A STUDY OF BRAINS:
An Exercise in the Understanding of Evolutionary Trends at Work

Frank Pace

It is perhaps important to point out that not all animals have a "brain". In fact, being unicellular or colonial conglomerations of cells, Protozoa have not yet acquired the complexities of differentiation found in higher animals. Althouh these simple animals do show sensitivity and respond to environmental stimuli they still lack nerve cells. In the Coelenterates (jellyfish, hydras and sea-anemones) one gets differentiation of the body into different cell types... some of these being directly concerned with the transmisson of nerve impulses. The multipolar neurons and their axons ramify through the bodies of the these diploblastic animals and the systems are so diffuse that the set-up is usually referred to as a "nerve-net". However this tends to become aggregated to form specialized nerve tracts in animals which are higher up in the evolutionary tree. Since many sense organs become concentrated in the head (cephalization) concommitantly the nerve tracts in these regions become further elaborated and nerve masses or ganglia are formed. These in fact become the rudiments from which higher and more complex brains arise.

In Turbellarians a mass of nervous tissue becomes associated with the eyes, the chemoreceptors and the rheoceptors (current detectors). Removal of such a brain will produce a disorganization of complex forms of locomotion, the animal becomes hypersensitive and the "inhibiting" effect of the brain is lost. A simpler kind of response is obtained when the supra-oesophageal or cerebral ganglia of annelids and arthropods are removed. The cerebral ganglia act primarily as a sensory relay centre which passes information to the motor sub-oesphageal ganglia via the commisures. If one of the latter is cut, the limbs on the cut side show additional activity and "circus" movements ensues due to the inability of the cerebral ganglia in inhibiting these responses. One gets a tendency in the animal kingdom towards an increase in the centralization of the control of activities. Thus the primitive local reflexes tend to get a certain degree of dependence on the integrating areas and higher motor centre. These excite lower motor centres and finally one gets the response from the effectors. Concommitantly with this trend one gets more elaborate connections and interrelations in the higher animal's brain.

SENSORY CENTRES —— HIGHER MOTOR AND INTEGRATING CENTRES —— LOWER MOTOR CENTRES

Environment Stimuli Effectors

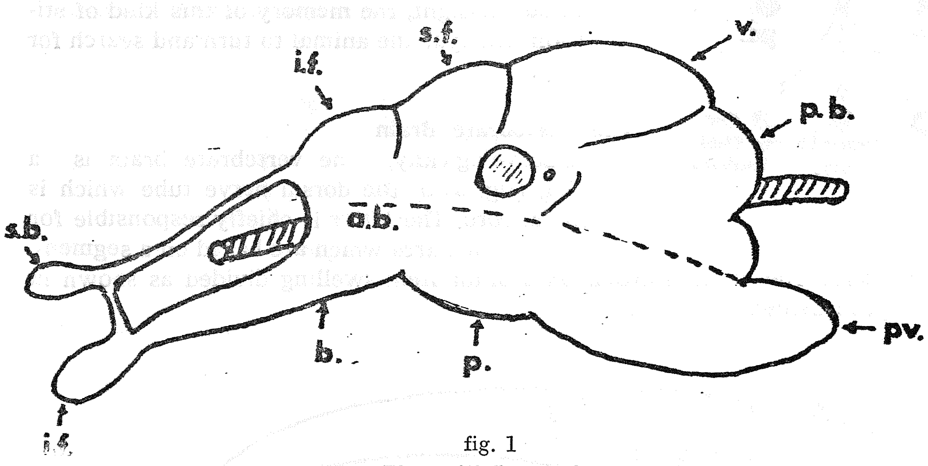


fig. 1

The Cuttlefish Brain

Guide to labelling: a.b. anterior basal lobe, i.f. inferior frontal lobe, s.f. superior frontal lobe, v. vertical lobe, p.b. posterior basal lobe, b. branchial lobe, p. pedal lobe, pv. pallio-visceral Lobe, s.b. superior buccal lobe.

A Complex Invertebrate Brain as exemplified by that of the Cephalopod Mollusc. (fig. 1)

Using classical neurological techniques one can work out the function of the different parts. Removal of the supraoesophagal part or mass results in the usual restlessness and hypersensitivity as with the annelids. The squid swims about continuously and if just one side has been removed circus movement is shown. If more local incisions are made, one finds that the anterior lobe of the basal part acts as a higher motor centre for co-ordinating swimming. It inhibits the action of the palliovisceral lobe which is responsible for the continual mantle contractions and funnel and fin movements. The anterior basal lobe itself seems to be controlled by higher sensory centres around the optic nerve. This centre is a very important sensory centre in Cephalopods. Stimulation of all lobes one by one resulted in co-ordinated activity of different sets of muscles as shown in the ordinary behaviour of the animal. One would therefore conclude that the different lobes are arranged on a hierarchial principle, and thus one gets multiple control of lower motor centres from the higher motor centres.

