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FUNCTIONAL ORGANIZATION IN THE TRIGEMINAL MAIN SENSORY AND ROSTRAL SPINAL NUCLEI OF THE CAT

BY I. DARIAN-SMITH, GILLIAN PHILLIPS AND R. D. RYAN

From the School of Physiology, University of New South Wales, Kensington, N.S.W., Australia

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In a previous study of single neurones within the trigeminal main sensory nucleus (Darian-Smith, 1960) considerable variation in the characteristics of the cell population was observed. The discharge latency following electrical stimulation of the skin varied greatly from different neurones, as did the size of their receptive fields. Recent investigations on the gracile and cuneate nuclei (Gordon & Paine, 1960; Gordon & Seed, 1961; Kruger, Siminoff & Witkovsky, 1961; Perl, Whitlock & Gentry, 1962) are relevant to these observations, since these structures have long been considered functionally homologous with the rostral part of the brain-stem trigeminal complex. These investigations have demonstrated that a pattern of distribution of the neurones, according to their functional characteristics, occurs within the dorsal column nuclei. The average receptive field size and the proportion of cells whose axons project to the contralateral ventrobasal complex of the thalamus differ in different regions of the nuclei.

In view of these findings the present experiments were carried out to examine neurones within the anterior subdivisions of the brain-stem trigeminal complex (main sensory nucleus, nucleus tractus spinalis oralis and nucleus tractus spinalis interpolaris; Olszewski, 1950) and to characterize them according to anatomical position and to some of their functional properties. Particular attention was paid to the identification of neurones whose axons projected to the contralateral arcuate nucleus of the thalamus, the trigeminal relay within the ventrobasal complex. A similar investigation of the nucleus tractus spinalis caudalis has previously been made by Gordon, Landgren & Seed (1961).

METHODS

Preparation of animal. Cats weighing 2·6–4·0 kg were used for all experiments. After induction with ether, anaesthesia was maintained with intravenous chloralose (50–55 mg/kg). This dosage was sufficient to maintain light surgical anaesthesia throughout the experimental period. After mounting the animal in a stereotaxic instrument in the standard Horsley-

Clarke position, the ventilatory rate and volume were measured. An initial intravenous injection (12–16 mg) of the muscle relaxant gallamine triethiodide (Flaxedil; May & Baker) was given and respiration maintained with a pump at the previously measured respiratory rate and tidal volume. 100% oxygen was used as the inhalant throughout the experiment. Intravenous Flaxedil was administered at approximately 20 min intervals (4–6 mg). Under these conditions the arterial oxygen and carbon dioxide contents were maintained at normal levels, being checked in several early experiments by blood gas analysis. The level of anaesthesia was checked intermittently by allowing the animal to recover from the relaxant drug. The mean arterial blood pressure was recorded via a femoral arterial catheter, with a Statham strain gauge (Type P 23) in conjunction with a Grass 2-channel Polygraph, Model 5. Results from animals with a mean pressure sustained below 100 mm Hg were rejected. In the nine animals used the pressure range was between 100 and 145 mm Hg during the period of recording neurone activity. Body temperature was maintained at 37–38° C by means of a d.c. electric blanket.

A unilateral occipital craniotomy and a contralateral parietal craniotomy were performed. The arch of the atlas was also largely removed. The exposed brain was covered with a paraffin pool maintained at 37–38° C. The dura overlying the cerebellum and medulla, and the parietal cortex respectively, was then removed.

Recording. Tungsten micro-electrodes (Hubel, 1957) with a tip diameter of less than 1 μ were used for extracellular neural-unit recording. Penetrations of the brain stem were made at an angle of 30° to the vertical plane to reach structures under the sloping tentorium cerebelli. For amplification, a capacity-coupled amplifier was used, the working frequency band width being 80 c/s–10 kc/s. Oscilloscope traces were recorded with a Grass kymograph camera attached to a single-beam oscilloscope. Respiratory pulsation occasionally interfered with unitary recording, but was not a serious problem.

Serial Nissl-stained sections (Einarson's gallocyanin method, 1932) were made of the brain stem after each experiment, for identification of the electrode tracks. This, however, allowed the identification only of the lateral and rostro-caudal position of the penetration. In these experiments it was important that the positions of all the units in a transverse plane could be referred to each other. The only way in which we could fulfil this requirement was to make all the recordings on the same electrode, when the combination of the histologically identified electrode tract and co-ordinates of the electrode tip fixed the positions accurately relative to each other. There was, however, still inaccuracy up to $\pm 0{\cdot}15$ mm in the vertical positions of units when we attempted to place them on photographs of the appropriate vertical section. For this reason we have not attempted to define the exact position of units recorded in the ventromedial region of the trigeminal nuclei. In all the following experiments two full transverse planes were explored in each of which at least 40 units were isolated and in several cases twice this number of units were identified in a single plane.

Stimulation of skin and thalamus. Cells were initially identified by an evoked discharge in response to electrical stimulation (bipolar, interpole distance 2–3 mm) of the ipsilateral upper lip. The electrical pulse was a square wave 50 μsec in duration. The stimulus isolation unit used was similar to that described by Fein (1960). Then by means of a small brush the unit's response to light mechanical stimulation of the skin was examined, and its receptive field size determined.

