VIII. *An Experimental Investigation of the Central Motor Innervation of the Larynx.*

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Received June 17,—Read June 19, 1890.

[Plates 31, 32.]

Part I.—Excitation-experiments.

a. *Introduction.*

In the course of observations dealing with the physiology of the motor innervation of the larynx, the results of which were embodied in a paper recently presented by one of us (F. S.) to the Royal Society,* it was shown that the central innervation of the larynx played a much more important *rôle* in the function of respiration than had previously been accorded to it. More especially it was shown that certain nerve-centres were constantly at work in maintaining a reflex-tonus of the abductor muscles (posterior crico-arytænoids) indispensable for the mechanism of quiet respiration in Man.

In 1880, 1881 and 1883† it had been shown by one of us (F. S.) that these same muscles (the abductors) were more liable to degenerative changes in cases of organic disease of the motor nerves of the larynx from the medulla oblongata downwards, and at the same time that functional disorders of the laryngeal motor apparatus almost exclusively affected their antagonists, the adductors. The explanation of all these different phenomena presented great difficulties, and, although light was thrown upon them in very various and unlooked-for ways, it soon became evident that neither clinical and pathological observations in Man alone, nor experiments upon the peripheral nerve-mechanism of animals, would suffice to solve all the questions here involved.

Now, the fact just mentioned—viz., that in functional disorders (*e.g.*, hysterical aphonia) those motor laryngeal nerve-fibres only which subserve the volitionary function of the larynx (*i.e.*, phonation) ordinarily suffer, whilst, on the other hand, in

* "On the Position of the Vocal Cords in Quiet Respiration in Man, and on the Reflex-tonus of their Abductor Muscles." 'Roy. Soc. Proc.,' 1890 (vol. 48, p. 403).

† (*a*) Foot note in German Edition of Morell Mackenzie's 'Diseases of the Throat and Nose,' vol. 1, p. 574.

(*b*) 'Archives of Laryngology,' July, 1881

(*c*) 'Berliner Klinische Wochenschrift,' No. 46, *et seq.*, 1883.

organic disease those fibres are usually primarily affected which are engaged in maintaining the automatic process of laryngeal respiration—seemed to indicate that there must be a central differentiation corresponding to these varied phenomena. Hence it was that the idea of the present research occurred to us.

In planning such an investigation we naturally turn first to the subject of the cortical representation of the larynx—a problem which, first touched upon by FERRIER and DURET, has been treated in detail by H. KRAUSE at the instigation of H. MUNK, and by MASINI.

From this point we might proceed to the consideration of the fibres leading from the cortex to the lower centres in the medulla, as they pass through the corona radiata and the internal capsule. The investigation of these fibres by means of the excitation-method has, so far as we know, not been undertaken by any previous observer, though some work by the ablation and degeneration method has been performed by KRAUSE. This latter method and its results will be fully dealt with by us in a subsequent paper.

Finally, we discuss the results of excitation of the central mechanism in the bulb, a branch of the subject which we commenced four years ago, and which also has not been treated, to our knowledge (confirmed by Professor GAD), by any previous observer.

Before passing to a complete historical retrospect of the question, and before describing the method of our own experiments, we may state that, since we have found certain important differences in the central structural arrangements in different species of animals, and also in animals of different ages belonging to the same species, it is essential that these should first be prominently and clearly expressed, in order that some discrepancies which exist in the statements of previous investigators and the classification of our own results might be properly understood.

To the same category belongs the question of the action of anæsthetics upon the neuro-muscular system, a question the importance of which for the present investigation can hardly be exaggerated; since, for reasons which we will further discuss, the effect attained by exciting any given centre may be entirely modified by the mere degree of anæsthesia affecting the peripheral mechanism of nerve-endings and muscles.

In a previous communication* we have shown the importance of the action of ether upon the peripheral nervous system, a factor which must be properly discounted in considering the action of the anæsthetic upon the nervous mechanism as a whole.

These considerations of species, age, and anæsthesia will compel us to further subdivide the great groups into which we have arranged our facts.

In the following historical retrospect of the results obtained by previous investigators we have thought it best (to avoid misconception) to place each writer in the chronological order of the appearance of his publication.

* "On an apparently peripheral and differential action of Ether upon the laryngeal muscles," 'British Medical Journal,' 1886.

b. *Historical Retrospect.*

Although various authors have observed the changes in thoracic respiration following excitation of the central nervous system, but few have studied the relationship of the latter to the larynx, either so far as respiration or as phonation is concerned.

As this relationship is the immediate subject of this paper, we shall confine ourselves in this retrospect to a brief *résumé* of the results of those authors who have directly investigated, either experimentally or clinically, the question here at issue.

On the experimental side undoubtedly FERRIER* was the first worker in the field of excitation. In the first edition of his well-known work he describes an instance in which excitation of a certain cortical area in the Dog elicited barking, and observes that similar observations had been made by him repeatedly.

Shortly afterwards DURET,† of Paris, referred to the same subject in connection with his cortical ablation and compression experiments, and reported similar results.

Although subsequent experimentation has shown that both these observers did not accurately localise the *focus* of the representation of phonation in the cortex, to them, undoubtedly, belongs the priority of the idea of a special representation of this function in the cortex.

Seven years after FERRIER'S reference to the question the subject was, at the suggestion of H. MUNK, specially studied by H. KRAUSE,‡ who was the first to localise accurately the phonatory area in the cortex of the Dog's brain. He made six excitation-experiments on Dogs, from which he localised the movement of closure of the glottis (always bilateral adduction) to be represented in the isthmus ("STIEL") of the præfrontal (præcrucial) gyrus. To his ablation and degeneration experiments we shall make reference in a future communication.

In his great work on the functions of the brain, FRANÇOIS FRANCK§ states that excitation of the "zone motrice" of the cortex produces changes in the thoracic respiratory movements according to the duration and intensity of the excitation. These changes are acceleration, slowing, and variations of amplitude. He does not consider that respiratory centres can be considered to exist in the cortex cerebri, or that there is any differential representation of the larynx or other parts of the respiratory apparatus.

In the epileptic convulsion evoked by cortical excitation he observed what we have confirmed and extended, viz., that in the tonic stage the glottis is shut, whereas in

* 'Functions of the Brain.'

† 'Traumatismes cérébraux,' 1878, p. 142.

‡ "Ueber die Beziehungen der Grosshirnrinde zu Kehlkopf und Rachen," 'Archiv für Anatomie und Physiologie, Physiol. Abth.,' 1884. This was preceded by a note under the same title, in the 'Sitzungsberichte der Kgl. Preuss. Akademie der Wissenschaften zu Berlin,' November, 1883.

§ FRANÇOIS FRANCK, 'Leçons sur les Fonctions Motrices du Cerveau,' Paris, 1887 pp. 146–8.

the clonic stage the cords execute movements synchronous with the twitchings of the thoracico-abdominal respiratory muscles.

MASINI* made in 1888 a series of both excitation and ablation experiments on the cortex of Dogs. In the former he found in four cases that excitation with weak currents produced earlier movements of the opposite vocal cord, followed by later and slower movements of the cord corresponding to the side of stimulation. He is the only experimenter, so far as we know, who has obtained such unilateral results. With stronger currents he obtained bilateral movements. According to his views the representation of the adductory movements of the vocal cords is spread over the whole motor area, though focussed in the centres for the soft palate and tongue.

ARONSOHN† mentions in a paper, published in the same year, briefly, that in his experiments he could not obtain any definite reply to the question whether the adductory movements of the vocal cords observed by him were actually due to the stimulation of the brain.

MOTT,‡ in repeating our observations, corroborated our results.

Two very important papers on the root-fibres of the motor nerves of the larynx, by GROSSMANN§ and GRABOWER‖ respectively, we only desire in this connection to mention by title, as the subject of their researches rather refers to the peripheral part of the nervous mechanism of the larynx.

The above short list comprises, so far as we know, all experimental contributions to this question, in which the intrinsic laryngeal movements have been actually observed or recorded, when the central nervous system has been stimulated.

The clinical evidence concerning the relationship of the larynx to the higher nervous centres is also very limited.

That lesions of the medulla oblongata may and do occasionally cause laryngeal paralysis, is, of course, admitted on all hands. In such cases it is, correctly speaking, rather a lesion of the vago-accessory nucleus and fibres in the medulla oblongata than a genuine central affection, to which the laryngeal paralysis must be attributed.

With regard to the higher nervous centres, however (cortex and internal capsule), matters are very different.

Although a certain number of cases have been published (*e.g.*, by ANDRAL, GERHARDT, FRIEDREICH, FOVILLE, DUVAL, LÖRI, LEWIN, LIVIO RONCI, LUYS, CARTAZ, MASSEI, &c.¶), in which simultaneously with organic lesions of the higher centres

* 'Archivi Italiani di Laryngologia,' Napoli, April, 1888, p. 45.

