

JAMES ARTHUR LECTURE ON
THE EVOLUTION OF THE HUMAN BRAIN
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- Frederick Tilney, *The Brain in Relation to Behavior*; March 15, 1932
- C. Judson Herrick, *Brains as Instruments of Biological Values*; April 6, 1933
- D. M. S. Watson, *The Story of Fossil Brains from Fish to Man*; April 24, 1934
- C. U. Ariens Kappers, *Structural Principles in the Nervous System; The Development of the Forebrain in Animals and Prehistoric Human Races*; April 25, 1935
- Samuel T. Orton, *The Language Area of the Human Brain and Some of its Disorders*; May 15, 1936
- R. W. Gerard, *Dynamic Neutral Patterns*; April 15, 1937
- Franz Weidenreich, *The Phylogenetic Development of the Hominid Brain and its Connection with the Transformation of the Skull*; May 5, 1938
- G. Kingsley Noble, *The Neural Basis of Social Behavior of Vertebrates*; May 11, 1939
- John F. Fulton, *A Functional Approach to the Evolution of the Primate Brain*; May 2, 1940
- Frank A. Beach, *Central Nervous Mechanisms Involved in the Reproductive Behavior of Vertebrates*; May 8, 1941
- George Pinkley, *A History of the Human Brain*; May 14, 1942
- James W. Papez, *Ancient Landmarks of the Human Brain and Their Origin*; May 27, 1943
- James Howard McGregor, *The Brain of Primates*; May 11, 1944
- K. S. Lashley, *Neural Correlates of Intellect*; April 30, 1945
- Warren S. McCulloch, *Finality and Form in Nervous Activity*; May 2, 1946
- S. R. Detwiler, *Structure-Function Correlations in the Developing Nervous System as Studied by Experimental Methods*; May 8, 1947
- Tilly Edinger, *The Evolution of the Brain*; May 20, 1948
- Donald O. Hebb, *Evolution of Thought and Emotion*; April 20, 1949
- Ward Campbell Halstead, *Brain and Intelligence*; April 26, 1950
- Harry F. Harlow, *The Brain and Learned Behavior*; May 10, 1951
- Clinton N. Woolsey, *Sensory and Motor Systems of the Cerebral Cortex*; May 7, 1952
- Alfred S. Romer, *Brain Evolution in the Light of Vertebrate History*; May 21, 1953
- Horace W. Magoun, *Regulatory Functions of the Brain Stem*; May 5, 1954
- Fred A. Mettler, *Culture and the Structural Evolution of the Neural System*; April 21, 1955
- Pinckney J. Harman, *Paleoneurologic, Neoneurologic, and Ontogenetic Aspects of Brain Phylogeny*; April 26, 1956
- Davenport Hooker, *Evidence of Prenatal Function of the Central Nervous System in Man*; April 25, 1957
- David P. C. Lloyd, *The Discrete and the Diffuse in Nervous Action*; May 8, 1958
- Charles R. Noback, *The Heritage of the Human Brain*; May 6, 1959

THE HERITAGE OF THE HUMAN BRAIN

Heritage means inheritance. In this sense the present discussion pertains to the heritage of the human brain. However, the term "heritage" has another, more pertinent definition in phylogeny. It takes me back to the days when I was exposed to the dramatic world of evolution and the paleontology of the vertebrates here at the American Museum of Natural History by Professor William K. Gregory. To this master (1951), the heritage characters are the older, basic, conservative, and deep-seated traits in an organism. The heritage characters reveal the true place of an animal within the orders, classes, and families of the animal kingdom.

The human brain is the product of a long phylogenetic history. The past resides in the fabric of its structural and functional components. In this presentation I would like to discuss the possible evolution of some of these components. The elements selected include some with "long" phylogenetic histories and others with relatively "short" phylogenetic histories. Because many of these examples also apply to other units of the brain, some specific points will illustrate principles with a broader scope and significance. In addition a glimpse into this history will indicate that the human brain is a product of both "old" and "new" elements.

