though superficial to cells with respiratory rhythms. This region seems to correspond to the 'nucleus reticularis ventralis' of Brodal (1957); though further work will be needed for its precise definition in terms of known anatomical structures. It lies ventrolateral to the reticular region in which Torvik (1956) found degeneration after trigeminal nerve section. It is of some interest that these '*B*' cells, excitable only from the ipsilateral face, and lying adjacent to the spinal trigeminal nucleus, lie in a nucleus of the reticular formation. They seem to belong to an organized facial afferent system rather than to show the spatially unspecific properties which are often attributed to sensory cells in these

nuclei; though this organization may merge spatially with other similar organizations, for a few ('*B*-type') cells were excitable from the limbs. Apart from one '*B*' cell fired antidromically from the contralateral medial lemniscus we have no knowledge of their efferent projections, and cannot therefore decide to what extent they belong to a rostrally-directed sensory system, or to a reflex system, or to both. Certainly these cells respond to stimuli in the range which one would call nociceptive; and it would be of great interest if their projections could be determined. The antidromic stimuli which we have used here may well have had access to only a limited part of the ascending trigeminal projections, about whose detailed anatomical organization there seems to be considerable uncertainty (see Rose & Mountcastle, 1959).

The complete absence of responses to small thermal stimuli in our experiments serves to emphasize that we have only examined a restricted region of the trigeminal nuclei. The thermal anaesthesia after Sjöqvist's tractotomy would lead one to expect such responses in the spinal nucleus; and by exclusion we should now expect that they would be found in its more rostral parts.

SUMMARY

1. The caudal part of the spinal nucleus of the trigeminal nerve was investigated, in anaesthetized cats, with extracellular micropipette electrodes, and responses recorded from single cells and fibres. A variety of mechanical and thermal stimuli were used to investigate the receptive areas and ranges of response. In some experiments attempts were also made to stimulate cells antidromically from the region of the contralateral medial lemniscus.

2. The majority of the cells (classed here as '*A*') had properties similar to those of 'tactile' cells in e.g. the dorsal column nuclei, responding to hair movement or light touch on skin or mucous membranes of the ipsilateral face. The responses were usually rapid in adaptation. Receptive areas ranged from 0·04 to 26 $cm^2$, the majority being rather small; and the smallest areas lay on hairy skin near the mouth or nose, or on the lips. Minimal latencies of response to electrical stimuli in the receptive area ranged from 1·7 to 4·2 msec. 40 % of '*A*' cells responded antidromically to lemniscal stimulation.

3. Some '*A*' cells responded to stimulation of maxillary vibrissae or of the long supra-orbital hairs. Some but not all of these responses showed the slow adaptation and directional sensitivity characteristic of vibrissal sensory fibres.

4. Mechanical stimulation of neighbouring hairs was shown to inhibit the responses of some '*A*' cells.

5. Histological evidence shows that '*A*' cells lay in the spinal trigeminal nucleus. There was a systematic topographical arrangement in the transverse plane, mandibular cells lying medial and dorsal, ophthalmic lateral and ventral, with maxillary in between.

6. A smaller group of deeper-lying cells ('*B*') had larger receptive areas. These spread over a great part of the ipsilateral face, were often discontinuous, and tended to vary in extent with time. Thresholds for mechanical stimulation were often low in the centre of the area, but increased peripherally to values far exceeding those of '*A*' cells. Responses adapted slowly and often outlasted the stimulus. A number of '*B*' cells responded to extreme thermal stimuli. Minimal latencies for electrical skin stimulation lay between 2·2 and 12·5 msec. Only one '*B*' cell (out of ten tested) responded antidromically to lemniscal stimulation. A few cells, otherwise similar, could be excited by strong pressure on some or all of the limb extremities.

7. The anatomical location and possible functional significance of '*B*' cells is briefly discussed.

8. No cells were found which showed any appreciable response to thermal skin stimuli within the range 10–45° C.

We are very much indebted to Dr T. P. S. Powell and Dr W. M. Cowan for their generous help with histological reconstruction, for supplying the photomicrograph of Plate 1, and for much useful discussion.

## REFERENCES

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

BRODAL, A. (1957). *The Reticular Formation of the Brain Stem.* Edinburgh and London: Oliver and Boyd.

DARIAN-SMITH, I. & MAYDAY, G. (1960). Somatotopic organization within the brain-stem trigeminal complex of the cat. *Exp. Neurol.* **2**, 290–309.

FITZGERALD, O. (1940). Discharges from the sensory organs of the cat's vibrissae and the modification in their activity by ions. *J. Physiol.* **98**, 163–178.

GORDON, G., LANDGREN, S. & SEED, W. A. (1960). Responses of single cells in the caudal part of the spinal nucleus of the trigeminal nerve of the cat. *J. Physiol.* **153**, 12–13*P*.

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

GORDON, G. & SEED, W. A. (1961). An investigation of nucleus gracilis of the cat by antidromic stimulation. *J. Physiol.* **155**, 589–601.

