THE UNCROSSED LATERAL PYRAMIDAL TRACT IN HIGHER PRIMATES

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I. INTRODUCTION

Bilateral degeneration in the lateral column of the spinal cord following a unilateral lesion of the motor cortex in the chimpanzee was first described by Leyton and Sherrington (11) in 1917. In three animals, one after ablation of the left arm area, and two in which the left leg was removed, Marchi studies revealed, in addition to the contralateral pyramidal degeneration in the cord, uncrossed degenerations in the lateral and ventral columns of the ipsilateral side. In the experiments involving the lower extremities, the fibres of this uncrossed lateral pyramidal tract could be traced as far down as the third sacral segment. Fulton and Keller ((5), p. 101) examined the degeneration in the cord of one chimpanzee following complete removal of the motor representation of the left lower extremity. Their findings confirmed the observations of Leyton and Sherrington and they were able to estimate that nearly ten per cent. of the pyramidal degeneration passed into the uncrossed postero-lateral area.

The course of the cortico-spinal fibres arising in the *premotor* and motor areas of the monkey, as demonstrated by the Marchi method, has been carefully analysed by Kennard (10), and the synaptic terminations of such fibres in the cord have been studied by the bouton method by E. C. Hoff (8). These authors have shown in the monkey that ipsilateral cortico-spinal tracts arise both in motor and premotor regions and that the motor area sends fibres both to the lateral and ventral spinal columns of the same side, while from the premotor area the ipsilateral fibres are found only in the lateral column. However, the total ipsilateral degeneration from the premotor cortex proved relatively greater than from the motor area. Hoff's studies indicate, furthermore, that a large proportion of the ipsilateral descending tracts actually terminate on the ipsilateral side and do not ultimately cross in the lower segments of the cord as some have suspected.

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II. EXPERIMENTAL RESULTS

During the past two years further experiments confirming the existence of this bilateral representation of the motor cortex in the chimpanzee have been carried out in this laboratory (2). Four chimpanzees have been studied and the following example is presented since the Marchi staining in this experiment was the most satisfactory. The results obtained will direct attention to the lack of agreement in most standard texts of anatomy and neurology concerning ipsilateral cortico-spinal pathways. It is generally stated that in higher mammals there is an ipsilateral ventral tract lying close to the ventral sulcus of the spinal cord. The existence of an uncrossed *lateral* pyramidal tract in the spinal cord is, however, omitted completely from most standard descriptions of the pyramidal pathways, in spite of the numerous confirmatory reports gathered from histological studies on the cat, dog, monkey, chimpanzee and Man.

Experiment 1

Subadolescent male chimpanzee. Removal of left leg area; flaccid monoplegia and positive Babinski. Sacrifice for Marchi studies on 15th day; rich ipsilateral degeneration in cord ("Mike").

The subject of this experiment was a well-developed male chimpanzee (*Pan satyrus*) approaching adolescence and weighing 14,000 gm. The animal was used for a degeneration experiment because it was difficult to handle and because its breathing movements were abnormal, due, as the autopsy disclosed, to a huge lymph node at the hilus of the right lung. There was no other evidence of tuberculosis.

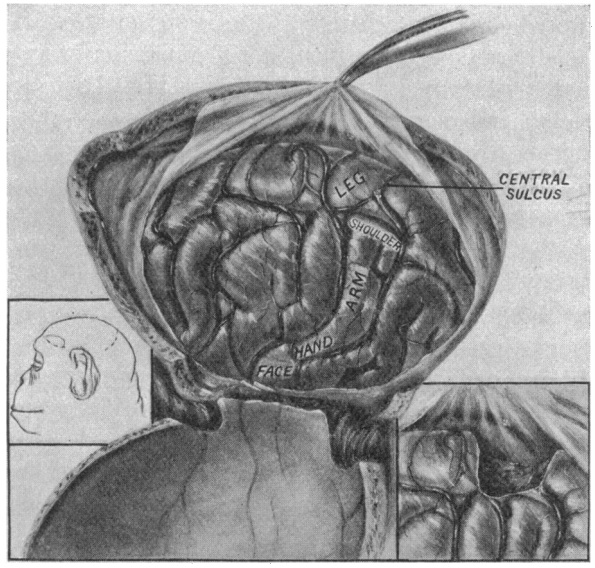
Operation (29 *March*, 1932). Under sodium amytal anaesthesia the left hemisphere was freely exposed by means of a bone flap and the chief markings traced upon cellophane. The motor area was identified by faradic stimulation and the motor representation of the left lower extremity was ablated, all tissue being removed well to the bottom of the central sulcus (text-fig. 1). The wound was approximated as usual with silk and it healed by primary union.

