AN EXPERIMENTAL INVESTIGATION OF THE CEREBRAL HEMISPHERES OF *LACERTA VIRIDIS*

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ALMOST all our knowledge of the structure of the reptilian brain is based on the histological study of normal material. The limitations of this method are too well known to need detailed discussion. By its use it is rarely possible to trace any fibres with precision from their origin to their termination. Only comparatively large bundles of fibres can be followed accurately, and these are usually composite, difficult and sometimes impossible to disentangle into their component parts. The direction in which any given fibre normally conducts is often left in doubt. One can, in short, do little more than map in broad outline the chief cell masses and fibre tracts, an insecure foundation on which to base functional or phylogenetic conclusions.

Conclusions of this kind have been frequently drawn, however, particularly in relation to the so-called neopallial primordia at the anterior end of the hemisphere. It was decided therefore to investigate the connexions of this region by the Marchi degeneration technique. In addition various parts of the brain have been stimulated electrically, and the results of the removal of large parts and in some cases the whole of both hemispheres have been studied; these experiments have been few in number, and proportionate caution must be used in basing conclusions on them.

The work has been done in the Anatomy Department of the University of Cambridge. I am particularly indebted to the technician, Mr Walter Calcott, for the preparation of the Marchi series of sections.

MATERIAL AND METHODS

Specimens of *Lacerta viridis* with ether as an anaesthetic were used in all the experiments.

Degeneration experiments. The skull was opened with a dental drill, the dura incised and a lesion made in the brain, sometimes with a cautery, sometimes by cutting with a fine knife. The olfactory bulbs, tracts and cerebral hemispheres are all easily accessible in this way. The opening in the skull was closed with a little cotton-wool on which a melted mixture of beeswax and resin was painted. This made a firm adhesive dressing and an adequate substitute for the bone removed. The mortality was fairly heavy, due as much to the general condition of the lizard before the operation as to the operation itself. In a few cases death was due to bleeding into the cranial cavity. Warmth is essential to satisfactory recovery; a temperature of between 70 and 80° F. was maintained in the cages.

After varying periods the lizards were killed, the skulls opened, and the brains fixed *in situ* with formalin. The brain was removed from the skull the next day and treated by the Marchi technique. All were cut in serial sections, a few in celloidin but most in paraffin.

No staining of degenerated fibres was found in brains which had been obtained less than 3 weeks after the operation. Of the six specimens which gave positive results, one had lived 29 days, two 37 days, and the others 33, 34, and 35 days respectively, from the date of operation. Probably the optimum period is about 34 days.

The results were not easy to interpret. Many fibres in these brains are not myelinated, and even those that are do not produce a very plentiful crop of fat droplets when degenerated. Artefacts in the shape of a fine sprinkling of black droplets in tracts that could not possibly have been affected by the operation were frequent. All the lesions were unilateral, and Marchi staining in a tract was considered as good evidence of degeneration resulting from the operation only when a definite difference, constant through the series, could be observed between the tract in question and the same tract on the normal side. The large number of unmyelinated fibres and the difficulty of keeping the animals alive for a long enough period are serious limitations to the usefulness of the method with this species and in this climate.

Stimulation experiments. A large bone flap on the dorsum of the head was cut with a small circular saw on a dental drill and turned back. The dura was dissected away and the midbrain and forebrain exposed. Faradic stimulation was used with fine bipolar electrodes of silver wire, the animals being under fairly deep ether anaesthesia.

Ablation experiments. Apart from the smaller lesions made in the degeneration experiments, complete decerebration was attempted in three cases and a hemi-decerebration in one. A bone flap was turned back and one or both hemispheres cut away anterior to the optic chiasma. After bleeding had stopped the flap was replaced and sealed in position with beeswax and resin. These animals were not easy to keep alive, but one, after removal of most of both hemispheres, lived for 17 days. After death the brains were removed and cut in serial sections so that the amount of tissue destroyed at the operation could be determined.

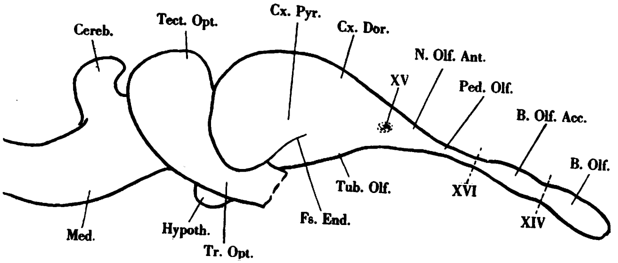
DEGENERATION EXPERIMENTS

The first series of experiments was designed to investigate the primary olfactory connexions of the hemisphere.

Lizard XIV. Right olfactory bulb destroyed with the cautery; killed after 34 days; Marchi's stain.

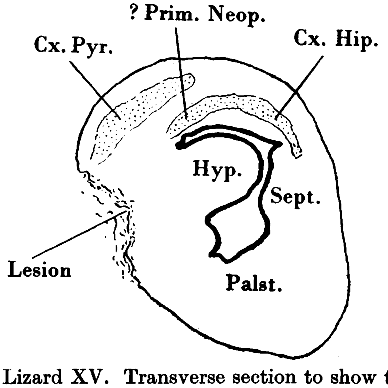
The sections showed almost complete destruction of one olfactory bulb. The accessory bulbs, being well behind the main bulbs, were both intact. In Text-fig. 1 the mark XIV shows the posterior limit of the tissue destroyed.

Degeneration in the olfactory tracts was slight but definite on the injured side. Fine black stippling could be traced from the deeper parts of the injured bulb to a superficial position in the peduncle. It could not be traced further than those cells that extend from the hemisphere into the root of the peduncle —Herrick's anterior olfactory nucleus. No significant degeneration could be seen in the hemispheres posterior to this. The lateral olfactory tract, the cortex, the paraterminal body (septum) and striatum were all free from degenerated fibres. The scantiness of degeneration even in the olfactory peduncle is a surprising feature of this specimen.



Text-fig. 1. A sketch of the lateral aspect of the brain of *Lacerta viridis*. XIV and XVI mark the posterior limits of the parts destroyed in these two lizards, and XV the site of the lesion in lizard XV.

Lizard XV. A small lesion was made with the cautery in the lateral part of the root of the olfactory peduncle and the animal killed after 35 days. Marchi's stain.



Text-fig. 2. Lizard XV. Transverse section to show the position and extent of the lesion.

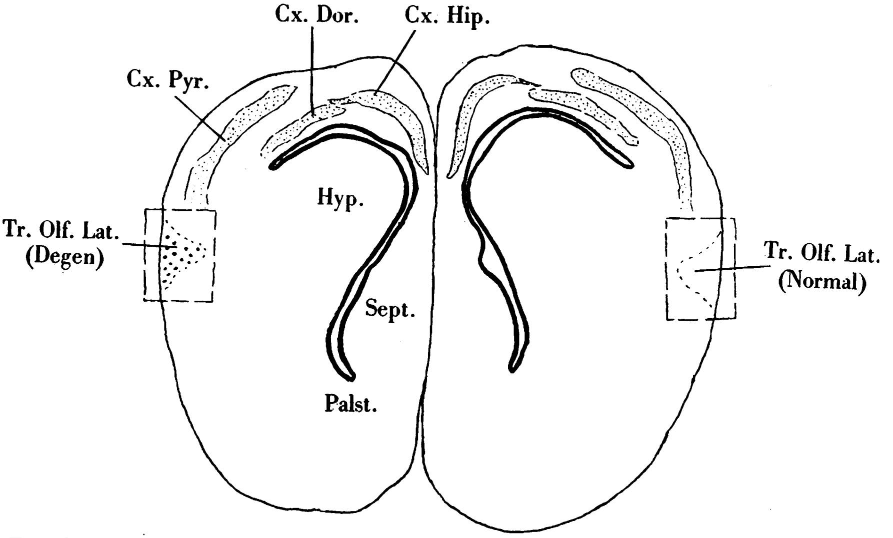
The sections showed a lesion ventro-laterally situated in the posterior part of the anterior olfactory nucleus (Text-fig. 1, XV, and Text-fig. 2). It divided the lateral olfactory tract and involved the pyriform cortex to a small extent.

