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SECONDARY NEURONES WITHIN A TRIGEMINO-CEREBELLAR PROJECTION TO THE ANTERIOR LOBE OF THE CEREBELLUM IN THE CAT

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The neurone population which is excited within the brain stem of the cat by light mechanical stimulation of the skin of the face is not homogeneous. Some differentiation of cell types has been attempted in terms of receptive field size, latency of discharge and rate of adaptation following cutaneous stimulation, anatomical location within the brain stem, and site of termination of the cell's axon (Darian-Smith, 1960; Gordon, Landgren & Seed, 1961; Kruger & Michel, 1962; Wall & Taub, 1962; Darian-Smith, Phillips & Ryan, 1963; Darian-Smith, Proctor & Ryan, 1963). A large component of this population consists of cells with small ipsilateral cutaneous receptive fields, which have a long axon projection to the contralateral arcuate nucleus of the thalamus, and whose cell bodies lie within one of the anatomical subdivisions of the brain-stem trigeminal complex (Gordon *et al.* 1961; Darian-Smith, Phillips *et al.* 1963). A significant proportion of the cells examined, however, do not belong to this 'lemniscal' group. These cells usually have a large receptive field which often extends over the contralateral part of the face, or beyond the peripheral distribution of the trigeminal nerve.

Further differentiation of the non-lemniscal trigeminal neurones in terms of their long axon projection was prompted by observations of Gordon & Seed (1961) on the homologous nucleus gracilis. They found in the rostral part of this nucleus cells with a direct axon projection to the anterior lobe of the cerebellum, which had large cutaneous receptive fields. Whilst previous investigations have demonstrated potentials evoked in the cortex of the anterior cerebellar lobe by stimulation of the skin of the face (Snider & Stowell, 1942, 1944; Adrian, 1943), functional properties of the trigemino-cerebellar pathway involved have not been examined. Two possible trigemino-cerebellar pathways for this projection are apparent. The anatomical basis of a direct pathway, such as was found by Gordon & Seed (1961) from the gracile nucleus, is provided by the findings

of several histological investigations (Woodburne, 1936; Larsell, 1947; Pearson, 1949; Carpenter & Hanna, 1961). An alternative pathway to the anterior lobe of the cerebellum from the limbs and trunk, which relays within the lateral reticulum nucleus, has been demonstrated by Brodal (1943, 1949, 1954). This nucleus lies ventral to a large part of the brain-stem trigeminal complex in the cat (cf. Walberg, 1952).

In the present experiments trigemino-cerebellar cells within the brain-stem which were excited by stimulation of the skin of the upper lip were identified. The anatomical position of most of these cells was shown to be within the lateral reticular nucleus, and some of their functional characteristics were examined.

METHODS

Preparation of animals. Cats weighing 2·8–5·3 kg were used for all experiments. After induction with ether, anaesthesia was maintained with intravenous chloralose (55–65 mg/kg), a dose sufficient to maintain light surgical anaesthesia throughout the experiment. In nine animals an initial intravenous injection (12–16 mg) of the muscle relaxant gallamine triethiode (Flaxedil, May and Baker) was given and respiration maintained with a pump. Flaxedil was administered at approximately 20 min intervals (4–6 mg). The level of anaesthesia was checked intermittently by allowing the animal to recover from the relaxant drug. These animals breathed 100 % oxygen. In 4 animals no muscle relaxant was used and they breathed air spontaneously; the results obtained in the two groups did not differ significantly.

After mounting the animal in a stereotaxic instrument, the occipital part of the skull was opened enough to allow the removal of the dorsal third of the tentorium cerebelli. The arch of the atlas was also removed. The whole exposed brain stem and cerebellum were covered with paraffin which was maintained at 37–38° C. The body temperature was also held at this temperature, by means of a d.c. electric blanket. During the whole operative period the mean systemic blood pressure was continuously recorded with a Statham 23 A.C. strain gauge and Grass polygraph: during the recording period intermittent measurements were made. The range for the 13 animals was 95–145 mm Hg, usually rising 5–10 mm Hg during the recording period.

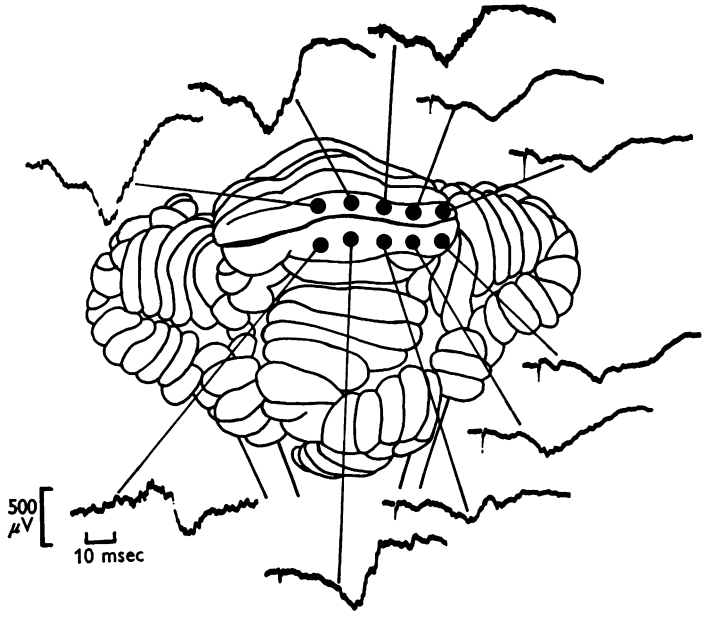
Recording. Tungsten micro-electrodes (Hubel, 1957) were used for extracellular neural recording. Penetrations of the brain stem were made at an angle of 30° to the vertical plane to reach structures under the tentorium cerebelli. A capacity-coupled amplifier was used for amplification, the working frequency bandwidth being 80–10,000 c/s. Permanent records of the responses of all units were made by means of a Grass Kymograph camera attached to the oscilloscope.

