THE ANATOMY OF THE NERVOUS SYSTEM.

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Owing to the difficulties of investigating the sensory organization of the nervous system experimentally, for many years experimental neurologists tended to direct their attention rather to the motor mechanisms, for these can easily be studied and recorded objectively. During the last few years, however, research investigations have been more concentrated on the anatomical basis of sensation and, accordingly, this review will be mainly concerned with this aspect.

CUTANEOUS SENSATION.

In 1940, Woollard, Weddell and Harpman published the results of their work on the neuro-histological basis of cutaneous pain, based on the study of methylene blue preparations correlated with physiological observations. They found that cutaneous pain in Man is subserved only by the finer medullated and non-medullated nerve fibres bearing free endings, and that these fibres and endings, which are specific, are arranged in a plexiform interlocking manner in the skin. They also determined that, contrary to Waterston's earlier conclusion that cutaneous pain has no basis in the epidermis, it can in fact be elicited from the deeper layers of the epidermis as well as the dermis. However, it seems that pain receptors in the epidermis are comparatively few. Fibres and endings morphologically identical with pain receptors are also to be found in the adventitia of blood-vessels, and supplying an accessory innervation to encapsulated touch receptors as well as to nerve endings subserving pressure, cold and proprioception. Incidentally the authors confirm the earlier observations of Woollard that pressure, warmth, touch, cold and pain are represented in the skin in punctate form, and that each primary modality of cutaneous sensation is related to a receptor of specific morphological type. They stress the fact that the theory of punctate sensibility must be interpreted from a three-dimensional point of view, and they find no anatomical basis for Head's classic theory of protopathic and epicritic systems. The paper contains an excellent composite diagram illustrating the innervation of the human skin in relation to punctate sensibility.

Continuing the field of work opened up by Woollard, Weddell (1941a) has further studied the pattern of cutaneous innervation in Man and lower animals. He finds a similar pattern of cutaneous nerve plexuses in widely different vertebrates, but there is a progressive differentiation of nerve endings. Thus in *Acanthias* only one type of ending was found, and in the rabbit two, while in

monkeys and Man there are multiple types. The same author also showed that each unit area of skin is evenly innervated by fibres approaching it from all directions, and that this arrangement explains the concentric shrinkage of an area of anaesthesia which occurs during the regeneration of a cut sensory nerve. Further, he was able to demonstrate that the distance between neighbouring receptors of pain, as determined histologically, bears a close relation to the limen of two-point discrimination for this sensation. In the same paper a description is given of the different patterns of sensory loss after nerve root, nerve plexus and nerve trunk lesions in Man, the value of which for the diagnosis of nerve lesions is indicated. Incidentally it may be noted that the frequent occurrence of recurrent nerve fibres in the trunks of sensory nerves serves to explain how it is that stimulation of the distal stumps of a completely divided cutaneous nerve may sometimes give rise to sensation.

Another interesting feature to which Weddell draws attention (1941*b* and 1941*c*) is the multiple innervation of sensory spots in the skin. It seems that, for example, each single group of hair follicles is innervated by two or more separate fibres which approach it from different directions. Meissner's corpuscles usually occur in compact groups, and a cold-spot overlies two or more groups of Krause's end-bulbs. It is believed that this normal condition serves to explain the " protopathic " phase which occurs in the recovery from sensory loss, for in the course of regeneration nerve fibres will arrive at each separate spot at different times because they approach it from different directions, and the ultimate course followed by the individual fibres will necessarily be of different lengths. Thus, during regeneration there will be a phase in which each sensory spot is innervated by a single fibre instead of multiple fibres. In this phase, recognition of graded stimuli and accurate localization will hardly be possible. Such an anatomical condition in the course of regeneration has actually been demonstrated histologically in a patient by Weddell. Reference should here be made to a paper by Weddell, Guttmann and Gutmann (1941), in which attention is called to another phenomenon which may complicate the clinical picture during the regeneration of a sensory nerve. This is the experimental demonstration that the initial shrinkage of an area of sensory loss (which may commence soon after injury) is brought about by the outgrowth into the area of nerve fibres from the surrounding intact cutaneous plexuses.

Just as Head's postulate of a double system of cutaneous nerve fibres to explain the phenomenon of protopathic and epicritic sensation has been shown by Woollard, Weddell and their co-workers to have no anatomical basis, so Lewis's conception of a separate organization of fibres to subserve his " nocifensor " mechanism has not been confirmed by these histological studies. It is some years ago that Lewis elaborated his hypothesis of a nocifensor system (see his lectures published in 1937), but in a recent book (1942) he deals with it at some length. However, it has received adverse criticism from Walshe (1942) in a general review of the anatomy and physiology of cutaneous sensation.

The relation of the sensations of tickling and itching to other sensory modalities of the skin, and their anatomical basis, still remain somewhat obscure. It is generally held either that they involve both the elements of touch and pain, or that they represent the finer gradations of pain only. The

latter view is supported by the fact that in the affected regions in syringo-myelia the sensation of superficial tickle is abolished together with that of pain, while that of light touch remains intact.   Zotterman (1939) has studied the problem experimentally by electro-physiological methods, and concludes that tickling and itching sensations are mediated by thin afferent fibres of the same type as those which are known to mediate pain.   It appears also that in cases of trigeminal neuralgia treated by Sjöqvist's operation of trigeminal tractotomy (Sjöqvist, 1938) there may be complete analgesia with an intact tactile sensibility, and over the same area tickling reactions are abolished.