Marked degeneration could be traced back in the lateral olfactory tract to the amygdaloid region of the hypopallial ridge or Hunter's eminence. It was lost in the core of a nucleus to which many names have been given: archistriatum (Kappers), nucleus occipitobasalis (Meyer), nucleus sphericus

(Edinger), etc., and which corresponds in part to the amygdaloid complex of mammals. The degeneration was more marked in the anterior than in the posterior extent of this tract.

Degeneration could also be traced ventro-medially from the lesion into the superficial aspect of the olfactory tubercle and, less certainly, into the olfacto-striatum.

A characteristic of degenerated tracts common in this series of experiments was shown by this specimen. In addition to the ordinary Marchi stain the tract showed a loose reticular structure in contrast to the finely granular appearance of the normal tract in transverse section.



Text-fig. 3. Lizard XVI. Transverse section showing the degenerated lateral olfactory tract. The rectangular outlines indicate the areas photographed in Pl. I.

Lizard XVI. The right olfactory bulb and anterior part of the peduncle were destroyed with the dental drill, and the animal killed after 37 days. Marchi's stain.

The sections showed complete destruction of the right main and accessory olfactory bulbs. In Text-fig. 1, XVI marks the posterior limit of the tissue destroyed.

Degenerated fibres could be seen peripherally in the injured peduncle and traced back to the anterior olfactory nucleus where they became scantier and disappeared completely dorso-medially. Dorso-laterally the degeneration was rather diffuse but behind this level became concentrated in the lateral olfactory tract and could be followed into the amygdaloid region. The photographs (Pl. I and Text-fig. 3) are taken from a transverse section about the middle of the hemisphere where the tract is still superficial and compact. In this specimen the black stippling was much more marked than the reticulated appearance mentioned for lizard XV. From the point of view of the Marchi staining this is the best specimen in the series.

In the ventro-medial part of the anterior olfactory nucleus degenerated fibres were scanty, but could be traced through into the superficial aspect of the olfactory tubercle and paraterminal body (septum). No further significant evidence of degeneration was found.

The following conclusions seem justifiable on the basis of these experiments, remembering always that they apply only to myelinated fibres.

Olfactory fibres which arise in the main olfactory bulb run superficially in the peduncle and end for the most part in the anterior olfactory nucleus. Few if any of these fibres run directly to the olfactory centres in the hemisphere behind this nucleus. Fibres from the accessory bulb, on the other hand, appear to run mainly through the anterior olfactory nucleus and to constitute the main part of the lateral olfactory tract. Many of these fibres reach as far as the amygdaloid region, but some end on the way, probably in the pyriform cortex. The evidence also suggests that olfactory fibres which run directly to the septum and olfactory tubercle are of similar origin. Here one is dealing with far fewer fibres and the conclusion is less certain.

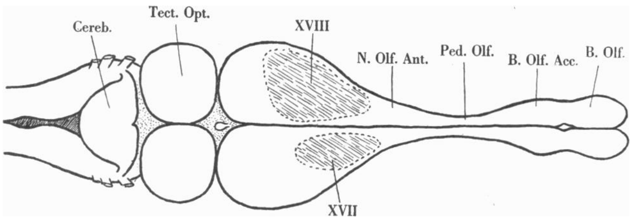
The constitution of the lateral olfactory tract of reptiles is of interest in view of Herrick's work on amphibians (1921). He has shown that in Anura there are two components of the lateral olfactory tract: (i) ventro-lateral, from the accessory bulb to the amygdaloid nuclei, and (ii) dorso-lateral, from the main bulb to the lobus pyriformis. This was the result of histological investigation, and the degree to which either of these tracts is a direct bulbar connexion and not relayed in the anterior olfactory nucleus is not clear. This subdivision is not found in the Urodela, where the accessory bulb is less distinct from the main bulb, and no clearly differentiated amygdaloid nuclei exist.

The accessory olfactory bulbs receive their afferent fibres from the vomero-nasal organs, so that in lizards it appears that the amygdaloid nuclei have developed largely under the influence of impulses that come from these organs. In this respect they resemble the Anuran amphibia. The absence of a vomero-nasal organ in the Crocodilia may account for the apparent lack of differentiation in the amygdaloid region as seen in Crosby's figures.

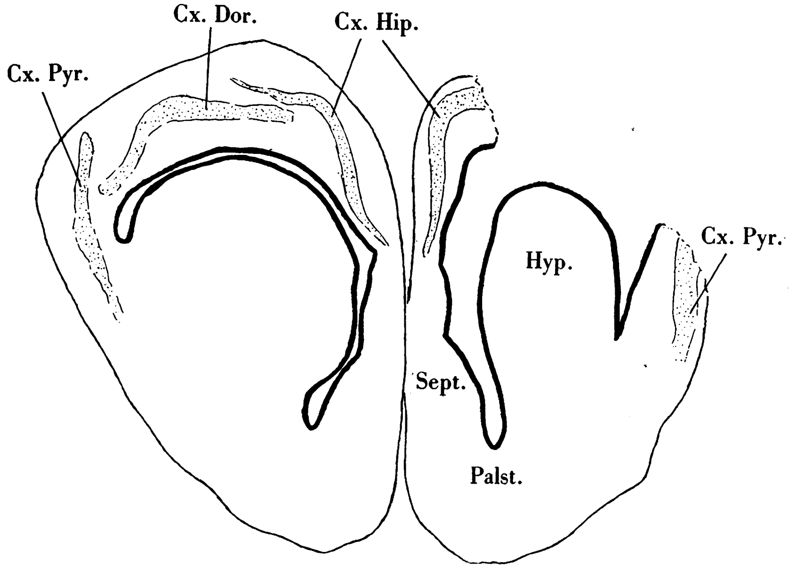
In mammals the condition is not yet clear. Cajal has denied any direct connexion of the lateral olfactory tract with the amygdaloid complex, and in the anosmatic dolphin this complex remains well developed. Other workers, Röthig, Herrick, Johnston and Loo in marsupials, and Herrick in the rat, have described such a connexion, but the histological evidence suggests that the lateral olfactory tract receives fibres from all parts of the main and accessory olfactory bulbs indiscriminately. There may therefore be well-marked differences between the mammals and the reptiles in the relationship of the amygdaloid complex to the vomero-nasal inflow, and this throws some doubt on the rather exact homologies between reptilian and mammalian amygdaloid nuclei that have been instituted by Johnston (1922). In reptiles, apart from Crocodilia, it appears that vomero-nasal impulses have been an important factor in the differentiation of the amygdaloid nuclei. In mammals the evidence is against any predominant influence of this kind.

The second series of experiments bears upon the efferent connexions of the cortex and corpus striatum, and was as follows:

Lizard XVII. A longitudinal incision was made in the dorsal aspect of the hemisphere just behind the anterior olfactory nucleus. The animal was killed after 37 days and Marchi's stain was used.

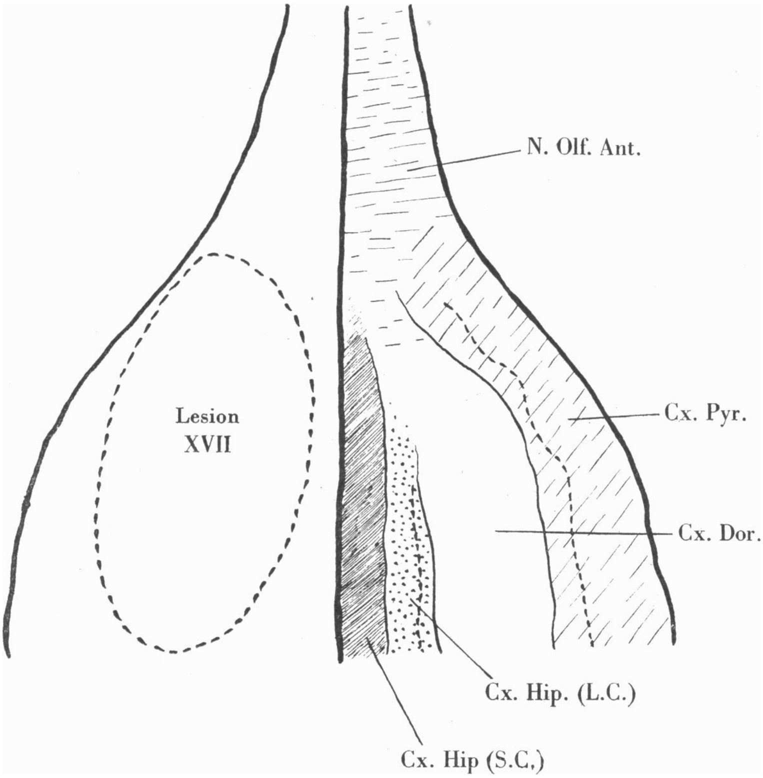


Text-fig. 4. Sketch of the dorsal aspect of the brain of *Lacerta viridis.* XVII and XVIII show the superficial extent of the lesion in these two lizards.