† "Zur Pathologie der Glottiserweiterung," 'Deutsche Med. Wochenschr.,' 1888.

‡ 'Brit. Med. Journal,' 1890.

§ "Ueber die Athembewegungen der motorischen Kehlkopfnerven, II. Theil," 'Sitzungsberichte der Kais. Akad. d. Wissensch. zu Wien,' November, 1889.

‖ "Das Wurzelgebiet der motorischen Kehlkopfnerven," 'Centralblatt für Physiologie,' January 4, 1890.

¶ The literature of these cases will be found in MASINI'S, GAREL and DOR'S, and in ROSSBACH'S papers hereafter referred to in the text. They are not quoted here at length, because these authors themselves admit that they cannot claim to be of a decisive character for the question at issue.

vocal disturbances or even laryngeal paralyses have been observed, no conclusions can be drawn from them for the decision of the present question, because all of them are in some way or other incomplete. In some of them the diagnosis of a cerebral lesion is not at all beyond doubt, in others multiple lesions existed, in a third category no laryngoscopic examination had been made, and again in others either no autopsy had taken place, or the descriptions of the latter, when made, are defective with regard to the condition of the medulla oblongata, the peripheral parts of the laryngeal nerves, the microscopic examination of the medulla, the nerve fibres, and the muscles themselves, &c.

In 1884 Bryson Delavan* called attention to the possibility which existed in his opinion, viz., of localising from clinical observation the cortical motor centre for the larynx. Of the two cases, however, upon which he based his views, in one (Seguin's) no laryngoscopic examination had been made, whilst he himself frankly stated some years afterwards,† that in the second one, his own, in which he had attributed the laryngeal paralysis to a cortical lesion, the post-mortem examination had established the fact that in reality it was of bulbar nature.

In 1886 Garel‡ recorded an observation, to which he added, in conjunction with M. Dor, another in 1890, which proved,§ in the opinion of these authors, that unilateral laryngeal paralysis could be caused by a unilateral lesion of the opposite hemisphere or internal capsule. We have elsewhere‖ taken exception to the interpretation given by these authors to the paralysis observed in their cases, because (*a*) the medulla oblongata was not microscopically examined at the post-mortem examination, and (*b*) the *total* paralysis (respiratory as well as phonatory) of the vocal cord observed in their cases is according to our ablation-experiments absolutely incompatible with the idea of its being due to a *cerebral* lesion.

Recently Rossbach¶ has published a very interesting paper on the subject, in which from a carefully observed case under his own care he draws the conclusion that unilateral paralysis of a vocal cord may be caused by a lesion of the opposite insula. Seeing however, that in his case there was atrophy of the corresponding side of the tongue due to an undoubted lesion of the ganglionic cells of the hypoglossal nucleus in the medulla oblongata, and that the integrity of the vago-accessory nucleus in the medulla was merely *surmised* from the fact, that the fibres of the nerve itself, and of the laryngeal muscles, had undergone no atrophy, while it was not at all shown that the

* 'Compte-rendu des Travaux de la Section de Laryngologie du VIII. Congrès International Périodique des Sciences Médicales.' Copenhague, 1884, p. 17.

† 'Transactions of the American Laryngological Association,' 1888, p. 195.

‡ 'Annales des Maladies de l'Oreille et du Larynx,' May, 1886.

§ *Ibidem*, April and May, 1890.

‖ 'Annales des Maladies de l'Oreille et du Larynx,' May and June, 1890.

¶ "Localisation des corticalen Stimmcentrums beim Menschen." 'Deutsches Archiv für klinische Medicin,' vol. 46, March, 1890.

laryngeal paralysis had existed so long that atrophy ought necessarily have followed, we cannot admit this case as actually proving such a relationship as that claimed by the author.

Finally, at this moment a paper on the subject is in course of publication from the pen of SCHEFF,* the outcome of which cannot yet be foretold.

The general observations of LANNOIS† bring nothing new, whilst GOTTSTEIN‡ considers the question of the existence of a cortical centre for the larynx in man as still open.

This short list practically exhausts the clinical material in connection with the subject.

c. *Methods of Experimentation.*

The different points to be considered under this heading may conveniently be grouped in the following manner :—

1. Electrical methods.
2. Operative technique.

1. *Electrical methods.*—The excitation either of the cortex, corona radiata, or bulb was furnished by the secondary coil of a DU BOIS-REYMOND inductorium of the ordinary pattern, the distances of the secondary coil being marked in millimetres from a zero point where the primary coil was completely covered. In the later experiments we always employed a special inductorium with the HELMHOLTZ side wire, very kindly graduated for one of us by Professor KRONECKER, according to the manner he has published elsewhere, and by means of which alone is obtained an accurate knowledge of the increase in the strength of the stimulus when the secondary coil is pushed towards and over the primary. To facilitate the various references to the strength of the current in this paper we now give in parallel columns the divisions in millimetres according to the old method, and opposite them the divisions according to KRONECKER'S method. The battery elements employed were either one Daniell cell, one 1 litre bichromate cell, (GRENET), or a thermoelectric element, 16 cm. high, 14 cm. diameter, of 19 metallic junctions.

DU BOIS-REYMOND inductorium.

cm.	0.	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.	18.	19.	20.	21.	22.	23.	24.	25
Divisions of current KRONECKER inductorium.	13,000	12,500	12,000	11,250	10,270	9,250	8,500	7,300	6,300	5,300	4,300	3,300	2,400	1,700	1,000	Fraction over 600	420	300	250	180	130	87	70	58	48	41

The electrodes employed were always fine platinum points which, in exciting the cortex, were fixed 2 mm. apart, but in exciting the corona radiata, internal capsule, or

* "Zur Pathologie d. Motilitätsstörungen d. Kehlkopfs." 'Allg. Wien. Med. Zeitung,' June, 1890.

† "Y a-t-il un Centre cortical du Larynx ?" 'Revue de Médecine et de Chirurgie,' August, 1885.

‡ 'Die Krankheiten des Kehlkopfs,' Dritte Auflage, 1890, p. 344.

bulb were placed 1 mm. apart. The stimulus was kept applied to the cortex for different periods of time according to varying circumstances. Thus if a very minimal stimulus was being employed it was necessary, in order to judge of its effect upon the cortex, to prolong the excitation during several respiratory movements of the vocal cords, *i.e.*, from 5 to 10 seconds. If, however, the stimulus was markedly adequate so that an unmistakeable effect was produced immediately and ceased directly the stimulation was discontinued, then the application of the electrodes was only maintained for from 1 to 2 seconds, so as not to exhaust the cortex.

2. *Operative technique.*—The first point to be considered of course is the anæsthesia, the importance of which has been already alluded to, and is considered in further detail on p. 195. We may say at once that we have almost invariably used ether, in a few cases also in part chloroform; but inasmuch as the latter did not show any specific effect, differing much from that of ether, it is sufficient only to allude to it here as it may chance to be mentioned hereafter. The narcotisation was always conducted in the following manner:—The ether was first given by inhalation, and then complete unconsciousness having been produced tracheotomy was next performed and the anæsthetisation continued through a funnel and short* piece of rubber tubing, the funnel resting on cotton wool wet with ether and covered with a cloth. This method had the advantage that as it was usually found far more convenient to inspect the larynx from below all trouble connected with the inhalation of the narcotic was avoided, and as the trachea was always completely divided it was readily moved aside without twisting the larynx to either side, and consequently an uninterrupted view obtained. Furthermore, if too much anæsthetic was given by mistake, it was easy to restore the animal by inflation.

The tracheotomy having been done, as large a cannula as possible was inserted and fitted as above stated.

The animal was secured in a prone position and the operation proceeded with to expose the central parts of the brain. These may be referred to as cortex, corona radiata, internal capsule, and bulb. The second and the third of course consist only of fibres, whereas in the first and last case additional complications arise and extra precautions have to be taken owing to their being central apparatuses.

Cortex.—The anterior third of the skull, including the roof of the orbit, was then removed by first making a trephine opening and subsequently removing the bone piecemeal with fine bone forceps. All bleeding from the bone, which was always free, was immediately checked by wax. In this way the whole of the anterior extremity of the hemisphere, including the orbital surface, was completely exposed, *i.e.*, as far as the margin of the olfactory tract. For the better exposure of the same the tissues filling the orbit were drawn forward, the ocular contents having previously been removed from the eyeball through an incision in the sclerotic.† By means of constant irrigation

* Purposely short to allow of proper change of the respiratory gases in ventilation of the lungs.

† Or the eyeball removed (Hitzig).

with warm water or normal salt solution shock was in very great measure avoided. This was also provided against in the usual way with hot vessels, coverings, &c.

In no case was the dura mater opened until immediately before the commencement of the excitation.

The animal was then fixed on its side so that when the anterior wall of the trachea had been removed a perfect view from below was obtained of the vocal cords in their whole length.