GENERAL SENSORY PATHS IN THE SPINAL CORD AND BRAIN-STEM.

It is well known that general sensory impulses are carried up in the spinal cord by two main paths, the spino-thalamic tracts and the posterior column tracts.   The former convey those impulses which underlie pain and temperature and the coarser aspects of tactile sensation, while the latter transmit proprio-ceptive impulses and those impulses which subserve the finer aspects of tactile sensation, including tactile localization and discrimination.   The course of the spino-thalamic tract in Man has lately been studied by Walker (1940a) in two patients who died shortly after chordotomy.   The fibres, after arising from cells in the posterior horn, pass across the mid-line in the anterior commissure to the opposite anterior column.   As they ascend they become more laterally situated, partly because more fibres of the spino-thalamic 'tract are being added at higher segments, displacing laterally those from lower segments. There is thus a topical localization within the tract, in the sense that the fibres from the lowest segments are situated at the periphery of the cord. There may be a varying admixture of the fibres conveying different categories of sensory impulse, " temperature fibres," predominating dorsally and " touch and pressure fibres " ventrally, while " pain fibres " occupy an intermediate position.   It is of some importance to note, also, that in the cervical region of the cord the sacral fibres lie practically lateral to the pyramidal tracts, and thus they may be spared in upper dorsal or cervical chordotomies in which the incision is made 1 to 2 mm. anterior to the ligamentum denticulatum. As regards the topical arrangement of the spino-thalamic tracts, Walker's observations confirm those made in the previous year by Hyndman and Van Epps (1939) on the basis of anatomico-clinical studies.   In the brain stem Walker found that the spino-thalamic tract lies just ventral to the descending nucleus and root of the trigeminal nerve, and further up just dorso-lateral to the inferior olivary nucleus.   In this position it has been sectioned surgically for the relief of intractable pain (Schwartz and O'Leary, 1941).   In the pons the tract runs immediately medial to the middle cerebellar peduncle and lateral to the medial fillet.   In the midbrain it turns dorsally and comes to lie right at the periphery, just above the lateral sulcus.   This peripheral position makes it possible to interrupt also at this level all the pain pathways from the entire opposite half of the body.   Indeed, such a surgical procedure has been put into practice by Dogliotti (1938).   Walker (1942a) has described a technique for mesencephalic tractotomy which differs from that of Dogliotti in placing

the lesion further up in the mid-brain. The advantages are the greater ease of surgical approach, and the fact that at this level the surface markings allow the position of the pain tracts to be more precisely located. Both the spino-thalamic and the secondary trigeminal paths can be interrupted at the same point by a comparatively small lesion. Walker (1942b) has accurately mapped out the somatotopic localization of the spino-thalamic and trigeminal tracts in the mesencephalon by experimental studies on the monkey's brain.

Approaching the thalamus by passing just medial to the brachium of the inferior colliculus, the spino-thalamic tract turns laterally to become dispersed in the basal portions of the ventral thalamic nucleus. The topography of the termination of the fibres conveying impulses from different parts of the body could not be determined in Walker's human material, but it may be supposed that it probably corresponds to the arrangement indicated by earlier experiments in the monkey (Le Gros Clark, 1936; Walker, 1938a), i.e. those originating from the more rostral parts of the body terminating medially and those from the caudal parts ending laterally.

During the period covered by the present review there has been little further study of the course of sensory impulses conveyed by the posterior column tracts of the spinal cord. For the sake of completeness, a brief reference may be made to the slightly earlier work of Ferraro and Barrera (1934, 1936a and b) because of its anatomical importance. These investigators have confirmed that the fibres from the lower extremities terminate in the nucleus gracilis, and that the latter sends its fibres entirely to the medial lemniscus. Consequently a lesion of the nucleus gracilis involves no appreciable cerebellar connection of the lower extremities. On the other hand, the main cuneate nucleus, which receives impulses from the upper extremities, possibly sends some fibres to the cerebellum besides those which enter the medial fillet. But it is difficult to say how far this is the case, for the external cuneate nucleus (nucleus of Clarke-Monakow), which lies immediately adjacent to the main cuneate nucleus and which receives fibres of the posterior columns from the cervical segments of the cord, does send its efferent fibres to the cerebellum. Thus, when a lesion of the posterior column nuclei involves also the external cuneate nucleus, the resulting symptoms are more pronounced because of the involvement of the cerebellar component. A study of the topography of fibres in the medial lemniscus by the same authors has shown that in the interolivary space of the medulla the fibres from the nucleus gracilis occupy the most ventral position, and those from the nucleus cuneatus the dorsal portion. More frontally the fibres from the nucleus gracilis are displaced laterally and ventrally and come to occupy the ventro-lateral angle of the medial lemniscus, while the fibres from the nucleus cuneatus occupy the dorsomedial portion.

A recent experimental study on the topical organization and termination of the fibres of the posterior columns in the macaque monkey by Walker and Weaver (1942) confirms the earlier work of Ferraro and Barrera.