Text-fig. 5. Lizard XVII. Transverse section showing the extend of cortex destroyed at about the middle of the lesion. The underlying hypopallium is intact.

The sections showed almost complete destruction of the dorsal cortical area with slight damage to the anterior olfactory nucleus. The lateral part of the hippocampal and the dorso-medial part of the pyriform area were slightly involved. Text-fig. 4, XVII, shows the approximate position and extent of the lesion. Text-fig. 5 is a transverse section through about the middle of the lesion; it shows that in spite of the extensive destruction of cortex, the hypopallium and corpus striatum generally have escaped injury. Since much has been written about the homologies of this particular region of the cortex, a graphical reconstruction has been prepared in Text-fig. 6 to show the exact areas involved. The figure gives a dorsal view of both hemispheres anterior to the lamina terminalis and the commissures, extending forwards to the root of the olfactory peduncle. Measurements were taken at right angles from the medial sagittal plane to the margins of the cortical areas and plotted on the right-hand side of the figure. Only areas whose boundaries are so clear and definite as to be beyond all controversy have been marked. The intermediate dorsal area has been left unshaded and only its medial and lateral margins marked by interrupted lines. It is overlapped medially by the hippocampal and laterally by the pyriform cortical areas, De Lange's medial and lateral superposition. Anteriorly it can be seen that all the areas blend with cells scattered in the olfactory peduncle for which Herrick's name, nucleus olfac-



Text-fig. 6. A graphical reconstruction showing the dorsal aspect of the anterior parts of the hemispheres of *Lacerta viridis*. For description, see text, p. 338.

torius anterior, is adopted. In order not to confuse the picture the area destroyed by the lesion is marked on the opposite hemisphere.

This area covered by the lesion includes all the antero-dorsal parts of the hemisphere which can conceivably be reached by fibres of the lateral forebrain bundle system, except the anterior olfactory nucleus. Actually few if any fibres of this bundle can be traced into the region of the anterior olfactory nucleus. It is therefore true to say that the so-called primordium neopallii (Elliot-Smith), or the primordium of the general cortex (Crosby), or the parapyriform neopallial primordium (Dart), has been wholly, or in large part, destroyed by the lesion.

I feel bound to put the reasons for this conclusion at length, since I have been unable to define such a primordium in *Lacerta viridis* as a clear-cut cortical area. All that there appears to be is an ill-defined area including parts of what has been called dorsal cortex (subiculum, Dart), the pyriform area, and perhaps the nucleus olfactorius anterior, which appear to have connexions with the lateral forebrain bundle. In this species I have been unable to find anything so definite as the parapyriform and parahippocampal primordia described by Dart, nor indeed to find the thalamic radiation in the medial forebrain bundle on which so much of his interpretation rests. These findings, or lack of findings, are derived from a study of normal brains stained by the usual histological methods.

Evidence of degeneration in this specimen was extremely scanty. A fine black stippling was rather more marked in the alveus system on the injured side medial to the lesion, and could be traced, but with some uncertainty, into the dorsal part of the homolateral paraterminal body (septum). In a few of the sections behind the lesion the forebrain bundles on the injured side seemed to show similar slight evidence of degeneration, but as the appearance was not consistent from section to section, it can probably be discounted.

No other evidence of Marchi degeneration was found, but the paraterminal body on the injured side was, as a whole, smaller than on the normal side. Its cells appeared shrunken, hyaline and very refractile, but this cannot be counted as firm evidence of degeneration in the absence of any cell stain.

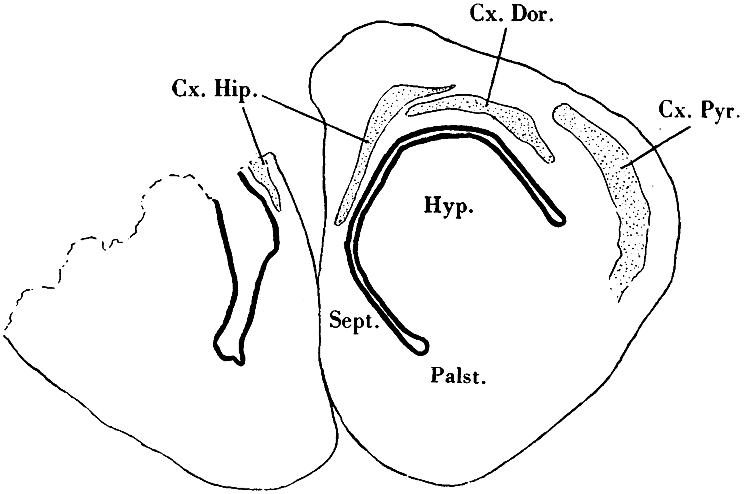
Lizard XVIII. A lesion was made with the knife in the antero-lateral part of the cortex. It was more extensive than in lizard XVII. The animal was killed after 33 days and stained by Marchi's method.

The approximate superficial extent of the lesion is shown in Text-fig. 4, XVIII. In the sections a large lesion was found in which nearly the whole of the dorsal cortex and all but the most ventral part of the pyriform and the most medial part of the hippocampal cortex had been destroyed. There was no damage posterior to the lamina terminalis. Text-fig. 7 is a transverse section through about the middle of the lesion, and it can be seen that there is also fairly extensive damage to the dorso-lateral part of the hypopallium, but that the palaeostriatum and septum are intact.

Anterior to the lesion no evidence of degeneration was found. On its medial side rather doubtful traces were seen in the alveus system leading into the superficial part of the septum (homolateral). Similar traces were present in the anterior commissure extending into the amygdaloid region (again homolateral), but these are probably not significant.

Definite evidence of degeneration was seen in the form of a fine dust-like stippling throughout the palaeostriatum on the injured side. It could be traced back into the diencephalon in the ventral peduncle of the combined forebrain bundles, but not with certainty into the midbrain.

It was noticed in addition that the fine network of fibres in the somatic part of the palaeostriatum and the septum was looser and less uniform than on the normal side. The septum was slightly swollen as if with oedema fluid. There was no evidence of inflammation, and it seems fair to accept these changes as degenerative.

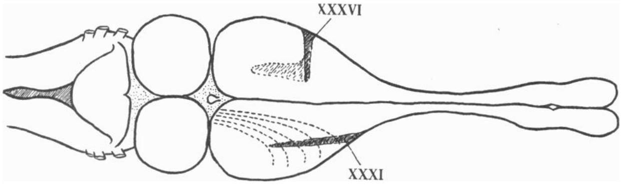


Text-fig. 7. Lizard XVIII. A transverse section showing the damage to the cortex and hypopallium at about the middle of the lesion.

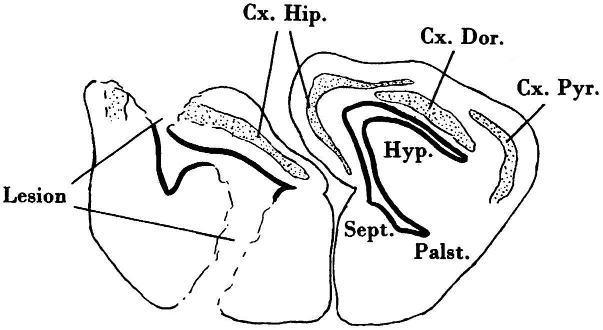
Lizard XXXI. An attempt was made at hemi-decerebration, the incision being carried longitudinally between the hemispheres and then laterally behind the left hemisphere. The animal lived 31 days and was then killed and the brain stained by Marchi's method.