Background statement

The vertebrates have a recorded history of over four hundred million years (fig. 1), back into the Ordovician period when the oldest vertebrates, fish of the Class Agnatha (lampreys and hagfish are living examples), first ap-

peared in the fossil record. The Class Placodermi of fish appeared during the Silurian period and became extinct by the end of the Paleozoic era. The Class Chondrichthyes (cartilage fishes, including sharks and rays) and the Class Osteichthyes (bony fishes, including carp, trout, and flounder) were first found in the fossil record in the Devonian period. The fish that left the water gave rise to the Class Amphibia (living frogs and salamanders) during the late Devonian. The Class Reptilia appeared later in the Carboniferous period. During the first half of the Mesozoic era is found the first fossil evidence of the Class Aves (birds) and the Class Mammalia (warm-blooded, hairy animals). The orders of mammals were all established by the Paleocene period approximately 60,000,000 years ago. The evolution of all eight classes of vertebrates took place over a

Eras	Periods or Epochs	Approximate Time Since Beginning, in Millions of Years
Cenozoic	Recent	[About 20,000 years]
	Pleistocene	1
	Pliocene	10
	Miocene	25
	Oligocene	35
	Eocene	50
	Paleocene	60
Mesozoic	Cretaceous	120
	Jurassic	150
	Triassic	180
Paleozoic	Permian	210
	Carboniferous	270
	Devonian	300
	Silurian	330
	Ordovician	420
	Cambrian	510

FIG. 1. The geologic time scale.

tremendous span of time, during which the brain and the other organs had the opportunity to undergo a multitude of changes.

A characteristic of phylogeny is the persistence of change that continuously takes place in the successions of living organisms. The alterations result in change of complexity and modification of the subsequent and surviving forms which replace their antecedents. The procession of families, genera, and species within each of the eight classes throughout geologic time persisted until today's living vertebrates represent the culmination of prior evolution. Many forms became extinct. Some living fossils persist, such as the reptilian *Sphenodon*, a relic of the Permian, and the mammalian hedgehog and opossum, survivors of the Paleocene. Other living fossils also exist.

One of the grand expressions of the complexity and diversity of animal forms is the concept of adaptive radiation expressed by Henry F. Osborn, a former President of the American Museum. This concept implies the exploitation of the ways of life by organisms that utilize the opportunities that occur. Accompanying this invasion into the many ecological niches are the changes that occur within the organisms themselves. The source of this expression within the organism are genetic mutations, while many of those that persist have survival value. The interactions between the species and their environment express themselves in change and diversity. I am utilizing this concept to interpret the phylogeny of the brain, although this concept is usually applied to organisms.

Why stress these established concepts, which are obvious to any student of evolution? The fact is that these concepts are overlooked by some unwary biologists, including neuro-anatomists. A list of living mammals arranged in order of a sequence of structural differences has been interpreted as having phylogenetic significance, although it may have no

relation to the true phylogenetic position of the mammals. The "sequence" may in reality be an expression of adaptive radiation. For example, the number of uncrossed nerve fibers in the mammalian optic chiasma is correlated primarily with the location of the eyes (adaptive radiation) rather than with the phylogenetic position of the animal (see The Visual System, below). A mistaken notion of the relation between two mammals may be indicated by a statement such as, the cow and horse are closely related, when, in fact, these species are in two distinct orders (the former in the Artiodactyla and the latter in the Perissodactyla) the common ancestry of which is probably in the Paleocene when the orders of mammals were established.

The basic outlines of the phylogenetic tree have been worked out by the astute analyses of the fossil record by paleontologists. For obvious reasons it is difficult (impossible in most cases) to interpret the evolution of soft tissues from the direct fossil record. In a remarkable study, Tilly Edinger (1948) reconstructed the outlines of the evolution of the horse's brain from fossil brain casts and was able to draw a number of penetrating conclusions from this study. One such conclusion was that the surface anatomy of the brain of *Eohippus* (dawn horse) was similar to that of the common opossum—a living fossil.