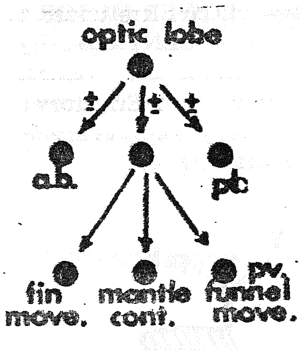


fig. 2

Stimulation of the vertical and frontal lobes of the cephaloped brain does not affect muscles and swimming. These regions seem to be important for learning and integrated complex behavioural patterns found in the animals e.g. as soon as a prey moves out of sight, the memory of this kind of stimulation will spur the animal to turn and search for the prey.

The Vertebrate Brain

Embryologically, the vertebrate brain is a swelling (fig. 3) of the dorsal nerve tube which is the spinal cord. The latter is chiefly responsible for involutary reflex arcs which are based on a segmental pattern. The brain is based on a brain stem swelling divided as shown in the figure below.

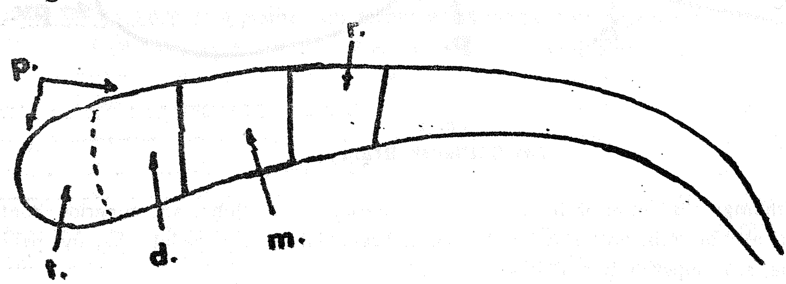


fig. 3

Guide to labelling: p. prosencephalon, t: telencephalon, d. diencephalon, m. mesencephalon, r. rhombencephalon.

Early on in evolution, occurs the division of the prosenccephalon into a telencephalon and a diencephalon. All these parts have been elaborated further in evolution so that the diencephalon, to quote this part as an example, gave rise to the thalamus, epithalamus, hypothalamus and the infundibulum. Primitivily, in fact, the brain shows an acute resemblance to the spinal cord both in its structure and segmental pattern. Thus somatic dorsal nerves carry sensory impulses from skin and muscle proprioreceptors. Visceral nerves carry sensory impulses from the smooth muscles of the viscera e.g. gut, uterus and blood vessels. Correspondingly one gets the somatic motor nerves supplying the voluntary muscle and the visceral motor nerves supplying the smooth and involuntary masculature. This set up is found in all vertebrates. In addition one may get in the higher forms, the visceral part of this pattern contributing towards the specialized autonomic nervous system with antagonistic sympathetic and parasympathetic contributions by which involuntary muscles are under a more highly elaborated control. Concommitantly with this one gets ventrally situated gangalia which establish new connections with dorsal and ventral nerve roots. The medulla oblongata, being the hinder part of the brain, shows this differentiation of entry of somatic sensory, visceral sensory, visceral motor and somatic motor nerves quite clearly by a sulcus limitans. (fig. 4)

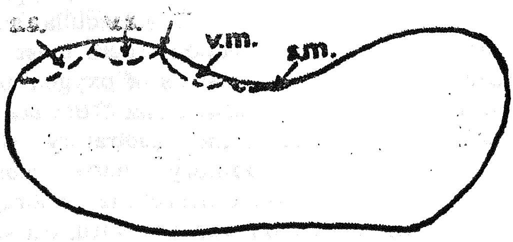
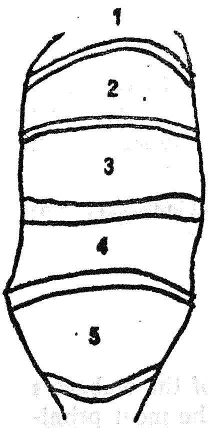


fig. 4

Gudie to labelling: s.s somatic sensory, v.s. visceral sensory, s.l. sulcus limitans, v.m. visceral motor ,s.m. somatic motor.