Correct positioning of the battery of four stimulating electrodes in the contralateral arcuate nucleus of the thalamus was achieved in the following way. By mapping the focal and unitary activity evoked in the ventrobasal complex the vertical, lateral and antero-posterior ordinates were determined. The usual finding was that evoked unitary activity was recorded in two transverse planes 1 mm apart. In the transverse direction this was recorded in penetrations extending over 2–2·5 mm and had a similar vertical extension. The stimulating electrodes were placed transversely in the more posterior plane, the

Horsley-Clarke plane Anterior 6·5 mm (A 6·5 mm, most commonly). The vertical position varied between 0 and + 1 mm above the Horsley-Clarke zero plane and the lateral position was most commonly such that the middle of the battery was 4·5–5·0 mm lateral to the mid line. By appropriate switching adjacent pairs of the electrodes were used as a bipolar electrode (interpolar distance 1·5 mm, bared ends of 125 μ tungsten wire). Stimulus duration was 50 μsec. Usually one combination was much more effective than the other two, although all cells were tested with the three electrode pairs.

The differentiation of antidromically and trans-synaptic evoked discharges following stimulation of the contralateral arcuate nucleus

For trigeminal neurones in which contralateral thalamic stimulation evoked a discharge with a latency of more than 3 msec there was no difficulty in establishing the trans-synaptic nature of the discharge. For cells which fired with a shorter latency, however, there was difficulty in differentiating trans-synaptic and antidromically induced responses; e.g. the ability of the discharges to follow repetitive stimulation at varying frequencies allowed no sharp separation of these two types of response. The technique adopted to make this distinction was a modification (suggested by Professor A. S. Paintal) of a previously described method (Paintal, 1959). The technique has also been used recently by Bishop, Burke & Davis (1962) to identify antidromic activation of lateral geniculate neurones. Consider first the anatomical situation shown diagrammatically in Fig. 1*a*. If the cell body is initially

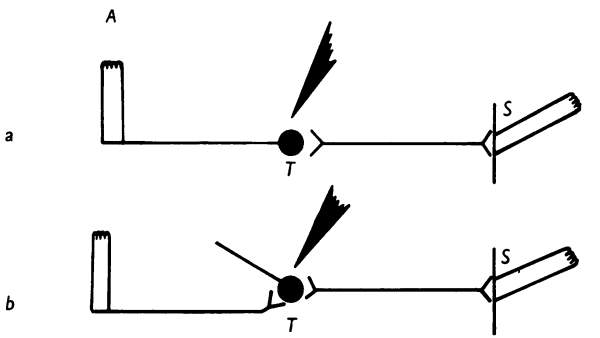

Fig. 1. Diagrams illustrating pathways for activating trigeminal neurones (*T*) from the contralateral arcuate nucleus of the thalamus (*A*). *S* is the stimulus site on the skin of the ipsilateral upper lip. In *a* the trigeminal neurone may be antidromically activated from the thalamus, whereas in *b* only trans-synaptic activation is possible.

activated synaptically from the skin, an impulse will be propagated along its axon up to the contralateral arcuate nucleus. If at any time during the time of conduction from its cell body to the arcuate nucleus the impulse collides with an antidromically propagated impulse, extinction of both impulses occurs. Further, if the fibre terminal in the arcuate nucleus is stimulated after the orthodromic impulse has reached the nerve endings, but within the absolute refractory period of the axon, no antidromically propagated impulse will develop. The earliest time following synaptic activation of the cell at which a stimulus applied to its axon terminals in the arcuate nucleus will generate an antidromically activated impulse which invades the cell body is the conduction time from brain stem to contralateral arcuate nucleus (*T*) plus the refractory period of its axon (*R*). This impulse will be recorded in the nerve cell body in the brain stem only after travelling back from the arcuate nucleus to the cell body, i.e. $2T + R$ (assuming orthodromic and antidromic propagation rates to be equal).

If the stimulus order is reversed in the situation shown in Fig. 1*a*, the shortest response time will be an estimate of the recovery time for the neurone's soma.

In the situation illustrated in Fig. 1*b*, where trans-synaptic activation occurs following thalamic stimulation, the factor determining the shortest response time following successive stimulation of the skin and thalamus respectively, will again be the recovery time of the cell soma, which for trigeminal neurones is only slightly longer than that of the cell's axon (*R*) (Darian-Smith, 1960).

Thus a much shorter response interval will be observed with trans-synaptically activated neurones than with antidromically activated neurones, allowing ready identification.

RESULTS

Characteristics of evoked single neurone activity within the nucleus tractus spinalis oralis and main sensory nucleus

Each neurone was initially identified by its discharge evoked by electrical stimulation of the ipsilateral upper lip in the region of the base of the vibrissae (Olszewski, 1950; Brodal, Szabo & Torvik, 1956). Its response to light mechanical stimulation of the skin was then determined and the receptive field size determined. The cell's response to electrical stimulation of the contralateral arcuate nucleus was then examined.

Cutaneous stimulation. In the early experiments a careful examination of the rostral part of the nucleus tractus spinalis oralis was made, because at this level previous experiments have demonstrated a peak of evoked activity on stimulating the upper lip (Darian-Smith & Mayday, 1960). In a total of 494 neurones examined at this level less than 1 % failed to respond to light mechanical stimulation of the skin. Differentiation according to the type of mechanical stimulation most effective in evoking activity (Hunt & McIntyre, 1960) was not attempted. Spontaneous discharge at rates above 1–2/sec in these cells was uncommon. Most cells fired repetitively in response to electrical stimulation of the skin (Fig. 2, left-hand column). In Fig. 3 is shown a histogram of the distribution of their shortest discharge latency to this stimulus. The receptive fields (for mechanical stimulation) varied greatly in size and are considered below. These findings are similar to those previously made in a small series of neurones in this region (Darian-Smith, 1960), although the general anaesthetic used in the early series was sodium pentobarbital.