The sections showed a much less extensive lesion than had been intended. There was an incision parallel to the midline but some distance from it (see Text-fig. 8, XXXI), passing dorsally through the lateral part of the dorsal cortex and ventrally just lateral to the olfactory tubercle and the olfactory part of the palaeostriatum. Text-fig. 9 is a transverse section which shows the relation of the lesion to these parts. There was no damage posterior to the lamina terminalis, and the cerebral peduncles were both intact. There was a little damage to the lateral part of the septum. The main effect of the lesion was to divide the lateral olfactory tract anteriorly and also those fibres of the lateral forebrain bundle which connect with the hypopallium and cortex. In Text-fig. 8 the position of these fibres has been marked with interrupted lines and their relation to the lesion can be seen.

The main positive finding in this specimen was a fairly well-marked degeneration in the ventro-medial part of the lateral forebrain bundle on the injured side. This degeneration could be traced into the subthalamic region of the diencephalon. Text-fig. 10 gives a diagram of the forebrain bundles in this part of their course. Both medial and lateral bundles are combined, and the composite tract is separating into dorsal and ventral peduncles. The dorsal peduncle consists of coarse fibres compactly arranged (Text-fig. 10, *Ped. Dor.*). It is derived probably entirely from the lateral forebrain bundle and connects chiefly with the nucleus rotundus of the thalamus. No evidence of degeneration was found in it. The ventral peduncle, consisting of finer and more scattered fibres, is derived from both medial and lateral bundles. It runs mostly to the hypothalamus. In the photographs (Pl. II) the evidence of degeneration can be seen moderately clearly in this peduncle. There is a scattering of rather coarse fat droplets stained black in the area within the dotted line, and a fairly marked loosening of the texture of this part of the bundle, giving rather a honeycomb appearance which does not show very clearly in the photograph. These findings were consistent on the injured side throughout the diencephalon.

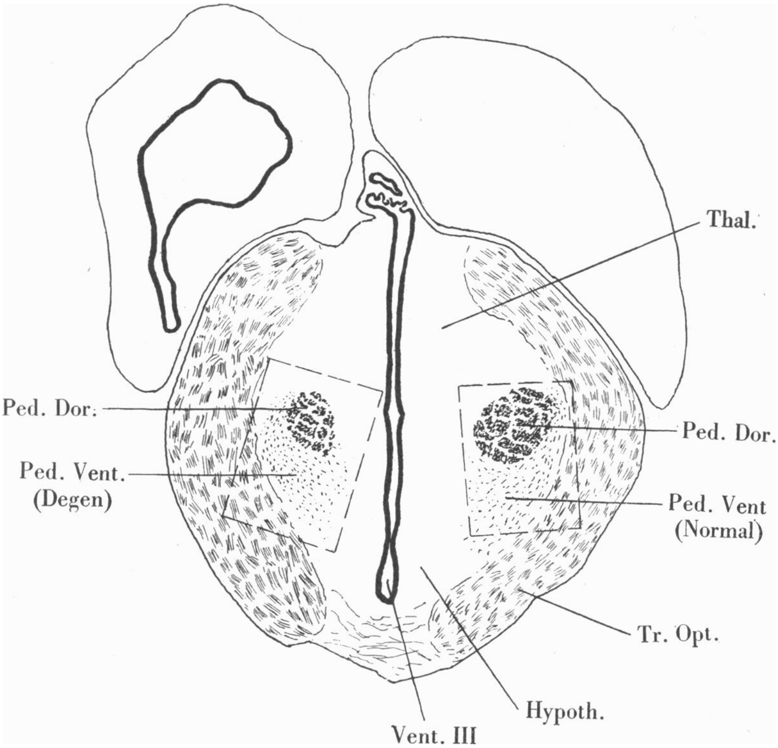


Text-fig. 8. Sketch of the dorsal aspect of the brain of *Lacerta viridis*, showing the position of the lesions in lizards XXXI and XXXVI. The dotted lines in the right hemisphere indicate the position of the lateral forebrain bundle.



Text-fig. 9. Lizard XXXI. A transverse section, considerably distorted on the injured side. The position of the cut, passing through the cortex dorsally and the striatum ventrally, is shown.

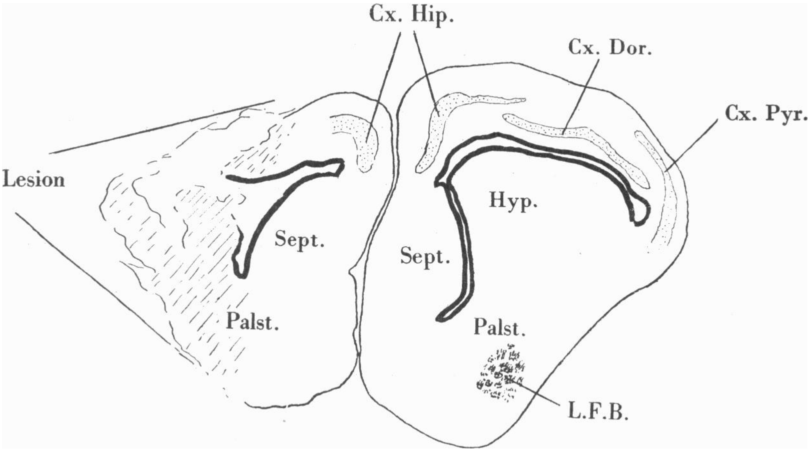
A little degeneration could be traced through into the midbrain, where it lay in the tegmentum, dorso-medial to the basal optic root (see Text-fig. 12, from another specimen), in the position of De Lange's tractus septo-mesencephalicus. This is shown in his Fig. 17 of *Varanus salvator*, p. 90, 1913. Most of the degenerated fibres, however, end in the diencephalon, probably in the hypothalamus.



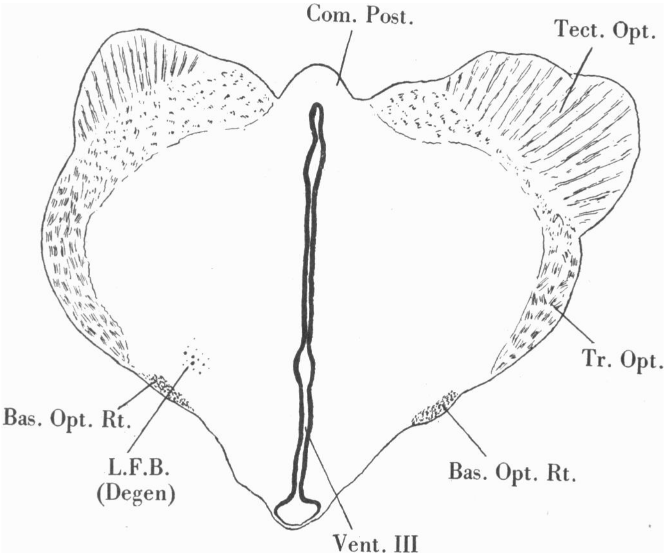
Text-fig. 10. Lizard XXXI. A transverse section about the middle of the diencephalon. The position of the forebrain bundles and their subdivision into dorsal and ventral peduncles is shown. No attempt has been made to show the degeneration in the ventral peduncle on the left side, but photographs of the areas outlined are shown in Pl. II.

Beyond this there was considerable diffuse stippling in the hippocampal cortex and septum on the injured side, although this could not be traced posteriorly in the medial forebrain bundle. A similar finding in the stria medullaris may be significant. Some stippling among the fibres of the commissures was too diffuse to be capable of interpretation. Anterior to the lesion slight stippling and atrophy in the anterior olfactory nucleus and the olfactory peduncle was seen.

Lizard XXXVI. A transverse cut was made about half way through the hemisphere just behind the neopallial primordium. The animal was killed after 29 days, and Marchi's stain was used. The position of the lesion is shown in Text-fig. 8.



Text-fig. 11. Lizard XXXVI. A transverse section through the lesion at the level of maximal destruction of tissue. All that part of the left hemisphere shaded obliquely is necrotic.