Postoperative notes. An immediate postoperative examination revealed a well-marked Babinski response on the right side, and a feeble plantar extension response (? from anaesthesia) on the left; the arm, knee, and ankle-jerks were equal and hyperactive. The Chaddock, Oppenheim and Gordon responses could be elicited on both sides, but more easily on the right. The Rossolimo sign was absent bilaterally and there was flaccidity of all joints of both lower limbs. When the animal recovered from the anaesthetic, spasmodic conjugate deviation of the eyes to the right was observed.

On the *first postoperative day* the animal had not fully recovered from the anaesthetic. There was conjugate deviation of the eyes to the right. Both lower limbs were flaccid at all joints but there was some voluntary power of the hip and knee on the left. The knee-jerk was present and the ankle-jerk absent, bilaterally. The Babinski, Chaddock and Oppenheim responses were

present on the right side and weakly so on the left. The Rossolimo reflex was absent bilaterally. There was also some weakness of the right upper limb and face.

On the *second postoperative day* the animal had fully recovered consciousness. On the right side the Babinski, Chaddock and Rossolimo were all positive, all other reflexes being negative. On the left all pathological reflexes were absent. The voluntary power of the left lower extremity was recovering. There was considerable deficit of motor power on the right upper extremity and the limb was held in a semi-flexed hemiplegic posture and resisted passive manipulation. Marked improvement in motor power at the knee and hip on the right lower extremity was observed, but there was no evidence of voluntary movement of the ankle or toe.



Text-fig. 1. Drawing of the left motor cortex of the chimpanzee made at operation from a direct cellophane tracing. The lesion, comprising the cortical representation for the lower extremity, is shown in the detail on the right. The operative incision is shown in the detail on the left (chimpanzee "Mike").

On the *eighth postoperative day* the animal showed marked respiratory distress. There was considerable deficit of motor power of the right lower limb and both upper extremities appeared good. It was impossible to examine the animal neurologically owing to its aggressiveness. At the end of two weeks power had returned to the right hip and knee and slightly to the ankle, but there were no prehension movements of the digits; the limbs continued flaccid and there was evidence of some muscular atrophy. The Babinski and Chaddock were positive but the Rossolimo and the Mendel-Bechterew were absent.

Sacrifice (13 April, 1932). On the *fifteenth postoperative day* under ether

anaesthesia the bone flap was re-elevated and faradic stimulation of the motor cortex gave active responses in the right upper extremities and face, but there was no trace of movement of the lower extremity. When the electrode was applied to the crater of the lesion no response whatever was obtained.

While under the anaesthetic the vascular system of the animal was washed through with warm Ringer-Locke solution and finally with formalin-Mueller's solution (95 parts Mueller's solution, 5 parts 37 per cent. formaldehyde). The brain and spinal cord weighed 380 gm.

Lesion. A sharply circumscribed lesion extending to a depth of about 8 mm. was situated over the upper part of the pre-Rolandic gyrus. Except for a very slight infringement on the postcentral convolution superiorly the lesion was largely confined to the motor area; its anterior limit extended 2–3 mm. into the premotor region, i.e. as far as the precentral sulcus; inferiorly it reached a point which corresponded to the representation of the shoulder. Segments from all parts of the spinal cord and brain stem were removed immediately and were stained by the Marchi method. There were no signs of injury to the right hemisphere.