The question repeatedly arises whether fibres of the medial fillet terminate in other parts of the fore-brain besides the thalamus. For example, some authors in the past have described terminal connections with the hypothalamus, but, in spite of careful studies, these connections cannot be said to be satis-

factorily established. On the other hand, Dusser de Barenne and McCulloch (1939), using their method of local strychninization with the recording of electrical activity, have adduced evidence which suggests that some fibres from the nucleus gracilis and cuneatus may extend directly to the cerebral cortex without the intervention of the thalamus, while others terminate in the globus pallidus. These conclusions seem to be out of harmony with the general plan of organization of the sensory systems of the brain as this has been conceived in the past, and, while of course they should not be rejected on this account, they will no doubt require corroboration before their final acceptance.

Trigeminal paths.—Recent interest in the technique of trigeminal tracto-tomy for the relief of intractable neuralgia has focused attention on the anatomy of the trigeminal paths. As is well known, it is commonly held that the descending tract of the fifth nerve subserves pain and temperature sensa-tions. This conception receives some confirmation from the observations of Sjöqvist that the tract contains a great preponderance of very fine fibres (less than 3μ in diameter). However, more careful studies of the sensory loss following tractotomy has led to some qualifications of the usual view. Walker (1939*b*), for example, has reported slight impairment of tactile sensation in such cases, and points out that similar observations are also to be found in earlier literature. He concludes, therefore, that the spinal tract carries sensation of pain, heat, cold, deep pressure-pain, and to a slight degree touch. It may be noted in this connection that, even if fine fibres predominate in the spinal tract, there are also varying numbers of larger fibres, and it may be presumed that the latter mediate tactile impulses. Similar conclusions have been reported by Grant, Groff and Lewy (1940) and Weinberger and Grant (1942). The latter found evidence that pain fibres from the oral mucous membrane lie most medially in the tract and that, while the general distribution of fibres is in terms of the peripheral divisions, all three divisions may descend to a point below the level of the obex. In several of these cases the authors found on post-operative sensory examination that there was considerable discrepancy in the relative degree to which pain and temperature were affected ; hence they conclude (in agreement with some earlier observers) that separate pathways probably exist in the tract for these sensory modalities.

Some details of surgical importance regarding the anatomical relations of the spinal tract of the fifth nerve are given by Olivecrona (1942). This author also points out that the results of tractotomy are often by no means as successful as commonly supposed, partly because of the troublesome paraesthesiae which may develop in the anaesthetic areas.

The secondary trigeminal paths have been studied anew by Walker (1939*a*) in the macaque monkey, employing the Marchi method. Fibres from the spinal nucleus of the fifth nerve decussate and run up in the white matter between the inferior olivary nucleus and the pyramid ; in the pons they lie at the lateral margin of the medial lemniscus. Then, accompanying the spino-thalamic tract through the mid-brain, they end in the medial portion of the nucleus ventralis posterior of the thalamus. No evidence was found in the monkey for the existence of a dorsal secondary trigeminal tract, described more than forty years ago by Wallenberg and v. Gehuchten, and Walker

suggests that this pathway possibly serves to carry fibres from the nucleus of the fasciculus solitarius, conveying sensory impulses from the pharynx, larynx and the adjacent tongue region. From the main sensory nucleus of the trigeminal nerve, it seems that two groups of fibres probably arise. One crosses the midline and follows the medial lemniscus, lying on its dorsal and medial aspect to terminate finally in the dorso-lateral portion of the arcuate nucleus of the thalamus. The other group, which passes through the dorsolateral part of the reticular substance, is partly crossed, but mainly uncrossed. While some of these fibres appear to terminate in the pons and mid-brain, many end in the medial part of the arcuate nucleus.

A clinical and pathological study of the systematization and central connections of the trigeminal nerve in Man has been presented by Smyth (1939). This author finds definite evidence to support the view that the ophthalmic division of the fifth nerve is represented in the lowest part of the spinal tract, and the mandibular division in the highest, and he points out that these observations are incompatible with the opinion that the representation in the tract is in terms of concentric zones converging on the nose and mouth. No evidence was found of a dorsal quinto-thalamic tract in Man. In the medulla the secondary path probably · occupies the ventro-medial part of the medial lemniscus, and in the upper half of the pons it comes into fairly close anatomical relationship with the fibres of the spino-thalamic tract. The abolition of the corneal reflex after operative section of the spinal tract indicates that the afferent arc descends to its most caudal part. In a recent paper by Harrison and Corbin (1942) tactile impulses were traced into the spinal tract of the fifth nerve of the cat by means of an oscillograph. The results of these experiments show that impulses originating in the ophthalmic division reach as far down as the caudal part of the first cervical segment, those from the maxillary area as far as the rostral part of the first cervical segment, and those from the mandibular area as far as the junction of the medulla and cord. Moreover, in the tract the ophthalmic fibres assume a ventral position, the mandibular fibres a dorsal position and the maxillary fibres an intermediate position.