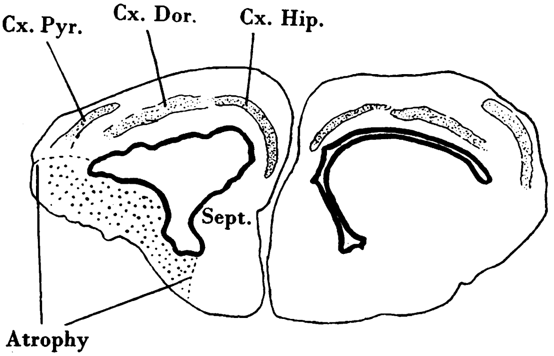


Text-fig. 12. Lizard XXXVI. A transverse section at the posterior end of the diencephalon, showing the beginning of the tectum of the midbrain. The position of the degenerated fibres is marked on the left side dorso-medial to the basal optic root.

In the sections it was found that at the level of the cut the whole striatum, with the exception of its most medial part, the pyriform cortex and the dorsal cortex had been destroyed (Text-fig. 11). Posteriorly there was some additional destruction of the dorsal cortex. The lateral forebrain bundle had been completely divided near its anterior end, and also, of course, the lateral olfactory tract. The medial forebrain bundle was practically intact.

Posterior to the lesion degeneration was definite in the medial part of the lateral forebrain bundle and could be traced through the subthalamic region in the ventral peduncle into the tegmentum nearly as far as the level of exit of the IIIrd nerve. Text-fig. 12 shows the position of the degeneration in a transverse section at about the junction of the diencephalon and the midbrain. Comparatively few of the degenerated fibres reached this level, most of them ending in the diencephalon, probably in the hypothalamus. The lateral olfactory tract was degenerated and some fine and rather doubtful degeneration could be traced in the alveus system into the septum.

Anterior to the lesion the whole striatum was atrophied and finely stippled with fat granules (Text-fig. 13). The cortical areas and septum were normal. A little rather doubtful degeneration could be traced round the lateral angle of the ventricle into the dorsal cortical area in the region of the primordium neopallii. The anterior olfactory nucleus was not appreciably affected.



Text-fig. 13. Lizard XXXVI. A transverse section anterior to the lesion. The whole ventro-lateral sector of the left hemisphere (stippled) shows marked atrophy. Marchi staining of degenerated fibres was present in this sector, but was not nearly as conspicuous as the stippling in the figure.

These experiments suggest the following conclusions. Destruction of the dorsal cortical area anteriorly, including any neopallial primordia that may be present, leads to no definite degeneration of myelinated fibres in the lateral forebrain bundle. There is therefore no long descending tract from this region of the cortex of *Lacerta viridis* leading to centres below the forebrain, and in any way comparable with the pyramidal tracts of mammals. There was some evidence for the presence of short fibres running medially in the alveus system to the septum.

When, in addition to the destruction of cortex the striatum is also damaged, degeneration appears in the more medial and ventral part of the lateral forebrain bundle and can be traced into the diencephalon and to a small extent into the midbrain. These fibres appear to be descending from the striatum, and comparable to some components of the ansa lenticularis of mammals.

The greater part of the lateral forebrain bundle consists of ascending fibres from the thalamus. The destination of some of these fibres is indicated in lizard XXXVI, where the anterior part of the forebrain bundle is cut off. In this anterior part degeneration is found, but can be traced only to a minor extent, and that rather doubtfully, into the lateral part of the cortex. The most anterior fibres of the lateral forebrain bundle end predominantly in the striatum itself, particularly its hypopallial part.

These results from the use of the Marchi technique, and the conclusions based on them, must be accepted with very great caution. Partly because myelinated fibres are not so numerous and partly because of the difficulty of the technique in cold blooded vertebrates, the actual histological findings are not so definite as they are in good mammalian preparations. Tracts are less clearly circumscribed and it is often difficult to be sure that a diffuse stippling is not an artefact, or that its presence on the injured side and not on the other only fortuitous.

It will be noticed that the conclusions concerning the composition of the lateral olfactory tract are really based on one specimen, lizard XIV, in which the results were for the most part negative. If in this specimen the lack of apparent degeneration in the lateral olfactory tract was due to some failure of technique, the greater part of the argument falls to the ground. In its favour it can be said that the lateral olfactory tract is one which showed evidence of degeneration more easily and more definitely than any other in this series of experiments, and that the technique used for lizard XIV was in no way different from that used for the others.

A further point that throws some doubt on the validity of these results is the lack of degeneration in some fibres which one would have expected to be affected. The alveus system was damaged, and sometimes quite extensively, in many of these experiments, yet it never showed more than very scanty evidence of degeneration. The system is known to contain many myelinated fibres, and these may of course be afferent to the cortex, but this conclusion is not secure without the corresponding positive evidence of degeneration to confirm it.

Finally, in defence of the conclusions that have been drawn, it may be said that there is some positive evidence to support all of them, and that they do not conflict with the known histology of normal material. It seems, therefore, justifiable to assume their truth provisionally and as a basis for discussion and further work.

STIMULATION EXPERIMENTS

Two of the largest specimens were used for these experiments, and with the following results.

No motor response could be obtained from any part of the hemispheres or the olfactory peduncle with a stimulus that was adequate to evoke movements easily from the midbrain, or by direct application, from a muscle. Movements resulted from stimulation of the forebrain only after the use of a stimulus so strong that it spread even to the adjacent temporal muscle and must have affected the whole brain at least. Such movements were always mass movements of the whole body, and clearly were valueless as evidence of a specific motor function in any part of the forebrain.

Stimulation of the tectum of the midbrain led constantly to a flexion of the tail towards the side stimulated. By increasing the strength of the stimulus this movement was converted into a fairly regular side to side movement of the tail; i.e. a regular series of muscular contractions travelling alternately down the two sides of the body. The extent to which the trunk muscles were involved varied, but the whole movement was very like that of the trunk and tail in normal progression. The limbs did not take part in this movement in any co-ordinate manner. Isolated movements of the limbs sometimes resulted from midbrain stimulation, but they were weak, inconstant, and sometimes homolateral, sometimes heterolateral. They never occurred apart from tail movements.

An attempt was made to investigate the effect of simultaneous stimulation of the forebrain on movements to be obtained from the midbrain. A continuous stimulus, of a strength just sufficient to evoke movements from the midbrain, was applied to the hemisphere in the region of the dorsal cortical area. It was found that movements of the tail could still be obtained from the midbrain. They tended to be rather slower; sometimes better sustained, sometimes less in extent, but not otherwise altered in character. This effect was soon lost, and could not always be repeated after an interval for the recovery of fatigue.

Stimulation of the midbrain after the removal of the hemispheres led to the adoption of a definite posture. The forelimbs were adducted back to the trunk, with the elbow at a right angle so that the body was held just off the ground. The hindlimbs were splayed out in semi-flexion at the hip and knee. This reaction was tested in only one specimen.

ABLATION EXPERIMENTS

(i) *Partial lesions of one hemisphere*

In several lizards (e.g. lizards XVIII and XXXI) fairly extensive lesions were made in one hemisphere. Some of the hippocampal cortex, the septum and a considerable part of the striatum were intact on both sides. None of these specimens showed any defect of motor behaviour once they had recovered from the immediate effects of the operation. This was often after so short a time as one or two hours. Under the conditions of the experiments, i.e. confinement in a small cage, they did not differ to superficial examination from normal lizards. They were active and fed well. In all these specimens a considerable part of the dorsal cortex including the region of the neopallial primordia had been removed.

(ii) *Hemidecerebration*

Lizard XXV. Practically the whole of one cerebral hemisphere was removed together with most of the septum and cortex of the opposite hemisphere (excluding the pyriform area). There was some slight damage to the opposite corpus striatum. The animal lived for 10 days after the operation.

This lizard remained rather sluggish. Stimuli, such as a touch or pinprick on any part of the body, led to quite normal reactions in the form of attempts to escape or run away. There seemed to be no defect in the performance of any ordinary movement, and this condition was reached within 24 hours of the operation.

It was not seen to feed at any time after the operation, but on the third day it snapped at a worm moving in its field of vision. It failed to take the worm into its mouth.