Location of the recording site. In these experiments it was important that the positions of all the units in each transverse plane could be accurately related. This was only possible if all the recordings were made with the same electrode. The co-ordinates of the electrode tip for each neurone then related their positions accurately. In addition, 20 μ serial paraffin sections were cut of each brain stem and every second slide stained by Einarson's (1932) gallocyanin method. After identifying electrode tracks, neighbouring sections were stained by Holmes' silver method (1947). The identification of vertical positions along electrode tracts was made by placing small electrolytic lesions (4·5 μA for 10 sec; Hubel, 1959). These lesions were difficult to find even in the silver-stained sections, but when identified were very useful.

Stimulation of skin and cerebellum. Cells were initially identified by their discharge

evoked by electrical stimulation of the ipsilateral upper lip (bipolar electrodes with 2–3 mm between poles; duration of square pulse 50 μsec). If the cell responded to light mechanical stimulation of the skin, its excitatory receptive field was mapped out with a brush.

The response evoked in the anterior lobe of the cerebellum by electrical stimulation of the upper lip was mapped with a surface electrode. Short-latency potentials such as those illustrated in Text-fig. 1 were evoked by this stimulus over a limited area of cortex of the culmen and simplex; they were mainly ipsilateral but also extended 2–3 mm across the mid-line. A battery of 10 stimulating tungsten electrodes was then arranged to cover the whole of this region of projection. These electrodes were arranged in 2 transverse rows



Text-fig. 1. Dorsal view of cerebellum showing typical position of stimulating electrodes. The potentials evoked at these points on the surface of the cortex by an electrical stimulus applied to the right upper lip are also shown.

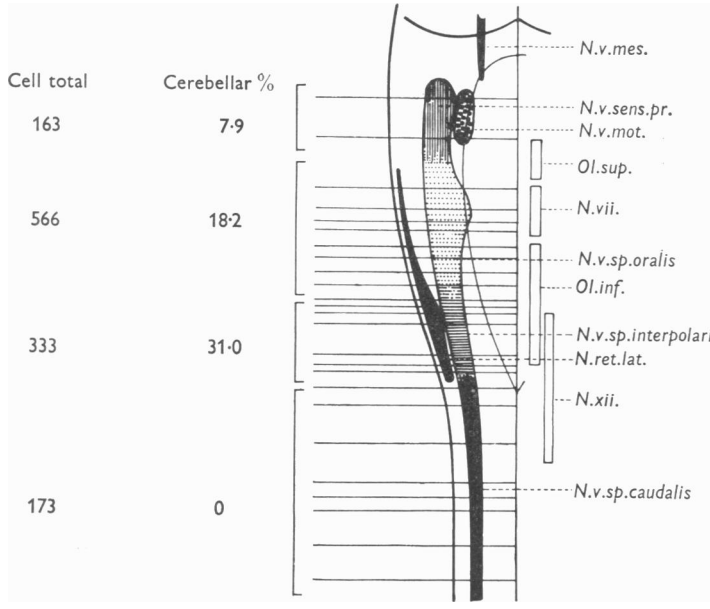
3 mm apart; within rows the electrodes were 2 mm apart. By using the uniselector switch previously described (Darian-Smith, Proctor *et al.* 1963), a square pulse of 50 μsec duration could be passed between successive pairs of electrodes on the cerebellum. This allowed rapid identification of any axon projection of the neurone being observed to this region of the anterior lobe of the cerebellum. In Text-fig. 1 a typical placing of the stimulating electrodes is shown, together with records of the evoked potential recorded at each of these sites following electrical stimulation of the lip.

The differentiation between an antidromic response and a trans-synaptic response in a trigeminal neurone following simulation of the cerebellar cortex was made by the 'collision' method previously described (Darian-Smith, Phillips *et al.* 1963), and illustrated in Text-fig. 3 of the present paper.

RESULTS

After the initial identification of neurones by the discharge evoked by electrical stimulation of the ipsilateral upper lip, their receptive fields were

mapped with a camel-hair brush. With a few cells no response to this kind of mechanical stimulation of the skin was seen; these cells have not been included in the series. Each neurone was then examined to see if a discharge could be evoked by electrical stimulation of the anterior lobe of the cerebellum. In Text-fig. 2 are shown all the planes within the brain-stem in which neurones were examined in this way. In most planes 60–70