Stimulation of the contralateral arcuate nucleus of thalamus. In Fig. 2 (right-hand column) the discharges evoked in these same neurones by stimulating electrically the contralateral arcuate nucleus are shown. Again a wide variation in the shortest latency of discharge was observed, shown by the histogram of Fig. 4. A large proportion of neurones fired with a discharge latency of 2 msec or less, either with a non-repetitive discharge such as is shown in the top trace of Fig. 2*a* or with an early single spike, followed after an interval of 1·5–4·0 msec by repetitive

discharge (Fig. 2*b*, *c*). With all discharges with a latency of greater than 3 msec the latency of the first spike was dependent on the stimulus intensity, commonly increasing by several milliseconds on reducing the intensity of the stimulus applied to the arcuate nucleus. This finding, together with the observations that these cells were unable to follow repetition rates of 100 c/s, strongly suggested that such discharges were synaptically evoked.

The differentiation of antidromically and trans-synaptically induced responses was carried out by using the technique described above. Figure 5

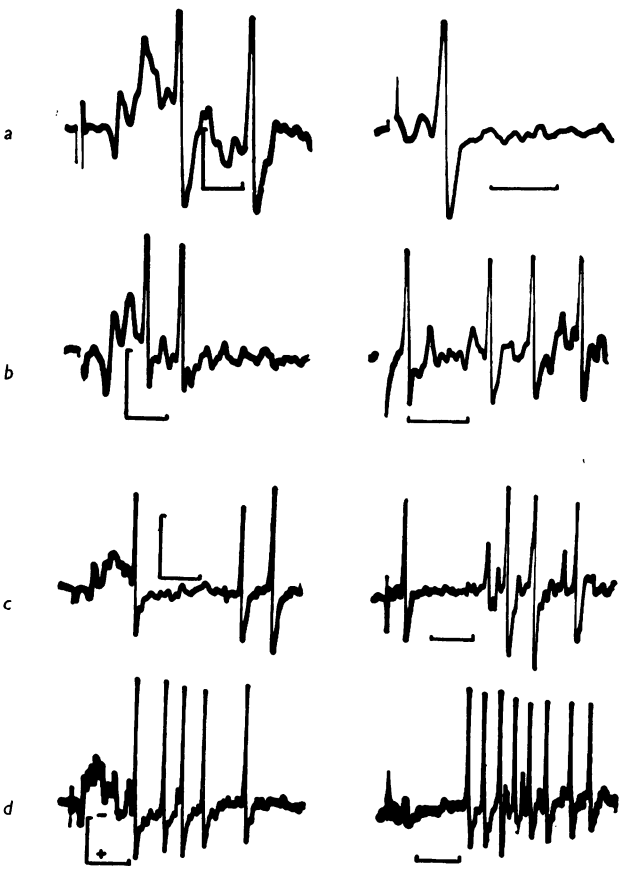

Fig. 2. Records of common discharge patterns observed in trigeminal neurones following electrical stimulation of the ipsilateral upper lip (left-hand column) and the contralateral arcuate nucleus of the thalamus (right-hand column). In *a*, *b*, *c* the neurone was fired antidromically from the thalamus; in *b* and *c* there was also a later trans-synaptic repetitive discharge. In *d* the neurone fired only trans-synaptically following stimulation of the contralateral arcuate nucleus. With all records the time calibration equals 1 msec, and the amplitude calibration 0·5 mV; upward deflexion represents a negative voltage change.

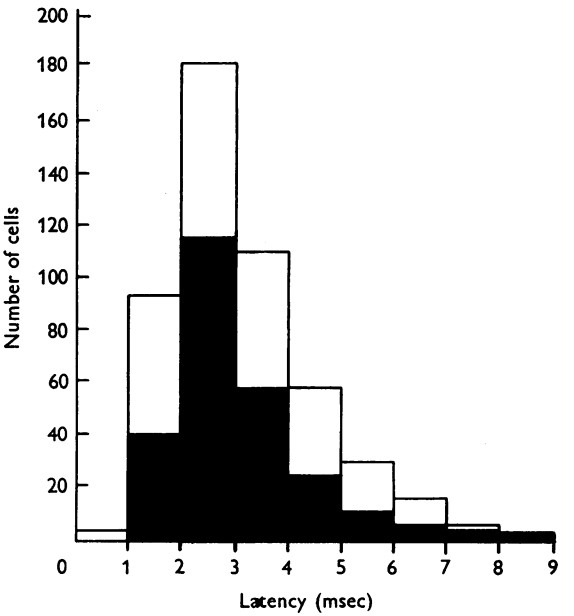

Fig. 3. Histogram showing the distribution of the shortest mean latency of discharge of trigeminal neurones evoked by electrical stimulation of the ipsilateral upper lip. All these units were within nucleus tractus spinalis oralis. The blackened area includes any cell whose axon projected to the contralateral arcuate nucleus of the thalamus (Type 1 cells).

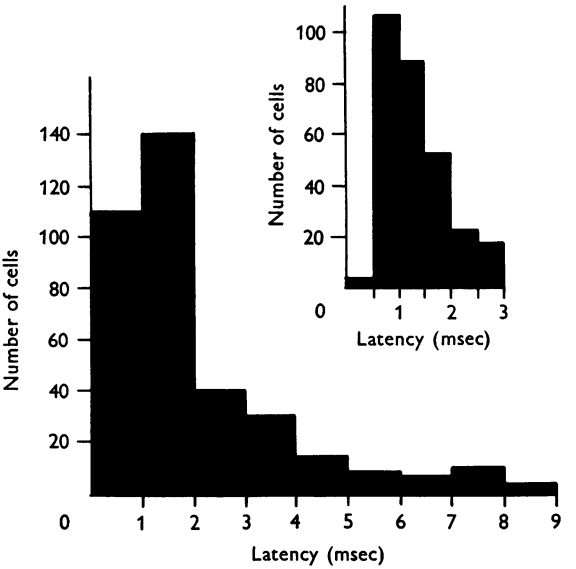

Fig. 4. Histogram showing the distribution of the shortest mean latency of discharge of neurones within nucleus tractus spinalis oralis following electrical stimulation of the contralateral arcuate nucleus of thalamus. The insert shows more detail of the distribution during the 3 msec following the stimulus.

illustrates typical responses. In Fig. 5*a*, *b* the responses observed in a neurone whose axon projected to the contralateral arcuate nucleus are shown. In Fig. 5*a* the response evoked on stimulating the upper lip preceded the thalamically evoked discharge. The latency of this latter response (T) was 1·1 msec. The shortest response interval was 2·9 msec.