In all this preparation of the trachea, larynx, &c., special care was necessary to avoid injury of the recurrent laryngeal nerves. Between every period of the excitation of the cortex it was douched with warm water or saline solution, protected by the skin-flap from the air and kept warm with hot sponges.

Corona Radiata.—The investigation of the corona radiata of course enables one to decide many points concerning the amount of representation of various functions in the cortex. Naturally, however, the excitation of the few fibres descending from the comparatively extensive area of the cortex is not easy unless the electrodes be placed exactly upon the cut ends of the fibres. It is for this reason, no doubt, that a stronger stimulus* is usually required to successfully excite the fibres. The removal of the cortex was always effected by a single incision with a sharp scalpel at right angles to the supposed direction of the fibres.

Internal Capsule.—This was exposed by horizontal section through the hemisphere in the same way as that just described for the corona radiata. The line of the incision taken is referred to on p. 202, and the only point noteworthy here is the arrest of hæmorrhage, &c. Naturally bleeding comes almost entirely from the middle cerebral, the lenticulo-striate arteries and their branches. Bleeding from these vessels can be certainly arrested if a fragment of amadou be gently pressed on the open mouth of the vessel and left there. Usually the various bundles of fibres in the capsule were then explored with the electrodes, and finally a careful transcript of the surface of the section made with compasses upon paper ruled with squares of 1 mm. a side, and the corresponding bundles of fibres indicated by arbitrary numbers placed on the squares into which the capsule was by this means divided.

The Medulla Oblongata.—This was exposed for excitation by reflecting the muscles and periosteum by the usual T-shaped incision from the occipital bone and the dorsal surfaces of the arches of the first two vertebræ without injury to the vertebral vessels. These same arches and the neighbouring portion of the occipital bone were then cut away with bone forceps. The dura mater was then divided in the middle line and the middle lobe of the cerebellum slightly drawn upwards or a portion removed in order to expose the lower end of the fourth ventricle. A drawing was then made with compasses of the surfaces of the ventricle thus exposed on the 1 mm. ruled paper. Oozing from the cerebellar vessels was always readily controlled, even in the dog, by irrigation with hot water or saline solution. This had a very notable effect also in raising

* Putnam, Franck.

the excitability of the bulbar centres when these were depressed by shock, exposure, &c.

In every case a post-mortem examination was made, the drawings verified and the specimen preserved.

d. *Influence of the Anæsthetic and Strength of Stimulus.*

We have assumed that the construction of the whole neuro-muscular apparatus of the larynx comprises (1) an area of cortex popularly, though incorrectly, termed the cortical laryngeal centre, (2) a similar area in the bulb or medulla oblongata which may in like manner be spoken of as the bulbar laryngeal centre and is connected with the cortical apparatus by fibres running in the corona radiata and internal capsule, while finally the vago-accessory nerve roots and peripheral branches contain the fibres supplying the laryngeal muscles and mucous membrane.

It was first observed by HOOPER* that even when the recurrent nerves were cut inhalation of large doses of ether produced paralysis of the closers (the adductors) of the glottis before the openers (the abductors). We repeated† and extended in further detail this observation and showed that this remarkable peripheral and differential action of ether was, in all probability, due to the fact that the antagonistic muscles of the larynx belong to classes of muscles biologically different.

HOOPER'S original observation was contested by DONALDSON,‡ who found that in certain cases one of the two groups of muscles predominated according to the strength of the stimulus, that with a feeble current, opening, with a strong current, closing, of the glottis was produced. A further, later research by HOOPER§ showed that the same effect is produced by varying the rate (*i.e.*, the intensity ?) of the stimuli, with a slow rate of interruption of a constant current abduction being obtained, with a quick rate adduction.

We have observed DONALDSON'S result to be occasionally present, and from general considerations are ready to believe that HOOPER'S second observation is correct. It is clear that the ether effect, and the intensity of stimulation effect mutually confirm each other. All these results apply in their entirety to Dogs only. Both, however, have to be kept in view when considering the results of exciting, as in the present research, the highest point of the efferent neuro-muscular track of the laryngeal apparatus in any animal, since it is obvious that the actual representation of movement (whether closure or opening of the glottis) might be masked by the condition of the peripheral mechanism; for instance, if this were poisoned with ether stimulation would give opening only of the glottis.

* 'Transactions of the American Laryngological Association,' vol. 7, 1886.

† 'Brit. Med. Journal,' 4–11 September, 1886. *Vide* also BIEDERMANN, 'Centralblatt für Physiologie,' and BOWDITCH, 'International Journal of the Medical Sciences,' April, 1887, p. 444.

‡ 'American Journal of Medical Sciences,' July, 1886.

§ 'Transactions of the American Laryngological Association,' 1888.

This combination of physiological relationship in the larynx has not, so far as we know, received much attention, we wish, therefore, to lay stress upon the fact that, until it has been further investigated, we shall not speak dogmatically upon the relative degree of representation of the two antagonistic movements in any one point of the cortex, but shall content ourselves with giving the results of our work. The further consideration naturally arises, that possibly what applies to the peripheral mechanism *may* also be true of the central apparatus, that, in short, the activity of the cortical corpuscles in which the representation of adduction exists may be more easily extinguished by ether than that of the representation of abduction. Considering, too, that this implies the earlier abolition of purposive function, it is not so fallacious to thus translate peripheral (*i.e.*, nerve ending ?) conditions to a centre. This, however, although a question of the utmost interest, does not appear to be capable of direct solution until it is possible to differentiate either anatomically or functionally the particular fibres in the pyramidal tracts in which closure or opening are respectively represented.

We hope that the results of excitation of the internal capsule, especially in the Cat, *vide infra*, will lend some aid in explanation of the difficulty as well as in the special examination of MASINI'S results for the reasons before given. We have carefully noted the effect of varying the strength of the excitation.

We have always employed the same rate of excitation (viz., 100 per second), since we believe that variation in rate is practically the same in effect as variation in intensity.

RESULTS.

Cortex.

General Statements.

We have directed our attention primarily to the investigation of the representation of phonatory laryngeal movements only, but we have not been unmindful of the concomitant representation of respiration. This is a point which has already been the subject of research, and especially at the hands of FRANÇOIS FRANCK. That author, as already mentioned in the Historical Retrospect, does not consider that a separate cortical apparatus exists for the phonatory and respiratory functions of the larynx respectively, but we believe that an extensive series of experiments will justify the course we have adopted.

We moreover think it right to discriminate between the representation of general respiration and that of the larynx, since we have, on the one hand, obtained laryngeal effects without any concomitant changes in general respiration,* and on the other hand, one excitation has often at the same moment induced changes of a

* Since this was written KRAUSE has stated in the 'Berliner Klinische Wochenschrift,' No. 25, 1890, that he has observed the same differentiation of representation.

different type in the larynx and general respiration, *e.g.*, closure of the rima glottidis with general acceleration of respiration. We shall therefore proceed at once to describe the laryngeal effects only, and shall reserve what we may wish to state relating to the effects produced on general respiration for another communication. In arranging our results we divide them as indicated on p. 188, *i.e.*, first, according to the species of animal employed, and we shall commence with the highest order.

Monkey.

Species employed.—We have explored the cortex in examples of *Macacus sinicus*, *Macacus rhesus*, and *Macacus cynomolgus*.

Among these *Macacus sinicus* afforded the best results. The general conclusions we derive from our excitation experiments are as follows :—

Intrinsic Laryngeal Movements.—That in the foot of the ascending frontal gyrus, just behind the lower end of the præcentral sulcus (*vide* Plate 31, fig. 1),* there is a focus of representation of the movements of the vocal cords which are independent of movements of the pharynx, when the most anterior part of the focal area of representation is excited.

This focus is limited anteriorly by the præcrucial sulcus (*p.c.*, fig. 1) and a line continuing the direction of that sulcus to the Fissure of SYLVIUS, superiorly, by a line drawn horizontally (parallel to Fissure of SYLVIUS) through the upper extremity of the small secondary sulcus marked *v*, see fig. 1, inferiorly, by the Fissure of SYLVIUS, and posteriorly, by the sulcus *v*.

The purely intrinsic movement of adduction of the vocal cords seems to be represented in the front half (marked darkly F, in fig. 1) of this focal area. In the posterior half, *i.e.*, just in front of *v*, it is accompanied by pharyngeal movements especially. (BEEVOR and HORSLEY.)

In this focal area the character of the movement represented is invariably adduction (Monkey), and not only complete, but also perfectly bilateral. We have never observed abduction to follow excitation. Outside the focal area the intrinsic movements are also represented, but in a greatly diminished fashion. Thus, from the rest of the facial region, as high as the lower border of the upper limb region, as defined by BEEVOR and HORSLEY, and, posteriorly, as far as the secondary sulcus in the foot of the ascending parietal gyrus, a slight degree of adduction (as far as the cadaveric position) is obtained on excitation. The relative degree to which this exists is shown in fig. 1 by the depth of the stippling. It need hardly be added that, of course, the movements of the face, jaws, and tongue noted to be represented in this region (FERRIER, SCHÄFER, BEEVOR and HORSLEY) also occur in concomitant association.