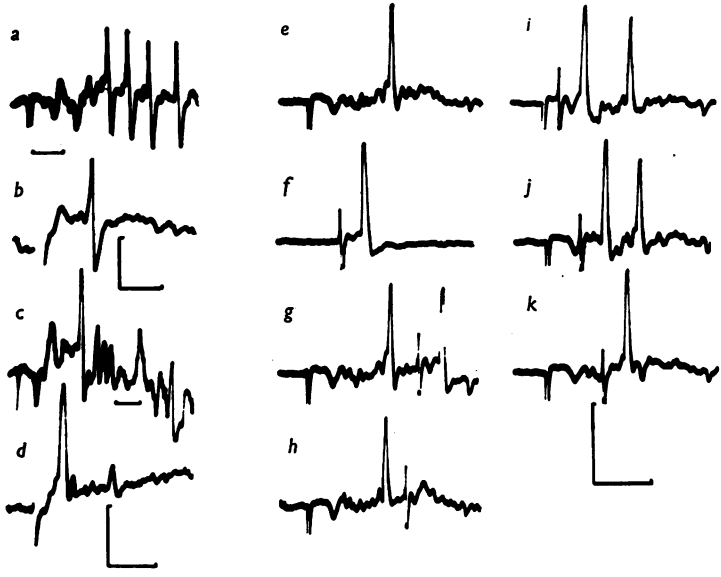


Text-fig. 2. Dorsal view of the brain stem, illustrating the rostro-caudal positions of all transverse planes examined in the present experiments. The number of neurones observed in each plane is indicated on the left-hand side, together with the percentage of these cells which fired following electrical stimulation of the anterior lobe of the cerebellum. *N.v.mes.*, Trigeminal mesencephalic nucleus; *N.v. sens.pr.*, main sensory nucleus; *N.v.mot.*, trigeminal motor nucleus; *Ol.sup.*, superior olivary nucleus; *N.vii.*, facial nucleus; *N.v.sp.oralis*, nucleus tractus spinalis oralis; *Ol.inf.*, inferior olivary nucleus; *N.v.sp.* interpolaris; *N.ret.lat.*, lateral reticular nucleus (Brodal); *N.xii.*, hypoglossal nucleus; *N.v.sp.*, caudalis, nucleus tractus spinalis caudalis.

neurones were isolated, although fewer were recorded caudal to the obex. To the left of the diagram the neurones have been grouped, the nuclear subdivisions of the trigeminal complex being used as landmarks. The total number of cells isolated within each brain-stem region, together with the percentage activated by electrical stimulation of the anterior lobe of the cerebellum, are indicated on the left side of the diagram.

Those neurones which discharged following cerebellar stimulation usually did so with a single short-latency spike (Text fig. 3*b*, *d*). A short

repetitive discharge was observed in only 8 %. The histogram in Text-fig. 4 illustrates the distribution of the latency of discharge of these cells following cerebellar stimulation. The latencies of 168 of the 185 (91 %) cells examined were 2 msec or less. Fourteen such cells were tested by the

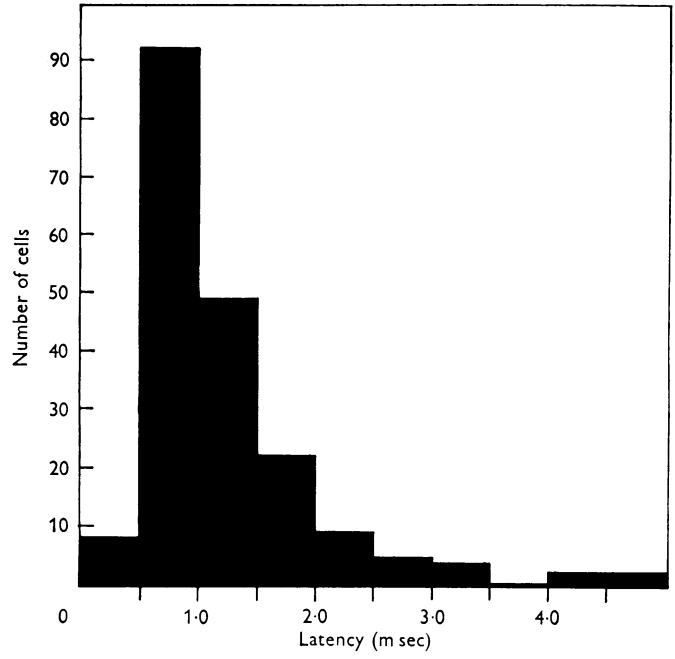


Text-fig. 3. The records *a* and *c* are typical discharge patterns in trigemino-cerebellar neurones, following electrical stimulation of the skin of upper lip: *b* and *d* are records of the discharges evoked in these two cells respectively by electrical stimulation of the anterior lobe of the cerebellum. In both examples the latter responses were shown to be antidromically evoked, by using the collision technique shown in *e–k*. *e*, Discharge following cutaneous stimulation; *f*, discharge following cerebellar stimulation (latency = 0·75 msec). In *g*, *h* the cutaneous discharge preceded the cerebellar evoked response; extinction of the cerebellar evoked response occurred when the interval between responses was less than 2·05 msec. When the cerebellar evoked response preceded the discharge evoked by cutaneous stimulation (*i*, *j*, *k*) extinction of the second spike occurred when the interval between responses was less than 0·95 msec. These observations demonstrate that the discharge in *f* was antidromically evoked. Voltage calibration 1 mV. Time scale shown by horizontal bars: for *a–d*, scale is 1 msec; for *e–k*, scale is 2 msec.

collision technique (Darian-Smith, Phillips *et al.* 1963) and shown to be antidromically fired by cerebellar stimulation. Text-fig. 3*e–k* illustrates such a sequence. Two cells with longer discharge latencies (2·9 and 3·4 msec, respectively) were similarly examined; both fired trans-synaptically.