All but two of the cranial nerves end either in a sensory or a motor centre. These two are the Optic nerve (II) and the Olfactory (I). Cranial nerve I is very old evolutionary speaking; in fact there are reasons to believe that it preceded the brain. The optic nerve is not a derivation from the brain but a sensory tract arising from the eye. Embryologically the brain is formed from neuricrest cells which link the fold ends of an ectodermal longitudinally directed invagination. Between five bridges of nervous (fig. 5) material one gets spaces of non-nervous tissue. These represent a sequence of five segments. These segments later contributed to the main parts of the brain and their dorsal and ventral roots gave existence to the cranial nerves.



	Corresponding Cranial nerves	
	Dorsal	Ventral
Seg I Cerebellum	VI	III
Seg II Optic Tectum	VII, VIII	IV
Seg III Habenular	VII	VI
Seg IV Anterior commisure	IX	XII
Seg V Corpus callosum		

The Rhombencephalon (Hind-Brain)

This comprises the myelencephalon (medulla oblongata) and the metencephalon which includes the cerebellum and the pons. Histologically it shows up as descrete nuclei of axons; nervous tissue randomly distributed surrounds these nuclei. At certain regions of the medulla oblongata one gets a set of interlacing fibres which form motor and sensory decussations. If one removes the medulla oblongata and all the other parts of the brain, the spinal animal shows, after a period of spinal shock, a certain amount of mascular tone. However the animal cannot respire and this is accompanied by a fall in blood pressure. A bulbal animal however (i.e. with an intact medulla oblongata) can exhibit local reflexes and other reactions such as vomiting, sneezing and swallowing. The animal can respire and can control its blood pressure to some extent. Thus in the medulla oblongata there are nuclei centres responsible for motor function. There must also be some kind of respiratory centre sensitive to the tensions of oxygen and carbon diovide in the blood. The work of Pitts et al. showed that there are two sets ofnuclei; the expiratory nuclei being dorsal to the inspiratory nuclei. Application of electrode shocks into the inspiratory centre caused an increase of discharges of potentials in the phrenic nerve, the diaphragm contracted for three minutes and rhythmic respiration was abolished. On stimulating the expiratory centre, one would get a decrease in phrenic nerve discharge, the animal would breath out for one minute and after this the animal would breath in again. In primitive vertebrates, the medulla receives impulses from the lateral line system. (fig. 6) In the evolution of the tetrapods this has been drastically reduced and the nervous connections became adapted to serve the labyrinth of the ear, the sole vestige and functional part of the lateral line system. With the medulla one gets the associated vascularised non-nervous posterior choroid plexus.

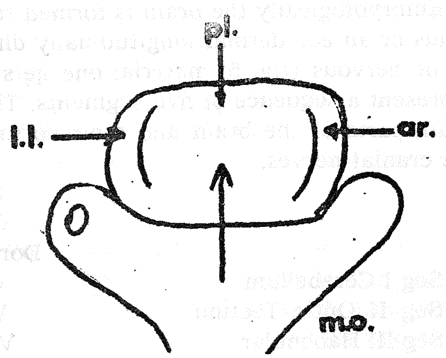


fig. 6

Guide to labelling: ar. archicerebellum, pl paleocerebellum, m.o. medulla oblongata, 1.1. lateral line reflex centre.

The Cerebellum

The cerebellum is the first of the five major commisures of the embryo's brain, its function being co-ordination of the central reflexes. The most primitive part of the cerebellum (fig. 7) is the archicerebellum which still retains some connection with the lateral line system.

The setup shown in the diagram persists in the case of fishes, amphibia reptiles and birds which lack the neocerebellum. The latter structure which is evolutionary more recent is found only in mammals. The archicerebellum at this stage retains its useful function as a centre of equilibrium in that it supplies the labyrinth of inner ear.

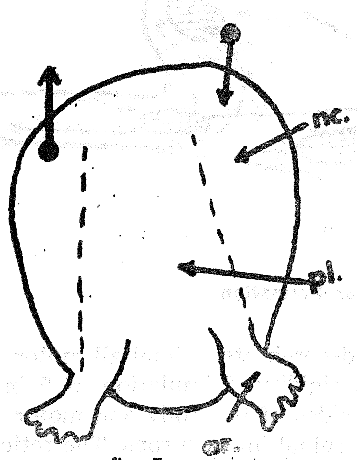


fig. 7

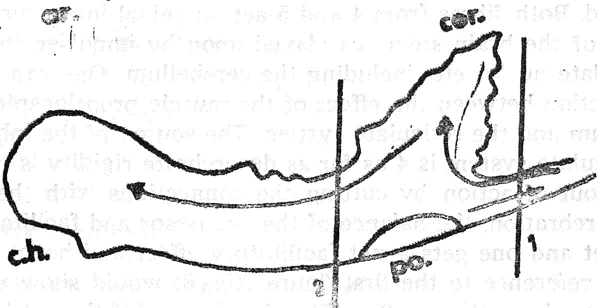


fig. 8

Guide to labelling: (fig. 7) nc. neocerebellum, pl. paleocerebellum, ar. archicerebellum. (fig. 8) c.h. cerebral hemispheres, cer. cerebellum, po. pons.

