

**EXPERIMENTAL DEMONSTRATION OF CEREBELLAR
CONNEXIONS FROM THE PERI-HYPOGLOSSAL NUCLEI
(NUCLEUS INTERCALATUS, NUCLEUS PRAEPOSITUS
HYPOGLOSSI AND NUCLEUS OF ROLLER) IN THE CAT**

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INTRODUCTION

During an experimental study of the cerebello-petal connexions of the reticular formation of the medulla oblongata, it was observed that after lesions of the cerebellum retrograde cellular changes occurred in the nuclei surrounding the hypoglossal nucleus. Since a perusal of the literature revealed that almost nothing is known of the connexions of these nuclei, and since therefore no sound ideas on their functional significance can be set forth, it was felt worth while to pursue this study. Although it has so far not been possible to decide precisely to which part or parts of the cerebellum the fibres pass, the existence of cerebello-petal fibres from the peri-hypoglossal nuclear complex has been demonstrated. In the present communication the evidence upon which this statement is based will be presented, and observations on the reticulo-cerebellar connexions will be published separately. In addition, a description of the normal structure of the peri-hypoglossal nuclei in the cat will be given because no detailed analysis of their cellular architecture in the cat is available. This knowledge is necessary for a proper evaluation of the pathological alterations observed in the experimental animals.

The term 'peri-hypoglossal nuclei', when used in this paper, is meant to include those nuclei which are found in mammals immediately around the nucleus of the hypoglossal nerve. They are the following: (1) the nucleus intercalatus of Staderini; (2) the nucleus praepositus hypoglossi; (3) the nucleus of Roller. Other names have also been employed, and opinions differ with regard to certain points in the delimitation of the nuclei. Questions of nomenclature and observations of previous authors working on this subject may appropriately be considered when the observations made in the present study are discussed.

MATERIAL AND METHODS

The normal features of the peri-hypoglossal nuclei in the cat were studied in serial transverse sections stained with thionine (15μ thick).

For the experimental study of the cerebello-petal connexions of the nuclei, young kittens, 2-3 weeks old, were employed. With sterile precautions and under Nembutal (pento-barbital) anaesthesia, lesions were made in the cerebellum by means of dissection, suction or thermocoagulation. Four to six days later the animals were killed by exsanguination under chloroform anaesthesia, and the cerebellum and brain stem immediately removed. After fixation in 96% alcohol the brain stem and cerebellum were embedded in paraffin and cut in transverse serial sections 15μ thick. The choice of very young animals and of the short post-operative period was

made in the light of previous experience gained with the modified Gudden method (Brodal, 1940), and in the nuclei at present under investigation the retrograde cellular changes are very clear-cut with the procedure adopted. The presence of altered cells makes possible a far more precise determination of the origin of the fibres in question than the equivocal determination of a partial loss of cells in the nuclei which would have to be studied with longer survival times.

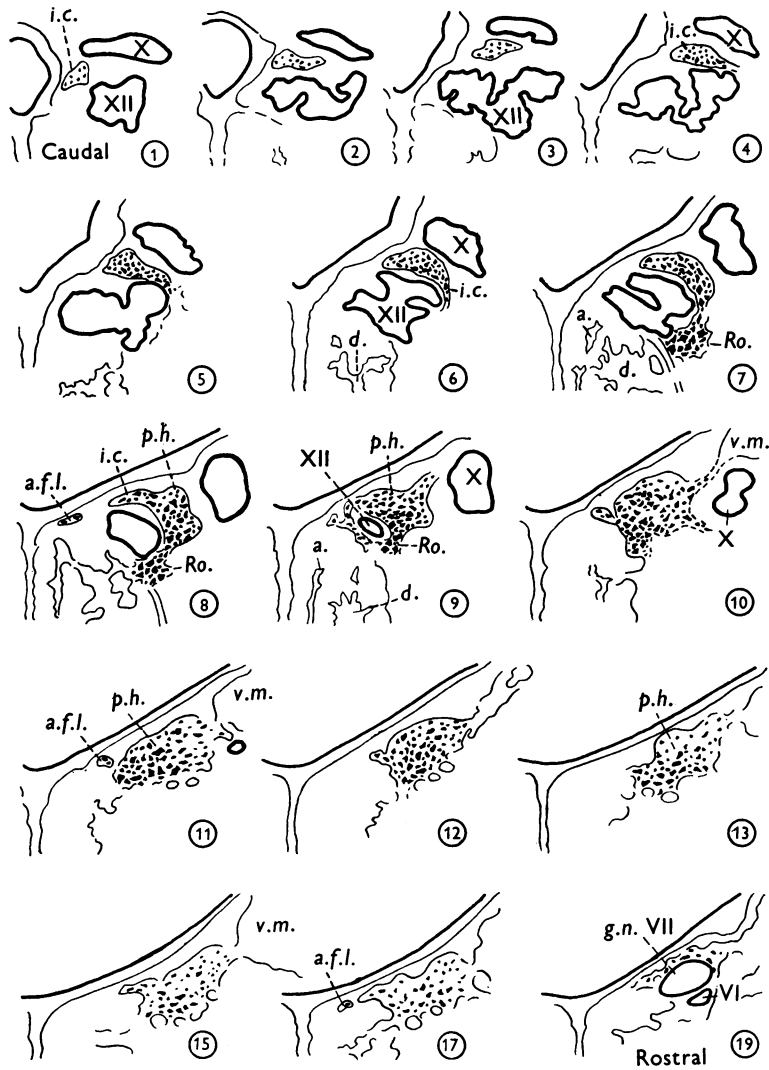
Supplementary and as yet provisional studies on some possible afferent connexions were made by means of the method of terminal degeneration. The modified Bielschowsky method of Glees (1946) was employed on adult cats for this purpose. The presence of terminal degeneration within the nuclei was sought after lesions of the midline structures of the cerebellum, hemisections of the brain stem at the level of the pons or after various lesions of the spinal cord.

NORMAL TOPOGRAPHY AND STRUCTURE OF THE PERI-HYPOGLOSSAL NUCLEI IN THE CAT

The description of the peri-hypoglossal nuclei to be given below is based on findings in cats 2–3 weeks old. In adult animals conditions are essentially similar, but the cells lie somewhat farther apart and contain more Nissl granules. The diagrams in Text-fig. 1 serve to illustrate the main topographical relations and cellular composition of the nuclei as seen at sixteen transverse levels in the medulla in a cat aged 15 days. The outlines were made by means of a projection apparatus, and the dots representing the cells filled in after direct examination under the microscope. The intervals between the sections drawn are equal except for the last three which are twice as large as the others. Pl. 1, fig. 1, shows drawings of the various types of cells composing the nuclei.

The nucleus intercalatus of Staderini is the first to appear when the region in question is traced caudo-cranially. It begins as a minute collection of small cells somewhat rostral to the caudal end of the hypoglossal nucleus, a little below the level of drawing 1 in Text-fig. 1. It is interposed between the hypoglossal nucleus ventrally and the dorsal motor (parasympathetic) nucleus of the vagus nerve dorsally, and retains this position for some distance. With the opening of the central canal the nucleus increases in size and lies between the hypoglossal nucleus ventromedially, the vagus nucleus dorso-laterally. Rostrally the nucleus intercalatus fuses imperceptibly with the nucleus praepositus. The transition appears to take place slightly below the level of the rostral end of the hypoglossal nucleus (8 in Text-fig. 1), since the cyto-architecture undergoes a change at this level (see below), and the nucleus increases markedly in size. In its rostral part the nucleus intercalatus shows some connexion ventrally with the nucleus of Roller (7 in Text-fig. 1). At more caudal levels its ventral or ventro-lateral border is sometimes indistinct (5 in Text-fig. 1), but otherwise it is everywhere clearly delimited from the hypoglossal and the vagal nuclei, although in places it is very closely related to the former. This is the case particularly at the ventral border of the nucleus intercalatus, where its cells may cover the dorso-lateral margin of the hypoglossal nucleus as a cap (5–7 in Text-fig. 1).