These findings agree with previous observations on antidromic and trans-synaptic activation of cells following arcuate nucleus stimulation (Darian-Smith, Phillips *et al.* 1963). It seems that trigemino-cerebellar

cells firing with a latency of 2 msec or less following cerebellar stimulation may be considered to fire antidromically, while responses with a longer latency are probably trans-synaptic.



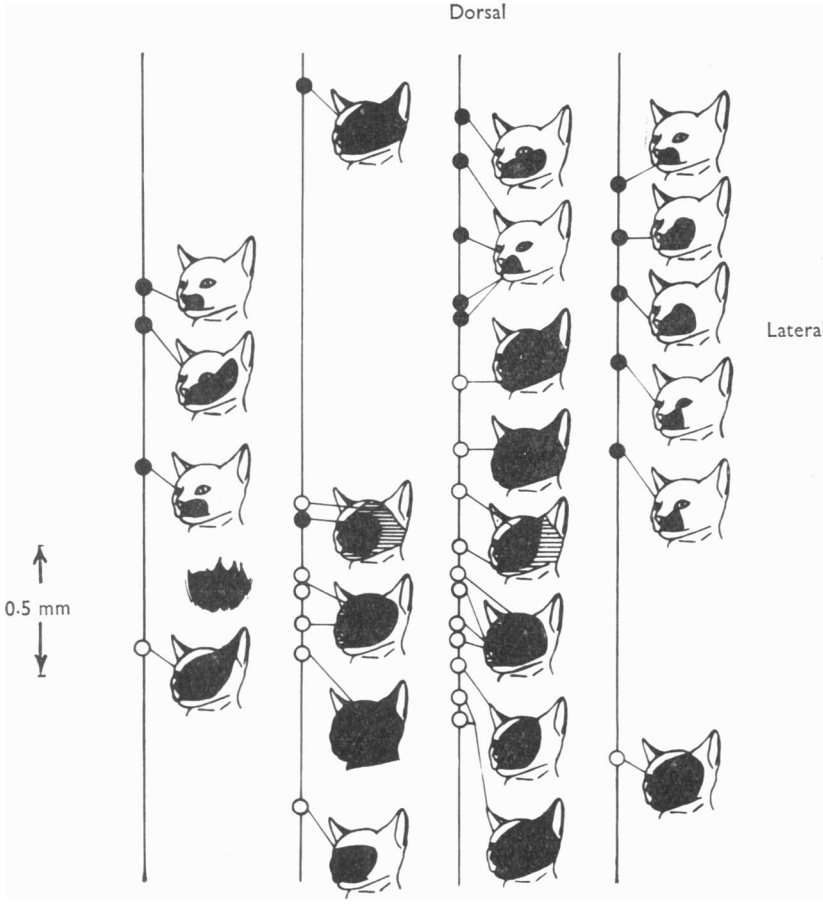
Text-fig. 4. Histogram showing the distribution of the discharge latency of trigemino-cerebellar cells following stimulation of the culmen-simplex area of the cerebellum.

The distribution of neurone types at different rostro-caudal levels in the brain stem

It is seen in Text-fig. 2 that in the neurone population excited by light mechanical stimulation of the skin of the face the highest proportion (25–57 %) of trigemino-cerebellar units was observed in the 3–4 mm rostral to the obex. The proportion fell to 5–7 % rostral to the facial nucleus, at the level of the main sensory nucleus, whilst of the 167 cells examined caudal to the obex, none had a long axon projecting to the anterior lobe of the cerebellum. Correlation of this rostro-caudal distribution of trigemino-cerebellar cells did not reveal any clear-cut relation to the sub-divisions of the trigeminal nuclear complex. However, it was apparent that trigemino-cerebellar cells were commonest at the levels of the nucleus tractus spinalis interpolaris and the caudal half of nucleus tractus spinalis oralis (Olszewski, 1950; Brodal, Szabo & Torvik, 1956). The

pattern of distribution of these cells in transverse planes at these levels was therefore examined.

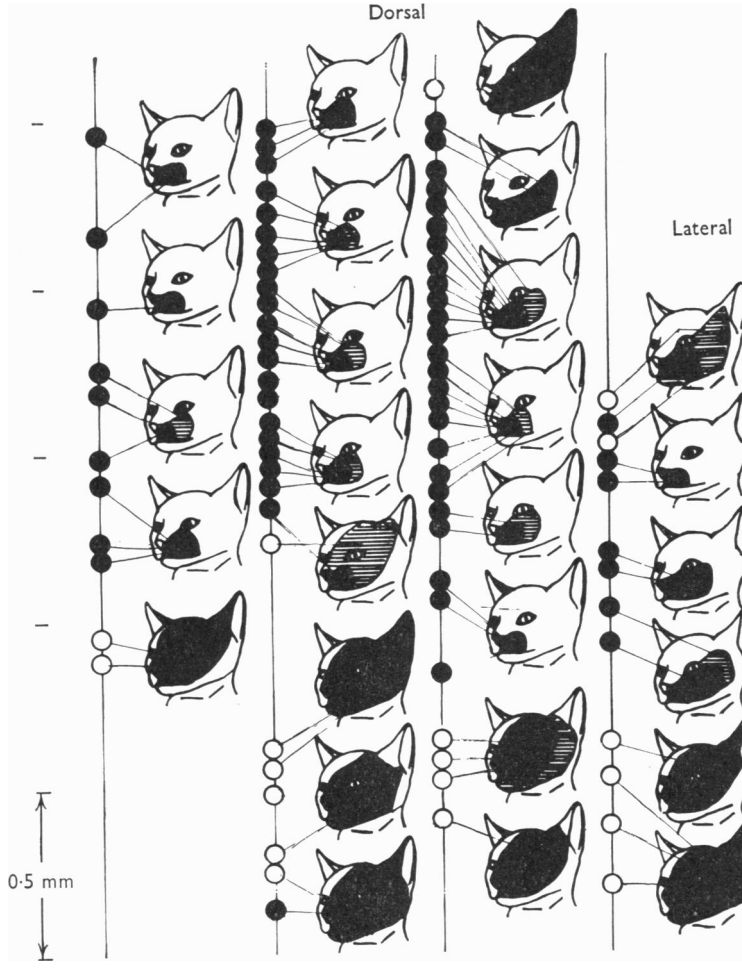
Text-figure 5 shows the pattern of distribution of trigemino-cerebellar