This gradual decrease in representation from a focus or centre of most complete function is typical of all cortical motor representation, especially in the lower apes.

Extrinsic Laryngeal Movements.—The movements of the larynx as a whole,

* Confirmed by MOTT and SCHÄFER, 'Brit. Med. Journal,' May 17, 1890.

of course, possess considerable interest. From anatomical reasons these resolve themselves under two headings—

(1) Upward Movement of the Larynx,
(2) Downward ,, ,, ,,

(1) *Upward movement* of the larynx we noted to occur only in front of the Fissure of ROLANDO, between it and the small secondary sulcus marked *v* in figure.

This movement is associated with swallowing and mastication, these actions being (BEEVOR and HORSLEY) represented in the strip of cortex thus indicated. Clearly, in this association, we have only the completion of the observed representation of these complicated acts.

(2) *Downward movement* of the larynx we obtained by exciting the cortex just behind the Fissure of ROLANDO between that sulcus and a line parallel to it, drawn from the lower end of the intraparietal sulcus to the Fissure of SYLVIUS.

Once we observed confusion between the movement of the larynx upwards and downwards to occur at this point, the downward direction predominating.

Epilepsy.—We have frequently observed epilepsy to follow excitation of the cortex in this region. At the commencement of the fit, the vocal cords are strongly adducted, often with tremors, *i.e.*, confusion between adduction and respiratory (?) abduction, this persisting during the tonic stage. Then, in the subsequent clonic stage, the movement of adduction alone occurs as single spasms and ceases, of course, often suddenly.

Carnivora.—Dog.

Phonation.—The following account applies only to the adult animal; we shall speak later of the differences which are caused in the cortical representation according to the age of the individual examined. The nomenclature of the sulci employed will be that given by LANGLEY in his admirable paper on this subject,* except that for brevity we shall speak of the anterior limb of the sigmoid gyrus as the præcrucial gyrus, and similarly of the posterior limb as the postcrucial gyrus. In the original description given by KRAUSE† of the cortical representation of the movements of the vocal cords, that author localised the focus of the representation to be situated in the præcrucial gyrus [or, as he called it, following MUNK, the gyrus præfrontalis (OWEN),] just where that gyrus terminates below in a narrow pillar or isthmus connecting it with the anterior composite gyrus. At this point he found that excitation, as a rule, produced bilateral adduction of the cords; this we have completely confirmed, but we have also found that while the spot indicated is a focus, nevertheless slight adduction can be obtained by excitation of the whole of the lower two-thirds of the præcrucial gyrus, and also a few millimetres of the upper extremity of the anterior composite gyrus.

* 'Journal of Physiology,' December, 1883, p. 248.

† 'Archiv f. Anatomie und Physiologie, Phys. Abth.,' 1884, p. 203.

This representation of the intrinsic movements of the larynx is not pure except very special care be taken to adjust the strength of the excitation sufficiently to prove a minimal stimulus to the point excited. As a rule, it is accompanied by movements of the tongue and of the pharynx, *e.g.*, swallowing.* Occasionally, however, we have obtained movements of the vocal cords without any concomitant action elsewhere. We have never, in the adult Dog, witnessed abduction, although we have explored the whole of the frontal lobe on its orbital and external nasal surfaces completely.

Respiration.—We now proceed to remark upon the representation of respiratory movements of the larynx also to be found in the cortex of the adult Dog. We have found that the following conditions may be produced with absolute certainty.

a. Acceleration of Respiratory Movements of the Vocal Cords.—This is chiefly represented just above the focus for the movements of the adduction of the cords, *i.e.*, just in the middle of the lower third of the præcrucial gyrus, but excitation of the whole of the præcrucial gyrus as a rule produces this effect in diminishing degree, as we move from the focal point just mentioned. In the performance of this act the abduction of the vocal cords is, as a rule, diminished in extent, as has already been mentioned in speaking of their phonatory representation in the same area, but they otherwise present the ordinary alternate rhythm of abduction and adduction.

Before passing to the next point observed we must here make a few remarks upon this extraordinary result, because it has not been, so far as we know, described in connexion with any function other than the respiratory.

Quickening of respiration has very properly been termed by RICHET† polypnœa, and has been proved by him to be the means whereby the thermo-taxic apparatus restores the equilibrium of the body by providing for extra loss or dissipation of heat.

Further, work of a memorable kind has been done upon this subject by OTT,‡ who has directed special attention to this point, and has produced by excitation the same acceleration of respiration, but from excitation of the internal capsule. (*Vide* our remarks on the internal capsule.) We provisionally quite agree with the conclusions and explanations offered by these writers, and we would here remark, that so far as we can see, the results obtained by CHRISTIANI,§ and probably those by MARTIN and BOOKER,‖ are to be explained as the results of excitation of the fibres leading down from this very extensive and cortical representation of the respiratory acceleration

* [While this paper was passing through the press MUNK published, in the 2nd edition of his 'Gesammelte Mittheilungen über die Functionen der Grosshirnrinde,' a statement on p. 178 to the effect that we have confounded the focal representation of phonation with laryngeal movements when accompanied by associated movements of the mouth, pharynx, &c. The justice of this statement we leave to the opinion of our readers.—August, 1890.]

† 'La Chaleur Animale.'

‡ 'Laboratory Researches,' Easton, Pa.

§ 'Zur Physiologie des Gehirnes.' Berlin, 1885.

‖ 'Journal of Physiology,' vol. 1, 1881.

that we have observed. (*Vide* also FRANÇOIS FRANCK, LÉPINE, BOCHEFONTAINE, DANILEWSKY, GOLDSTEIN, SIHLER, MUNK, &c., and our remarks on the internal capsule.)

b. Intensification of Respiratory Movements.—If the electrodes be moved over the surface of the sigmoid gyrus it will be noticed that as soon as they are placed opposite the lower or outer end of the crucial sulcus, there is then, together with the now very slight acceleration in rate, a distinctly more energetic action of the vocal cords. Both the abduction and the adduction movements are more pronounced, and as the electrodes are carried back to the lower end of the postcrucial gyrus, *i.e.*, over the area of representation of the fore-limb, this intensification becomes still more marked, and is occasionally accompanied by slowing, and may in short be said to be there localised, as from this point upwards it gradually diminishes over the surface of the gyrus.

These observations are interesting in connexion with those made by MASINI upon the distribution of the laryngeal represention in the Dog. (*Vide* History.)

In reviewing the results just noted, we wish to point out that if the excitation of the cortex be first attempted with an extremely weak current and if then the stimulus be increased, the first effect in response to the weak current is the respiratory acceleration before noted, and the next effect is the intensification of the respiratory movements. The purposive adduction obtained in the phonatory centre as a rule requires the strongest stimulus.

This has been found to be the case by most observers, the distance of the secondary coil from the zero point of the ordinary DU BOIS inductorium being required to be pushed, as KRAUSE himself first stated, to 7·5 or even 4 cm.* Although we have made a special investigation of this point with very weak as well as stronger currents, and although we have been very careful to preserve the vertical position of the larynx, and to record even the slightest action, we have never observed the unilateral movements described by MASINI.

Epilepsy.—As in the Monkey, we have not infrequently observed epilepsy to follow the excitation of the cortex, this being more readily produced in the carnivorous animals than in the higher. During the epileptic convulsions the vocal cords usually after preliminary adduction exhibit clonic adductory movements, in no wise differing from those previously described, save in their intermittent character.

Cat.

We have made a large number of experiments upon the cortex of the Cat because we found very early in our investigations, in 1886, that the movements of the larynx represented in the cortex of the Cat were not the same as those which we had obtained from the Monkey or even from the Dog. In other words: contrary to what we have just seen, the movement of abduction was well represented in the cortex of the Cat, although we had never been able to find any genuine trace of it in the cortex of

* Faradism, moreover, not HELMHOLTZ modification.

the Dog. It will be necessary, perhaps, first to explain that the arrangement of the convolutions in the Cat as regards the frontal lobe is in its chief features the same as in the Dog, only in miniature. See Plate 32, figs. 2, 3, 4, 5. The coronal fissure bounds the sigmoid gyrus below, and running forward is separated from the supraorbital sulcus by the pillar or isthmus of the præcrucial gyrus joining the anterior composite gyrus as before described. In front of the supraorbital sulcus and between that sulcus and the rhinal fissure is situated, as in the Dog, the orbital lobe. The rhinal fissure, of course, separates the orbital lobe from the olfactory tract. We mention all these points because their special bearing will be seen directly.