The majority of the cells composing the nucleus intercalatus are very small (Pl. 1, fig. 1 *b*). They are round or oval and few of them are piriform or spindle-shaped.



Text-fig. 1. Drawings made by means of a projection apparatus of transverse Nissl-stained sections through the medulla oblongata of a cat 15 days old, showing the topography of the peri-hypoglossal nuclei. The intervals between the sections represented are equal, except for those between drawings 13, 15, 17 and 19 respectively, which are twice as large. The dots indicate the distribution and density of cells of different types. See also Pl. 1, fig. 1.

Abbreviations employed in this figure and in Text-figs. 2 and 3

a.	accessory group of paramedian reticular nucleus	Ls.	lesion
a.f.l.	anulus fasciculi longitudinalis posterioris of Ziehen	ols.	superior olive
c.r.	restiform body	p.h.	nucleus praepositus of Marburg
c.v.	ventral cochlear nucleus	R.	right
d.	dorsal group of paramedian reticular nucleus	Ro.	nucleus of Roller
flocc.	flocculus	tr.sp.n.V	spinal tract of trigeminal nerve
g.n. VII	genu of facial nerve	v.l.	lateral vestibular nucleus
i.c.	nucleus intercalatus of Staderini	v.m.	medial vestibular nucleus
L.	left	VI	nucleus of abducent nerve
		VII	nucleus of facial nerve
		X	dorsal motor nucleus of vagus nerve
		XII	nucleus of hypoglossal nerve

The relatively scanty cytoplasm is provided with fine, sparse Nissl-granules. The nucleus is clear and has a distinct nucleolus. In addition some medium-sized cells occur (Pl. 1, fig. 1c). Most of these are piriform, and their nuclei, which are a little larger than those of the small cells, frequently have a slightly eccentric position. The Nissl-granules are fine, but more abundant than in the cells of the smallest type.

While in the caudal part of the nucleus intercalatus only one or two of the medium-sized cells occur in each section, their relative number increases at more rostral levels (see Text-fig. 1). At the same time the density of cells increases. Near the rostral end of the nucleus (i.e. approaching the rostral end of the hypoglossal nucleus) an increasing number of larger multipolar cells appears. At this level the medium-sized cells dominate the cellular picture and are more numerous than the small cells (8 in Text-fig. 1). It appears appropriate from this level to name the rostral continuation of the cell mass of the nucleus intercalatus the nucleus *praepositus hypoglossi*.

The nucleus praepositus hypoglossi. While the nucleus *praepositus* is fairly well delimited in its caudal part, except for its continuity with the nucleus intercalatus, referred to above, its limits are rather diffuse at rostral levels. Its rostral end is here, somewhat arbitrarily, placed at the level of the caudal end of the nucleus of the abducent nerve, where the nucleus *praepositus* tapers dorso-medially to the genu of the facial nerve. Laterally it is more or less continuous with the medial vestibular nucleus (10–17 in Text-fig. 1) and ventrally with the cells of the reticular formation, but, particularly at rostral levels, it may be separated from the reticular formation by some fine bundles of longitudinally running fibres. The medial surface of the nucleus faces the fibres of the medial longitudinal fasciculus and is usually quite distinct. The relation of the nucleus *praepositus* to the nucleus of Roller is very intimate, the two nuclei fusing almost completely (7–9 in Text-fig. 1; see also Text-figs. 2 and 3). The relation to the hypoglossal nucleus is also of interest. It will be seen from Text-fig. 1 (drawings 8 and 9; see also Text-figs. 2 and 3) that where the nucleus intercalatus passes into the nucleus *praepositus* the latter surrounds the rostral tip of the hypoglossal nucleus and thus comes to occupy the position of the hypoglossal nucleus at more rostral levels (10 in Text-fig. 1).

The cells of the nucleus *praepositus* are of the small, medium-sized and larger types (Pl. 1, fig. 1b–d). The large cells are usually multipolar, the medium-sized most often piriform or spindle-shaped. The latter and the small cells are similar to those in the nucleus intercalatus. The density of the cells in the nucleus *praepositus* decreases gradually in a caudo-rostral direction from the level of drawing 13. As will be seen from Text-fig. 1, the cyto-architecture of the nucleus varies somewhat at different levels. As a general rule the cells composing its ventral part are larger than those in its dorsal part. Large cells are particularly abundant ventrally in its caudal third, where the nucleus establishes contact with the nucleus of Roller, which contains a great number of similar cells. Rostral to the level of drawing 15 in Text-fig. 1 cells of the largest type are scarcely encountered, but here also the ventral part of the nucleus contains the largest of the cells present, which are of the medium-sized type.

Even if certain areas of the nucleus *praepositus* are composed predominantly of larger or medium-sized cells and others of predominantly small cells, these differences

are not distinct enough to justify a finer subdivision of the nucleus. From a topographical point of view the most cranial part of the nucleus praepositus might be called (in accordance with some previous authors) the *nucleus supragenualis nervi facialis*. However, no line of demarcation can be drawn between this and the rest of the nucleus praepositus. The rostral part of it (n. supragen. n. VII) is very loose in texture, and contains a few medium-sized and some small nerve cells.

The nucleus of Roller is not very clearly defined in the cat. However, at the ventral aspect of the rostral third of the hypoglossal nucleus fairly definite cell aggregations can be recognized. Most of the cells are situated lateral to the hypoglossal root fibres (7–9 in Text-fig. 1; see also Text-figs. 2 and 3) and are multipolar and rather large, but medium-sized and small cells also occur (Pl. 1, fig. 1e). These cells do not form a compact nucleus, but more massive parts alternate with regions in which only a few cells of the same types are found on the ventral surface of the hypoglossal nucleus. These groups, which are considered here to represent the nucleus of Roller, are frequently connected dorsolaterally by a cell strand with the nucleus intercalatus (7 in Text-fig. 1). At more rostral levels a similar connexion with the nucleus praepositus is even more convincing (8–9 in Text-fig. 1). The cell groups interpreted here as the nucleus of Roller are present also for some distance rostral to the hypoglossal nucleus where they appear as a ventral protrusion from the nucleus praepositus (10 in Text-fig. 1). This indication of a close relationship between the nucleus of Roller and the nucleus praepositus is emphasized by the similarity of the cells composing the parts of the nuclei in question.

Ventrally the nucleus of Roller is only indistinctly separated from the reticular formation. However, particularly along its rostral part, a certain separation from the reticular formation is established by some fine longitudinal fibre bundles, the same bundles, which, as mentioned above, are found ventral to the nucleus praepositus. The presence of these fibres makes the connexion between the nucleus of Roller and the nucleus praepositus more impressive.

While the nucleus of Roller can thus be recognized as a rather well-defined unit only where it lies ventral to the rostral third of the hypoglossal nucleus, in some cases similar smaller collections of cells are found ventral to the hypoglossal nucleus at more caudal levels. This, however, is not always so in normal material, an observation in keeping with the fact that the nucleus of Roller in the restricted sense presents considerable individual variations.