One of the elements of the trigeminal nerve, the mesencephalic root, has aroused discussion and controversy for many years. Two main theories have been held regarding its function, both based on quite inadequate evidence. One of these is that the root conveys proprioceptive impulses from the extrinsic ocular muscles, and the other that it conveys proprioceptive impulses from the masticatory musculature. The controversy seems now to have been finally settled by the work of Corbin and Harrison (1940). Using the Clarke-Horsley stereotaxic instrument for localization, these authors picked up the action potentials in the mesencephalic root in cats after applying various peripheral stimuli. They found conclusive evidence that the root (and its nucleus) is concerned with the reception of impulses from stretch receptors in the masticatory muscles and pressure receptors related to the teeth and in the hard palate. It thus appears probable that these impulses play an inhibitory role, and, in constituting the afferent side of masticatory reflex arcs, co-ordinate and control chewing movements. No action potentials could be elicited from the mesencephalic root as the result of stretching the extrinsic

ocular muscles. The precise anatomical distribution of the fibres of the mesencephalic root of the fifth nerve has been determined by Corbin (1940), using the Marchi method after destruction of the mesencephalic nucleus with the Clarke-Horsley stereotaxic instrument. The fibres were found to be distributed to the ethmoidal branch of the ophthalmic division, the palatine and superior alveolar branches of the maxillary division, and the pterygoid, temporal, masseteric and inferior alveolar branches of the mandibular division.

THE THALAMUS.

The thalamus constitutes in general a system of relay stations whereby diverse somatic afferent impulses are projected on to the cerebral cortex.* It is, so to speak, a filter through which these impulses must pass before they reach the highest integration levels of the central nervous system. In the past ten years the structural analysis of the thalamus has been greatly advanced, partly by the delineation of its component nuclei and their fibre relations in preparations of normal material, partly by tracing the termination in the various nuclei of ascending tracts from the spinal cord and brain stem, and partly by establishing the relation of the nuclei to the different cortical areas of the cerebral hemispheres. All this work has served to demonstrate that the thalamus is composed of a congeries of functional " centres " each with its specific afferent and efferent fibre connections ; in other words, it has thrown a great deal of light on the nature of the functional localization which exists in this part of the brain. During the last few years our knowledge has been made more precise by the detailed study of normal, experimental and clinical material.

The nuclear composition and the fibre connections of the thalamus have recently been analysed in a number of different vertebrates : *Amblystoma* (a teleostean fish) (Herrick, 1939) ; *Corydora* (Miller, 1940) ; the American water-snake (Warner, 1942) ; Virginian opossum (Bodian, 1939, 1940, 1942) ; pig (Solnitzky, 1938) ; sheep (Rose, 1942) ; chimpanzee (Walker, 1938c) ; rat (Lashley, 1941) ; *Hyrax* (Ibrahim and Shanklin, 1941) ; phalanger (Goldby, 1941, 1943) ; and rabbit (Stoffels, 1939). A study of these papers will show that in all mammals the thalamus is constructed on the same plan. There is, for example, no striking difference between the thalamus of marsupials and that of eutherian mammals. There are, of course, differences in the relative development of individual nuclear elements, and these show a direct relation with the extent and differentiation of the cortical areas with which they are connected.

A study of a remarkable clinical case in which a diffuse porencephaly had led to almost complete hemidecortication (Le Gros Clark and D. S. Russell, 1940) has shown that, in the human brain, practically the whole thalamus projects on to the cerebral cortex. The only elements which remain unaffected by destruction of the cortex are the centre median nucleus and a narrow subependymal zone of small cells lining the third ventricle. It appears, therefore, that the cells of all the other thalamic elements send their axones to

* In this article the term " thalamus " refers to the main part of the diencephalon exclusive of the epithalamus, hypothalamus and subthalamus.

the cortex and to no other region of the brain—otherwise it would be difficult to explain the total retrograde cell degeneration which occurs after cortical lesions. This anatomical fact is clearly of the greatest significance in the consideration of the part which the thalamus may play in sensory functions, for it appears finally to dispose of any structural basis for Head's conception of the " essential organ " of the thalamus. It likewise disposes of such elements as the thalamo-olivary·tract and the thalamo-striate connections which have found their place in text-book descriptions for many years. It may be noted that in lower mammals the thalamic atrophy which follows hemidecortication is apparently not quite so complete as it is in Man (Waller, 1938 ; Papez and Rundles, 1938 ; Walker, 1938a, 1938b). This suggests a progressive " corti- calization " of thalamic functions which reaches its acme in the human brain.

Reference may be made to an excellent monograph by Walker (1938a) on the Primate thalamus, which gives full information on the subject up to date. Subsequent researches have added more details concerning many of the thalamic nuclei. By the use of electro-physiological methods the topographical representation of the body in the ventral nucleus has been confirmed—that is, the lower limbs are represented most laterally, the upper limbs occupy an intermediate position, and the sensory impulses from the head region are projected most medially (Magoun and McKinley, 1942). The latter terminate in that part of the ventral group of nuclei which is termed the arcuate nucleus, and this element projects on to the lower extremity of the sensory cortex in the opercular region of the hemisphere. Suggestions have been put forward that the arcuate nucleus is concerned, at least partly, with the sensation of taste, but the evidence for this is by no means conclusive.

The ventral group of nuclei may be divided into anterior, middle and posterior parts from the point of view of their ascending connections. It is in the posterior part (nucleus postero-lateralis and nucleus arcuatus) that the fillet systems end. These elements appear to project entirely on to the sensory (post-central) area of the cortex. The middle part receives fibres of the brachium conjunctivum from the opposite cerebellar hemisphere—this has recently been confirmed in the monkey by Crouch and Thompson (1938b)— and it projects on to the motor cortex. Experiments by Sjöqvist and Weinstein (1942) suggest that (at least in monkeys and chimpanzees) the cerebellar projections to the thalamus may subserve the recovery of proprioceptive functions following interruption of the medial lemniscus. The afferent connections of the anterior ventral nucleus are not certainly known.