Text-fig. 5. The relative positions of trigeminal neurones observed in a transverse plane in the brain stem passing through nucleus tractus spinalis interpolaris. Four electrode penetrations were made at 0·5 mm intervals with the same electrode. The cutaneous receptive field of each cell is shown on the adjacent electrode diagram. Cells which fired antidromically following electrical stimulation of cerebellum, ○; cells not firing following cerebellar stimulation, ●. Pl 1, figs. 1 and 2, are photographs of histological sections passing through the electrode tracks shown above.

and other cells excited by mechanical stimulation of the lip in a transverse plane through the brain stem at the level of nucleus tractus spinalis interpolaris. Plate 1, fig. 1 is a photograph of the corresponding histological section. It can be seen that most trigemino-cerebellar cells lie ventral and

have uniformly large receptive fields. It is seen on comparing Text-fig. 5 with similar maps in a previous examination (Darian-Smith, Phillips *et al.* 1963) that most Type 3 and Type 4 cells of the earlier series probably had

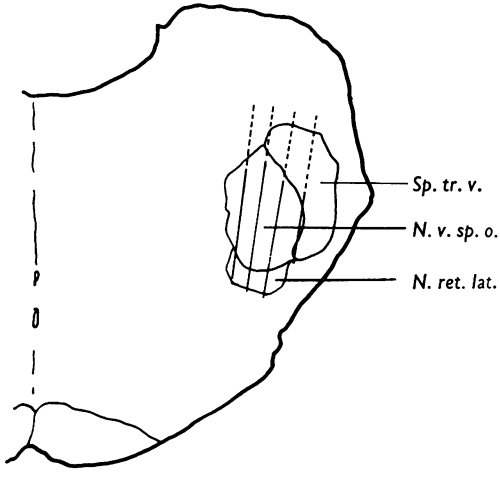


Text-fig. 6. The relative positions of trigeminal neurones observed in a transverse plane in the brain stem traversing nucleus tractus spinalis oralis. Four electrode penetrations were made with the one electrode, at 0·5 mm intervals. The cutaneous receptive field of each unit is shown in the adjacent diagram. Neurone types are indicated by the same symbols as used in Text-fig. 5.

long axons terminating in the anterior lobe of the cerebellum. In the photograph of the section it is evident that electrode tracks extended ventral to the nucleus tractus spinalis interpolaris and on further examination, with marking lesions, it was found that most of these trigemino-

cerebellar cells were within the lateral reticular nucleus (Brodal, 1943; Walberg, 1952). Plate 1, fig. 2, illustrates the apposition of this nucleus to the ventral part of the nucleus tractus spinalis interpolaris and an electrode penetration passing through it. It is not possible from the present results to be sure that all ventrally placed trigemino-cerebellar neurones lay within the lateral reticular nucleus, particularly those near the common border of the two nuclei, but the majority certainly did so.

At more rostral levels trigemino-cerebellar neurones, activated by mechanical stimuli to the upper lip, were also observed ventral to the nucleus tractus spinalis oralis. Text-figure 6 illustrates such a plane.

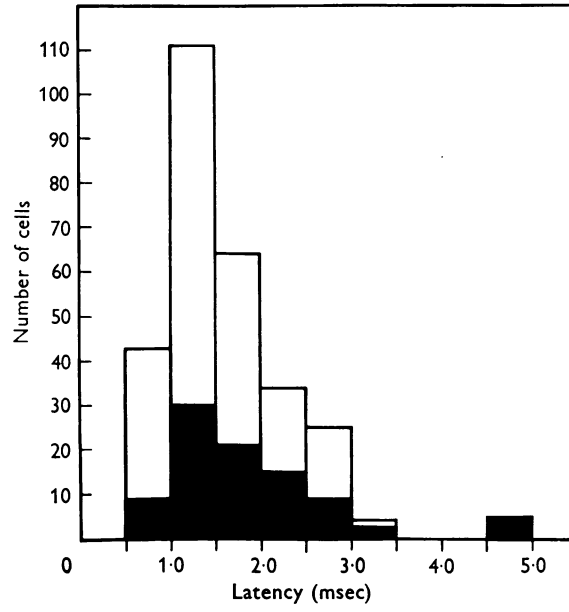


Text-fig. 7. Transverse section through brain stem, illustrating the electrode penetrations along which the neurones of Text-fig. 6 were identified. *Sp.tr.V.* Trigeminal spinal tract; *N.ret.lat.* lateral reticular nucleus; *N.v.sp.o.* nucleus tractus spinalis oralis.