In the cat no nuclear group can be identified which might reasonably correspond to the *nucleus paramedianus dorsalis* of Jacobsohn, described in man (see discussion). The only cell complex, in addition to those already mentioned, which may deserve attention as a fairly distinct group is a tiny collection of medium-sized cells forming a sort of cap on the dorsal aspect of the medial longitudinal fasciculus. It is very variable, present as a rule only in a few sections, and medial to the nucleus praepositus (8, 11 and 17 in Text-fig. 1). It sometimes shows a connexion with the latter, but in any section seldom consists of more than two to five cells. This cell group has been identified with the *anulus fasciculi longitudinalis posterioris*, described in man by Ziehen (1934).

EXPERIMENTAL FINDINGS

In the young animals employed in the present study characteristic changes are observed in the cells of all the peri-hypoglossal nuclei 4–6 days after extensive lesions of the cerebellum. These changes are most clearly seen in the large cells, containing many Nissl-granules, but in the main they are similar in the smaller ones. In Pl. 1, fig. 1, drawings of representative specimens of altered cells of different types are reproduced. As will be seen from this figure and from the photographs in Pl. 1, figs. 2–5, there is a tigrolysis which affects almost the entire cytoplasm of the cell, leaving only a narrow zone with fine Nissl-granules along its periphery, thus indicating that the tigrolysis begins centrally. The nucleus is constantly found close to the periphery of the cell, frequently without any visible zone of cytoplasm between it and the cell border. In cells which are much affected, the nuclear membrane appears to disintegrate and the cytoplasm loses its milky appearance and becomes vacuolated. On account of the varying size of the cells it is impossible to decide whether the changes described are accompanied by any change in cell volume. Where many nerve cells are affected, astrocytes and microglial cells are increased in number and appear more active.

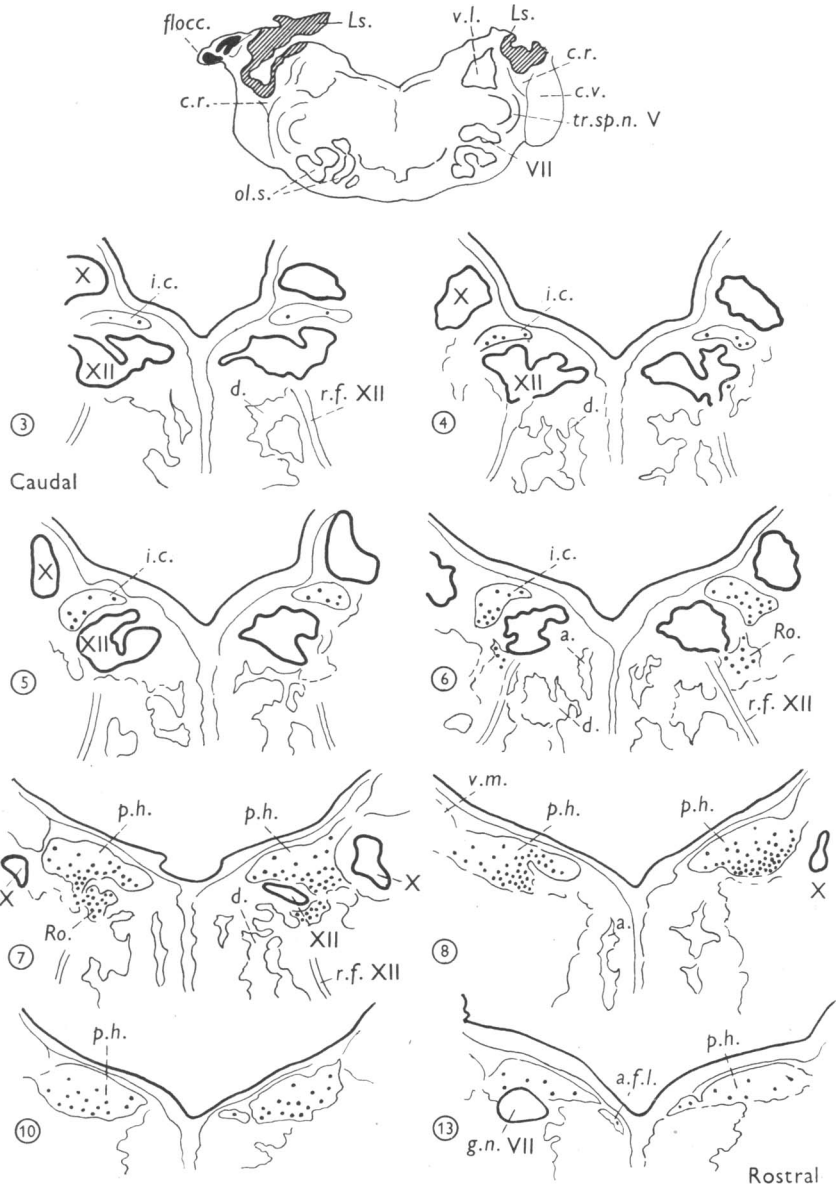
Only cells presenting the features mentioned have been considered as definitely pathological. When present there are usually interspersed between them others which show a diffuse tigrolysis but lack the homogenous appearance of the cytoplasm. Their nuclei are situated somewhat peripherally, but not extremely so as in the cells shown in Pl. 1, fig. 1. Probably they are cells in an earlier stage of change, but since somewhat similar cells may be seen in normal animals they have not been considered pathological.

The cellular changes observed are of the same type as those seen in other instances following transection of axons, the so-called retrograde cellular changes. For comparison a cell from the hypoglossal nucleus is included in Pl. 1, fig. 1. This cell, from a cat 21 days old at operation and killed 5 days later, shows the changes following transection of the root fibres of the hypoglossal nerve. The occurrence in the peri-hypoglossal nuclei of cells presenting similar changes after lesions of the cerebellum is taken to indicate that these cells project on to the cerebellum.

Cat O 93. Age at operation 15 days; survival period 5 days (Text-fig. 2, and Pl. 1, figs. 2–4).

After exposure of the caudal half of the cerebellum an attempt was made to remove the entire cerebellum by suction and blunt dissection. Serial sections show that this has almost been achieved; only small remnants of both flocculi and of the left paraflocculus are left. Probably the fibres to these parts have also been destroyed, since there is a necrosis extending for some distance into both restiform bodies and both brachia pontis (hatched in Text-fig. 2).

In the nuclei of the peri-hypoglossal complex cells showing typical retrograde changes are present, but they are not uniformly distributed, as will be seen from the diagram in Text-fig. 2. In the caudal part of the nucleus intercalatus cells that have undergone definite changes are rare. In its rostral half a moderate number of medium-sized and small cells present the typical picture of retrograde changes (Pl. 1, fig. 2). In its extreme rostral part (6 in Text-fig. 2) in which larger multipolar cells are present in increasing number a considerable proportion of these, as well as of the medium-sized piriform cells, are changed.



Text-fig. 2. Semi-diagrammatic representation of the findings in cat O 98 with an almost total cerebellar removal. Above, a drawing showing the remnants left of the cerebellum. Hatchings indicate partially destroyed tissue. Below, a series of drawings through the peri-hypoglossal nuclei. Dots indicate cells showing retrograde changes, the density giving an approximate impression of the distribution and relative number of changed cells. The level of the sections reproduced will be seen from their numbers, no. 1 (not included) passing through the most caudal part of the complex, no. 13 through its rostral end. For abbreviations see legend to Text-fig. 1.

The intensity of the changes increases somewhat, and reaches its maximum in that part of the nucleus praepositus which is particularly rich in large cells (Pl. 1, fig. 3, 8 in Text-fig. 2).

In the nucleus of Roller the majority of cells are altered (Pl. 1, fig. 4). Scattered changed cells are also found in the anulus of the medial longitudinal fasciculus.

Following a practically total removal of the cerebellum cells presenting retrograde changes are thus found in the nucleus intercalatus, the nucleus praepositus and the nucleus of Roller. Other experiments confirm these findings and give some additional information.