Right lung. There was some consolidation in the upper and middle lobe with a huge caseous nodule at the hilum. The left lung, heart and abdominal viscera showed no evidence of abnormality.

Histological findings

In the sections through the *pons* there is degeneration of the pyramidal bundles entirely confined to the left side. The sections through the *upper part of the medulla* (Plate I, fig. 1) show a similar unilateral degeneration in the left pyramid. No Marchi granules can be seen on the right side. At the *level of the pyramidal decussation* (Plate I, fig. 2) the large majority of the degenerating fibres can be seen crossing to the right side; a few remain ipsilateral but pass dorsally to take up a position in the left lateral column of the spinal cord.

Sections through the level of the *fifth cervical segment* (Plate I, fig. 3) show a heavy degeneration in the right lateral column, the degenerating fibres forming a comma shaped bundle which extends laterally to the periphery. On the left side in an exactly corresponding position are degenerated fibres in significant number, although considerably less than on the right. This ipsilateral tract forms a comma shaped area exactly comparable in size and shape to that of the contralateral pyramidal tract. In addition, a small number of degenerating fibres can be seen in the left ventral column lying close to the central sulcus. There is no evidence of degeneration in any other part of the section.

In sections through the *tenth thoracic level* (Plate I, fig. 4) an exactly similar arrangement is seen, except that the degenerating pyramidal tracts, both contralateral and ipsilateral, although still comma shaped, now lie more medial so that they do not quite extend to the periphery. The ipsilateral ventral tract

is still present in all levels of the thoracic cord though considerably smaller in its extent in the lower segments.

In the *first lumbar* and *first sacral* segments, the contralateral and ipsilateral tracts are still present, but gradually decreasing in size in the lower levels. Here they tend to extend out once more to the periphery. The proportion of degenerating fibres on each side appears the same as in the cervical region although the total number on each side is considerably less. The ipsilateral ventral tracts at this level have all but disappeared. In no segment of the spinal cord could degeneration be traced in the anterior commissure.

This case illustrates clearly the existence of bilateral representation for the motor area in the spinal cord. The fibres from area 4 appear to descend on the same side as far as the pyramidal decussation in the medulla. At this point three divisions can be recognised: (1) The large majority cross to the opposite side to run down in the lateral column of the cord. (2) A significant number (about one-tenth of the crossed tract) pass dorsally to the lateral column of the same side. (3) A few fibres remain ventrally and continue down the cord in this position as the direct or ventral pyramidal tract. In the chimpanzee this tract is well circumscribed.

III. DISCUSSION

Bilateral descending degeneration in the lateral columns of the spinal cord is a constant finding after unilateral lesions of the motor cortex in lower animals. This degeneration, extensive on the contralateral side, less marked but nevertheless distinct on the ipsilateral side, was first observed by Schafer (19) in 1883. In a monkey in which the central convolution and the adjoining parts of the frontal and parietal lobes had been removed on the left side of the brain, the left pyramidal tract was found degenerated throughout its entire extent, and in addition there existed "an unexplained tract of degeneration in the left lateral column of the cervical cord." Schafer wrote: "The only gleam of elucidation as to the source of the degenerated fibres in the left lateral column in this region which it has been possible to obtain is to be found in the observation above recorded of the apparent passage of a small part of the degenerated left anterior pyramid *towards* the left lateral column whilst the larger part took the more usual course towards the opposite lateral column. I have searched in vain for any sign of degeneration along the pyramidal tract of the right side of the medulla, pons and crus cerebri, and of the right internal capsule."

Uncrossed degeneration in the lateral column was subsequently traced by the Marchi method in dogs by Sherrington (20, 21) and Muratoff (14); in cats by Boyce (1) and Redlich (16); and in monkeys by Sherrington (22), Mott (13), Mellus (12), Rothmann (17) and Simpson and Jolly (23). In the higher Primates the evidence presented in this communication confirms the presence of the direct lateral pyramidal tract in the chimpanzee.