Again these cells had uniformly large receptive fields. The majority of units in this plane, however, had small receptive fields, and had axons projecting to the contralateral arcuate nucleus (Darian-Smith, Phillips *et al.* 1963). When located accurately on the appropriate histological section it was found again that the trigemino-cerebellar neurones occurred not in the nucleus tractus spinalis oralis but in the lateral reticular nucleus, now much reduced in cross-sectional area.

In addition a few trigemino-cerebellar cells were regularly found along the dorsal margin of the nucleus tractus spinalis oralis (Text-fig. 6). We observed no functional differences between these cells and those trigemino-cerebellar cells observed ventrally. Whether these cells lay within the trigeminal nucleus or within juxtaposed nuclei was not determined.

In transverse planes at the level of the main sensory nucleus trigemino-cerebellar units were observed only along the dorsal margin of that nucleus; no such cells were found ventral to the trigeminal nucleus.



Text-fig. 8. Histogram showing distribution of the shortest latency of the discharge evoked in trigeminal cells by electrical stimulation of the ipsilateral upper lip. The distribution for trigemino-cerebellar units (■) and for those cells lacking an axon projection to the anterior lobe of the cerebellum (□) are illustrated. Comparison is made only between cells which were identified within the same transverse planes, as the mean latency of discharge of the trigeminal neurone population varies with the rostro-caudal level in the brain stem.

Latencies of discharge of trigemino-cerebellar neurones following electrical stimulation of upper lip

In Text-fig. 8 the distribution of the shortest latencies of unitary discharge evoked by electrical stimulation of skin is shown and compared with that of the remainder of the population (largely 'lemniscal' units projecting to the contralateral arcuate nucleus). Because the mean latency of discharge varies at different rostro-caudal levels (Darian-Smith, Proctor *et al.* 1963) the comparison has been made only between cells of the two groups recorded in the same planes. From the histogram it is evident that no marked latency differences between the two populations occurred. As the latency of the presynaptic volley in the spinal tract at this level in the brain stem is 1·3–1·5 msec it is apparent that those cells with a latency of 2 msec or less were monosynaptically excited. Hence primary afferent

fibres from the skin terminated directly on at least some of the trigemino-cerebellar cells. From our results it is not possible to tell if a preceding relay occurred within the trigeminal nucleus proper in the presynaptic pathway for the longer latency trigemino-cerebellar cells.

Interrelation of trigemino-lemniscal and trigemino-cerebellar neurones excited by mechanical stimulation of the lip

In one experiment both trigemino-cerebellar and lemniscal neurones (see Darian-Smith, Phillips *et al.* 1963) were identified in each transverse plane. The two groups were quite discrete, no units being antidromically fired from both the cerebellum and the contralateral arcuate nucleus. However, most trigemino-cerebellar units discharged trans-synaptically following electrical stimulation of the region of the contralateral arcuate nucleus. Trans-synaptic excitation of 'medial lemniscal' limits was not observed following electrical stimulation of the anterior cerebellum. Thus an excitatory link exists between the two systems in one direction only.

These findings within the same animal were fully supported by the much larger series of observations in separate animals reported previously (Darian-Smith, Phillips *et al.* 1963). In those experiments trigeminal cells with large receptive fields found in the ventral part of the trigeminal complex, whilst having no axon projection to the arcuate nucleus of the thalamus, were commonly trans-synaptically excited by thalamic stimulation. Most of these cells, called Type 3 and Type 4 neurones in that report, must have been trigemino-cerebellar neurones of the type described in the present experiments.

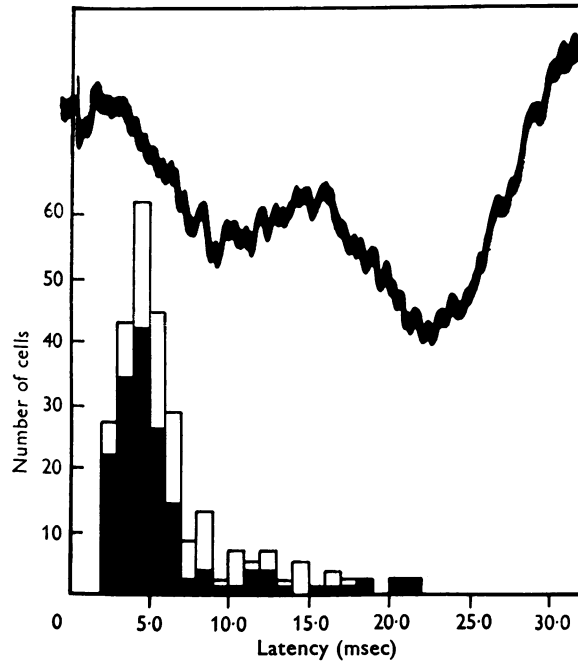
The input to the anterior lobe of the cerebellum following electrical stimulation of the skin of the face

From the data obtained in the present experiments the volley arriving at the anterior cerebellar lobe following an electrical stimulus (duration 50 μsec) applied to the skin of the upper lip may be defined in terms of the relative number of separate impulses reaching the cortex at successive intervals after the stimulus. The time after the stimulus of arrival at the cortex of an impulse along any particular trigemino-cerebellar cell equals the latency of discharge of the cell within the brain stem plus the time taken for the impulse to pass from the cell body in the brain stem to the cerebellar cortex. The latter component is the same as the latency of the antidromic discharge of the cell following cerebellar stimulation, assuming that orthodromic and antidromic propagation along the axon are identical.