The medial nucleus of the thalamus (n. dorsomedialis) projects on to the granular area of the frontal cortex. The topographical details of these connections have been studied by Walker (1940c) in the monkey and by Waller (1940a) in the cat, and the same connections have been established for Man by Stern (1943) from the study of a brain in which the frontal cortex had been partly destroyed by a traumatic lesion. These connections of the medial nucleus are of particular interest in relation to problems of functional localization in the frontal cortical areas, more especially because of the modern development of surgical measures for treating certain psychological conditions by the operation of leucotomy. Unfortunately, little is known of the nature of the

impulses which are relayed on to the cortex by the medial nucleus. Connections have been described with adjacent thalamic nuclei—particularly the lateral and ventral nuclei—but it seems doubtful if these really exist, seeing that all the cells of these nuclei appear to undergo degeneration after hemi-decortication. More certain are the ascending connections which the medial nucleus receives from periventricular·fibres which ascend to it alongside the third ventricle, and which probably have their origin in the hypothalamus. On the basis of these connections it was suggested some years ago by the present author (1932) that the medial nucleus provides a mechanism whereby the highest functional levels of the brain are enabled to control the more primitive elements of mental activity, such as are expressed in emotional reactions, and that the frontal cortical areas represent a final product of cerebral development, where the activities of the purely cortical mechanisms underlying the intellectual components of personality are equated with the activities of the hypothalamic region, which are in some way associated with the more fundamental and primitive components. No doubt this speculative hypothesis is an over-simplification of a process which is clearly very complicated and which must involve many parts of the brain, but it seems probable that the medial nucleus may play at least a part in such integrative functions. In a recent clinico-pathological study of thalamic tumours, Smyth and Stern (1938) observe that in cases where gliomas invade the thalamus from the ventricular wall, involving the medial nuclei and periventricular connections, mental deterioration is an early sign. Further detailed studies of clinical cases in which the medial nucleus is involved are required to elucidate its precise functions.

The centre median nucleus of the thalamus remains a mystery. As already stated, this well-defined element is unaffected by cortical lesions, and it may thus be assumed that it has no cortical connections. A clinical case of complete cortical deafness following bilateral thrombotic lesions in the external capsule has been described by Le Gros Clark and Ritchie Russell (1938) in which the centre median nucleus had undergone complete atrophy, and the suggestion was put forward that it may have connections with the insular cortex which had hitherto escaped notice. However, an experimental investigation undertaken to inquire into this possibility by the same authors (1939) showed no evidence of such connections. Possibly it may project on to elements of the corpus striatum (as suggested by some previous workers), but the evidence for this is far from conclusive. The consensus of opinion at present seems to be that the centre median nucleus is purely a thalamic association centre, sending its efferent fibres to the surrounding thalamic nuclei (Crouch, 1940). In this connection reference may be made to the observations of Magoun and McKinley (1942), who investigated the termination of ascending sensory tracts in the thalamus by the oscillographic recording of potential changes in the latter after stimulating various peripheral nerves. They found that the centre median nucleus is actually " fired " by the peripheral stimulation, but the potentials are of a character significantly different from those of the lemniscal systems, and moreover occur considerably later. It may be assumed, therefore, that the centre median discharge is the result of activity delayed in some relay system.

For a general experimental study of the efferent connections of the various thalamic nuclei in the monkey, reference may be made to papers by Crouch and Thompson (1938*a*) and Crouch (1940). The anatomical relationship of the thalamic nuclei to the " thalamic syndrome " has been lately discussed by Smyth and Stern (1938), Kleist and Gonzalo (1938) and Walker (1938*b*).

VISUAL PATHS.

In the past few years a considerable amount of work has been completed on the detailed analysis of retinal connections and visual centres. Of quite outstanding importance is a book by Polyak (1941) on the retina, in which he records at some length his studies of retinal histology. These studies provide a sound basis for the investigation of the retinal mechanisms involved in the perception of light and colour. Particularly interesting is the author's recognition of several types of bipolar cell, each of which has a different pattern of intra-retinal connections, for it is suggested that these elements may constitute the analysers postulated by the classical trichromatic theory of colour vision.

The main terminal stations of the optic tract are well known to be the lateral geniculate body and the tectum of the mid-brain. Connections with the basal regions of the fore-brain in lower mammals have also been described by way of the so-called anterior and posterior accessory optic tracts. It now seems doubtful whether the former is an independent terminal connection of the main tract, and in spite of recent studies (Gillilan, 1941) it is not definitely established that the latter is present in the higher mammals (see Jefferson, 1940).

In the higher primates a large proportion of the fibres of the optic tract end in the lateral geniculate body. In Man, apes and catarrhine monkeys this is composed of six layers of cells, of which three receive homolateral retinal impulses and three heterolateral. It has been found by the method of trans-neuronal degeneration that from every spot in the central part of the retina fibres pass back to terminate in three layers of cells in the geniculate body, and it is inferred, therefore, that the conducting unit of the optic nerve is a unit of three fibres, each fibre passing to a separate cell layer. The interest of this observation lies in its possible relation to the trichromatic theory of colour vision (Le Gros Clark, 1941*a*).