Phonation.—The bilateral adduction of the vocal cords, as in phonation, we have observed in the Cat to be more frequently represented in the coronal gyrus at its anterior extremity, near the anterior composite gyrus, at a point which is in a line with the crucial sulcus and in the upper part of the gyrus, *i.e.*, close to the coronal fissure, at *d'*, figs. 2, 4, 5. We have further observed that representation of bilateral adduction is also to be found in the area corresponding to that discovered by KRAUSE in the Dog, *i.e.*, just above and in front of the anterior end of the coronal fissure, at *d*, figs. 2, 4, 5. This representation of adduction, whether in one place or the other, is very soon exhausted, although it is, when present—*i.e.*, in a full-grown old Cat—well marked. It requires a moderate stimulus for its production, *i.e.*, 7000 to 8000 of the KRONECKER coil.

Respiration, Abduction, Acceleration.—We have found that in the Cat there exists a point (at *b*, figs. 2, 3, 4, 5) in the lower border of the hemisphere, just above the rhinal fissure—*i.e.*, in the anterior composite gyrus—and just below the depression representing the antero-supra-sylvian sulcus, excitation of which produces well-marked—*i.e.*, as long as the excitation lasts—abduction of the vocal cords; and that the same effect is produced, in a diminishing degree, round this point as a focus, and occasionally passes above the supra-sylvian sulcus on to the coronal and upper part of the anterior composite gyrus. This cortical representation of abduction in the Cat is very interesting, as probably indicating special respiratory requirements* in that animal, this deduction being confirmed by the experiments of LEGALLOIS† and others. Although we have found occasionally that in the Cat the præcrucial gyrus gave upon excitation, as in the Dog, acceleration of respiration, yet this was not so marked.

Intensification.—Similarly, intensification also was observed, but in no great degree.

Concomitant Movements.—Concomitant movements were observed (movements of the tongue, licking, mastication, and swallowing) when the anterior composite gyrus was excited, *i.e.*, when opening of the glottis (abduction) was produced. But we constantly observed the abduction to be completely maintained while thoracic respira-

* In the discussion following a demonstration of some of our experiments at the 10th International Medical Congress, 1890, Prof. DU BOIS-REYMOND stated that he had observed phonation in the Cat and Cow to be of an inspiratory nature. Prof. EXNER stated the same with regard to the Pig.

† 'Sur le Principe de la Vie.'

tion went on unhindered. On the other hand, when closure of the glottis was evoked, the respirations were distinctly slowed.

We cannot pass from this part of the subject without adverting to the remarkable way in which the laryngeal apparatus of the Cat is, as we have before remarked, extremely sensitive to the operation of the anæsthetic. Especially was this the case in making these experiments upon the cortex, since we found that a moderately deep narcotisation was sufficient to change the effect observed from adduction to abduction. The discussion of this we resume further on.

Epilepsy.—We have occasionally observed epilepsy, and when it occurred the vocal cords were preliminarily brought together, and then moved in clonic adductory spasms. We would now like to state that it is the phonatory—or, as we may say, the purposive—adductory representation of the laryngeal movements which is invariably brought out in the epileptic discharge of the cortex; another proof, if proof be required, of our position that adduction is a movement characteristic of the highest cortical evolution as far as the larynx is concerned.

Rodents.—Rabbit.

Cortical representation of movement in the Rabbit is, of course, well known to be very limited indeed, both in extent and in degree, the cortical centres being soon exhausted and the effects produced being relatively insignificant. We therefore only made two experiments upon this animal. We obtained no focal representation of the larynx, but the intrinsic movement observed concurrently with the movements of other parts were, as a rule, adduction; and, where this was most marked, the concomitant movement was that of swallowing.

Corona radiata.

We have, in a certain number of experiments, removed the cortex and excited the fibres beneath. As might be expected, our results all point to one conclusion, viz., that excitation of the fibres which lead in a direct line from the particular part of the cortex removed to the internal capsule gives the same effects as did the cortex when that was excited. Thus, in the Dog we have observed that the white fibres leading down from the præcrucial gyrus gave acceleration and those from the isthmus of that gyrus adduction, whereas the fibres coming from the lower end of the postcrucial gyrus gave intensification of the respiratory movements of the vocal cords. Exactly the same is observed in the Cat, viz., that acceleration is coupled with adduction, and that, on excitation of the fibres coming from the abductor focus, we have as distinctly abduction.

In no case, in accordance with the previous observations of various authors, did we obtain epileptic movements of the laryngeal muscles, after the cortex had been excised, by stimulation of the fibres leading therefrom.

Internal Capsule.

It will be necessary to give a slight anatomical introduction before describing our results of the excitation of the internal capsule. In the first place we invariably have exposed the internal capsule by a horizontal section carried through the substance of the hemisphere from before back, after the usual preliminary ligature of the middle cerebral artery. In this manner the internal capsule in its whole length, basal ganglia, &c., were exposed, and readily distinguishable. The horizontal section before referred to passed in the Carnivora through the sub-prorean gyrus, the lower part of the orbital lobule just above the rhinal fissure, through about the middle of the Sylvian fissure, and so backwards through the lower end of the curved external convolutions and sulci, *i.e.*, ecto-sylvian, &c.

In the Monkey the section was carried horizontally backwards through the third frontal gyrus, the foot of the ascending frontal and parietal gyri respectively, across the Sylvian fissure, through the uppermost part of the temporo-sphenoidal lobe, and so through the occipital lobe. The anatomical features of the cerebral sections thus produced, although, of course, differing considerably in the various orders of animals, nevertheless are not so diverse as might be anticipated (see figs. 6, 7). In each case the section exposed both the caudate and lenticular nuclei of the corpus striatum as well as the optic thalamus. The sections in the Monkey thus correspond to about the level of Group 4, as described by BEEVOR and HORSLEY. These authors in their paper (*ante*, pp. 49–88), on the arrangement of the excitable fibres of the internal capsule of the Bonnet Monkey, just referred to, observed phonation to occur in one section of the capsule when these fibres were excited (*ibid.*, p. 83), but they did not directly observe the laryngeal movements.

In this connection it must be remarked that in the Carnivora the lenticular nucleus is relatively extremely narrow (see figs. 6, 7), so that the angle made by the two limbs of the capsule is a very open one, almost 150 to 160 degrees. Therefore, as will be seen directly, the general arrangement of the fibres, as far as the antero-posterior order goes, is the same in the two classes of animals, although the actual positions are not quite the same, owing to the non-development of the præfrontal region in the Carnivora. Since the irruption of præfrontal fibres which makes up the mass of the anterior limb in the Monkey and pushes the excitable fibres further backwards into the posterior limb does not occur in the brain of the Dog or Cat, in these animals it is the anterior limb which principally contains the excitable laryngeal fibres.

In all animals the most anteriorly placed laryngeal effect observed was the accelerated movements of the vocal cords connected with quick movements of the thorax in the polypnœa, which we have described to be produced by excitation of the præcrucial gyrus. In the Cat and in the Dog this acceleration of respiration is produced by excitation of a considerable number of fibres occupying the anterior half of the anterior limb, *i.e.*, opposite about the anterior half of the caudate nucleus as exposed in the

section before referred to. At the same time that acceleration was produced there was also obtained from the most posterior bundles of these fibres, in all animals, abduction, this combination being concentrated in the Monkey at the genu, where the fibres subserving the acceleration of respiration are chiefly grouped. In the Cat and in the Dog these abductor fibres were found just before the genu.

Taking the various species individually we find that, in (1) the Monkey, acceleration is first produced when the fibres immediately in front of the genu and exactly at the genu are stimulated; this is, of course, just opposite the sharp angle made by the middle zone of the lenticular nucleus. The fibres in the posterior limb immediately behind the genu when excited either give a mixed movement or simply produce on excitation diminution of abduction, and it is not until we get to the junction of the middle and posterior fourths of the capsular border of the middle zone of the lenticular nucleus that we get distinct adduction. There, however, the adduction is very accurately localised to a few bundles of fibres about 2 square millimetres in area. Just behind this point for a short distance diminished abduction was observed on stimulating the capsule in one case; it is clear, therefore, that in the Monkey the acceleration of respiration is only brought about by a few fibres at the situation of the genu, while the phonatory adduction of the cords is subserved by a few fibres in almost exactly the middle of the posterior limb of the capsule.

It may be interesting at this point to state that this is what might have been expected, inasmuch as it is just at this region that the observations before referred to* show that these fibres similarly subserve the movements of the tongue and pharynx.

(2). In the Dog the condition appears to prevail which is found in the Cat, about to be described, that is to say, that excitation of almost the whole of the anterior limb produces acceleration of respiration and that adduction begins to be produced at the genu. (*g*, fig. 7.) We will therefore proceed to describe the condition as it is seen in the Cat, in which animal we have investigated this point closely.