If the cell population in the whole of the nuclear region from which the trigemino-cerebellar projection to the anterior lobe of the cerebellum arises is sampled without bias, the temporal distribution of impulses

arriving at the cerebellar cortex may be estimated. One additional factor which contributes to this distribution is the repetitive discharge observed in many trigemino-cerebellar units following electrical stimulation of the skin.

In Text-fig. 9 we see the temporal distribution of incoming impulses to the cerebellar cortex, constructed from the present series of (168) units.



Text-fig. 9. Upper record: potential changes recorded on the surface of the cortex of the culmen, and evoked by a single electrical stimulus (duration 50 μsec) to the skin of the ipsilateral upper lip; a positive potential change is recorded as a downward displacement. Below is a histogram illustrating the distribution of the latencies of impulses arriving at the culmen evoked by stimulation of the ipsilateral upper lip. The stimulus parameters were similar to those of the stimulus used to evoke the surface record. The 'black' histogram includes only the first spike arriving at the cerebellar cortex along each axon; the full histogram includes any repetitive discharge in each axon.

For comparison a typical record of a potential evoked at the surface of the ipsilateral simplex by the same electrical stimulus is shown. It is a complex wave, composed of at least 2 early positive components followed by a long-latency negative potential (Dow, 1939; Carrea & Grundfest, 1954). The black histogram shows the temporal distribution of arriving impulses when only the first spike in the discharge in each axon is con-

sidered. The extended histogram shows the full latency distribution of impulses arriving at the cerebellar cortex when the whole repetitive discharge in each axon is included.

Comparison of the latency distribution of impulses arriving at the cerebellar cortex of the anterior lobe with the surface evoked potential in this region demonstrates that the invading volley may well have contributed to the generation of the first positive phase of the surface response. Grundfest & Campbell (1942), Carrea & Grundfest (1954) and others have previously suggested that this positive potential (Potential I) is entirely presynaptic. The present experiments demonstrate that this is possible, but in no way rule out an additional significant post-synaptic contribution to the generation of the early positive wave.

DISCUSSION

While it has long been known that most cells within the lateral reticular nucleus have an axon projection to the cerebellum (Blakeslee, Freiman & Barrera, 1938), it was Brodal (1954) who first suggested that this nucleus might be an important synaptic relay within a spino-cerebellar pathway excited by stimulation of cutaneous 'tactile' receptors. This suggestion was based on the known spinal afferent fibres of the nucleus (Blakeslee *et al.* 1938; Brodal, 1949) and its efferent projection to the cerebellum, and on the observations of Berry, Karl & Hinsey (1950) and Bohm (1953), in which evoked potentials were recorded in the region of the lateral reticular nucleus following stimulation of various peripheral nerves. The present observations have demonstrated the correctness of this suggestion in relation to cutaneous afferents from the face.

Our observations concerning receptive-field size of these trigemino-cerebellar cells are in agreement with those on neurones examined in excitatory spinal pathways from the skin to the anterior lobe of the cerebellum (the *E*-cells of Oscarsson, 1956); and on cells within the gracile nucleus reported by Gordon & Seed (1961) to project to this region of the cerebellum.

Our observations that trans-synaptic excitation of trigemino-cerebellar neurones occurs following stimulation of the contralateral ventrobasal complex of the thalamus demonstrates a linkage between the medial lemniscal projection system to the cerebral cortex and the skin-cerebellar projection, in addition to the well recognized cortico-cerebellar linkage via the pons (Adrian, 1943; Hampson, Harrison & Woolsey, 1952). In contrast, an excitatory linkage in the reverse direction, from the cerebellum to the medial lemniscal pathway, was not observed. Whether the excitatory pathway from the contralateral thalamus to the skin-cerebellar cells included collaterals from medial lemniscal cells, or, alternatively, separate

axons arising from cells in the region of the arcuate nucleus, was not determined in the present experiments. However, as the latency of discharge of the skin-cerebellar neurones following thalamic stimulation for most cells was 5–10 msec (see Fig. 10, Darian-Smith, Phillips *et al.* 1963) it is unlikely that the pathway was monosynaptic, involving only the axons and collaterals of medial lemniscal neurones.

Previous observations (Gordon *et al.* 1961; Darian-Smith, Phillips *et al.* 1963), together with those in the present experiments, define the cell groups excited within the different trigeminal subnuclei by mechanical stimulation of skin. Within the main sensory nucleus and nucleus tractus spinal oralis, most cells so excited are 'lemniscal', projecting to the ventrobasal complex of the contralateral thalamus. Within the nucleus tractus spinalis interpolaris very few cells were in fact excited by mechanical stimulation of the skin. At this level in the brain stem, however, many cells were excited by cutaneous stimulation, but most of these had large receptive fields and their cell bodies lay within the lateral reticular nucleus; about one-third of these were shown to have an axon projection to the cerebellum. However, the very few lemniscal cells observed at this brain-stem level did have their cell bodies within the nucleus tractus spinalis interpolaris. No other cells excited by cutaneous stimulation were isolated within this nucleus. Gordon *et al.* (1961) showed that within nucleus tractus spinalis caudalis only 40% of excited neurones were lemniscal. No cells from this nucleus have been shown in this series to project to the anterior lobe of the cerebellum, so that the axon termination of many cells excited by cutaneous stimulation is still not accounted for. It is likely that a proportion of these cells have an ipsilateral projection to the thalamus, as well as to the brain-stem reticular formation (Åström, 1952; Carpenter & Hanna, 1961) and to the cervical cord (Kerr & Olafson, 1961). It is also probable that, unlike the situation in more rostral trigeminal subnuclei, internuncials occur at this level.