However, for interpretations of the phylogeny of the brain, great reliance must be placed on a judicious selection of living forms and the utilization of living fossils. It is really a game of selecting controls out of nature's vast experimental design. In essence the successful reconstruction of the evolution of the brain requires the selection of animals that represent critical stages. One complication is that a "living fossil" may retain a multitude of primitive characters, but the one in question may be modified. For example, although the insectivores are living representatives of basic mammalian stock, the poor sight in many con-

temporary insectivores (mole and shrew) may be a regression. After this warning, I may fall into this trap.

Units under discussion

To illustrate the heritage of the human brain, I have selected several functional units of the nervous system. These include (1) the visual system, (2) the pyramidal system, (3) the reticular system and the lemniscal systems, and (4) the cortex of the cerebrum (fig. 2).

The visual system is a structurally compact sensory system with a long phylogenetic history. The pyramidal (corticospinal) system is a structurally compact motor system with a relatively short phylogenetic history. The reticular system is a diffuse, yet organized afferent and efferent system with a long phylogenetic history, and the lemniscal systems are structurally compact systems with phylogenetically new additions. The cortex of the cerebrum is the gray mantle of the cerebrum, of which portions have long phylogenetic histories and other portions, short phylogenetic histories.

The prefossil vertebrates

The vertebrates that preceded those in the fossil record developed or evolved from forms that possessed a cephalocaudal (head-tail) orientation and a bilateral symmetry. How this occurred is a matter of speculation, but the results are a matter of record. A constellation of general receptors (pain and so forth) and specialized receptors (smell, sight) were grouped at the head end. Along with this the brain differentiated in the central nervous system. A series of decussations and commissures (nerve cells with their cell bodies on one side and axons that cross the midline to the opposite half) apparently developed in the central nervous system as a mechanism for correlating the activities of the two halves of the body.

Two other fundamental morphologic features were ap-

parently established early in vertebrate evolution: (1) Blood vessels invaded the central nervous system and became intimately related to the neural elements of the brain and spinal cord. This feature is present only in chordates of all the animal phyla (von Bonin, 1950). (2) Three fundamental divisions are present in the brain of all vertebrates; prosencephalon (telencephalon and diencephalon), mesencephalon, and rhombencephalon (metencephalon and myelencephalon). Within these structures are the substrates from which the brains of all the vertebrates evolved throughout the more than four hundred million years of vertebrate phylogeny.

THE VISUAL SYSTEM

Man is a member of the primate order—an order which is difficult to characterize because of its many primitive features. However, two basic primate characters are the coordination of a well-developed visual sense and varying degrees of manual dexterity (Simpson, 1949).

Let us turn our attention to a consideration first of the visual system.

In most vertebrates, sight is the dominant sensation. The visual system is a window to a narrow band of radiation which creates a sensory awareness and a mental reaction. To the biologist, the sensory response is the crucial point. The significance of vision in man can be gauged from the fact that, of all the nerve fibers entering or leaving the central nervous system, more than one-third are in the optic nerves. Whereas the fibers of the optic nerve number over a million, those of the auditory nerve, in contrast, contain approximately thirty thousand fibers.