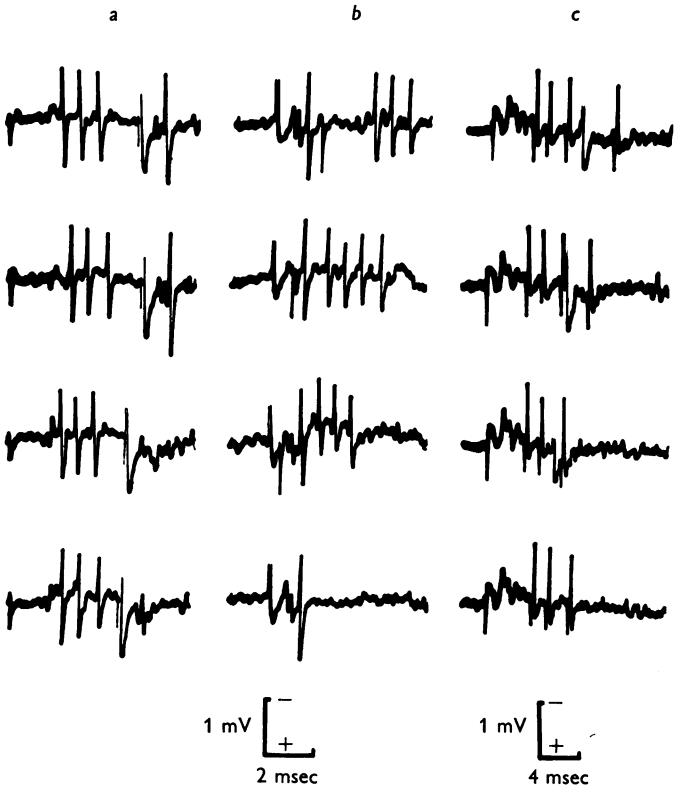

Fig. 5. Interaction of discharges evoked in trigeminal neurones by electrical stimulation of ipsilateral upper lip and contralateral arcuate nucleus. Records *a* and *b* are from same neurone; in *a* the response evoked from the lip preceded that evoked by thalamic stimulation, whereas in *b* the stimulus sequence was reversed. Records in *c* were from another unit, the stimulus sequence being that seen in *a*. Upward deflexion indicates a negative voltage change. The voltage and time scales for *a* and *b* below *b*, and for *c* below *c*.

In Fig. 5*b* the response evoked by thalamic stimulation preceded the cutaneous response. The shortest response interval was then 0·8 msec R. It is seen that $2T + R = 2{\cdot}2 + 0{\cdot}8 = 3{\cdot}0$ msec, approximately the observed shortest response time in Fig. 5*a*. This neurone, then, was antidromically fired on stimulating the contralateral arcuate nucleus.

The responses of a second neurone, illustrated in Fig. 5*c*, contrast with those of the cell of Fig. 5*a*, *b*. In this sequence the cutaneous response preceded the thalamically evoked discharge. The latency of the latter response was 2·1 msec (*T*). The shortest response interval was 2·5 msec. Thus, antidromic activation of the neurone by stimulation of the thalamus was precluded by this observation, and the exciting pathway considered to be trans-synaptic.

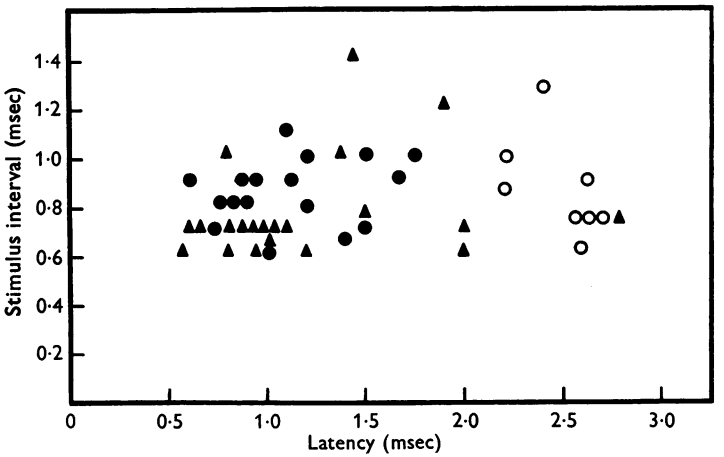

Fig. 6. Relations between shortest discharge latency of trigeminal neurones evoked by electrical stimulation of the contralateral arcuate nucleus and the nature of the activation. ●, neurones demonstrated to be antidromically excited; ○, neurones demonstrated to be trans-synaptically excited; ▲, neurones not tested. The graph also shows the lack of correlation for these cells between the nature of excitation of the unit and the shortest interval between the two successive supra-maximal thalamic stimuli which evoke a double response.