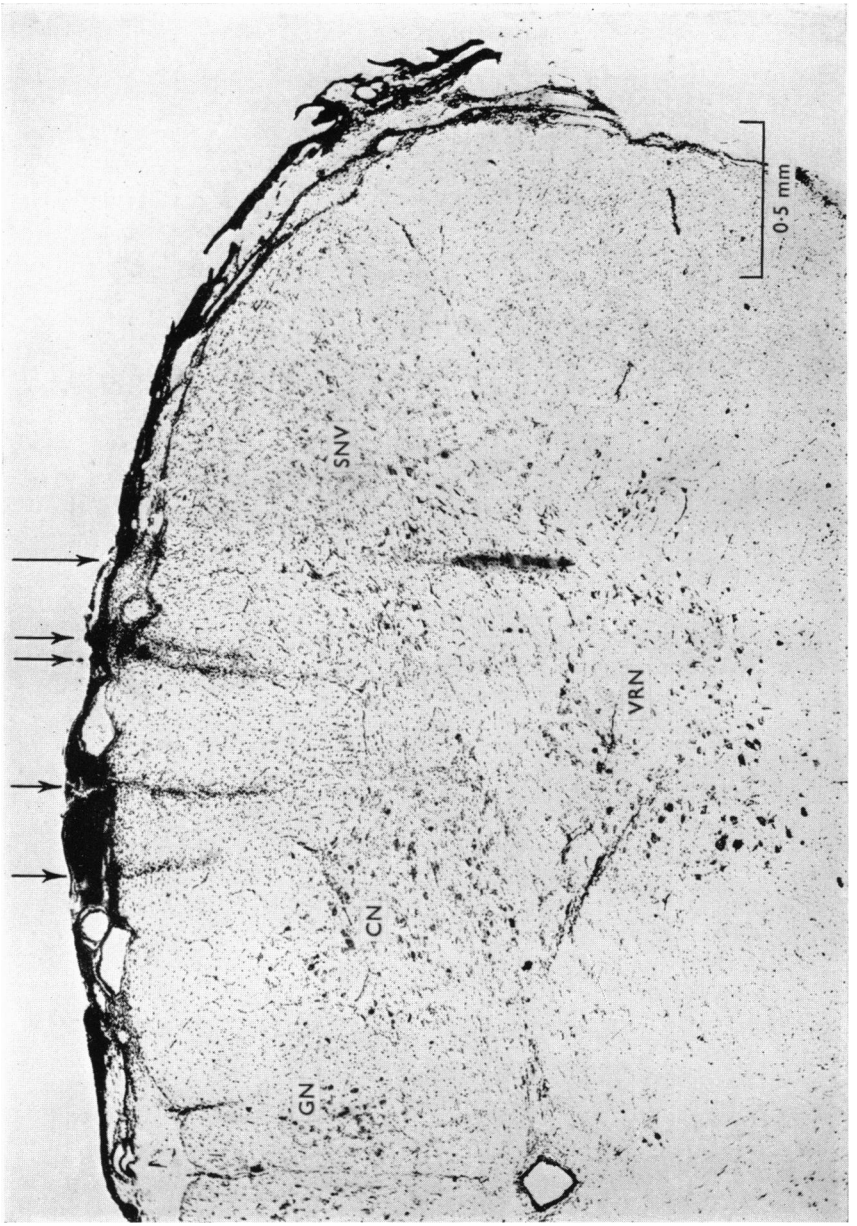
HARRISON, F. & CORBIN, K. B. (1942). Oscillographic studies on the spinal tract of the fifth cranial nerve. *J. Neurophysiol.* **5**, 465–482.

KUHN, R. A. (1949). Topographical pattern of cutaneous sensibility in the dorsal column nuclei of the cat. *Proc. Amer. neurol. Ass.* pp. 227–230.

MEESEN, H. & OLSZEWSKI, J. (1949). *A Cytoarchitectonic Atlas of the Rhombencephalon of the Rabbit.* Basel: Karger.

MOUNTCASTLE, V. B. (1957). Modality and topographic properties of single neurons of cat's somatic sensory cortex. *J. Neurophysiol.* **20**, 408–434.

POGGIO, G. F. & MOUNTCASTLE, V. B. (1960). A study of the functional contributions of the lemniscal and spinothalamic systems to somatic sensibility. *Johns Hopk. Hosp. Bull.* **106**, 266–316.


0·5 mm
SNV
VRN
CN
GN

ROSE, J. E. & MOUNTCASTLE, V. B. (1959). Touch and kinesthesis. In *Handbook of Physiology*, Section 1, Neurophysiology, **1**, 387–429, ed. FIELD, J. Washington, D.C.: American Physiological Society.

SJÖQVIST, O. (1938). Studies on pain conduction in the trigeminal nerve. *Acta psychiat., Kbh.*, Suppl. 17, 1–139.

TORVIK, A. (1956). Afferent connections to the sensory trigeminal nuclei, the nucleus of the solitary tract and adjacent structures. An experimental study in the rat. *J. comp. Neurol.* **106**, 51–142.

WALL, P. D. (1960). Cord cells responding to touch, damage and temperature of skin. *J. Neurophysiol.* **23**, 197–210.

## EXPLANATION OF PLATE

Plate 1. Photomicrograph from a transverse section of the spinal cord showing (in part) five electrode tracks, which are marked by arrows. Facial responses were recorded from the most lateral (i.e. right-hand) track, in which a '*B*' cell was found at a depth from the surface of approximately 1·2 mm (figure corrected for shrinkage in fixation). Tactile facial responses were recorded from the cellular region immediately superficial to this. CN, cuneate nucleus; GN, gracile nucleus; VRN, ventral reticular nucleus; SN*V*, spinal trigeminal nucleus. Section 25 $\mu$ thick: thionine stain.