Cat O 84. Age at operation 14 days; survival period 5 days (Text-fig. 3)

The lesion is bilateral, but chiefly affects the right half of the cerebellum. From Text-fig. 3 it will be seen that certain parts have been destroyed (black), while others are partially damaged (hatched). On the right side the knife has passed so far ventrally as to cut a considerable number of the fibres of the restiform body where they fan out just after reaching the white matter of the cerebellum. The areas of cerebellar cortex to which these cut fibres pass are stippled (the determination of these areas was facilitated by a comparison with the alterations in the inferior olive, since the topography of the olivo-cerebellar localization is known from previous studies).

In the peri-hypoglossal nuclei cells of all types show retrograde changes. Their number is clearly smaller than in the preceding series (cat O 93), but their distribution is essentially similar (Text-fig. 3). The changes are bilateral, but they are more marked on the right side than on the left.

In this experiment, as well as in some others with extensive lesions of the cerebellum (e.g. cats O 91 and O 94), the retrograde cellular changes within the peri-hypoglossal nuclei are of the same type as in the first case described. Furthermore, the distribution of altered cells is similar. With asymmetrical lesions, the peri-hypoglossal nuclei present the most marked changes on the side of the most extensive cerebellar lesion. This might be explained if the peri-hypoglossal fibres to the cerebellum are either exclusively uncrossed, or if they are crossed as well as uncrossed, the uncrossed ones being more numerous. The following experiment gives information on this point.

Cat O 54. Age at operation 21 days; survival period 5 days (Pl. 1, fig. 5)

The right brachium pontis has been completely, and the right restiform body almost completely, transected. There is some accidental damage to the superficial aspect of the right side of the medulla, injuring chiefly the spinal tract of the fifth nerve.

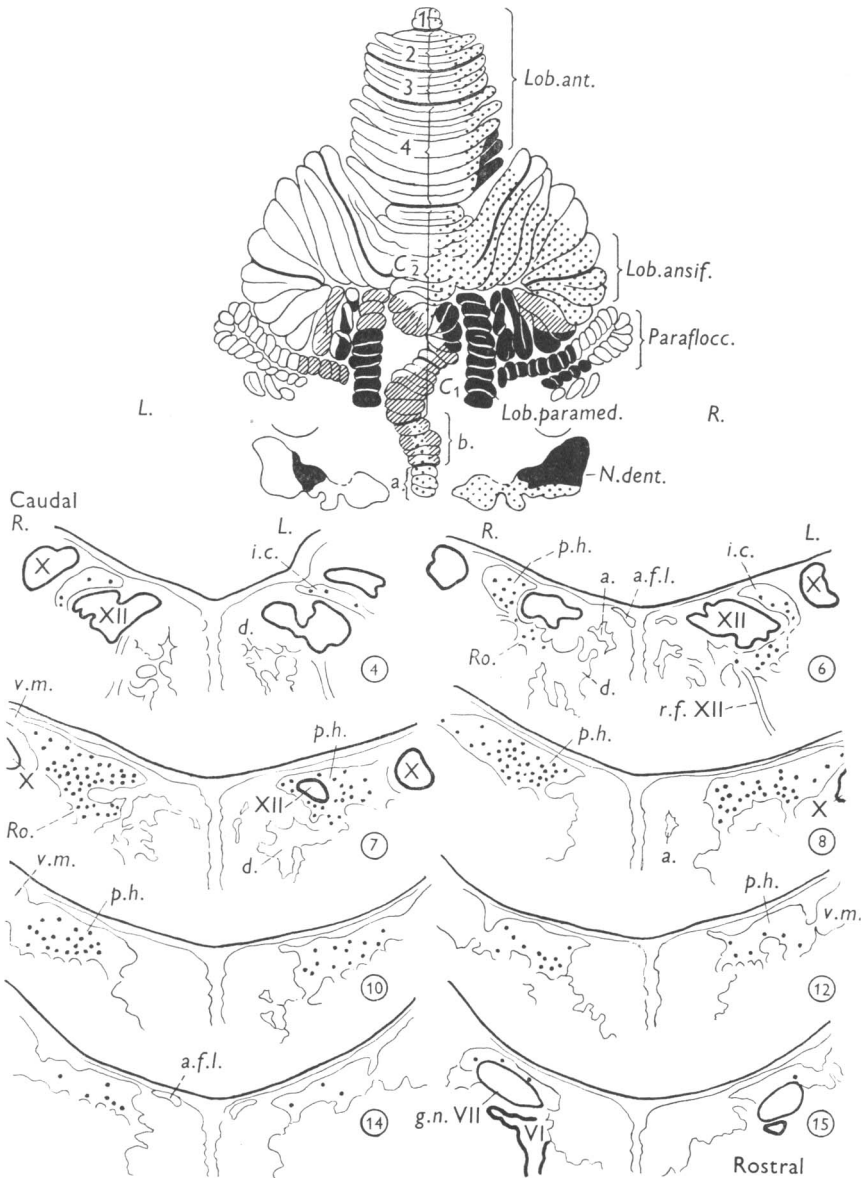
Again the peri-hypoglossal nuclei show retrograde changes on both sides with a distribution corresponding to that observed in the other cases. The changes are somewhat more intense in the nuclei of the right side than in those of the left.

Since in this case practically all afferent fibres to the cerebellum have been interrupted on one side only, the occurrence of bilateral changes in the peri-hypoglossal nuclei demonstrates that their connexion with the cerebellum is crossed as well as uncrossed. From a comparison of the changes of the two sides it appears that the proportion of crossed to uncrossed fibres is approximately as 1 to 1.5-2.

Terminal degeneration within the peri-hypoglossal nuclei

Five days after extensive lesions of the brain stem at the pontine level abundant and typical terminal degeneration was observed in the peri-hypoglossal nuclei (adult cats, Glees's method). Particularly in the nucleus praepositus, numerous

degenerating terminal boutons and fine degenerating terminal fibres were found (Pl. 1, fig. 6), in addition to some coarser degenerating fibres seen to enter from the



Text-fig. 3. Semi-diagrammatic representation of the findings in cat O 84. Above a diagram of the cerebellum unfolded into one plane. Black: areas totally destroyed. Hatching: partially damaged areas. Stippled: areas the fibres to which have been cut. Below a series of drawings through the peri-hypoglossal nuclei arranged as in Text-fig. 2. For abbreviations see legend to Text-fig. 1.

white matter close to the midline. Thus fibres descending in the brain stem must terminate in the peri-hypoglossal nuclei. This preliminary finding is of some interest,

although further studies are needed to decide from what structures these fibres take origin and to establish their exact course and their exact pattern of termination within the peri-hypoglossal nuclei.

In a cat in which a lesion of the posterior vermis of the cerebellum (including both nuclei fastigii) had been made 5 days before sacrifice the peri-hypoglossal nuclei were searched for signs of terminal degeneration. Sparse and not quite conclusive changes are present in the nucleus intercalatus. The findings are difficult to evaluate, and since one case only has been studied the projection of fibres from the cerebellum to the peri-hypoglossal nuclei cannot be considered as proved although their presence may be suggested.

Following lesions of the spinal cord terminal degeneration was seen in the peri-hypoglossal nuclei in several cases. However, although unequivocal, the degeneration is far less, even with lesions of the highest cervical segments, than that which follows interruption of descending fibres.