By the above means of identifying cells whose fibres projected to the contralateral arcuate nucleus, other characteristics of the antidromic response were examined. In particular it was found that for a small series, all cells whose thalamically evoked discharge had a latency of less than 2 msec were antidromically activated. These observations are illustrated in Fig. 6. In view of these findings all cells in the present samples, whose thalamically evoked response had a latency of less than 2 msec, were considered to project directly to the contralateral arcuate nucleus.

With this group of neurones we determined the shortest interval between two successive identical supra-maximal stimuli, applied to the arcuate nucleus, which evoked a double response. It is seen from Fig. 6 that over the range 0–3 msec there was no significant increase in the recovery time, indicating that this test is not suitable for differentiating antidromically and trans-synaptically evoked discharges in this situation. Similarly it

was found that the maximal stimulus repetition rate which the thalamically evoked response followed, whilst falling gradually from over 900 c/s for spikes with a latency of less than 1 msec to a frequency of about 300–400 c/s for spikes with a latency of 2–3 msec, permitted no clear differentiation of antidromically and trans-synaptically induced discharges.

Examination of the unitary discharge patterns observed in trigeminal cells, following stimulation of the contralateral arcuate nucleus, revealed three main discharge patterns. In Fig. 2*a* the commonest pattern for an antidromic response is illustrated—a single non-repetitive spike. Figure 2*b* and *c* shows another common pattern, a single early spike, followed after a pause of 1·5 msec by a repetitive discharge varying in latency, and evoked commonly only by increasing the stimulus intensity. The reverse sequence on progressively increasing the stimulus intensity was however observed with some units. In Fig. 2*d* a common trans-synaptic response is shown, with a long repetitive discharge.

TABLE 1. Neurone types identified within trigeminal nuclei

Neurone type	Receptive field	Response to thalamic stimulation	No. of neurones: Main sensory N. and N.V.Sp.O.	No. of neurones: N.V.Sp.I.
Type 1	Ipsilateral, within distribution of V	Antidromic	287	6
Type 2	Greater than ipsilateral V	Antidromic	5	0
Type 3	Ipsilateral, within distribution of V	Trans-synaptic	121	59
Type 4	Greater than ipsilateral V	Trans-synaptic	41	15
Type 5	Varied	No response	130 (26 tract fibres)	16

N.V.Sp.O. = nucleus tractus spinalis oralis; N.V.Sp.I. = nucleus tractus spinalis interpolaris.

The method used for stimulating the arcuate nucleus does not preclude the stimulation of neighbouring nervous tissue. For this reason the anatomical basis for trans-synaptic activation of trigeminal cells has not been identified. However, the discharge patterns illustrated in Fig. 2*b* and *c* are suggestive of an excitatory pathway involving recurrent collaterals from neighbouring axons projecting to the arcuate nucleus (cf. Amassian & de Vito, 1957).

By means of the above criteria for characterizing neurones isolated in the trigeminal complex the population sample may be grouped into the subdivisions indicated in Table 1.

Cell pattern within transverse planes through nucleus tractus spinalis oralis and main sensory nucleus. Within different planes through the nucleus tractus spinalis oralis and main sensory nucleus a common pattern of the distribution of all types was regularly observed. Figure 7 illustrates a typical distribution, recordings from these neurones being obtained during a sequence of four electrode penetrations 0·5 mm apart in the same transverse plane, in the rostral part of the nucleus tractus spinalis oralis.

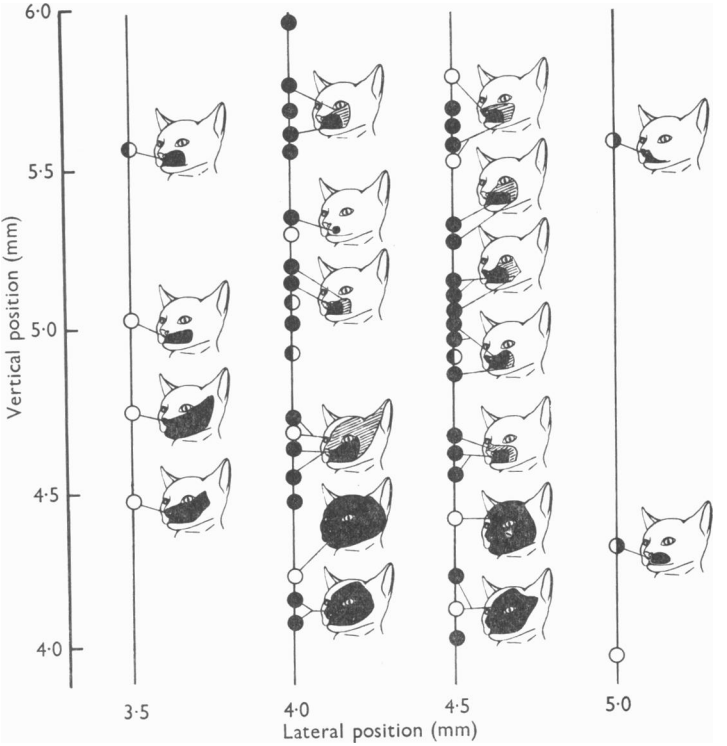

Fig. 7. Transverse plane through nucleus tractus spinalis oralis 5 mm anterior to obex. Four electrode penetrations were made, the most lateral traversing the spinal tract. The position and receptive field of each neurone is shown except for a few cells whose receptive fields were not determined. The cell types are indicated by the following symbols: ◑, tract fibres; ●, Type 1 neurones; ○, Type 3 and 4 neurones; ◐, no evoked thalamic response, but unit synaptically activated from skin.