Its posture was normal, but 7 days after the operation slight hypertonus seemed to be present in the extensor muscles of the neck. At this stage, in running forwards, it made repeated leaps upwards with the forepart of its body, as if attempting to surmount imaginary obstacles. There was no further change till its death on the tenth day.

(iii) *Complete decerebration*

Lizard XXXII. It was found post-mortem that the attempt at complete decerebration in this lizard had removed all the anterodorsal parts of the hemispheres including the septum and commissural region. There was a little damage to the anterodorsal part of the thalamus. The hypopallium had been removed anteriorly, but a little of the palaeostriatum, the posterior part of the hypopallium and the amygdaloid region were intact on both sides, although much damaged by haemorrhages, the probable result of infection.

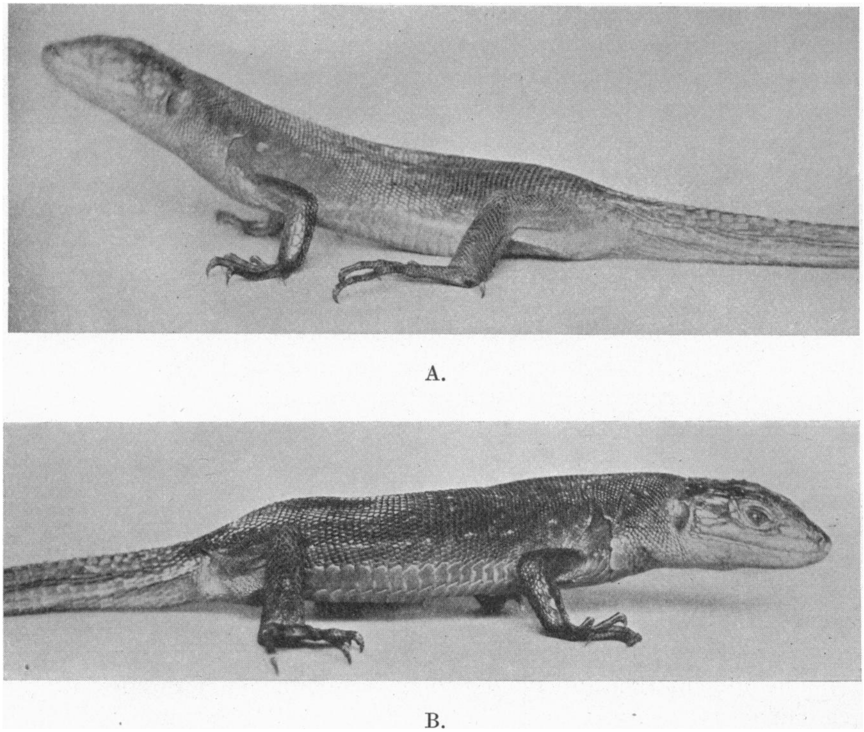
No detailed notes were kept of this lizard, but there was no obvious defect of motility or posture, and no rigidity. It was never seen to feed, and at death the intestine was completely empty. It lived 22 days.

Lizard XX. This lizard lived only 2 days. Post-mortem it was found that the whole of both hemispheres had been removed with the exception of the posterior end of Hunter's Eminence, i.e. the amygdaloid region. The preoptic nuclei, thalamus and hypothalamus were intact.

Apparently voluntary movements of the forelimbs were noted 1 hour after the operation. Four hours later the lizard could walk in a perfectly co-ordinated manner if strongly stimulated by touch or pinprick. There seemed to be a slight general increase in the tone of all the muscles of the body, most marked however in the muscles which extend the trunk and neck. It was extremely sluggish and it was difficult to determine the posture of the limbs, since they tended to remain in any position to which they were passively moved.

There was no change 24 hours later, but it was noted that it could climb up the side of its cage.

Lizard XXI. This lizard lived for 7 days. Post-mortem both hemispheres were found to be completely removed. There was in addition much diencephalic damage due to haemorrhage and infection. An abscess in the tegmentum had probably interrupted the tecto-spinal tract on one side.



Text-fig. 14. Lizard XXI. Photographs to show typical postures on, A, the second, and B, the third, day after the decerebration.

Five hours after the operation the lizard was walking normally, but showed the same sluggishness and general increase of tone as the preceding specimen. There was the same tendency to remain in any position to which it was brought by passive movement, but tilting or inversion of the whole animal always led to brisk attempts to regain a normal position.

No marked changes occurred throughout the remaining 6 days of life. As a rule it stood in an extended posture with the body lifted off the ground (Fig. 14 A), but was often found in a more normal position, although usually with the body raised above the ground (Fig. 14 B). The right eye had been slightly damaged in the operation and the head was usually held abducted towards the left.

It noticed a worm moving in its field of vision and turned towards it. On one occasion it turned and snapped when pricked with a pin, but on no occasion made any attempt to feed.

In running it held its head hyperextended and made repeated jumps into the air like lizard XXV. Its sluggishness persisted throughout the whole period of its post operative life.

Lizard XXIV. This animal lived for 17 days. After death it was found that the cortex had been destroyed in both hemispheres, except for the medial part of the hippocampal area. The septum and the greater part of the striatum were present, but much damaged by small haemorrhages. These were present also in the thalamus and hypothalamus.

In its sluggishness, a slight general increase in tone and a tendency to remain in any position in which it was placed, this lizard resembled the preceding ones. It was not seen to feed. The increase in tone was rather doubtful, and the posture was always normal, the belly not being raised off the ground except in response to stimulation. It walked quite normally and ran with no attempt to jump like lizards XXV and XXI.

DISCUSSION OF THE STIMULATION AND ABLATION EXPERIMENTS

In *Lacerta viridis* there is no region on the dorso-lateral aspect of the hemisphere or in the olfactory peduncle where faradic stimulation leads to a motor response. There is, in fact, no evidence for the existence of a pallial area with characteristics resembling those of the motor part of the neopallium of mammals. This finding is in accord with the results of Marchi experiments where no trace of a long cortico-fugal tract like the pyramidal tract of mammals could be found. The conclusions reached on p. 345 indicate that the lateral forebrain bundle consists predominantly of thalamo-striatal fibres and a striofugal system running to the subthalamus, hypothalamus and tegmentum. A similar fibre system is found associated with the corpus striatum of mammals, and it is with this system rather than with the internal capsule that the lateral forebrain bundle of reptiles is comparable. Although the corpus striatum and its associated fibre systems are undoubtedly related to motor function, they are not electrically excitable. Such excitability is a characteristic limited to certain parts of the neopallium of mammals, and these parts and their typical connexions do not appear to exist in reptiles.

Stimulation of the hemispheres, however, did influence movements which could be obtained from the tectum of the midbrain. The result was not obtained constantly and it needs confirmation in larger reptiles. At least it indicates that the method of simultaneous stimulation of two parts of the nervous system may lead to information about regions which give no response when stimulated alone.

As far as they concern the inexcitability of the cortex, these results agree with those of Dr W. H. Wilson, of Cairo, who, in *Varanus* and *Uromastix*, was unable to obtain movements from the hemispheres with a stimulus strong enough to excite the midbrain. They conflict with those of Johnston (1916), Bagley & Richter (1924), and Bagley & Langworthy (1926).

Johnston obtained his results under deep chloroform anaesthesia, which he says is a necessary part of his technique. In three species of turtle and in a lizard (*Gerrhonotus*) movements were obtained from the antero-lateral part of the cortex. He does not specify the kind of movement very precisely, e.g. he states that from the antero-lateral pallial border in a turtle he obtained "movements of eyes, jaw, neck, legs and tail". These movements were not constantly homolateral or heterolateral, but only usually one or the other. He does not state how far the movements obtained in different animals resembled or differed from each other, except for two lizards. One of these, from the motor area in question, gave movements of the "foreleg, jaw and eye muscles, neck and throat muscles, and anterior body musculature". The other, from the anterior part of this motor area, gave "strong contractions of the pelvic muscles, and movements of the hindlegs", and from the lateral part of the area a "definite torsion of the forepart of the body".

