THE CORTICAL PATHS FOR MASTICATION AND DEGLUTITION. By F. R. MILLER, M.A., M.B.

(*From the Laboratory of Physiology, Western University, Canada.*)

THE observation that movements of mastication may be elicited in the rabbit by stimulation of the cerebral cortex is due to Ferrier(1), who found the cortical area yielding the response to be rather extensive and to be situated on the lateral surface of the frontal lobe. Réthi(2) obtained mastication and also deglutition by excitation of the cortex of the rabbit. Stimulation applied to the infracortical paths yielded both responses as far posteriorly as the subthalamic region. On arrival at the crus cerebri, however, stimulation produced a continuous jaw closure, in place of the rhythmical mastication, whilst swallowing was absent. He argued from these results for the existence of a centre for mastication and deglutition situated within or below the thalamus and above the crus cerebri. A study of the cortical area and subcortical tracts involved in mastication in the rabbit was made by Carpenter(3). He followed the tracts into the medial portion of the crus cerebri. But he makes no mention of a change from masticatory rhythm to continuous jaw closure, as was recorded by Réthi. The cortical masticatory centre as localised by Mann(4) is somewhat smaller than Ferrier's area and is situated slightly ventral to it.

The present research represents an attempt to investigate somewhat more completely the cortical paths concerned in mastication and deglutition. The rabbit served as the experimental animal and anæsthesia was induced by ether or by the injection of chloral hydrate intraperitoneally (about ·35 gm. per kilo.) or by a combination of both procedures.

The inductorium used for stimulation was fed by two storage cells; an ammeter and a rheostat were arranged in the circuit and the rheostat was adjusted so that, whilst the interrupter of the inductorium vibrated, the ammeter indicated a reading of approximately 0·2 ampère. Stimulation was applied by the bipolar and unipolar methods, the latter method serving for the purpose of localisation. The stimulating terminals were of platinum fused at their extremities into small beads. The terminals of the bipolar electrodes were 1 mm. apart. The average secondary distance was 9·5 cm. for both methods of stimulation. At 13·5 cm. the current from the bipolar electrodes was just perceptible on the tip of the tongue.

The first problem presenting itself was whether the masticatory movements elicited from the cortex are bilateral, that is whether the muscles of both sides of the jaw participate in the reaction. For the purpose of deciding this question the mandible was sawn through at the symphysis and the soft tissues were divided in the middle line as far back as the angle of the jaw. Under these conditions the masticatory movements were seen to be not only bilateral but also synchronous, the muscles of the two sides functioning harmoniously. It appeared just possible that mere contact between the divided halves of the jaw might be responsible for the bilateral character of the reaction. Such a contingency was, however, readily excluded by stimulating the cortical area, whilst, at the same time, the contralateral half of the jaw was drawn aside. Stimulation under these conditions yielded again synchronous, bilateral jaw movements. Moreover, direct observation of the exposed, ipsilateral masseter muscle during the stimulation showed it to be executing rhythmical movements of mastication. It is clear, then, that bilateral, synchronous movements of mastication result from stimulation of the appropriate cortical area of one cerebral hemisphere.

Mention has already been made of the fact that Réthi elicited rhythmical mastication from infracortical paths as far posteriorly as the subthalamic region. In view of the somewhat vague nature of this statement it appeared desirable to determine more accurately the posterior limit for the reaction. Anæsthesia was effected by chloral hydrate injected intraperitoneally and by ether. Tracheotomy having been performed, the animal was secured with its abdomen on the table, a hot water bottle being placed crosswise so as to support it just in front of the hind legs. The head was placed on a block of suitable size. The skull was trephined in front of the coronal suture and the opening enlarged to an adequate extent.