The precise mode of termination of optic fibres in the lateral geniculate body of the rabbit and cat has recently been studied by Glees (1941, 1942) by making use of the characteristic degenerative changes which occur in the optic terminals a few days after section of the optic nerve. In both these animals each optic fibre is in terminal relation with a number of geniculate cells (ten or more), and there appears to be a considerable overlap. Moreover, a single geniculate cell receives a large number of terminals, estimated (in the cat) at about forty. In the monkey the condition is very different (Glees and Le Gros Clark, 1941). Here each optic fibre commonly terminates in a spray of five or six branches, each of which ends in synaptic relation with one geniculate cell, and in no case was it possible to find more than one synaptic contact with each cell. Clearly, such an arrangement would provide for the utmost

precision in the recording at the geniculate level of a retinal image. In the cat, on the other hand, the profusion of synaptic contacts, together with the overlap of the terminals of different optic fibres, would presumably provide an anatomical basis for a high degree of sensitivity even in low intensities of illumination. The work of Glees and Le Gros Clark provided the first *direct* evidence that crossed and uncrossed retinal fibres end in different cell-laminae of the geniculate body, and also indicated that the terminal of each fibre is confined to one lamina only. . Thus there appears to be no anatomical basis for a fusion at the geniculate level of crossed and uncrossed retinal impulses. A similar conclusion has been reached by O'Leary (1940) on the basis of Golgi studies of the cat's brain. These anatomical observations receive confirmation from electro-physiological methods of investigation, for Bishop and O'Leary (1940), by leading off from the geniculate body of one side in the cat while stimulating simultaneously or in succession both optic nerves with single shocks, found no evidence of any phenomena of interference or facilitation which might suggest fusion of retinal images at the geniculate level.

In the Primates it seems that destruction of the visual cortex leads to complete degeneration of all the cells of the geniculate body. Hence it may be assumed that these cells are entirely concerned with the cortical projection of retinal impulses—i.e. there are no intercalated cells which might subserve purely intrageniculate neural activities. It has been known for some time that minute lesions in the visual cortex of the monkey lead to retrograde atrophy involving all six cell-layers of the geniculate body—in other words, it may be inferred that the conducting unit of the optic radiations is a 6-fibre unit. Hence, while the impulses from corresponding points in the two retinae evidently remain distinct within the limits of the geniculate body, they must be brought into the most intimate relation as soon as they are projected on to the cortex, and it may be inferred that the cortical mechanism for the fusion of two images necessary for stereoscopic vision is very localized spatially.

For further details regarding recent work on the visual paths, reference may be made to Le Gros Clark (1942a, 1943).

Sensory Areas of the Cerebral Cortex.

By studying the effect of local strychninization of the sensory cortex on the electrical activity of the thalamus, and the effect of local strychninization of the sensory thalamic nuclei on the electrical activity of the cortex, Dusser de Barenne and McCulloch (1938b) have provided further evidence of the reciprocal anatomical connections which exist between each nucleus and its corresponding cortical area. Moreover, they found that sharp functional boundaries are present between the adjoining sensory systems. It is pointed out that the cortico-thalamic neurones (the existence of which seems finally to be established by their methods) can hardly provide the basis for the inhibitory functions originally ascribed to them by Head, for their stimulation leads to an increase and not a decrease in the electrical activity of the thalamic cells. The same authors (1940) have shown that the spontaneous electrical activity of the cortex remains after decapitation and decerebration, but vanishes when

the cortex is separated from the thalamus. This observation further emphasizes the importance of the reciprocal thalamo-cortical connections in the establishment of a common functional unit.

For a number of years it has been contended by anatomists—on the ground of histological and experimental studies—that the general sensory area of the cortex (receiving impulses conveyed by the fillet system) is probably quite limited in extent and (in the higher Primates) practically confined to the post-central gyrus. On the other hand, physiologists have been reluctant to accept such a clear-cut and restricted type of localization ; they have depicted the sensory area of the cortex as much more extensive, spreading in the monkey over a considerable part of the frontal and parietal cortex. Lately, however, the conception held by the anatomists has been vindicated by the employment of much more refined physiological methods. By recording the potential waves in the cortex after the excitation of skin receptors by normal stimuli, Adrian (1941) has mapped out the somatic sensory area of cortex in the rabbit, cat, dog and monkey. In each case the area appears to correspond precisely with the histological area delineated many years ago by Brodmann (area postcentralis). No evidence for a bilateral representation was found in the cat, dog or monkey. The simplicity and directness of the relay mechanism in the thalamus is suggested by Adrian's observation that signals from tactile receptors are handed on to the cortex without much alteration, though they are accompanied by additional signals from the thalamus which are rather variable. Observations by Woolsey, Marshall and Bard (1942) on the sensory cortex in the monkey (also using electrical methods for recording cortical potentials) have led to results similar to those of Adrian, and, in addition, they have analysed the topographical localization of different regions of the body in the post-central cortex in considerable detail. Reference on the same subject should be made to papers by Bard (1938), Marshall, Woolsey and Bard (1941), and Marshall (1941).