Bagley & Richter and Bagley & Langworthy made use of alligators and obtained their best results without any anaesthetic. Movements were obtained from a similar motor area, and appear to have been of the same irregular type, usually involving both neck, trunk and tail and more than one limb. Single movements of a limb were never obtained. Their results differ from Johnston's in two important respects. They state that the striatum is completely inexcitable, whereas Johnston obtained movements from the striatum which he though were due to stimulation of the crus passing through it. They also state that the movements were obtained most easily from the medial side of the hemisphere (i.e. from the surface of the septum) and that the conduction of the motor impulse is down this medial wall, presumably in the medial forebrain bundle system. Johnston could get no response from the medial wall of the hemisphere in the turtle.

None of these workers found any evidence for the localization of precise movements. Johnston states "tentatively and with reserve that leg movements have been obtained most often from the anterior part of this area, and eye, jaw and neck movements from the lateral portion". Bagley & Langworthy found that the outer part of their area favoured movements of the legs, and the medio-dorsal part those of the head and tail.

It is clearly impossible to bring these varying results into any uniform scheme. It may be that different reptiles, even different species of lizards, differ far more than one would expect. On the other hand, differences in technique may also explain the inconsistences. The obvious fallacy in dealing with a small brain is the possibility of the spread of the stimulus to adjacent structures. The workers who have obtained positive results appear to have taken efficient precautions against this, and to have controlled their experiments with care, particularly in the case of Bagley & Langworthy's experiments on the alligator. On the other hand, it is difficult to discredit negative results on technical grounds, since technical errors are more likely to give false positive results in experiments of this kind than negative ones. It is possible that the anaesthetic had depressed the excitability of the cortex although Johnston obtained his results under far deeper anaesthesia than was used here. Operative damage to the cortex and interference with its blood supply might account for negative results, but care was taken to avoid these accidents, and, as far as could be seen, with success.

In this unsatisfactory state of affairs one must be very cautious about basing any conclusions on the results of forebrain stimulation in reptiles. It can at least be said that these negative results, and Bagley & Langworthy's results, although at variance over the main question whether the cortex is excitable or not, agree in finding no evidence of a descending motor tract from the antero-lateral part of the cortex which passes like the pyramidal tract of mammals through the striatum. They indicate the possibility of the conduction of motor impulses down the medial side of the hemisphere. Histological evidence shows that such a path may be present as part of the alveus system, and the Marchi experiments suggest that it is not a long tract, but consists of short fibres which connect the cortex with the septum, whence their impulses could be relayed to lower levels in the medial forebrain bundle system.

The ease and constancy with which movements can be obtained by stimulation of the tectum of the midbrain indicate that this is a very important and perhaps the dominant motor mechanism of the lizard brain. Its extent is considerable and its histological complexity far in advance of anything found in the forebrain. It is surprising that the main response affected always the tail and trunk muscles, but this may be because in such a small animal it is impossible to localize the stimulus to discrete parts of the tectum. The larger trunk and tail movements might then overshadow the finer ones. There was some evidence that the cortex might modify the activity of the tectum, but as a whole the results suggest that the control of movements, which is a function of the motor area of the neopallium of mammals, is localized in the midbrain of reptiles. This function of the midbrain is modified in a general way, e.g. by facilitation or inhibition, by impulses from the forebrain. There is no evidence for the exact and detailed representation of movements in the hemisphere of the lizard as there is in that of mammals.

The ablation experiments are for the most part in accord with this conclusion and with the similar experiments of Steiner (1900) on the lizard, and of Bagley & Langworthy (1926) on the alligator.

It appears that large unilateral lesions of the cortex lead to no obvious change in the behaviour of a lizard. In the only case in this series (XXIV) where the cortical lesions were bilateral, the animal was sluggish, refused to eat, and showed slight hypertonus. In this animal there was some striatal and diencephalic damage due to infection and haemorrhage. It is probable that this damage is really responsible for the changes in behaviour observed, since Steiner found that complete decortication left the animal apparently normal.

Extensive damage to the basal centres, comprising the striatum and septum or paraterminal body, led constantly to an extreme sluggishness with almost a complete lack of any spontaneous activity, an inability to feed, slight hypertonus chiefly of the muscles of the neck and trunk, and to the curious jumping gait after strong stimulation. These changes were seen even after the attempted hemidecerebration (XXV), where the whole thalamus and one corpus striatum were still intact and found to be free from any damage by infection and haemorrhage after 10 days. Steiner states that he observed the jumping gait only after the removal of the thalamus. From his diagram of the brain after the removal of the hemispheres alone it appears that a very considerable part of the striatum was left intact, and it may well be that it was the removal of this part of the striatum and not of the thalamus which led to the appearance of this type of progression in his second series of experiments. He did not check the amount of brain tissue removed after death by the method of serial sections.

Steiner observed no hypertonus and no postural change after decerebration, and with this Bagley & Langworthy are in agreement in their experiments on the alligator. As in the stimulation experiments, the negative finding is less open to criticism on technical grounds than the positive, but in spite of this it seems worth while to put these observations on lizards on record. As far as they go, they suggest on the positive side some participation of the basal centres of the hemispheres in the distribution of tone and in feeding activities. In addition these parts seem to have an influence on mechanisms in lower levels of the nervous system, perhaps of the nature of facilitation, which shows itself in the apparently spontaneous activity of the normal animal. On the negative side there is complete agreement in all the results so far published. There is no evidence from ablation experiments that any movement is localized in the forebrain in such a way that removal of the forebrain, or of any part of it, leads to the loss of that movement. In other words there is nothing to suggest a localization of motor function of the type found in the motor area of the mammalian neopallium.

Structurally there is no evidence for the presence of long efferent projection tracts from the cortex. The efferent cortical fibres are short and run mainly to the septum whence they are relayed into the medial forebrain bundle, and perhaps laterally by way of the striatum into the lateral forebrain bundle. It seems unlikely that this relay is a simple affair, transferring the impulse with little alteration to lower centres. There is some evidence that in birds the striatum is responsible for the co-ordination of different movements into an orderly behaviour sequence (the complete performance of the act of feeding is one of the simpler sequences which are dependent on the integrity of a part of the corpus striatum in birds; Rogers, 1922), and it is likely that the basal centres of the reptilian brain have similar functions. From the results recorded above this appears to be true in relation to feeding at least. Cortical impulses will probably play upon these basal co-ordinating mechanisms, modifying their activity in some way that these experiments are too crude to reveal. They would not control movement directly, and therefore differ functionally as well as structurally from the motor parts of the neopallium of mammals.

SUMMARY

Marchi experiments

The ordinary technique was used, but it was found that a post-operative life of at least 30 days, during which degeneration could take place, was necessary. Warmth is essential during this period.

Though not so striking as the results obtained with mammalian material, positive staining of degenerated myelinated fibres was found after lesions in the olfactory tracts, the lateral forebrain bundle and, less certainly, in the alveus system.

Evidence was found for the following conclusions:

(i) Primary olfactory fibres from the main olfactory bulb are for the most part relayed in the anterior olfactory nucleus before passing to other forebrain centres.

(ii) The lateral olfactory tract consists predominantly of fibres from the accessory olfactory bulb and many of them reach the amygdaloid nuclei without an intermediate relay.

(iii) There is no efferent projection tract from the antero-dorsal region of the cortex. There is some evidence for the presence of short efferent fibres from the cortex passing medially in the alveus system to the paraterminal body (septum).

(iv) The lateral forebrain bundle contains efferent fibres from the corpus striatum, mainly its hypopallial part, which can be traced into the subthalamic region. Many end here, probably connecting with the hypothalamus. A few can be followed through into the tegmentum of the midbrain.

These conclusions naturally take no account of unmyelinated fibres.

Stimulation and ablation experiments

Under ether anaesthesia faradic stimulation of the cortex failed to elicit any motor response. From the tectum movements chiefly of the trunk and tail were obtained, and it was found that these movements could be modified by simultaneous stimulation of the cortex. This effect was not constant; it was usually of the nature of a partial inhibition, but sometimes the movement became better sustained although less in extent, and sometimes no effect could be detected.

Partial and complete removal of the hemispheres failed to demonstrate the localization of any precisely definable motor function in these parts of the brain. To some extent the experiments supported the idea that the striatum, and probably other basal centres, function as coordinating mechanisms in the synthesis of motor behaviour patterns, e.g. the feeding activities. They suggest that these centres participate in the control of muscular tone, and that they can facilitate or inhibit motor reactions in lower levels of the nervous system.