(3). In the Cat the most anterior effect is acceleration. This commences, according to the level of the section, either just in front of, or just opposite to, the anterior extremity of the caudate nucleus, and it persists throughout the front half of the anterior limb of the capsule. (1–3, fig 6.) At this centre point of the anterior limb the respirations become intensified, abduction much more notably marked, and in some cases persistent. (See fig. 6.)

Exactly at the genu, or in many cases just in front of it, *i.e.*, opposite the posterior extremity of the caudate nucleus (*vide* figs. 6 and 7), adduction is very sharply marked.

In most cases the bundle of fibres subserving this phonatory adducton is small, in others—possibly owing to slight difference in the obliquity of the section—

* Beevor and Horsley, *loc. cit.*

adduction can be obtained from almost any point in the front half of the posterior limb, and in some cases there is, in addition, diminished abduction as far as the hinder end of the lenticular nucleus.

We are now in a position to discuss further the points postponed in speaking of the relative representation of respiration and phonation in the cortex.

It will be seen that in the capsule we have thus arranged antero-posteriorly the fibres subserving portions of the cortex which are placed rather transversely to the mesial plane than parallel to it, and that, as might be expected, the acceleration which is the highest and most anterior is similarly most anteriorly placed in the internal capsule. To return now to the polypnœa obtained by exciting these fibres in the internal capsule, OTT describes how by using needle electrodes he was enabled in the Rabbit and in the Cat to evoke exactly the same polypnœic condition that we produced in the above-mentioned circumstances. He was exciting the fibres, according to our view, of the capsule leading from the cortex. The very important results which he obtained, and the bearing which these facts have upon heat regulation and the pathology of fever will be found in his communication.

The next point is of course the relation which the laryngeal movements thus described bear to the other respiratory movements. Where we had to do simply with the acceleration of the laryngeal movements, of course such acceleration was exactly synchronous with acceleration of thoracic respiratory excursions.

But when the fibres posterior to this were excited, viz., those which produced persistent abductory movements of the vocal cords, then it was noticed that while the larynx remained wide open in persistent abduction as long as the excitation lasted, nevertheless the respiratory excursions of the thorax were greatly accelerated; another instance of the differentiation of representation which we have before described. Next, when the vocal cords were brought together in adduction, as a rule there was some slowing of respiration and frequently movements of the opposite fore limb and swallowing.

Epilepsy.—After what has gone before it will be easily understood that we never saw epilepsy to occur from excitation of the internal capsule, and that all intrinsic laryngeal movements observed were strictly and completely bilateral.

Medulla oblongata.

We come now to the consideration of the laryngeal movements produced by direct excitation of the medulla oblongata. It will readily be conceded that here there is more than usual difficulty in discriminating between those laryngeal movements which subserve the process of respiration and those which have to do with phonation. We do not propose in the present case to do more than indicate what those movements are, and to leave the consideration of the shares which they individually possess in serving the two functions before mentioned to another time.

But we may observe incidentally that we are naturally inclined to regard that small area of the medulla from which adduction can be produced as a transit-station for the corresponding cortical, and as a centre for reflex phonatory impulses. Whether this is really so the future will show. What is, for the present, of more practical import in this connection is how far the bulbar apparatus for the larynx is bilateral or unilateral in its composition. It will be seen directly that we have obtained from the one half of the medulla oblongata both bilateral and unilateral effects, that is, as far as they go the bilateral effect is for the most part complete, sometimes, *i.e.*, when the electrodes are moved outwards, with a preponderance of movements on the part of the cord on the same side, and the unilateral effect is of course movement of the cord on the same side as that stimulated.

We shall discuss the results then from these two standpoints, viz., (1) the bilateral effect, and (2) the unilateral effect.

We have only made observations on the Carnivora, and in this respect it is interesting and important to note that the results in the Cat are not different from those in the Dog. In fig. 9 is given a photograph of the floor of the fourth ventricle in the Dog, the calamus scriptorius (*c.s.*, fig. 9) is well seen bounded laterally by the fasciculus gracilis passing up on each side towards the restiform body with the ala cinerea (*a.c.*, fig. 9) well marked. The cerebellum has been divided and the right half removed, so as to expose the lower surface of the inferior peduncle completely, and only the upper part of the inferior vermiform process is seen to be in contact with the floor of the ventricle.

Within the area thus exposed are included all the movements of the vocal cords which may be reasonably attributed to phonation, and also almost all which are connected with respiration. However, in accordance with what we have stated above, we shall now proceed to describe the movements of the vocal cords independently of the function they may be supposed to subserve.

1. *Adduction.*—Closure of the glottis is sharply and invariably produced when the upper margin of the calamus scriptorius, *i.e.*, the nucleus of the spinal accessory nerve, is stimulated, and the same thing is observed if the electrodes are carried outwards and upwards along the margin of the posterior pyramid for about 3 mm. from the middle line. This action is distinctly bilateral.

Immediately above the calamus, in the situation of the ala cinerea, abduction is invariably produced. This movement, like that of adduction, is also absolutely bilateral and persistent. It extends upwards as high as the line drawn horizontally across the fourth ventricle at the transverse level of the upper end of the representation of the adduction. (See fig. 9.) Above this point, especially in the middle line as high as the level of the eighth nerve, excitation evokes movements of the cords about the cadaveric position (see dotted area, fig. 9), which may be looked upon as either a confusion or imperfect adduction. This movement is strictly bilateral.

We have obtained unilateral adduction of the vocal cord on the same side by

excitation of the restiform body in a vertical direction beginning below, opposite and close to the upper end of the region just referred to as giving bilateral adduction, and proceeding along the outer part of the floor of the fourth ventricle as high as the centre of that cavity. (See fig. 9.)

Whether the adduction of the vocal cord of the same side obtained by excitation in the line thus drawn is due to excitation of the nucleus reserved for the movements of the vocal cord of the same side, or whether it is rather excitation of those fibres which run through the substance of the medulla, to appear at once as the roots of the vago-accessory nerves, remains doubtful, though we are naturally more inclined towards the latter view. However, we do not consider that any positive opinion can at present be expressed upon this point.

Abduction.—It has been mentioned above that the movement of abduction is obtained over the situation of the upper two-thirds of the ala cinerea and also from about the origin of the eighth nerve. This latter area is evidently more important and extends upwards to close to the debouchment of the aqueduct of SYLVIUS. (See fig. 9.) Further, this movement of abduction is persistent, and is better marked a short distance, about 2 mm. from the middle line, than in the middle line itself. We have never observed unilateral abduction similar to the unilateral adduction before mentioned.

It may be that fibres exist in the tegmentum or crusta which directly connect together the cortical and bulbar mechanisms now described, and that, as before suggested, the observations which would point to respiratory mechanisms existing in the basal parts of the cerebral hemisphere and in the mesencephalon have been the results of stimulation of such fibres by those looking for respiratory centres in these positions.

Before we had recognised completely the degree to which the etherisation must be carried we obtained some results upon the larynx when the dorsal surface of the spinal cord, *i.e.*, below the calamus scriptorius, was stimulated, but we saw from the first that the results obtained here were probably those of a reflex nature, and further investigation has confirmed this opinion. For the effects were only produced in their entirety as the excitation approached successively the posterior roots, and diminished as the electrodes were moved to intermediate parts of the spinal cord. Further, the effects were far more in the nature of acceleration of thoracic respiration than primary changes in the movements of the larynx.

We never observed any after effects, *e.g.*, clonus, &c., upon cessation of the stimulation of the medulla oblongata.

Influence of Age.

Those acquainted with the history of previous research on the subject of the innervation of the larynx know well that, from the first, experimental investigation has shown that there exists, according to the age, a great difference in the same

species of animal in the representation in the nervous system of respiration and phonation respectively.

The need for efficient respiratory action on the part both of the larynx and the thorax is much greater in the younger animal than in the adult, and is greater, as LEGALLOIS more especially has shown, in the Cat and the Horse than in any other animal, especially more than in the Dog. The present part of our paper will be devoted to summarising the facts that we have observed and the differences noted according to the age of the animal, and we shall group the results, as before, according to the species, beginning again with the highest.

(*a.*) *Monkey.*—In the Monkey we have only incomplete observations owing to the difficulty of obtaining many Monkeys, but all our observations went to show that phonatory adduction was less represented in the young animal than in the older adult.

(*b.*) *Dog.*—In the Dog these differences are also marked. In the young Dog even with strong currents we have frequently only obtained from the focus of laryngeal phonatory representation a high degree of acceleration of respiration with marked diminution of abduction, but no complete adduction; in fact in the cortex of such an animal, while respiration is most efficiently represented, phonation is only imperfectly evolved.

(*c.*) *Cat.*—In the Cat, again, the same thing prevails in its entirety, with the additional point, viz., that this want of differentiation in the laryngeal movements was not confined to the larynx, but also prevailed in the centres for the movements of the limbs.