The receptive cortical area for auditory impulses has now been defined with great accuracy in the cat and monkey by the use of a variety of methods— Marchi (Woollard and Harpman, 1939), retrograde cell degeneration (Waller, 1940b), combined oscillographic and cyto-architectonic methods (Bremer and Dow, 1939) and electrical methods (Ades, 1941 ; Ades and Felder, 1941). In the monkey the area is astonishingly small, occupying the upper face of the superior temporal gyrus, and in diameter not more than 12 mm. An anatomical study of a case of complete cortical deafness by Le Gros Clark and Ritchie Russell (1938) indicates that in the human brain the area is correspondingly limited. By the study of surface potentials produced by stimulation of cochlear fibres, Woolsey and Walzl (1941) have presented evidence suggesting that there is a regional localization in the acoustic area of the cat, in the sense that impulses from the basal end of the cochlea are projected on to the anterior part of the area, and those from the apical end to the posterior part, while impulses from intermediate positions end in band-like zones of acoustic cortex between these two limits.

The precise extent of the visual cortex in Man and a number of other mammals has been known for many years, and it has also been established

that the topographical projection of retinal impulses on to the cortex is organized on a very precise plan. Attempts have more recently been made to analyze the structural basis of visuo-cortical processes, but progress along these lines is slow. Numerical computations show that in the monkey about 1,350 afferent fibres (conveying retinal impulses from the lateral geniculate body) project on to each square millimetre of visual cortex (Le Gros Clark, 1941b), compared with 1,700 in the rat (Lashley, 1939). O'Leary and Bishop (1931) have demonstrated that in the rabbit there is an extremely close correspondence between the optically excitable cortex and the anatomically defined area striata. The study of the structural changes which occur in isolated portions of the cortex in the monkey has confirmed, *inter alia*, that the afferent fibres ascend very obliquely into the cortex from the subjacent white matter, while the association fibres are collected in the radiated bundles (Le Gros Clark and Sunderland, 1939), and that the stria of Gennari is predominantly made up of intracortical connections of an entirely local character. The study of Golgi material has enabled O'Leary (1941) to analyse the structural plan of the area striata in the cat, with detailed descriptions of the neurones of which the various cellular laminae are composed and their interconnections. The author found that the distribution of the plexus of afferent fibres is more limited than it is in the rabbit, being almost entirely confined to lamina IV (internal granular layer). He also notes that in the cat the afferent fibres extend over a significant area of the cortex, giving off a number of ramifying collaterals in its course, so that the point-to-point localization between retina and cortex can hardly be as precise as it seems to be in the higher Primates. Perhaps the most conspicuous elements in the visual cortex of the higher Primates are the large " solitary cells of Meynert " (see Le Gros Clark, 1942b). Each of these cells has widely spreading basal dendrites which bring it into contact with a relatively extensive area of cortex ; indeed, it is estimated that in the monkey the axone of each cell represents a " final common path " for a unit area of cortex of approximately half a square millimetre. The Meynert cells are thus appropriately disposed to serve rapid " mass reactions " from the cortex, that is to say, reactions which rapidly reflect the gross activities of the cortex. Experimental evidence has also been recorded which indicates that the axones of the Meynert cells extend down to the mid-brain to form at least a component part of the cortico-mesencephalic tract.

Organization of the Cerebral Cortex.

In 1938(a) Dusser de Barenne and McCulloch studied the interconnections of various parts of the cerebral cortex by the method of local strychninization, combined with the recording of the electrocorticogram over adjacent areas. The application of strychnine to an area *a* of the cortex may " fire " another area *b*, as shown by characteristic potential fluctuations (" strychnine spikes ") in the electrocorticogram. The authors have shown that the strychnine acts directly on the perikaryon of a neurone, and that the strychnine spikes are the result of impulses conveyed by the axon through the subcortical white matter to its terminal in the cortex elsewhere. The method has thus proved to be a

most useful technique for mapping out the course and distribution of association fibres interconnecting the various cortical areas. It has been found that the areas differ considerably in their connections, and in many cases the latter are far less widespread than anatomists have supposed to be the case. For example (Dusser de Barenne, Garol and McCulloch, 1941a; Bonin, Garol and McCulloch, 1941) in the monkey area 1 (post-central cortex) sends fibres to areas 4, 2s, 5 and 7, area 6 to areas 4s, 4, 1, 2s, 5 and 7, while area 17 (visual cortex) only sends fibres to the adjacent area 18. Within the limits of certain areas the intra-areal distribution appears to be extremely limited. Thus in area 17 and area 5 the strychnine spikes are restricted to the area actually strychninized and its immediate vicinity. In many other areas, on the contrary, the intra-areal distribution is widespread. In the chimpanzee's brain (Bailey, Dusser de Barenne, Garol and McCulloch, 1941) the organization of the cerebral cortex seems to be much the same as it is in the monkey, except that the distribution of association fibres is considerably less widespread.