SUMMARY

1. The discharges evoked in neurones within the brain stem by mechanical stimulation of the skin of the ipsilateral upper lip were recorded in anaesthetized cats with tungsten micro-electrodes.

2. A varying proportion of these cells at each level along the rostrocaudal axis discharged antidromically when the anterior lobe of the cerebellum was stimulated electrically in the region of the ipsilateral culmen and simplex.

3. The cell bodies of most of the trigemino-cerebellar neurones lay within the lateral reticular nucleus; these had receptive fields considerably larger than neighbouring cells within the trigeminal subnuclei, whose

long-axon projection was to the contralateral arcuate nucleus of the thalamus.

4. A few similar trigemino-cerebellar neurones were observed along the dorsal margin of nucleus tractus spinalis oralis. No such cells were observed caudal to the obex.

5. Trigemino-cerebellar neurones were trans-synaptically excited following electrical stimulation of the contralateral arcuate nucleus of thalamus.

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EXPLANATION OF PLATE

Fig. 1. Transverse section through brain stem illustrating the electrode penetrations along which the neurones of Text-fig. 5 were isolated. No neurones were isolated in the most medial penetration. Holmes' silver stain; thickness 20 μ.

Fig. 2. Transverse section immediately adjacent to that of Pl. 1, fig. 1, showing details of the ventral part of electrode track 3. This is placed within the lateral reticular nucleus, within which most trigemino-cerebellar neurones were observed. Einarson's gallocyanin method; thickness 20 μ. *N.v.sp.int.*, Nucleus tractus spinalis interpolaris; *Sp.tr.V.*, trigeminal spinal tract; *N.ret.lat.*, lateral reticular nucleus.

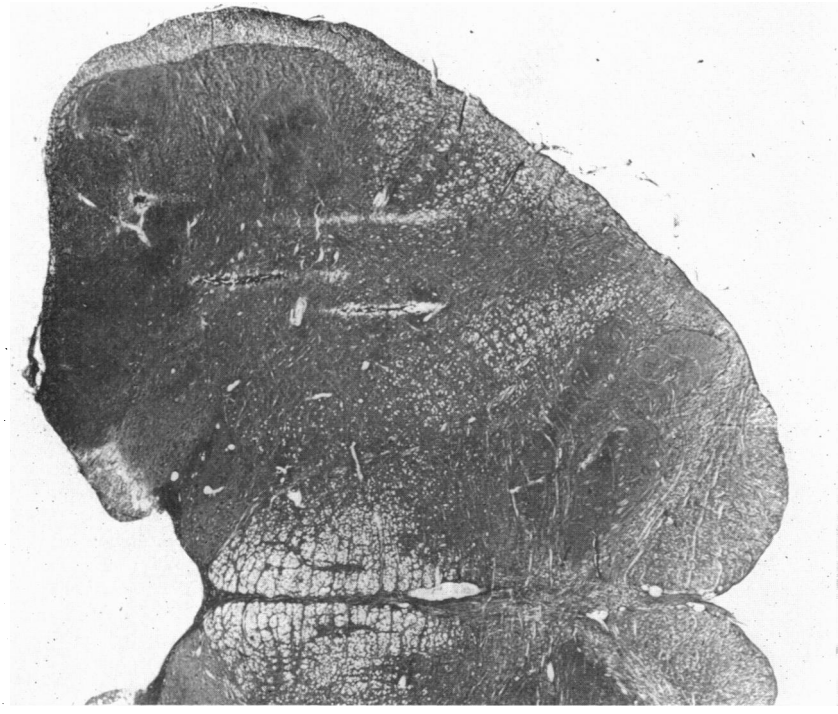

FIG. 1

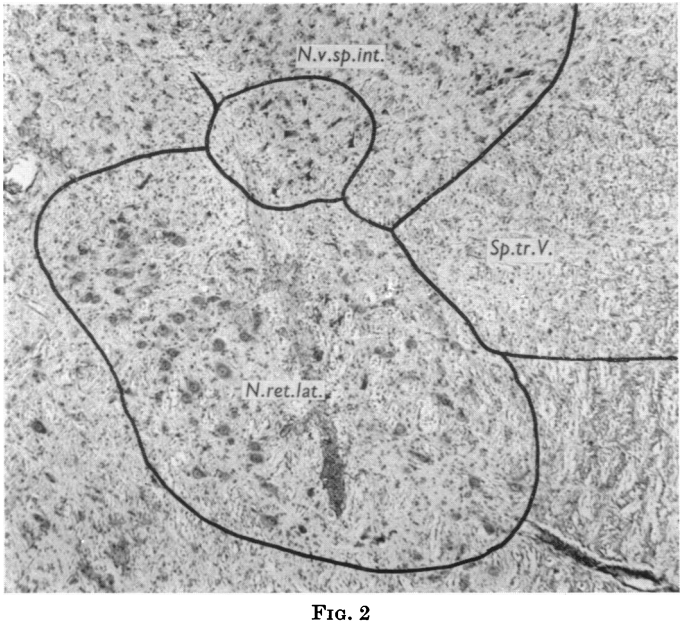

FIG. 2