DISCUSSION

A perusal of the pertinent literature reveals considerable confusion with regard to the designations employed for the various cellular groups surrounding the hypoglossal nucleus. This is probably due, at least to some extent, to the fact that these nuclei vary in different mammals and that there are considerable individual variations even in the same species. This has been pointed out by Jermulowicz (1934), among others, and is also evident in the present material. As long as knowledge of their fibre connexions is inadequate, the delimitation of the various nuclei must be based on topographical, cyto-architectural and comparative-anatomical criteria. The demonstration in this paper that all these cellular groups send fibres to the cerebellum emphasizes their close functional relationship, and serves to minimize the importance of a detailed separation into smaller cell groups. The subdivision of the nuclei employed in this paper, has therefore taken into account only the more conspicuous morphological features and before discussing the experimental findings some comment on the normal anatomy and terminology is appropriate. The nuclei have been most extensively studied in man.

(1) *The topography and delimitation of the peri-hypoglossal nuclei*

The nucleus intercalatus, described first in man by Staderini (1895), has been generally recognized by subsequent authors. Its position between the hypoglossal nucleus and the dorsal motor (parasympathetic) nucleus of the vagus is unequivocal. Among authors who have studied this nucleus in man may be mentioned Streeter (1903), Marburg (1904), Jacobsohn (1909), Weed (1914), Fuse (1914), Gagel & Bodechtel (1930), Jermulowicz (1934) and Ziehen (1934). Barnard (1940), in a comparative-anatomical study, found the nucleus intercalatus scarcely developed in the opossum but clearly present in the mouse, rat, rabbit, sheep, dog, cat, monkey and man. The continuity of the nucleus with the reticular formation, as described here, has been noted by several authors in various mammals and man.

Opinions differ only with regard to its rostral delimitation. Staderini originally applied the term nucleus intercalatus not only to the cellular group interposed between the hypoglossal and dorsal motor nucleus of the vagus, but to its rostral

continuation as well (Staderini, 1938). This terminology was adopted by Streeter (1903) and Weed (1914), among others. The part extending rostral to the hypoglossal nucleus, however, has been considered a separate nucleus by most authors, first apparently by Marburg (1904) who called it the nucleus praepositus hypoglossi. Since this designation has gained general recognition it has been adopted in the present paper, the more readily since it is more appropriate from a descriptive point of view than other names employed. However, as was mentioned earlier no clear-cut boundary can be seen between the nucleus intercalatus in the restricted sense and the nucleus praepositus. According to available descriptions this appears to be the case not only in the cat but also in most other mammals including man.

In the cat, the cyto-architecture of the cell mass under consideration undergoes a change slightly caudal to the level of the rostral end of the hypoglossal nucleus. The chief feature of this change is an increased number of multipolar cells, medium to large in size. In the cat, therefore, it seems natural to place the transition between the nucleus intercalatus and the nucleus praepositus slightly caudal to the rostral end of the hypoglossal nucleus. In their atlas of the rabbit's brain stem Meessen & Olszewski (1949) appear to have done this, but it should be noted that the distinction is of importance chiefly for descriptive purposes.

The nucleus of Roller, described in man by Roller in 1881, has attracted the interest of several authors (Streeter, 1903; Marburg, 1904; Cajal, 1909; Jacobsohn, 1909; Weed, 1914; Nakamura, 1930; Gagel & Bodechtel, 1930; Goldin, 1934; Ziehen, 1934; and others). Jacobsohn (1909) called it the 'nucleus sympathicus sublingualis'. Goldin (1934) labels it 'nucleus comitans hypoglossi dorsalis secundus'. On the whole, subsequent descriptions are in accord with Roller's original report. The nucleus of Roller in man is found immediately ventral to the rostral half or third of the hypoglossal nucleus and medial to the root fibres of the hypoglossal nerve.

In mammals, generally the nucleus of Roller is, on the whole, less well developed and more difficult to identify than in man. Comparative studies have been made by Nakamura (1930) and Barnard (1940). Barnard found it well developed in the monkey and could identify it in the dog, cat, rabbit and sheep; he found it less distinct in the mouse, rat and shrew, but clear-cut in the opossum. In the rabbit the nucleus was also identified by Kimmel (1940) and by Meessen & Olszewski (1949). Berkelbach van der Sprenkel (1924) found it in *Erinaceus*. In monkeys the nucleus of Roller may be found medial to the root fibres of the hypoglossal nerve (Nakamura, 1930; Barnard, 1940), but in the other mammals in which it has been identified it lies lateral to these fibres. As we have seen, this is also the case in the cat, a point previously mentioned by Cajal (1909).

In keeping with the varying development of the nucleus of Roller in mammals, its cellular composition appears not to be the same throughout, as far as can be judged from the available literature. In man its cells are described as being small, having a diameter of some 15μ against the 60μ of the hypoglossal cells (Roller, Ziehen). Gagel & Bodechtel (1930), as well as other authors, stress the reticular appearance of the nucleus and mention its continuity with the nuclei interfasciculares nervi hypoglossi of Jacobsohn. The cellular strands connecting the nucleus of Roller with the nucleus praepositus have been noted also in the monkey by Barnard (1940).

There can be no doubt that the nucleus in the cat, described in the present study

as the nucleus of Roller, corresponds with the nucleus of the same name in man. Its position agrees with that described for other mammals, and also the diffuseness of its border adjacent to the reticular substance. Its rostradorsal connexion with the nucleus praepositus, which is very definite in the cat (see Text-fig. 1, drawings 8-9), has been noted also in man. With regard to its cells, it is interesting to note that Goldin (1934), who is one of the few authors to give a detailed account of the cells of the nucleus of Roller in man, distinguishes three types: (a) very small, rounded cells, with a comparatively large nucleus and scanty, finely granulated cytoplasm; (b) elongated cells; (c) large cells with a great mass of cytoplasm. This agrees well with the three different cell types present in the cat (Pl. 1, fig. 1*e*). An arrangement of its cells with their long axes parallel to the circumference of the nucleus, as described by Barnard (1940) in the dog, is not marked in the cat, as Cajal (1909) also found.

In addition to the well circumscribed nucleus of Roller, scattered collections of cells of a similar type are frequently found in the cat also at more caudal levels ventral to the hypoglossal nucleus. Such cell groups, present in some sections only, have been noted in other animals, and have been considered part of the nucleus of Roller. Since these cell groups in the cat react to cerebellar lesions in the same way as the cells of the nucleus of Roller, this view appears to be justified.

The nucleus praepositus. With regard to the rostral continuation of the nucleus intercalatus there is considerable confusion in the literature. In this paper the name nucleus praepositus nervi hypoglossi, proposed by Marburg (1904), is given to the cell column in question. From Marburg's atlas of the human brain it appears that his nucleus praepositus extends in a rostral direction to the level of the abducent nucleus. Marburg does not describe the cells of this nucleus, but its position as a longitudinal column occupying a position similar to that of the hypoglossal nucleus at more caudal levels, is clear, and justifies its name. Meessen & Olszewski (1940), in their atlas of the rabbit's rhombencephalon, use the name nucleus praepositus hypoglossi in the sense of Marburg. Since this terminology appears less equivocal than the name 'nucleus funiculi teretis', it has been adopted in the present paper, although the nucleus in question does not present a uniform appearance throughout in the cat. Since cells projecting on to the cerebellum are found even in its most rostral part, there seems to be little reason for applying different names to the various parts of this nuclear complex.