Sea-sickness pills probably act on this centre. Examine now the set-up of a cat's brain (fig. 8). If one cuts the brain at 2, the animal becomes stiff, the extensor muscles become contracted, the tail is raised and the head elavated. All these are symptoms of "decerebrate rigidity". For a good understanding of the cause of this phenomenon one would have to consider the reticulate system (reticulate formation) of the mammalian brain. The work of Magoun at al. has shown this to be made up of scattered grey matter intersected by fibres running in all directions.

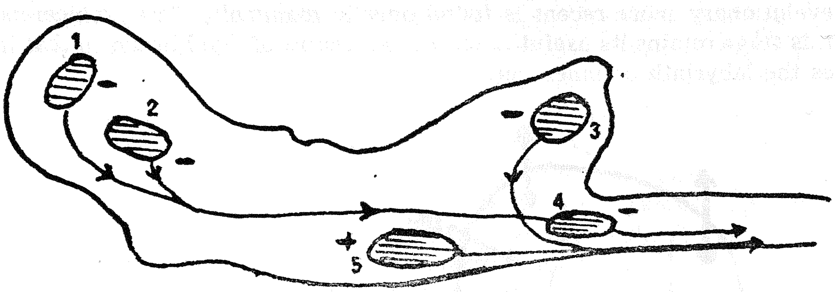


fig. 9

The Reticular Formation

When area 4 is stimulated in a decerebrate animal all motor activity is abolished and one gets a decrease in rigidity. Stimulation of 5 in a normal animal facilitates movements on both sides of the body and motor activity is aided. Both fibres from 4 and 5 act on spinal interneurons. The reticular neurons of the brain stem are played upon by impulses from the cerebral cortex, caudate nuclei etc. including the cerebellum. One can now understand the interaction between the effect of the muscle proprioceptor impulses at the cerebellum and the reticulate system. The source of the inhibitory impulses on the reticulate system is 4 as far as decerebrate rigidity is concerned. When this is put out of action by cutting the connections with the rest of the system by decerebration, the balance of the suppresor and facilitatory reticular system is offset and one gets a net facilitatory effect and hence decerebrate rigidity. In fact reference to the first figure (fig. 8) would show that the short-circuiting process by cutting at 2 will not be obtained if the cut is made through plane 1.

The Mesencephalon (Mid-Brain)

The mid-brain includes the area above the sulcus limitans or the sensory tectum associated with the eye and derived from the embryo's second commisure and the area below the sulcus limitans or the tegmentum made up of unspecialized reticulum. Primitively, apart from functioning as optic centres, the mid-brain structures were even responsible as an association area. In fact, in fish and amphibia (fig. 10) the optic tectum is a dominant structure and is responsible for such reactions as those associated with fight or flight. Sanders has demonstrated the learning behaviour of goldfish to be entirely dependent on the integrity of the optic tectum. In fact stimuli from the two optic lobes and olfactory regions pass through the brain (diencephalon) and go to the primary visual centre in the the tectum and in the association area. These will evoke well-coordinated responses by the motor neurons leaving the area. In fact the set-up can be summarised diagramatically by consideration of a teleost's brain mid-brain nervous system.

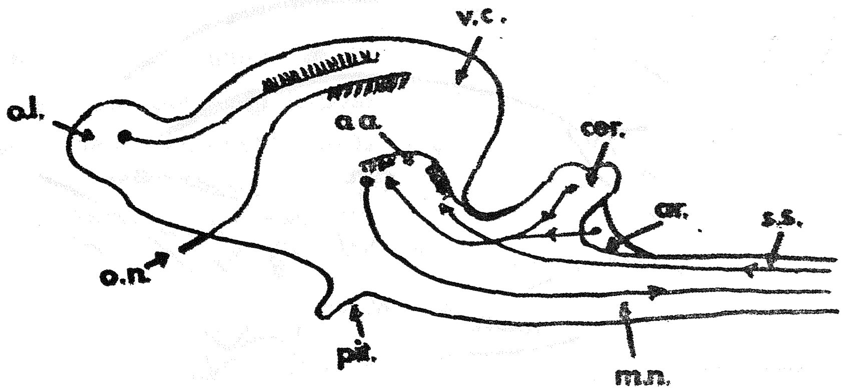


fig. 10

Teleost Brain

Guide to labelling: o.o olfactory lobe, a.a. association area, v.c. primary visual centre, cer. cerebellum, ar. archicerebellum, s.s somatic sensory m.n. motor nerves, pit. pituitary, o.n. optic nerve.