Recordings from axons in the spinal tract (two on the right-hand side in Fig. 7) were uncommon, and only 26 tract axons were isolated. No spontaneous activity was observed in these units. The spike discharge evoked on stimulating the upper lip was always initially positive and non-repetitive; no thalamically evoked response was recorded. The mean

latency of the electrically evoked response from skin was 1·08 msec (S.D. ± 0·14 msec). Conduction velocities along the fastest and slowest conducting fibres from which records were obtained were 75 m/sec and 42 m/sec respectively. These recordings were made 4–5 mm behind the entrance of the root into pons. The receptive fields of the units varied but were mostly quite small (mean diameter = 12·6 mm; S.D. = ± 8·5 mm; n = 24) except for two axons whose receptive fields extended over most of the ipsilateral face.

Type 1 cells were characterized by having an axon projection to the contralateral arcuate nucleus, and a small receptive field lying wholly within the peripheral cutaneous distribution of the ipsilateral trigeminal nerve. These neurones were concentrated in the dorsolateral part of the nucleus as is shown in Fig. 7. Within this part of the nucleus practically all neurones were Type 1 cells and formed part of the trigeminal contribution to the medial lemniscal system. Their ipsilateral receptive fields varied from less than 5 × 5 mm to 60 × 50 mm (mean = 475 mm^2). Their shortest latency of discharge following electrical stimulation of the skin is shown for the series in the histogram in Fig. 3 (mean latency = 3·03 msec; S.D. = ± 1·26 msec; n = 287). It is evident from the long latencies of some of these units that they were activated from the skin via a polysynaptic pathway.

The majority of neurones trans-synaptically activated on stimulating the contralateral arcuate nucleus (cell types 3 and 4) occurred in medial and ventromedial parts of the nucleus.

Type 4 cells with extensive receptive fields, extending beyond the peripheral distribution of the trigeminal nerve, probably were neurones within the reticular nuclei adjacent to the ventromedial aspect of the trigeminal nucleus.

Only five neurones were Type 2 cells, with axons projecting to the region of the contralateral arcuate nucleus, but differing from Type 1 cells in having receptive fields extending beyond the peripheral distribution of the trigeminal nerves to forelimbs and trunk. Presumably these cells were also part of the brain-stem reticular formation; they were observed only at the dorsal or ventral and medial margin of the nucleus (see Fig. 8).

The present experiments did not demonstrate any differences in the pattern of distribution of the different cell types at different rostro-caudal levels within the main sensory nucleus and nucleus tractus spinalis oralis. Figure 8 illustrates the cell pattern in a transverse plane near the anterior pole of activity. An additional 90 cells were examined in this region. It was observed, however, that unitary evoked activity was very slight in the anterior part of the main sensory nucleus, agreeing with previous observations on evoked activity in this region (Darian-Smith & Mayday, 1960).

Evoked neurone activity within the nucleus tractus spinalis interpolaris. A profound change in the characteristics of the neurone population was observed when the recording site was moved to nucleus tractus spinalis interpolaris. This is seen in Fig. 9, illustrating the pattern of distribution

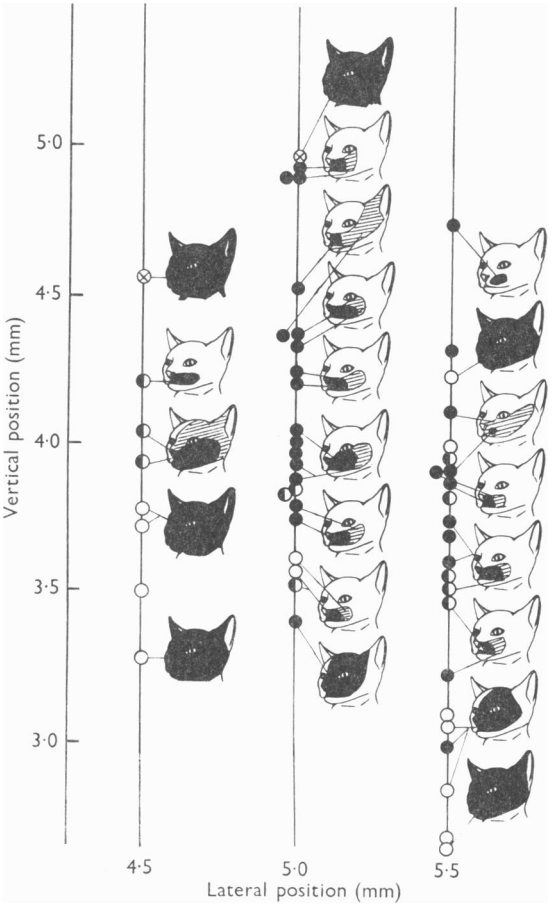

Fig. 8. Transverse plane through main sensory nucleus 8 mm anterior to obex. Three electrode penetrations were made through the nucleus; an additional penetration 0·5 mm lateral to the most lateral illustrated traversed the spinal tract but no units were recorded. Neurone types are indicated by the same symbols as used in Fig. 7, the additional symbol ⊗ indicating a Type 2 neurone.

of cell types in a transverse plane through the nucleus. Very few neurones were antidromically activated on stimulating the contralateral arcuate nucleus, but most were trans-synaptically activated from this region.