The discussion of the terminology of the nuclear complex, labelled here the nucleus praepositus, cannot, however, be abandoned without some references to the different terms found in the literature. Situated medial to his nucleus praepositus Marburg (1904), in man, distinguishes a slender longitudinal column of small cells, the nucleus funiculi teretis. The term nucleus funiculi or eminentiae teretis, unfortunately, has been used with different meanings. Thus Jacobsohn (1909) employs it for the cell group called nucleus praepositus by Marburg, while the small-celled column medial to the nucleus praepositus is termed nucleus paramedianus dorsalis. Jermulowicz (1934) uses the term in the sense of Jacobsohn, and claims that within the nucleus funiculi teretis three minor subdivisions, containing larger cells, should be separated as follows: caudally, a nucleus praepositus; rostrally a 'Kappenkern des Facialisknies' (nucleus supragenualis nervi facialis); and as a third complex the

dorsal part of the *anulus fasciculi longitudinalis posterioris* of Ziehen, a group of medium-sized cells dorsal to the medial longitudinal fasciculus. Because of its inconsistent use, Ziehen (1934) argues that the term *nucleus funiculi or eminentiae teretis* should be deleted from the anatomical vocabulary. Instead he uses the designation 'raphe part of the *nucleus paramedianus dorsalis*' for the medial small-celled column, corresponding, it appears to Jacobsohn's *nucleus paramedianus dorsalis*, and the name 'ventricular part of the *nucleus paramedianus dorsalis*' for what appears to be Jacobsohn's *nucleus funiculi teretis* or Marburg's *nucleus praepositus*. Other variations in the use of the term *nucleus funiculi teretis* may also be encountered, but there is no need to review the confusing problem of nomenclature of the peri-hypoglossal nuclei more completely for this paper. Suffice it to say that according to most descriptions it is possible in man to distinguish a longitudinal column of small cells extending from the level of the hypoglossal nucleus to the level of the abducent nucleus (*n. paramed. dors.* of Jacobsohn, *n. em. teretis* of Marburg) and another column, situated just lateral to the first, composed of cells of different sizes but containing a certain proportion of medium-sized to larger cells (*n. fun. teretis* of Jacobsohn, *n. praep.* of Marburg). The larger cells in the latter are predominant at certain levels of its longitudinal extent, chiefly caudally and rostrally (*n. praep.* of Jermulowicz and *n. supragen. n. fac.* respectively).

In the cat no separate small-celled column can be seen which might correspond to the *nucleus paramedianus dorsalis* of Jacobsohn (1909). In his comparative-anatomical study Barnard (1940) illustrates in the medulla of the rabbit, sheep, dog, monkey and man a slender column of cells situated close to the midline, just beneath the floor of the fourth ventricle. He labels this column the *nucleus eminentiae teretis* and apparently uses this term in Marburg's sense (i.e. as equivalent to Jacobsohn's *n. param. dors.*). In his description, however, the nucleus is mentioned only in the dog, monkey and man, and in the dog it is said to be poorly represented. Since a similar nucleus cannot be found in the cat and is not mentioned or described by Meessen & Olszewski (1949) in the rabbit, it is possible that Barnard was mistaken with regard to the rabbit and the sheep. It appears that the *nucleus paramedianus* is a differentiation of the peri-hypoglossal grey matter which has appeared only late in phylogenesis. A *nucleus praepositus* (in the sense of Marburg) is mentioned by Barnard only in his account of monkey and man. Marburg (1931) emphasizes that the *nucleus praepositus* is more easily recognized the higher one proceeds in the phylogenetic scale, and that at the same time its continuity with the *nucleus intercalatus* becomes less marked.

It appears from the literature that the peri-hypoglossal nuclear complex becomes increasingly differentiated in higher mammals, reaching its peak in man. In the cat this differentiation has not yet proceeded to the formation of a *nucleus paramedianus*. Which cells of the *nucleus praepositus* (in the sense employed here), if any, correspond to this nucleus in monkey and man, it is impossible to decide. It is worth noticing, however, that the *nucleus praepositus* of the cat displays the same general topographical and cytological features as the corresponding structure in man. Thus, according to Jermulowicz (1934), in man the larger cells are at all levels concentrated in the ventral part of the nucleus. The same is the case in the cat, and is probably a feature of some functional importance. The concentration of larger cells at the

caudal and to some extent at the rostral ends of the nucleus is also similar in the cat and in man. The rostral condensation might be referred to as the *nucleus supra-genualis nervi facialis*. Its position close to the nucleus of the abducent nerve suggests a functional relationship similar to that which may exist between the caudal condensation and the hypoglossal nucleus. If this suggestion should be substantiated, it would be appropriate to separate the rostral condensation from the nucleus praepositus and to use a special name for it.

The anulus fasciculi longitudinalis posterioris of Ziehen (1934) is described by him in man at levels rostral to the nucleus of the abducent nerve. It more or less surrounds the fibres of the medial longitudinal fasciculus. Its cells are said to be larger than those of the nucleus paramedianus dorsalis, and the nucleus may be broken up into minor cell groups.

In the cat a few medium-sized cells seen at some levels medial to the nucleus praepositus resemble a little what Ziehen describes in man. However, in the cat these cell groups are found further caudally and they do not completely surround the fasciculus. Their relationship with cells of the raphe appears to be the same as in man. In spite of the differences mentioned, it was deemed appropriate to label the nuclear group the anulus of the medial longitudinal fasciculus, emphasis being laid on its close relation to that fibre bundle.

(2) Fibre connexions of the peri-hypoglossal nuclei

After extensive lesions of the cerebellum the changes in the cells of the peri-hypoglossal nuclei are those characteristic of the retrograde degeneration which occurs in nerve cells when the axon is transected. They are virtually identical with the changes seen in other cells known to project upon the cerebellum, e.g. the cells of the external cuneate nucleus, the lateral reticular nucleus and the pontine nuclei (Brodal, 1941, 1943; Brodal & Jansen 1946), and may therefore be taken as showing that the cells in question send their axons to the cerebellum.

In the experiments reported all cells of the peri-hypoglossal nuclei were never affected, not even when practically the entire cerebellum was removed. This seems to indicate that some send their axons to other regions of the brain, but another possibility must also be considered. It is well known from other instances that all the cells of a nucleus do not react with the same speed to damage to the axon (Brodal, 1939). Considering the short survival time employed in the present study it is, therefore, probable that some cells have not yet reached a sufficient degree of alteration to be recognized as changed. Experiments with total ablations of the cerebellum and a longer survival period would help to decide this question, but so far it has not been possible to keep such animals alive for more than 6 days. If only the cells seen to be definitely pathological are taken into account, it appears that at least the majority of the cells of the caudal third of the nucleus praepositus and of the nucleus of Roller project on to the cerebellum, while the rostral two-thirds of the nucleus praepositus contain a much smaller proportion of cells of this type.

With regard to the nucleus intercalatus the evaluation of this point is more difficult since the small cells, of which this nucleus is chiefly composed, are difficult to analyse with regard to cytological changes. However, a careful comparison of cells in the experimental animals with normal controls leaves no doubt that a certain

number of the small cells in the experimental animals are pathological: they are rounded, the nucleus is found in the extreme periphery of the cell and almost no Nissl-granules are left (Pl. 1, figs. 1 and 5). It is impossible from the material available at present to decide whether many of the other cells are normal or in the early stages of retrograde change. Until further evidence is brought forward, it seems safe to conclude only that a certain proportion of the cells of the nucleus intercalatus project on to the cerebellum; the proportion is somewhat greater in the rostral than in the caudal levels of the nucleus.

Apart from the conclusion that a somewhat greater proportion of the connexions described run to the homolateral rather than to the contralateral half of the cerebellum, no suggestions can be offered with regard to the finer organization of this projection. Thus no conclusions can be drawn concerning the exact area within the cerebellum in which the fibres from the peri-hypoglossal nuclei terminate. Nor can it be decided whether fibres from different parts of the nuclear complex terminate in different areas. Experiments are being undertaken to elucidate these questions, but even without knowledge of these details the present observations are of interest since they demonstrate a connexion of the peri-hypoglossal nuclei which, as far as is known, has not been suggested before, and which may contribute to our understanding of the function of these peculiar nuclei.