None of these experiments gives any support to the theory that the anterodorsal part of the cerebral cortex of reptiles is neopallial in nature.

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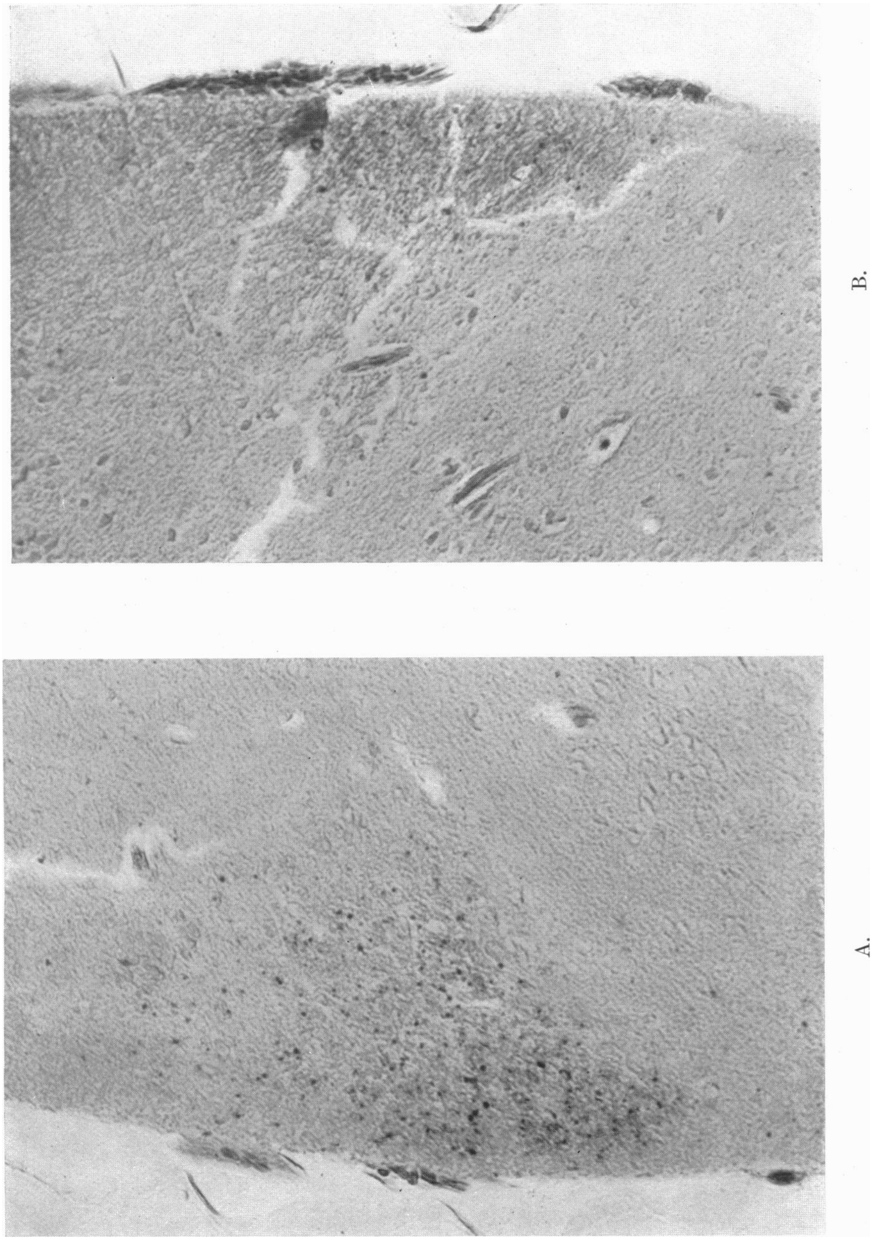
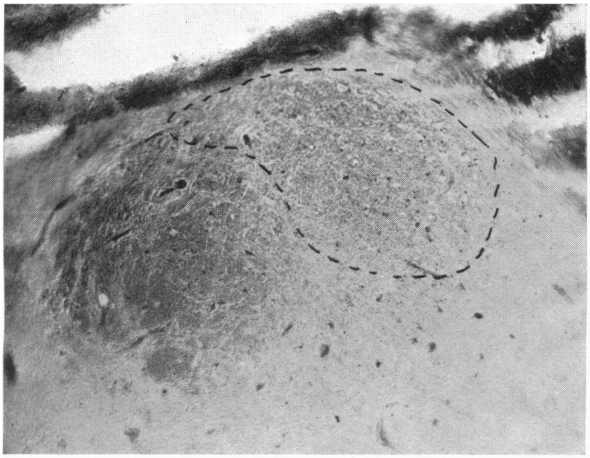


GOLDBY—Investigation of the Cerebral Hemispheres of *Lacerta viridis*



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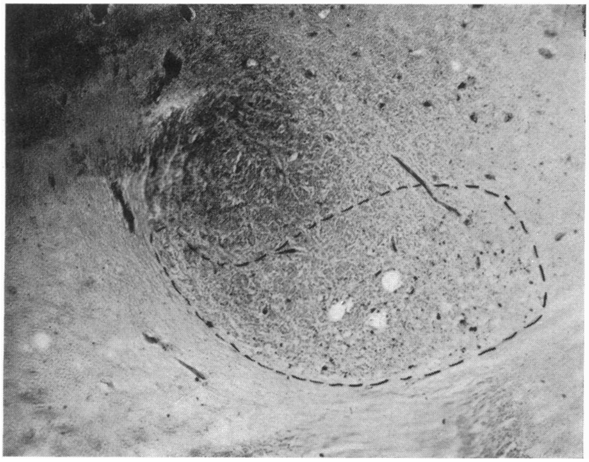

A.

GOLDBY—INVESTIGATION OF THE CEREBRAL HEMISPHERES OF *LACERTA VIRIDIS*

EXPLANATION OF PLATES I AND II

PLATE I

Lizard XVI. Photographs of the lateral olfactory tracts, A, from the degenerated, and B, from the normal side. Both photographs were taken from the same section which is drawn in outline in Text-fig. 3 (p. 335). The areas photographed have been marked in this figure.

PLATE II

Lizard XXXI. Photographs of the forebrain bundles in the subthalamic region, A, from the degenerated, B, from the normal side. The area covered by the ventral peduncle of the combined forebrain bundles is surrounded by a dotted line. Text-fig. 10 (p. 342) is a drawing of the section from which these photographs were taken, and the area covered by them is marked on it. For a description of the degenerative changes shown, see the text (p. 341).

ABBREVIATIONS USED IN THE FIGURES

Key to lettering

B. Olf.	Bulbus olfactorius.	*Med.*	Medulla.
B. Olf. Acc.	Bulbus olfactorius accessorius.	*N. Olf. Ant.*	Nucleus olfactorius anterior.
Bas. Opt. Rt.	Basal optic root.	*Palst.*	Palaeostriatum.
Cereb.	Cerebellum.	*Ped. Olf.*	Pedunculus olfactorius.
Com. Post.	Commissura posterior.	*Ped. Dor.*	Pedunculus dorsalis.
Cx. Dor.	Cortex dorsalis.	*Ped. Vent.*	Pedunculus ventralis.
Cx. Hip.	Cortex hippocampi.	*Prim. Neop.*	Primordium neopallii.
Cx. Hip. (*L.C.*)	Cortex hippocampi, large celled part.	*Sept.*	Septum (paraterminal body).
Cx. Hip. (*S.C.*)	Cortex hippocampi, small celled part.	*Tect. Opt.*	Tectum opticum.
Cx. Pyr.	Cortex pyriformis.	*Thal.*	Thalamus.
Fs. End.	Fissura endorhinalis.	*Tr. Olf. Lat.*	Tractus olfactorius lateralis.
Hyp.	Hypopallium.	*Tr. Opt.*	Tractus opticus.
Hypoth.	Hypothalamus.	*Tub. Olf.*	Tuberculum olfactorium.
L.F.B.	Lateral forebrain bundle.	*Vent. III.*	IIIrd ventricle.