The receptive field size of cells at this level was much larger than more anterior in the nuclear complex, and this in fact precluded any somatotopic

organization at this level (Darian-Smith, Proctor & Ryan, 1963). Like neurones in the more anterior nuclei, most cells fired on light mechanical stimulation of skin (2 cells in 96 failed to fire). In Fig. 10 the shortest discharge latencies on electrically stimulating the skin of the ipsilateral upper lip are plotted. An increase in the mean latency of the sample

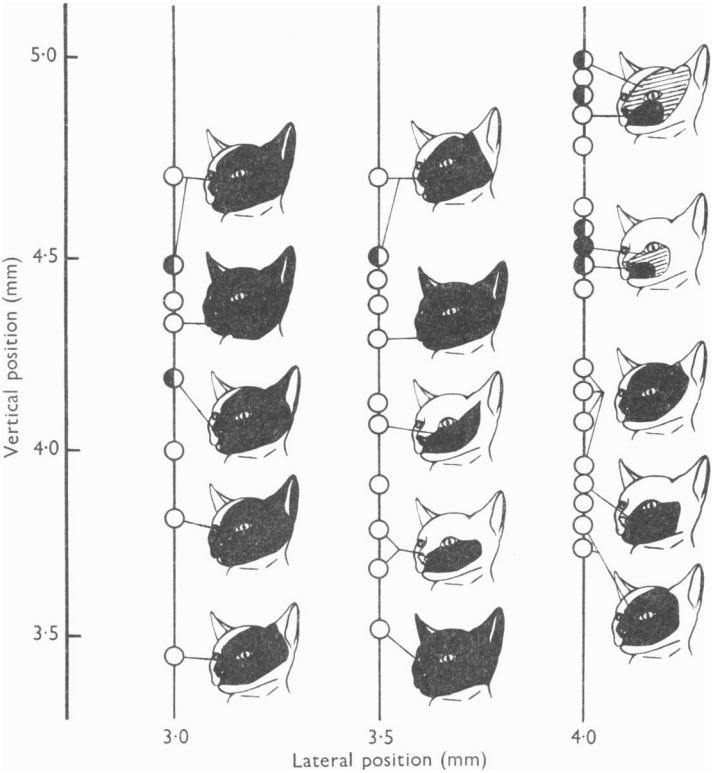

Fig. 9. Transverse plane through nucleus tractus spinalis interpolaris 2 mm anterior to obex. Three electrode penetrations are illustrated. The most lateral penetration passed down the lateral margin of the nucleus. Cell types are indicated by the symbols used in Fig. 7.

occurred (mean = 4·60 msec; S.D. = ± 1·77 msec) not adequately accounted for by the time of conduction down the spinal tract (see Darian-Smith *et al.* 1963). In Fig. 11 is shown the latency of the response evoked in these units on stimulating the contralateral arcuate nucleus. This distribution differs significantly from that observed in the population isolated in the nucleus tractus spinalis oralis (Fig. 4), the vast majority of units having a discharge latency greater than 5 msec. Along the rostrocaudal axis of the nucleus tractus spinalis interpolaris (about 3 mm), no variation

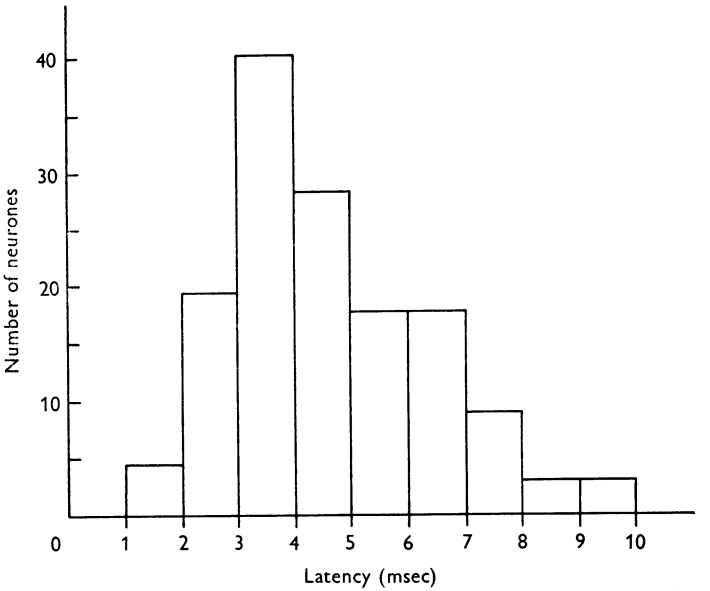

Fig. 10. Histogram of shortest mean discharge latencies of neurones within nucleus tractus spinalis interpolaris evoked by electrical stimulation of the ipsilateral upper lip.

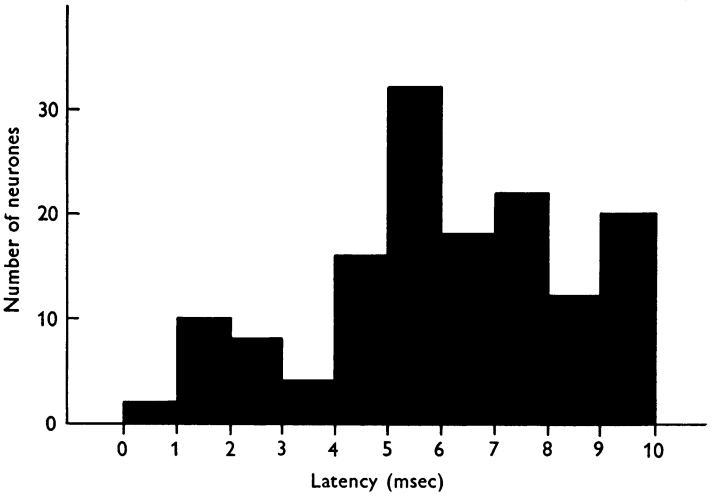

Fig. 11. Histogram of shortest mean discharge latencies of neurones within nucleus tractus spinalis interpolaris evoked by electrical stimulation of the contralateral arcuate nucleus of thalamus.

in the above pattern was observed. The caudal limit of the distribution of this neurone population coincided with the posterior limits of this nucleus.