As has been seen, the nucleus intercalatus fuses imperceptibly with the nucleus praepositus, and both these nuclei are connected by conspicuous cellular strands with the nucleus of Roller. These topographical features point to a functional relationship between the three nuclei, the existence of which is strongly emphasized by the demonstration of a common projection to the cerebellum. It is also of interest to note that the peri-hypoglossal nuclei fuse with other nuclei which have cerebellar connexions. Thus the nucleus praepositus is continuous with the medial vestibular nucleus, which, as has been verified in this material, sends fibres to the cerebellum. The nucleus of Roller establishes a cellular connexion with a particular group of cells of the reticular formation, situated just lateral to the raphe (labelled *d* in Text-figs. 1-3). This is one of three small reticular cell groups which project to the cerebellum and which have been termed collectively the nucleus reticularis paramedianus (Brodal, 1952). In addition, scattered cells along the course of the root fibres of the hypoglossal nerve (nuclei interfasciculares n. hypoglossi of Jacobsohn) behave in the same manner, so that here, as in so many other cases, topographical features reflect functional relationships.

The close topographical relation between the hypoglossal nucleus and the peri-hypoglossal nuclei naturally has been taken as an indication that the nuclei in question are of importance for the functions of the tongue. The demonstration of a quantitatively important projection from these nuclei to the cerebellum lends support to the contention, advocated by Du Bois (1929), that they are in some way concerned with the proprioceptive innervation of the tongue, and argues against the view that they are related to taste. The increasing development of these nuclei as the mammalian scale is ascended (Tagaki, 1925*b*; Kappers, Huber & Crosby 1936; Barnard, 1940) also points in the same direction.

The cerebellar connexions of the peri-hypoglossal nuclei described here appear at present to be their only definitely established efferent connexions. The original

contention of Roller (1881) that the axons from his nucleus join the root fibres of the hypoglossal nerve, although supported by some authors, has not been verified by controlled experimental studies (see Barnard, 1940) or by careful analyses of normal material (Cajal, 1909; Ziehen, 1934; Kimmel, 1940; Boyd, 1941; and others). Nor have changes been observed in the other peri-hypoglossal nuclei following transection of the hypoglossal nerve (Tagaki, 1925*a*; Barnard, 1940). It appears likely that the cells of these nuclei are functionally related to those of the hypoglossal nucleus proper, but whether axons or collaterals from the former are among the fibres passing in great number between the peri-hypoglossal and the hypoglossal nuclei has not been experimentally verified, although Kimmel (1940) in normal rabbit material thought this to be so. Future studies must decide whether all or some of those cells of the peri-hypoglossal nuclei which apparently do not send their axons to the cerebellum project on to other parts of the brain, or whether they are to be considered as internuncial cells, serving for the reception of afferent impulses to the nuclei. It has been suggested (Marburg, 1931) that the larger cells of the peri-hypoglossal nuclei are 'motor', giving origin to efferent fibres, while the small cells are 'sensory', receiving impulses from afferent fibres and transmitting them to other cells of the nuclei. However, as has been seen, cells of all types project on to the cerebellum, so that the presence in the nuclei of cells of different sizes can scarcely be explained on this basis alone, although the efferents to the cerebellum may take their origin chiefly from those regions which are particularly rich in larger cells. A more probable explanation can be given for the presence of cells of different sizes. Since large cells have in general thicker axons than small ones, it may be presumed that the consequent differences in physiological properties, such as the height and duration of the action potential and the conduction velocity, are the functional correlates of the morphological differences. If future studies should demonstrate that afferents from the same source establish synaptical contact with cells of all types, this interpretation would be supported. That it is possible is shown by observations made in the lateral reticular nucleus (nucleus funiculi lateralis) in which large as well as small cells project on to the cerebellum (Brodal, 1943), and both types receive spinal afferents (Brodal, 1949). If there are true 'sensory' or better, internuncial cells, in the peri-hypoglossal nuclei, it appears that they must be sought chiefly in the nucleus intercalatus and the rostral two-thirds of the nucleus praepositus.

The present study suggests that the peri-hypoglossal nuclei when discharging must influence first and foremost the cerebellum (possibly particular regions of it) and probably the hypoglossal nucleus as well. The peri-hypoglossal nuclei themselves appear to be influenced by impulses from different sources. According to the findings reported here, an important contribution must be represented by fibres from higher levels descending in the brain stem. Whether some of these fibres pass via the fasciculus longitudinalis dorsalis of Schütz as described by Nakamura (1930), but not verified by Barnard (1940), cannot be decided from observations made in normal material. Other afferents appear to come from the vestibular nuclei, particularly the medial nucleus, by way of Fuse's fasciculus triangulo-intercalatus (Fuse, 1914; Tagaki, 1925*b*), but in his experimental study of the efferent connexions of the vestibular nuclei, Buchanan (1937) does not mention such fibres. Of particular

interest is the question of possible cranial nerve afferents. In normal material from different mammals several authors have observed fibres of the vagus and glossopharyngeal nerves passing to the nucleus intercalatus (Du Bois, 1929; Barnard, 1940; Kimmel, 1940, 1941), to the nucleus praepositus (Fuse, 1914; Kimmel, 1941), and even to the nucleus of Roller (Kimmel, 1941, in the rabbit). In experimental studies with the Marchi method Du Bois (1929) found fibres of the vagus passing to the nucleus intercalatus, while Allen (1923) in the guinea-pig failed to do so. In a human pathological case Schwartz, Roulhac, Lam & O'Leary (1951) did not see them.

If the peri-hypoglossal nuclei are concerned in the regulation of the motor activities of the tongue, it would be reasonable to assume that they receive proprioceptive impulses from this organ. The problem of the proprioceptive innervation of the tongue is, however, far from clear. Widely diverging views on the presence and abundance of proprioceptive receptors in the tongue have been expressed in the literature (see, for example, Langworthy, 1924; Weddell, Harpman, Lambley & Young, 1940; Boyd, 1941), and the central course of possible proprioceptive fibres is uncertain. While some authors have observed a moderate number of ganglion cells along the hypoglossal nerve in different mammals and man (Tarkhan & Abd El-Malek, 1950), and suggest that at least some proprioceptive impulses may travel via this nerve, others have been unable to verify the existence of such cells (Carleton, 1938; Boyd, 1941), and Barron (1936) did not obtain action potentials from the hypoglossal nerve after deforming, stretching or burning the tongue in experimental animals. Boyd (1941) suggested that the cells of the so-called Frieriep's ganglion on the hypoglossal nerve may have become incorporated in the first or second cervical dorsal root ganglion, and the demonstration that some fibres of the hypoglossal nerve degenerate after removal of these ganglia in the rabbit (Yee, Harrison & Corbin, 1939) supports this view. However, the available evidence relating to possible afferents in the hypoglossal nerve indicates that they are very few in number and that other pathways for proprioceptive impulses from the tongue must be sought for. The disputed fibres of the vagus and glossopharyngeal nerves to the nucleus intercalatus may perhaps be of this kind, as suggested by Du Bois (1929).

The assumption of a relation of the peri-hypoglossal nuclei to motor functions of the tongue is strengthened by Allen's (1927) observation of fibres from the nucleus fastigii to the nucleus intercalatus in Marchi preparations of the guinea-pig. If further studies should verify their existence, they would provide evidence for a closed circuit between the cerebellum and the peri-hypoglossal nuclei.