A remarkably interesting observation recorded by Dusser de Barenne and McCulloch (1938a), and independently also observed by Hines (1937), is the existence of a narrow strip of cortex (4s) along the anterior margin of the motor cortex (area 4) which, when stimulated electrically, chemically or mechanically, leads to a suppression of the electrical activity of the whole of the rest of the cortex, and also to a disappearance of the motor response to stimulation of the motor cortex. The latter has a remarkable latency of about four minutes, and cannot be produced again for many minutes. By making various lesions in the brain, it was discovered that the integrity of the caudate nucleus is necessary for the suppression phenomenon. It was also found that strychninization of area 4s leads to the appearance of typical strychnine spikes in the caudate nucleus. Thus it seems certain that there are cortical cells in area 4s, whose axones terminate either directly or by means of collaterals in the caudate nucleus, even though (Verhaart and Kennard, 1941) it is not possible to demonstrate such an anatomical connection by the ordinary Marchi technique.* The suppression effect produced by the activity of the caudate nucleus appears to take place through the thalamus, for, while the absence of direct caudato-cortical connections is shown by the fact that strychninization of the caudate nucleus produces no strychnine spikes in the cortex, such an experiment does lead to changes in the electrical activity of the thalamus. However, the evidence suggests that the connection of the caudate nucleus to the sensory thalamic nuclei is not a simple direct axonal one, but has relays somewhere in between. Other suppression areas besides area 4s have been mapped out in the monkey's brain (Dusser de Barenne, Garol and McCulloch, 1941b), a narrow strip along the anterior border of the premotor cortex (8s), another along the posterior border of the post-central cortex (2s), and yet another adjacent to area 18 (19s). From all but the last of these, direct efferent connections with the caudate nucleus seem to have been established by the method of strychninization. In the course of this work evidence has also been adduced to show

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* Since this was written, Dr. P. Glees, working in the author's laboratory, has been able to demonstrate the efferent connection between area 4s and the caudate nucleus by the experimental use of a specialized silver technique.

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that fibres run from area 6 to the putamen and globus pallidus externus, and from area 4 to the putamen.

This recent work on the anatomical relation between the cerebral cortex and the corpus striatum is of outstanding importance, and will no doubt soon lead to a considerable clarification of the rolé played by the basal ganglia in cerebral functions. It becomes clear now that the corpus striatum is in some fundamental way essential for the normal activity of the cerebral cortex; indeed, it seems to constitute a necessary activating mechanism. This conception is likely to be fruitful in the interpretation of the mental disturbances which often accompany lesions in the region of the basal ganglia.

THE CEREBELLUM.

The morphological analysis of the cerebellum has been a bone of contention for many years, and the uncertainties regarding it are reflected in the different views of the cerebellar subdivisions which are presented to students in ordinary text-books. While previously the cerebellum was commonly subdivided on morphological grounds into three lobes, anterior, middle and posterior, recently there has been a tendency to recognize two main lobes only, anterior and posterior. Yet the former subdivision is no doubt the more reasonable, for it is based on several of the fundamental connections of different areas of the cerebellar cortex. The confusion regarding the subdivisions of the cerebellum has evidently arisen partly because anatomists in the past have expected them to be much more clear-cut than is really the case, and have tried to relate them rigidly to fissures which they have mistakenly supposed to be constant and fixed boundaries between different morphological elements and strictly comparable from one animal to another. It seems also that some anatomists have unwittingly confused the issue by their tendency to separate sharply the older and more recent phylogenetic components of the cerebellum, and this tendency, indeed, applies to several other parts of the brain as well. It would probably save a good deal of confusion if the prefixes " palaeo- " and " neo- " were debarred from use in cerebral morphology altogether.

A comprehensive review of the evolution and anatomy of the cerebellum has lately been published by Dow. (1942b). For this reason it would be superfluous to deal in great detail with recent studies of cerebellar morphology here, and some of the main points only will be mentioned.

The termination of spino-cerebellar fibres in the anterior and posterior lobes of the cerebellum has been established in a general way for a good many years, mainly on the basis of Marchi studies. By oscillographic methods the distribution of these fibres has now been mapped out with much more precision (Dow, 1939); they have been shown to reach the entire anterior lobe of the cerebellum, the lobulus simplex, pyramid and paramedian lobule, and they are most numerous in the anterior lobe. The work of Brodal and Jansen (1941) also makes it probable that some end in the uvula and perhaps in the nodule.

Cortico-pontine and ponto-cerebellar connections have been studied by Sunderland (1940). This work has thrown considerable doubt on the view held by some previous investigators that specific areas of the cerebral cortex

project on to specific areas of the cerebellar cortex, for while it appears that cortico-pontine fibres relate different parts of the cerebrum to different parts of the pontine nuclei, the latter project diffusely on to the lobus medius of the cerebellum. Such a conclusion receives further confirmation from the oscillographic studies of Curtis (1940) and Dow (1942a).

The olivo-cerebellar system has a point-to-point relationship of a very precise kind, and through it the inferior olive sends fibres to the whole extent of the cerebellar cortex. The details of these connections have been confirmed and extended by Brodal (1940). It may be argued indirectly from the nature of this relationship that the climbing fibres in the cerebellar cortex are the actual terminals of the olivo-cerebellar system, while the mossy fibres are the terminals of the vestibulo-cerebellar, spino-cerebellar and ponto-cerebellar systems.

Vestibulo-cerebellar fibres are related entirely to the basal part of the cerebellum, and according to Dow (1939) end in the flocculus, nodule, uvula and lingula of the cerebellar cortex, as well as in the fastigial nuclei.

The existence of long association fibres connecting distant parts of the cerebellar cortex has been disputed. They have been described on the basis of Marchi material, but the latter is hardly critical enough to provide a definite answer. Electro-physiological methods have now shown that they probably do not exist, for a strong stimulation of a cerebellar folium, sufficient to produce an after-discharge lasting several seconds, fails to modify the electrical activity further than 5 mm. from the site of stimulation (Dow, 1938). On the other hand, short association fibres linking up immediately adjacent folia of the cerebellum are undoubtedly present in abundance.

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