The Diencephalon (Posterior Fore-Brain)

The posterior fore-brain is made up essentially of three main parts. The dorsal region is the epithalmus or the third commisure known as the habenular. It lies on the root of the nerve tracts leading from the olfactory lobes to the brain. The thalamus is the second region and can be considered as a relay station on the ascending sensory pathways. It is a mass of grey matter with three main nuclei which receive impulses from the hypothalamus, cerebellum and sends these impulses to the cerebral cortex. The thalamus is responsible for the sensitivity of the superficial surface of the animal e.g. tactile, painful or thermal stimuli. Pain is in fact appreciated at the thalamic level and not at the cortical level since stimulation of the cerebral cortex does not evoke pain. There is still a lot of mystery enshrouding the functions of the thalamus. The final structure contributing to the diencephalon is the hypothalamus situated as the name implies venrally in the brain. It is very important structure physiologically since it can be considered to be the integrator of the autonomic nervous system. The nuclei can be conveniently divided into four groups: (fig. 11) (1) Anterior hypothalmic nuclei (paraventricular and supraoptic). (2) Middle hypothalamic nuclei (tuberal, dorsomedial and ventromendial). (3) Posterior nuclei (posterior nuclei proper and mamillary nuclei) (4) Lateral nuclei.

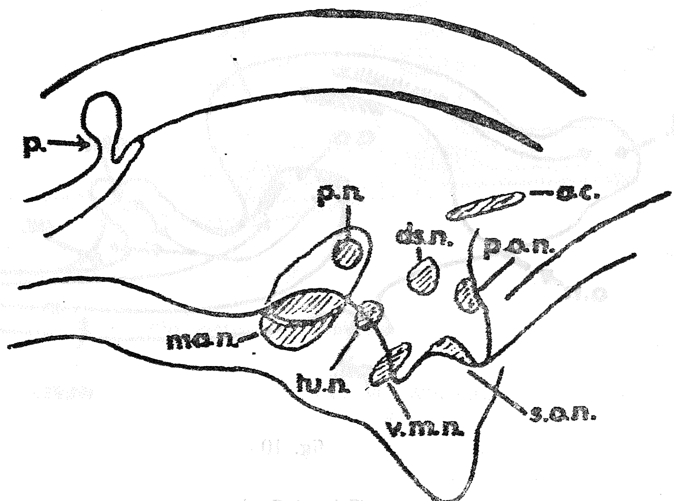


fig. 11

The Hypothalamus: Distribution of Nuclei

Guide to labelling: p. pineal organ, p.n. posterior nuclei, ds.n. dorsomedial nuclei, a.c. anterior commisure, p.o.n. preoptic nuclei, s.o.n. supraoptic nuclei. v.m.n. ventromedial hypothalamic nuclei, tu.n. tubernal nuclei, ma.n. mamillary nuclei.

Hess, by introducing electrodes into the hypothalamus of a conscious cat could evoke different reactions such as sleep, rage, hypersexuality, etc. More localised stimulation of the anterior and middle nuclei had a parasympathetic effect e.g. sweating, bladder contraction, cardiac inhibition and peristalsis of the gut. If on the other hand, the posterior and lateral nuclei are stimulated one gets piloerection, dilation of pupil, cardiac acceleration and inhibition of gut peristalsis. This shows that although the hypothalamus is not essential for sympathetic and para-sympathetic effects (a decerebrated animal from the pons retains cardiac reflexes) it comes into play under periods of stress. Moreover it is essential for body temperature regulation in homeothermic animals. In the cold, the posterior hypothalamus is responsible for vasocontriction and shivering. The anterior, on the other hand is sensitive to a

rise in body temperature and thus causes sweating and vasodilation. On destroy ing the supraoptic nucleus and removing the infundibulum, ADH or vasopressin production, from the pituitary stops and one gets diabetes insipidus. At the onset of this, no water absorption takes place in the kidney tubules. The animal drinks to compensate for the large volume of water lost in the urine which may reach up to forty litres a day! The area of the supraoptic nucleus is known to secrete antidiuretic hormone since this is released when the nucleus is injected with acetylholine.