In Man, Weigert studies of the spinal cord in cases of unilateral lesions,

nvolving the precentral cortex or the internal capsule, have been made by Pitres (15), Dejerine and Spiller (3)[1], Dejerine and Thomas (4), Hoche (7) and Russell (18). All have been able to confirm the bilateral degeneration of the pyramidal tracts following such unilateral cerebral lesions.

The histological evidence for the bilateral representation for the motor cortex (area 4 of Brodmann) thus seems unquestionable. It has been assumed by many that the direct ventral pyramidal tracts cross to the opposite side in the cervical and upper thoracic regions of the spinal cord through the anterior commissure, though the histological evidence for such a crossing is lacking. That the direct lateral pyramidal tract crosses likewise at some lower level seems highly improbable. It can be traced on the ipsilateral side as far as the sacral region and the studies of Hoff and Hoff (9) on the synaptic terminations of the cortico-spinal pathways lend no support to such a contention.

IV. CONCLUSIONS AND SUMMARY

1. Histological studies of a chimpanzee in which the left leg area was extirpated 15 days previously have revealed the presence of both an uncrossed ventral and an uncrossed lateral pyramidal tract. The direct ventral pyramidal tract has been traced as far as the lower thoracic segments. The direct lateral pyramidal tract has been traced on the ipsilateral side as far as the sacral region.

2. The evidence in support of a bilateral representation for the motor cortex in Man and in the lower animals may be considered as established on an anatomical as well as on a physiological basis (2).

REFERENCES

(1) Boyce, R. (1895). *Philos. Trans.* B, vol. clxxxvi, pp. 321–81.
(2) Bucy, P. C. and Fulton, J. F. (1933). *Brain*, vol. lvi, pp. 318–42.
(3) Dejerine, J. and Spiller, W. G. (1895). *C. R. Soc. Biol.*, Paris (sér. 10), t. ii, pp. 622–8.
(4) Dejerine, J. and Thomas, A. (1896). *Arch. Physiol.* (sér. 5), Bd. viii, S. 277–86.
(5) Fulton, J. F. and Keller, A. D. (1932). *The sign of Babinski: A study of the evolution of cortical dominance in primates.* Baillière; London: Springfield, Ill.: Thomas.
(6) Fulton, J. F. (1932). *Amer. J. Physiol.* vol. ci, p. 36.
(7) Hoche, A. (1897). *Neurol. Zbl.* Bd. xvi, S. 993–7.
(8) Hoff, E. C. (1934). *Arch. Neurol. Psychiat.*, Chicago (in press).
(9) Hoff, E. C. and Hoff, H. E. (1934). *Brain*, vol. lvii, p. 454.

[1] Dr Spiller writes us as follows: "In 1895 I spent ten months at the Salpetrière in the service of Dejerine, and wrote with him a paper entitled: 'Contribution à l'étude de la texture des cordons postérieurs de la moelle épinière' (see page 3). After completion of this work I undertook the investigation of the pyramidal tract in man. The spinal cords from a considerable number of hemiplegics, who had died within a suitable period after the paralysis developed, were studied by the method of Marchi, and I noted the bilateral degeneration of the crossed pyramidal tract from an unilateral lesion. My findings and notes were left with Dejerine with the understanding he would report them, as he had the previous paper, before the Société de Biologie. This he did not do, but André Thomas took up the work where I had left off, and it was published by Dejerine and him with the title 'Sur les fibres pyramidales homolatérales' (see page 4)."

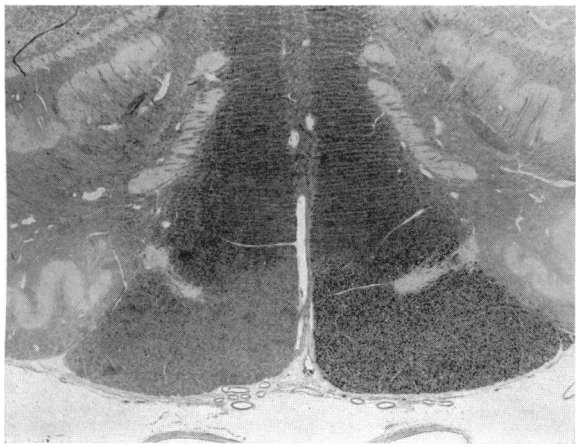


Fig. 1.