Evidence has been reported in this paper that fibres ascending from the spinal cord terminate in the peri-hypoglossal nuclei. This is surprising and the functional significance of such fibres is at present entirely obscure. There is little doubt, however, that investigations using the method of terminal degeneration will unravel many unexpected fibre connexions, at least as perplexing to our present-day conceptions of the organization of the nervous system as those just referred to. With regard to the peri-hypoglossal nuclei, we are as yet far from understanding their functional organization, which appears to be more complex than generally assumed. At present we can only state that they may be activated by impulses from numerous sources and that they have important relations with the cerebellum;

it may be assumed that they are probably involved in some way in the regulation of the motor functions of the tongue. Much work is needed to clear up the many obscure problems related to these small and peculiar nuclei. It is certain that they are functionally important, not least so in man.

SUMMARY

1. The topography and cellular architecture of the peri-hypoglossal nuclei in the cat are described. The nucleus of Roller, the nucleus intercalatus of Staderini and a nucleus praepositus in the sense of Marburg can be differentiated. The three nuclei are interconnected by cellular strands, and fuse also with certain parts of the reticular formation and the medial vestibular nucleus. The confusing terminology of the nuclei is briefly discussed.

2. After extensive lesions of the cerebellum typical retrograde changes are observed in the cells of the peri-hypoglossal nuclei in cats 2-3 weeks old. The changes occur throughout all of the nuclei, but are most marked in the caudal third of the nucleus praepositus and the nucleus of Roller. The occurrence of such cell changes is taken to demonstrate the presence of efferent fibres to the cerebellum. Somewhat more than half of these fibres are uncrossed. Small as well as larger cells show retrograde changes after lesions of the cerebellum. This contradicts the assumption that the larger cells are 'motor', the smaller ones 'sensory', and an alternative explanation is offered.

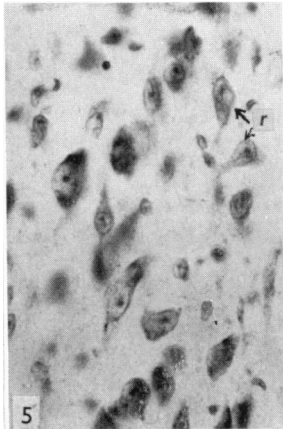
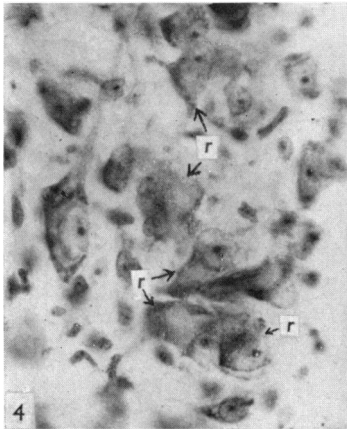
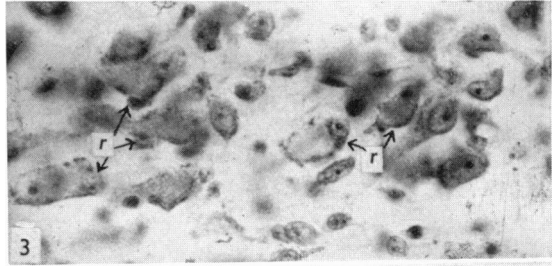
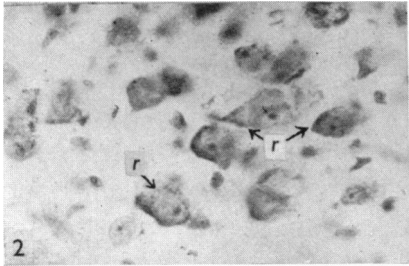
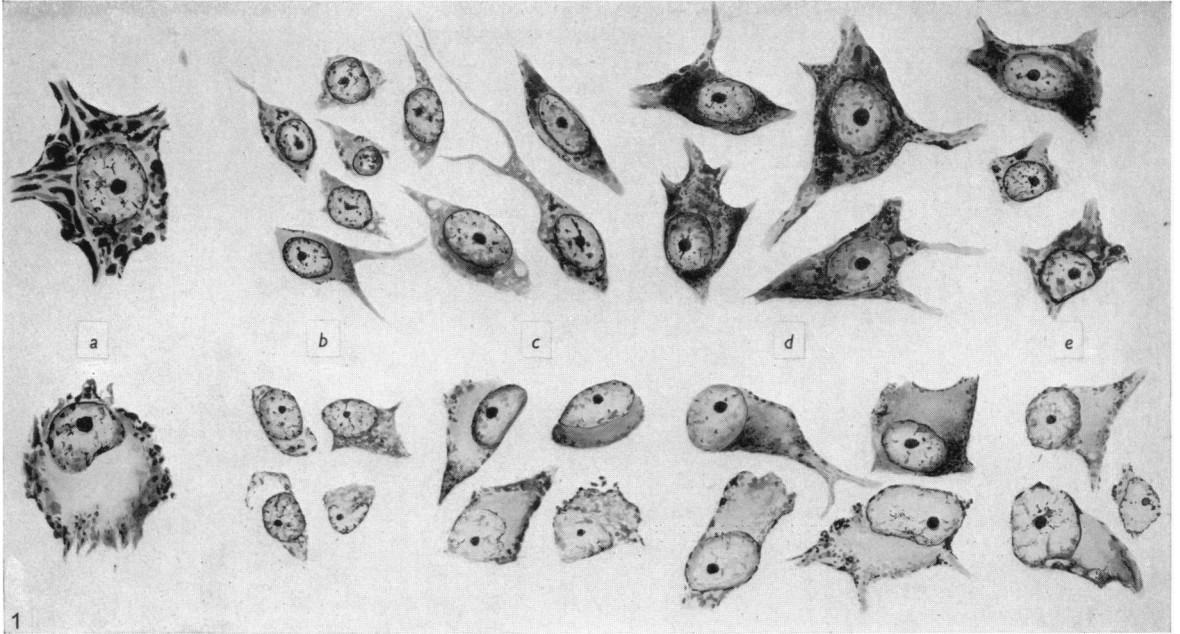
3. After lesions of the brain stem at the pontine level abundant terminal degeneration is seen in the peri-hypoglossal nuclei. Slighter, but convincing degeneration is seen after lesions of the spinal cord. Thus many descending and some ascending fibres terminate in the nuclei.

4. The functional implications of the findings are discussed. The projection on to the cerebellum supports the view that the peri-hypoglossal nuclei are concerned in some way with the motor functions of the tongue. Brief reference is made to findings in the literature concerning the connexions and function of the peri-hypoglossal nuclei.

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EXPLANATION OF PLATE

- Fig. 1. Camera lucida drawings of cells from the hypoglossal and peri-hypoglossal nuclei in the 14 days' old cat. Above, normal cells; below, cells of the various types as they appear when they are fully affected by retrograde (axonal) reaction. *a*, cells from the hypoglossal nucleus; *b*, small cells of the nucleus intercalatus; *c*, medium-sized piriform cells occurring in the rostral part of the nucleus intercalatus and in the nucleus praepositus; *d*, larger multipolar cells from the nucleus praepositus; *e*, cells from the nucleus of Roller. $\times 600$.
- Fig. 2. Cells showing retrograde changes (*r*) in the nucleus intercalatus of cat O 93, at a level between drawings 5 and 6 of Text-fig. 2. $\times 380$.
- Fig. 3. Cells showing retrograde changes (*r*) in the nucleus praepositus of cat O 93, at the level of drawing 8 in Text-fig. 2. $\times 380$.
- Fig. 4. Cells showing retrograde changes (*r*) in the nucleus of Roller of cat O 93. $\times 380$.
- Fig. 5. Small cells showing retrograde changes (*r*) in the nucleus intercalatus of cat O 54, contralateral to the side of the lesion. $\times 380$.
- Fig. 6. Terminal degeneration in the nucleus praepositus after lesion of brain stem at the pontine level. Glees's method. $\times 900$.