The Telencephalon

During evolution the forebrain telencephalon has developed from a primary olfactory area to the main association centre in the mammalian brain. Primitively it was an unpaired structure and later invagination caused a division of the most anterior part into two olfactory lobes. In the cyclostomes the telencephalon still retains its primitive condition in that it consists of two olfactory lobes and a paleopallium which is strictly olfactory in function. Olfac-

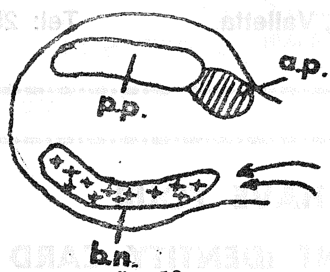


fig. 12a

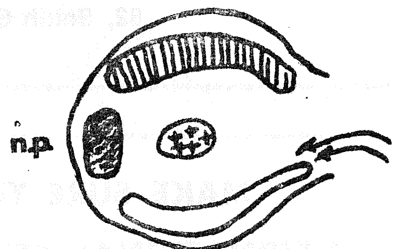


fig. 12b

Guide to labelling: p.p. paleopallium,, a.p. archipallium (hippocampus) b.n. basal nuclei (corpus striatum), n.p. neopallium.

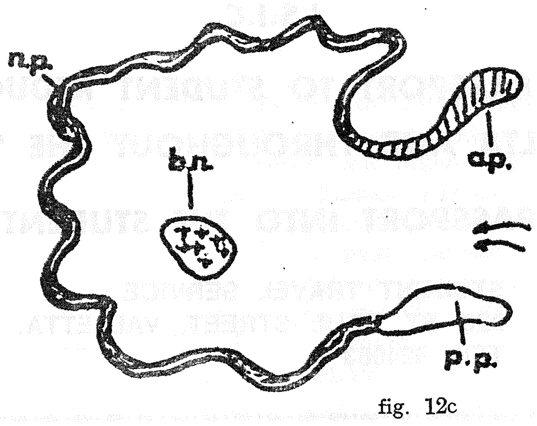


fig. 12c

tory sensations are sent along tracts through the diencephalon to be co-ordinated at other areas e.g. the cerebellum. In amphibians a new area is developed as an archipallium and a transverse section through the olfactory lobes of an amphibian will show the set-up (fig. 12a). The basal nuclei receive sensory impulses from the thalamus and this is in fact showing the beginning of a trend that is to follow. In reptiles one gets the development of the telencephalon into a correlation centre proper which gets more pronounced.

The neopallium, which is the fore-runner of the mammalian cortex is elaborated as an association centre and receives nervous connections from the thalamus region for interpretation (fig. 12b). In the mammals the neopallium expands and is elaborated into cerebral hemispheres (fig. 12c), two large correlation structures covering most of the brain; it acquires connections with the pons and the thalamus and a pyramidal tract shows up. Thus association which was primitively a function of the optic tectum (c.f. fig 10) is taken over by the neopallium or the cerebral cortex which receives optic, auditory and other impulses via the thalamus. This sensory information evokes appropriate motor response in the pons, the major motor region of the brain. The cerebral hemispheres cover the mid-brain and even part of the cerebellum (fig. 13). The cerebral cortex increases in surface area by convolution and folding of the surface. In man deeper grooves or sulci are prominent and show up as lines on the surface. These folds separate the different areas of the brain.

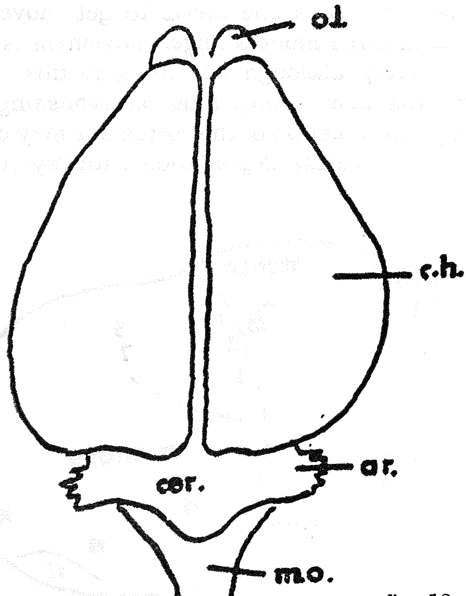


fig. 13

Guide to labelling: o.l. olfactory lobe, c.h. cerebral hemispheres, ar. archicerebellum, m.o. medulla oblongata, cer. cerebellum.