DISCUSSION

The present observations support the anatomical observation (Winkler, 1921; Torvik, 1957; Carpenter & Hanna, 1961) that an important contribution to the medial lemniscal system arises from the rostral part of the trigeminal brain-stem nuclei. Our observations are limited to those cells activated by electrical and mechanical stimulation of the skin. These neurones, however, were not restricted to the main sensory nucleus but rather extended throughout the whole of the nucleus tractus spinalis oralis also. Olszewski (1950) has previously observed the cytoarchitectural similarity of these adjacent nuclei and suggested the possibility of common function, which, in view of the present findings, is likely. Little evoked unitary activity was observed in the rostral part of the main sensory nucleus, confirming previous observations on field potentials evoked on stimulating the skin of the face (Darian-Smith & Mayday, 1960). This may result from the fact that in section the main sensory nucleus has a considerably smaller cross-sectional area adjacent to the trigeminal motor nucleus than at more posterior levels.

Neurones in these nuclei, whose axons projected to the contralateral arcuate nucleus, all responded to light mechanical stimulation of the skin, and most of these cells had restricted receptive fields, suggesting that they constituted at least part of the trigeminal contribution to the medial lemniscal system. This finding is not compatible with the recent suggestion of Wall & Taub (1962) that the trigeminal contribution to the medial lemniscus arises more caudad from nucleus tractus spinalis interpolaris and caudalis. In particular, nucleus tractus spinalis interpolaris in the present experiment contained practically no neurones whose axons projected to the contralateral arcuate nucleus, and in addition the receptive fields were uniformly large, extending over much of the ipsilateral face.

However, the similarity of these 'medial lemniscal' neurones and the 'A' cells of Gordon *et al.* (1961) in the nucleus tractus spinalis caudalis is evident. The axon projection and receptive field size of neurones in both groups were very similar. Functional differences may exist but have not been demonstrated by the present experiments. Tentatively both groups of these cells must be considered to contribute to the 'medial lemniscal' projection to the thalamus. Comparison of the observations of Gordon *et al.* (1961) with the present series suggest that the numerically greater contribution arises from the anterior nuclear components, nucleus tractus spinalis oralis and main sensory nucleus.

In parallel with the observations of Amassian & de Vito (1957) and Gordon & Seed (1961) on the cuneate and gracile nuclei, we commonly observed trans-synaptic activation of neurones within the trigeminal nuclei following electrical stimulation of the contralateral arcuate nucleus. Synaptic activation was observed not only in neurones whose axons did not project to the contralateral arcuate nucleus, but also in 'medial lemniscal' units; in the latter the discharge consisted of an initial antidromic response followed after a pause of 1·5–4 msec by a repetitive synaptic discharge (Fig. 2*b*, *c*). The anatomical pathways involved might be recurrent collateral from the axons of 'medial lemniscal' units, or alternatively interneurones within the nucleus. Cajal (1909) described recurrent collaterals arising from axons constituting the medial lemniscal outflow from the cuneate nucleus and other sensory relays and Amassian & de Vito (1957) have considered these to be the pathways responsible for this complex discharge following medial lemniscal stimulation. Whilst the anatomical evidence for the presence of interneurones in these anterior trigeminal nuclei is confusing (see Åström, 1952; Torvik, 1957) in the present experiments the regular distribution of non-lemniscal neurones along the ventromedial aspect of the nuclei does suggest the possibility of these being internuncials.

The markedly different population of neurones observed within the nucleus tractus spinalis interpolaris supports Olszewski's (1950) earlier suggestion that this region of the spinal nuclear complex might subserve a different function from that of the more anterior components. Recently Carpenter & Hanna (1961) have observed a considerable bundle of trigemino-cerebellar fibres originating from the nucleus tractus spinalis interpolaris and oralis, projecting largely to the ipsilateral culmen and declive, sites where evoked electrical activity has been recorded on stimulating the skin of the face (Snider, 1950). In the present experiments it was uniformly observed that cells in the nucleus tractus spinalis interpolaris had large receptive fields and resembled those cells shown to project to the anterior cerebellum from the rostral third of the nucleus gracilis (Gordon & Seed, 1961). It would thus appear likely that a major trigemino-cerebellar pathway excited by cutaneous stimulation within the peripheral distribution of the trigeminal nerve arises from the nucleus tractus spinalis interpolaris.

SUMMARY

1. Discharges evoked in neurones within the trigeminal main sensory nucleus, nucleus tractus spinalis oralis and interpolaris, by electrical stimulation of the skin of the ipsilateral upper lip were recorded in anaesthetized cats with tungsten micro-electrodes. Over 99% of these

cells were fired by light mechanical stimulation of the same cutaneous region.

2. Electrical stimulation of the contralateral arcuate nucleus of the thalamus enabled identification of neurones constituting the trigeminal contribution to the medial lemniscal system. Both antidromic and trans-synaptic activation of neurones were observed.

3. 'Medial lemniscal' neurones were identified throughout the nucleus tractus spinalis oralis and the caudal part of the main sensory nucleus. They formed a homogeneous cell group in the dorsolateral part of these nuclei; their receptive fields were small.

4. Neurones not antidromically activated from the contralateral arcuate nucleus were regularly observed along the ventromedial border of the nucleus. Many of these were trans-synaptically activated following thalamic stimulation. Their receptive fields were large: some cells have the characteristics of reticular formation neurones.

5. The axons of neurones within the nucleus tractus spinalis interpolaris did not project to the contralateral arcuate nucleus. Most were trans-synaptically activated from this nucleus. Their receptive fields were uniformly large. It is suggested that this nucleus is primarily a trigemino-cerebellar relay.

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