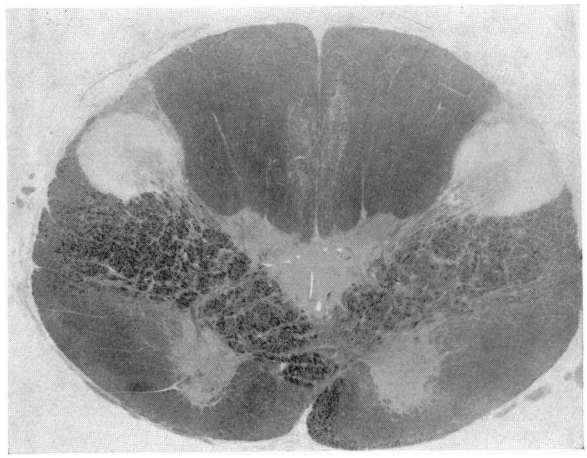


Fig. 2.

Fig. 3.

Fig. 4.

(10) KENNARD, MARGARET A. (1934). *Arch. Neurol. Psychiat.*, Chicago (in press).
(11) LEYTON, A. S. F. and SHERRINGTON, C. S. (1917). *Quart. J. exp. Physiol.* vol. XI, pp. 135–222.
(12) MELLUS, E. L. (1895). *Proc. roy. Soc.* vol. LVIII, pp. 206–14.
(13) MOTT, F. W. (1894). *J. Physiol.* vol. XV, pp. 464–87.
(14) MURATOFF, W. (1893). *Arch. Anat. Physiol.*, Lpz., *Anat. Abth.* S. 97–116.
(15) PITRES, A. (1884). *Arch. Physiol.* (sér. 3), Bd. III, S. 142–85.
(16) REDLICH, E. (1897). *Neurol. Zbl.* Bd. XVI, S. 818–32.
(17) ROTHMANN, M. (1900). *Arch. Psychiat. Nervenkr.* Bd. XXXIII, S. 292–310.
(18) RUSSELL, J. S. R. (1898). *Brain*, vol. XXI, pp. 145–79.
(19) SCHAFER, E. A. (1883). *J. Physiol.* vol. IV, pp. 316–26.
(20) SHERRINGTON, C. S. (1885). *J. Physiol.* vol. VI, pp. 177–91.
(21) —— (1890). *J. Physiol.* vol. XI, pp. 121–2.
(22) —— (1894). *Lancet*, vol. I, p. 265.
(23) SIMPSON, S. and JOLLY, W. A. (1906). *Proc. Roy. Soc. Edinb.* vol. XXVII, pp. 281–301.

EXPLANATION OF PLATE I

Fig. 1. Microphotograph of section through the upper part of the medulla oblongata. The ventral portion, including the region of the pyramids, is shown in the figure to demonstrate the unilateral degeneration of the cortico-spinal fibres above the pyramidal decussation (chimpanzee "Mike"). (Magnification × 10.)

Fig. 2. Microphotograph of section through the lower part of the medulla oblongata at the level of the pyramidal decussation. The major portion of the degenerating tract crosses to the opposite side, but a significant number of fibres can be seen passing dorsally to the lateral column of the same side (chimpanzee "Mike"). (Magnification × 10.)

Fig. 3. Microphotograph of section through the fifth cervical segment of the spinal cord, to show the degeneration in the crossed, the uncrossed lateral and the uncrossed ventral pyramidal tracts (chimpanzee "Mike"). (Magnification × 10.)

Fig. 4. Microphotograph of section through the tenth thoracic segment of the spinal cord. The degeneration is confined to the crossed pyramidal, the uncrossed lateral and uncrossed ventral pyramidal tracts, as seen in fig. 3 (chimpanzee "Mike"). (Magnification × 10.)