The fifth commisure of the neural crest cells in the embryo develops into the corpus callosum which bridges the two cerebral hemispheres. The main central sulcus and other important and prominent sulci enable the division of the brain into frontal lobe, pariental lobe, temporal lobe and occipital lobe. The minor sulci give the location of smaller areas knows as gyri. Histologically the cortical three layers of the embryo become differentiated into six layers of the adult.

These six layers are differentiated differently in different parts of the cerebral hemispheres and these histological studies or architectonics have enabled appropriate mapping out of the areas in the cerebral cortex and numbering of these areas as suggested by Brodman. The six histological layers are the molecular layer, the outer granular layer (small pyramidal) the medium pyramidal layer, the granular layer, the ganglionic large pyramidal layer and the polymorphous or tissiform layer. The granular layer is said to be the main arrival area of the thalamus fibres. The third layer is prominent in the frontal lobes and layer 5 or ganglionic is characteristic of the motor cortex.

In 1870, Fritsch and Hitzig applied electric stimulation to the frontal cortex and had movements of the dog on opposite sides of the body. Ferrier, a few years later tried a definite technique viz that of ablation. Removal of the area, which on stimulation gave movements of a chimpanzee's hand, made this hand go limp. This was due to lack of motor discharge from the cerebral cortex. In two or three days one starts to get movement in the proximal shoulder joints and in three months finger movement is developed. The remarable degrees of recovery although not 100% results from the acquisition of new connections from new tissues thus reestablishing the reflexes to some extent. To see the motor function of the cortex one may cut the nerve in the arm or spinal cord and trace the degradation pathway right back to the cor-

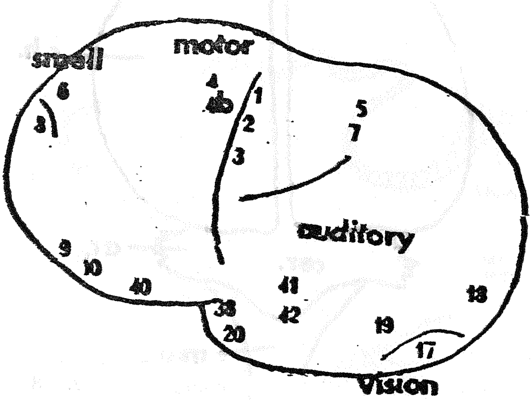


fig. 14

tex. The area in the cortex corresponding to the function usually degenerates and this can be seen by special staining (fig. 14).

Brodman's area 4 has the lowest threshold for electrical stimulation with a response in the body. In fact this is the motor cortex. Other areas do have a motor function but greater intensity of stimulation should be applid. The motor cortex is characterised histologically by having giant Betz cells, large neurons found in the V th layer associated with the large pyramidal neurons. If area 4 is exposed and a hot spatula is held longer than three seconds, all six layers of the cerebral ccrtex are killed. If only three layers are killed, one still gets motor activity displayed. The path of the Betz cell axons shows up as passing down through the pons to the pyramids where they cross over and form the pyramidal tracts. In all higher mammals, the part of the motor area near the vertex of the skull is concerned with movements of the leg, the middle part with the arms and the lowest part of area 4 with movements of the face.

A transverse secetion through the central sulcus will show up the mapping of the motor area in more detail. The problem is to what extent are the individual muscles represented in the cortex. Does every muscle have one cortical site? Ferrier found that there was considerable overlapping of areas. On stimulating the thumb area one also gets some amount of finger movement. Liddell tried to solve this problem by working on the motor cortex of *Papio papio*, the baboon. On altering the intensity of stimulation on area 4 he got a good seperation of the areas e.g. thumb, index, etc. It is believed by some that currents of suitable intensity and frequently applied to the motor cortex in man will evoke single muscle movements. Others believe that the cortex deals with co-ordinated movements. Penfield and others say that movements of cortical stimulation are quite simple and not skilled and acquired as in the adult. Area 6, (fig. 14), the premotor area of mammals lacks Betz cells and