It is in accordance with points noticed by one of us (V. H.) in the representation of the limb-muscles in the cortex of the Monkey that a wider extent of cortex provides for a higher evolution or development of the motor representation, and probably the differences we have just been describing as produced by age are due to the greater or less provision of cortical material for subserving the particular function represented.

CONCLUSIONS.

The conclusions which we feel may legitimately be drawn from the foregoing experiments—and which, we may be permitted to add, are based not only upon the results of the work just described, but also upon much which we have not alluded to, and which will be described in subsequent communications—may best be put forward upon the plan according to which we believe the central innervation of the laryngeal movements is arranged.

In consequence of the laryngeal muscles serving, as particularly insisted upon by one of us (F.S.), in this connection, two distinct functions (1) phonation, (2) respiration, and in consequence of these two functions being, one connected with so-called purposive or volitionary acts, the other, on the contrary, related to those functions

which are commonly spoken of as belonging to organic life, it is easy to understand that our results bring us to the conclusion that the phonatory movements of the laryngeal muscles, *i.e.*, adduction, &c., are represented principally in the cortex, whereas the respiratory movements, *i.e.*, abduction, chiefly in inspiration, adduction less commonly and imperfectly in expiration, usually find their origin in impulses emanating from the bulb.

We have seen that the first of these functions, phonatory adduction, is represented most completely in the cortex the higher we ascend in the animal scale, and the more completely as the cortex is developed in the life of the individual, *i.e.*, by age, while *pari passu*, the function of respiration, although present in a minor degree, as evidenced by acceleration, is least represented where phonation is most completely developed. In further detail, adductory phonation is centred in the Monkey at the junction of the foot of the ascending frontal gyrus, and the base of the third frontal gyrus, in the Carnivora at the junction of the præcrucial, or præfrontal gyrus, with the anterior composite and coronal gyri. Respiration is represented in the higher animals only as acceleration, and that above and rather in front of the focus of phonation.

In the Cat only have we found a deliberate representation of abduction in the cortex.

Turning now to the lowest part of the central apparatus, the bulb, we see that there is therein situated a small but concentrated focus on each side of the middle line for bilateral closure of the glottis, and outside that a small area, excitation of which produces unilateral adduction of the vocal cord on the same side. Above this region of adduction there is also a representation of abduction, *i.e.*, inspiration.

Finally we have found that, connecting the cortical apparatus with the bulbar apparatus, there exist numerous connecting fibres which can be analysed as they pass down from the cortex through the corona radiata and internal capsule towards the bulb; that as far as they are concerned they simply subserve the functions which are proved to exist in the cortex; that the anatomico-functional arrangement of these fibres in the capsule enumerated from before backwards is :—acceleration of respiration, abduction, intensification, adduction; and that their respective positions in the capsule are constant and strictly homologous in the different species of animals, according to the development of the cerebral hemispheres in the particular cases observed.

These results are in complete concord with the ideas concerning the whole central nervous mechanism which innervates the larynx, ideas which were put forward by one of us (F.S.) at the International Congress at Copenhagen in 1884. We are enabled to state this the more positively for the reason that we have in our hands the notes of a large number of ablation experiments which, by their control of excitation effects, prove to demonstration the correctness of the views and opinions we have enunciated.

Description of Plates.

PLATE 31.

Fig. 1. Photograph of right hemisphere of a Macacque's brain, *Macacus sinicus*.
The total or absolute representation of the larynx is indicated by dotting, the depth of the same showing the degree of representation.

R. Fissure of Rolando.
Pc. Præcentral sulcus.
F. Focus of highest development of laryngeal representation, *i.e.*, pure intrinsic movement of adduction.
v. The small secondary sulcus indicated by that letter.
Sy. Fissure of Sylvius.

PLATE 32.

Fig. 2. Three-quarters view of Cat's brain, half natural size.

c.s. Crucial sulcus.
d. Krause's centre of adduction.
d'. Centre of adduction also noted by the authors.
b. Focus of abduction.

Fig. 3. Base of Cat's brain, half natural size
Fig. 4. Side view of Cat's brain, natural size
Fig. 5. „ „ half natural size
} Lettering as above, fig. 2.

Fig. 6. View of Cat's brain from above. The right hemisphere has been sliced horizontally, as described in the text, to show the internal capsule.

olf. Olfactory lobe.
p.f. Præfrontal fibres.
Ca. Caudate nucleus.
g. Genu.
o.th. Optic thalamus.
n.l. Lenticular nucleus (putamen).
F.S. Fissure of Sylvius.

1. Anterior limit of fibres excitation of which produces acceleration of respiration.
2. Posterior limit of fibres representing acceleration and abduction and commencement of representation of adduction.
3. Centre of anterior limb marking commencement of representation of abduction.

Fig. 7. Horizontal section of the right hemisphere of the Dog. Lettering as in fig. 6.

Fig. 8. View of the bulb of a Cat, the cerebellum being split and drawn aside.

C.q. Corpus quadrigeminum.

cb.p. Posterior ditto and superior cerebellar peduncle.

r. Restiform body.

a.c. Ala cinerea.

c.s. Calamus scriptorius.

Fig. 9. View of the bulb of a Dog, the cerebellum having been split and the right half removed.

aq. Aqueduct of SYLVIUS.

i.v.p. Inferior vermiform process.

a.c., *c.s.* As above.

The close oblique markings at the calamus and extending outwards indicate the focus of bilateral adduction.

The vertical lines indicate the representation of bilateral abduction.

The horizontal marks on the outer side indicate the area of unilateral adduction.

The dotted area indicates the representation of incomplete adduction.

All are photographs of the parts in the recent state.

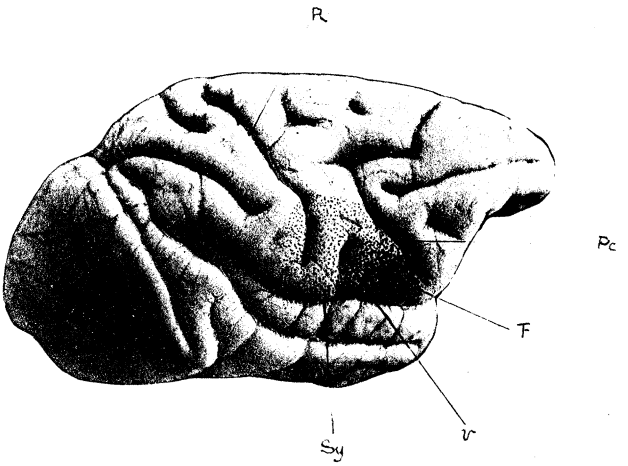

Fig. 1

L.B. Fleming Hanwell.

Photo-Print.