In the preliminary experiments the reaction of mastication was first excited from the cortex and then successive vertical slices were removed from one hemisphere with a flat spatula. The hæmorrhage resulting from each excision was checked by packing with absorbent cotton soaked in adrenaline solution. Following each extirpation bipolar stimulation was applied to the cross-section and in this way it was found that, as Réthi had reported, masticatory rhythm and swallowing could be evoked for a considerable distance backwards but that they were finally replaced by steady jaw closure. The muscles concerned in this closure appeared to be solely those on the same side as the stimulation. It was noted further that the reaction was more readily obtained from a point on the base of the skull than from the cross-section of the brain. The extreme posterior limit for obtaining mastication and deglutition was found to lie approximately 16 mm. behind the zygomatic process.

In order to ascertain the exact anatomical relations experiments were performed in which a section was made across both hemispheres at the level just mentioned. Stimulation of the appropriate place on the cross-section of each hemisphere now yielded, provided the posterior limit had not been exceeded, mastication and swallowing. A further portion of one hemisphere was now removed until it was found that, instead of chewing and swallowing, only steady jaw closure was elicited on excitation. The original point on the opposite side, however, still yielded chewing. Sections were then prepared from each hemisphere and stained by the Weigert method.

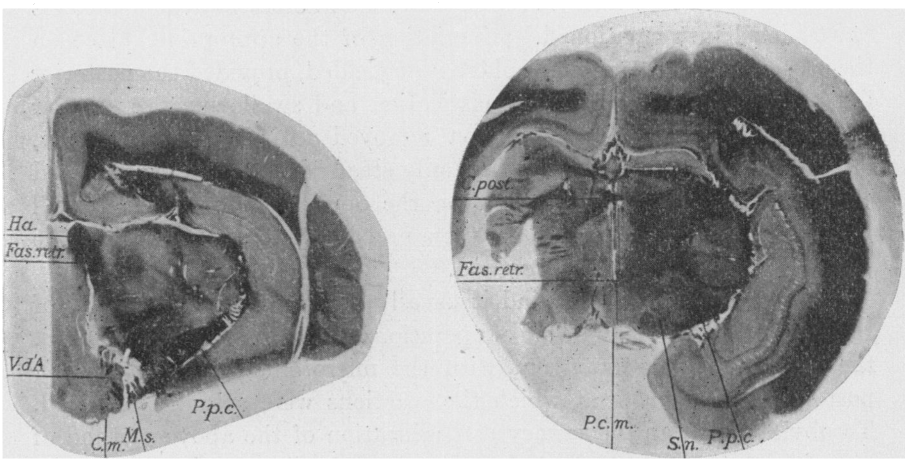
In experiments of this kind it usually happens that the section of the brain, as made at the time of operation, is not perfectly flat. Hence, the first complete section cut with the microtome lies very slightly posterior to the plane at which the reactions were actually obtained. To obviate such an inaccuracy a modification of the above method of experimentation was adopted as a control. In these experiments sections were cut from one hemisphere only and the extreme posterior limit for mastication and deglutition was determined as accurately as possible. A section was then made with the microtome through the intact hemisphere at the level which yielded mastication and deglutition on the opposite side. A similar procedure was adopted to ascertain the level yielding continuous closure.

In consequence of numerous experiments of the types described it can be definitely asserted that a masticatory rhythm and deglutition may be obtained as far backwards as the level of Fig. 1; from the level of Fig. 2 and beyond it, however, only steady jaw closure was noted.

Reference has been made to the interpretation placed by Réthi on the change in type of the reaction from a rhythm to continuous closure. He inferred the existence of a centre for mastication and swallowing within or immediately below the thalamus. Presumably he thought the continuous jaw closure evoked beyond the level of Fig. 1

was due to stimulation of fibres in the pes pedunculi. As already mentioned, my own observations show that the effect is produced by contraction of the ipsilateral closing muscles. This fact makes it appear improbable that the contraction depends on stimulation of the pes. Examination of the anatomical arrangements of the region shows that the contraction is caused by stimulation of the mandibular nerve at its emergence from the skull by escape of current from the electrodes.