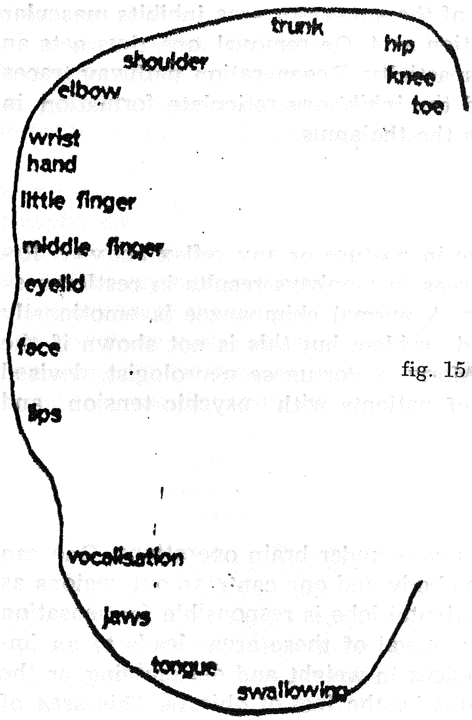


fig. 15

Motor Cortex (Man)

hence is not easily stimulated. Electrical stimulation of area 6 causes movements of groups of muscles and whole limbs. If the whole of the motor cortex of rabbit is removed, hopping and placing reactions are lost. If the area 4 in monkeys is destroyed, the animal develops hemiplagia i.e. paralysis and loss of voluntary movements on the opposite side of the body. If the pyramidal tracts in the medulla oblongata are cut, the abdomen protrudes the head sags and the limbs become flacccid. After some time sitting and walking become possible but the ability to perform accurate and delicate movements is lost. One would conclude that:

(1) Voluntary movment can be carried in fibres other than the pyramidal tracts
(2) pyramidal fibres are important in willed skilled movements
(3) most other reflexes and posture movements are under the influence of the cortex. If the ablation extends from area 4 to area 6 one gets spastic paralysis in contrast to the flacid paralysis brought by removal of area 4. In spastic paralysis one gets the arms with increased flexor tones and the legs with increased extensor tone (c.f. decerebrate rigidity).

It is found that if 4 is removed, spasticity is produced in an animal. Later it was also discovered that stimulation of the suppresor area inhibits mascular tone and movements following stimulation at 4. On removal ,one thus gets an incontrolled discharge of 4 and hence spasticity. Degeneration pathway traces has shown connections between 4 and the inhibitory reticulate formation in the brain stem and with the 4 area via the thalamus.

Frontal Association Area.

On stimulation one gets no change in posture or any reflex activity. Removal of both sides of these frontal areas in monkeys results in restlessness and defects in learning and behaviour. A normal chimpanzee is emotionally upset if he fails to solve a complicated problem but this is not shown if the front association areas are removed. Moriz, a Portugese neurologist, devised prefrontal leucotomy for treatment of patients with psychic tension and anxiety.

Sensory Areas.

This has been investigated in humans under brain operations. One can get sensations from various parts of the body and one can map out regions as for the motor cortex. The important pariental lobe is responsible for sensation of touch and pressure. Destrution or removal of these areas leads to an impairment of the ability to detect differences in weight and determining or the appreciation of form in three dimensions by the feel of objects. This area of the cortex is capable of fine descrimination of stimulus and small differences in the intensity.

Temporal Lobes

These receive impulses from the ear's cocklea. In the monkey pure tones of high frequency cause nerve discharges in the caudal part of this area and with low tones in the rostral part. In dogs three distinct areas have been traced, two capable of coarse and one of fine discrimination.

Occipital Cortex

It has for long been known that removal of the cerebral cortex was accompanied by blindness. Recently the precise area of the human occipital cortex has been localised to Brodman's area 17 (fig. 14). The path of the optic nerve fihres have been followed by degeneration pathways from the retina. Fibres from the optic nerve have been found to cross over at the optic chiasmata. The areas 18 and 19 adjacent to area 17 and association areas in which co-ordination of eye reflexes with other reflexes occurs.

The prefrontal areas in primates are large and this is associated with complex behaviour and ability of learning shown by these higher animals. The higher functions such as consciousness, intelligence and insanity are difficult to define. A stimulus which in an ordinary animal produces an activity A will after a process of learning provoke a different activity B.

So between the sensory and motor areas of the brain there must be developed a pathway of low resistance during the learning process. This need not necessarily be anatomical e.g. by growth of processes. In fact neurologists object to possibility of branching in neurons which are so densely packed.

A change in size of the synaptic knobs, in fact an increase has been proved to occur with activity. This would in fact decrease the width of the synaptic cleft and hence more acetylcholine is produced and one gets faccilitation of condition.

The establishment of the pathway will be helped by the "engraving" of a memory trace which gets clearer and easier to perform with increasing use. However there is still vagueness of unscientific terms in describing these phenomena. One knows that nerve cells are dying and are being replaced contiuously and this memory trace and engraving involves more than just facilitation.

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