Fig. 2

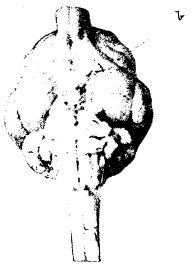

Fig. 3

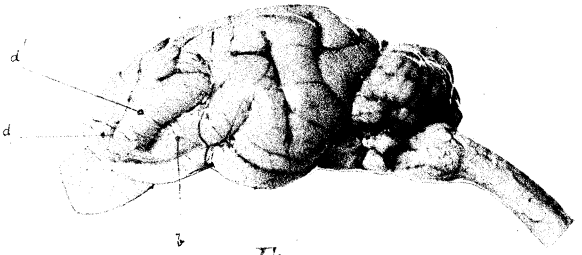

Fig. 4

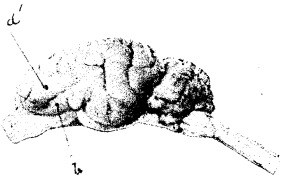

Fig. 5

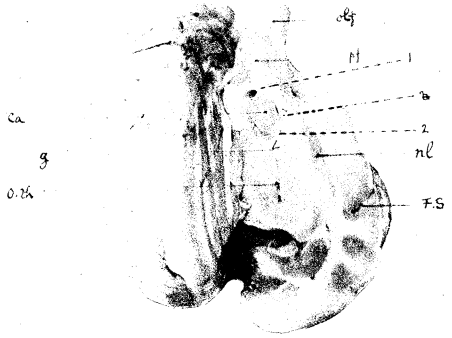

Fig. 6

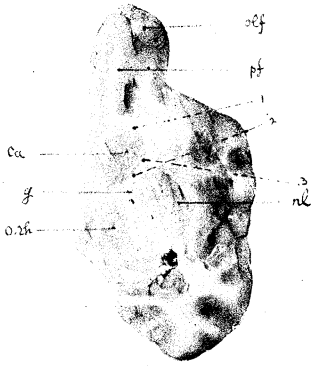

Fig. 7

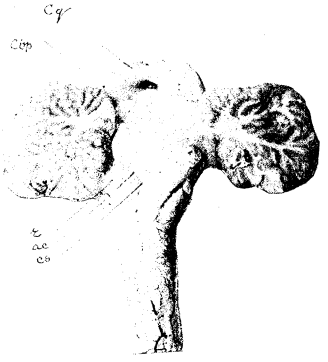

Fig. 8

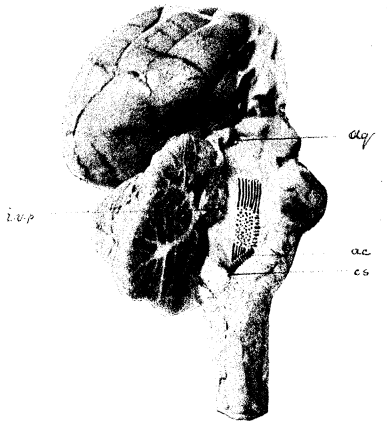

Fig. 9

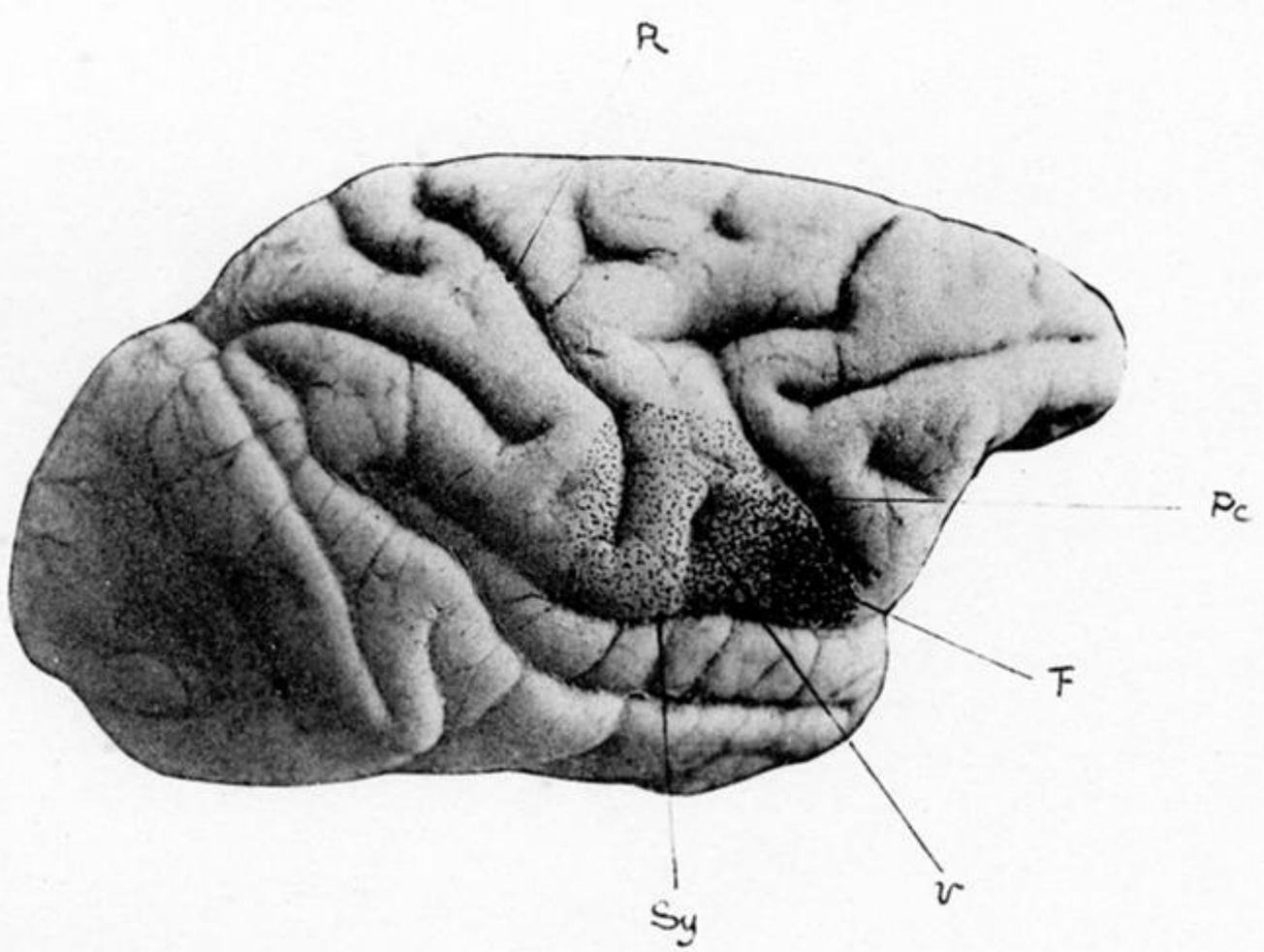

Fig. 1

PLATE 31.

Fig. 1. Photograph of right hemisphere of a Macacque's brain, *Macacus sinicus.*

The total or absolute representation of the larynx is indicated by dotting, the depth of the same showing the degree of representation.

R. Fissure of ROLANDO.

Pc. Præcentral sulcus.

F. Focus of highest development of laryngeal representation, *i.e.*, pure intrinsic movement of adduction.

v. The small secondary sulcus indicated by that letter.

Sy. Fissure of SYLVIUS.

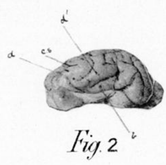

Fig. 2

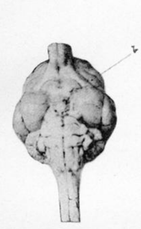

Fig. 3

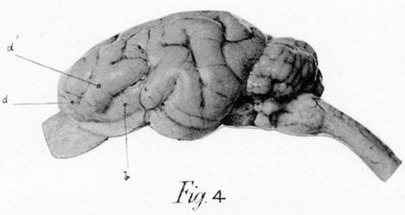

Fig. 4

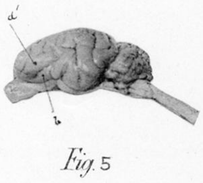

Fig. 5

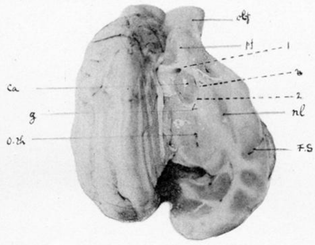

Fig. 6

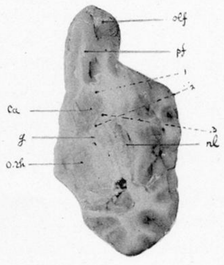

Fig. 7

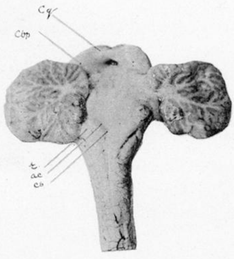

Fig. 8

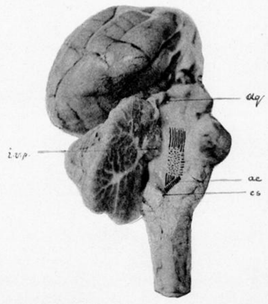

Fig. 9

PLATE 32.

Fig. 2. Three-quarters view of Cat's brain, half natural size.

c.s. Crucial sulcus.
d. KRAUSE's centre of adduction.
d'. Centre of adduction also noted by the authors.
b. Focus of abduction.

Fig. 3. Base of Cat's brain, half natural size
Fig. 4. Side view of Cat's brain, natural size
Fig. 5. ,, ,, half natural size
} Lettering as above, fig. 2.

Fig. 6. View of Cat's brain from above. The right hemisphere has been sliced horizontally, as described in the text, to show the internal capsule.

olf. Olfactory lobe.
p.f. Præfrontal fibres.
Ca. Caudate nucleus.
g. Genu.
o.th. Optic thalamus.
n.l. Lenticular nucleus (putamen).
F.S. Fissure of SYLVIUS.

1. Anterior limit of fibres excitation of which produces acceleration of respiration.
2. Posterior limit of fibres representing acceleration and abduction and commencement of representation of adduction.
3. Centre of anterior limb marking commencement of representation of abduction.

Fig. 7. Horizontal section of the right hemisphere of the Dog. Lettering as in fig. 6.

Fig. 8. View of the bulb of a Cat, the cerebellum being split and drawn aside.

C.q. Corpus quadrigeminum.
cb.p. Posterior ditto and superior cerebellar peduncle.
r. Restiform body.
a.c. Ala cinerea.
c.s. Calamus scriptorius.

Fig. 9. View of the bulb of a Dog, the cerebellum having been split and the right half removed.

aq. Aqueduct of SYLVIUS.
i.v.p. Inferior vermiform process.
a.c., c.s. As above.

The close oblique markings at the calamus and extending outwards indicate the focus of bilateral adduction.

The vertical lines indicate the representation of bilateral abduction.

The horizontal marks on the outer side indicate the area of unilateral adduction.

The dotted area indicates the representation of incomplete adduction.

All are photographs of the parts in the recent state.