With respect to the disappearance of mastication and swallowing beyond the level of Fig. 1 it would seem that a more plausible explanation may be offered than that of Réthi. According to Prof. Sherrington[1]



Figs. 1 and 2. Cross-sections of brain of rabbit. *C.m.*, corpus mamillare; *Fas. retr.*, fasciculus retroflexus; *Ha.*, habenula; *P.p.c.*, pes pedunculi cerebri; *V.d'A.*, bundle of Vicq d'Azyr; *M.s.*, situation of bristle indicating point from which mastication and swallowing were yielded; *C. post.*, posterior commissure; *P.c.m.*, pedunculus corporis mamillaris; *S.n.*, substantia nigra.

the explanation is to be found in the fact that the fibres concerned in these reactions have, beyond the level of Fig. 1, left the pes as "aberrant fibres" to proceed to their respective motor nuclei. Definite proof of the correctness of such a view would be furnished by demonstrating both mastication and swallowing in the decerebrate rabbit. Whilst swallowing is readily elicitable in the decerebrate cat (5) its demonstration in the decerebrate rabbit appeared desirable. Decerebration was, accordingly, performed in the rabbit by Sherrington's original method as described for the cat, both hemispheres being completely removed. The level of the transection was, of course, a considerable distance posterior to that

[1] Personal communication.

beyond which mastication and deglutition ceased to be elicitable by stimulation. In such a decerebrate preparation deglutition was found, after a short period of recovery, to be readily evokable by introducing water into the pharynx by means of a rubber tube. Efforts to induce mastication were, however, unsuccessful. Faradic and mechanical stimulation of the tongue, pharynx and various parts of the buccal mucosa failed to yield it. It appears probable that, could the decerebrate rabbit be kept alive for a sufficient length of time, mastication would eventually become elicitable. But in the few hours during which it retains its vitality I have not met with success in this direction. Since, however, swallowing is obtainable in the decerebrate rabbit it is evident that Réthi's hypothesis of a deglutition centre in the thalamic region must be definitely abandoned. And, in spite of the absence of experimental proof, the existence there of a centre for mastication would appear, from general considerations, extremely improbable.

The situation of the tract concerned in the masticatory rhythm was determined at various levels by the unipolar method of stimulation. A small bristle was inserted at the proper point and served as a record in the sections which were subsequently prepared. In Fig. 3 the bristle is situated in the lower part of the internal capsule.

In Fig. 1 the bristle is in the medial portion of the pes pedunculi. Deglutition accompanied mastication in these experiments but the specific tract involved has not yet been differentiated from that for mastication.

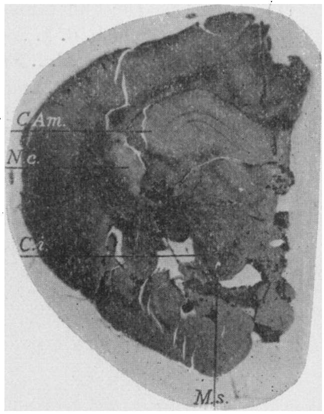


Fig. 3. Cross-section of brain of rabbit. *C. Am.*, cornu Ammonis; *C.i.*, internal capsule; *N.c.*, caudate nucleus; *M.s.*, situation of bristle indicating point from which mastication and swallowing were yielded.

SUMMARY.

1. The movements of mastication induced by stimulation of the cerebral cortex of the rabbit are bilateral.

2. Masticatory rhythm and deglutition can be elicited from the infracortical tracts as far posteriorly as the corpora mamillaria.

3. Beyond this level both reactions cease to be evokable, the reason

being that the fibres concerned have passed to their respective motor nuclei as "aberrant fibres."

4. The steady jaw closure which replaces rhythmical mastication is caused by escape of current to the mandibular nerve at its exit from the skull.

5. The existence of a deglutition centre in the thalamic region is disproved. The presence there of a centre for mastication appears improbable.

6. The infracortical tract for mastication and deglutition was traced through the lower part of the internal capsule at the level of the posterior extremity of the caudate nucleus to the medial part of the pes at the level of the corpora mamillaria.

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