Let us examine the optic chiasma (figs. 2 and 4), the site of decussation of the fibers of the optic system. Walls (1942) claims that there is “no discernible reason for any [type of crossing, including the optic chiasma]—they apparently just

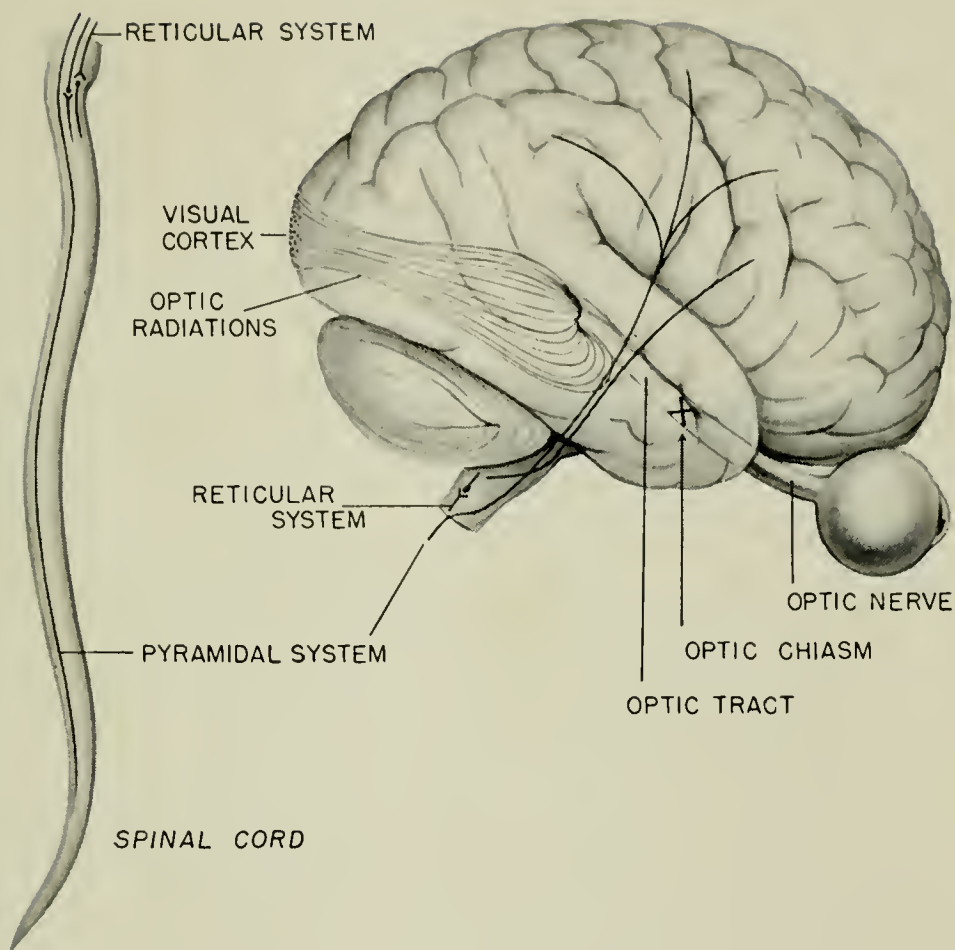


FIG. 2. The brain and spinal cord of man. Among the functional units of the nervous system discussed in the text are: (1) the visual system, represented by optic nerve, optic chiasma, optic tract, optic radiations, and visual cortex; (2) the pyramidal system—a motor system with a widespread cortical origin; (3) the reticular system, present throughout the central nervous system, represented by synaptic symbols indicating its multineuronal and multisynaptic nature; and (4) the cortex of the cerebrum which in man is folded into sulci and gyri.

happened . . . and became genetically fixed. . . ." Because chiasmata and commissures are frequent in the central nervous system of all vertebrates, they must have more than just chance significance. Possibly in primitive forms they may have been a chance affair associated with genetic mutations. Viewed pragmatically the crossing over was retained because it had biological and survival value to the organism. Ramón y Cajal's (1911) explanation is as brilliant and effective a hypothesis (Polyak, 1957) as has been advanced.

In reality there is no way of proving why crossing over occurred. In essence Cajal felt that the reaction to light, acting as a noxious stimulus to a prevertebrate, resulted in a withdrawal of the rostral end away from this stimulus. Hence the visual impulses were most effectively utilized in the economy of the organism by crossing to the opposite side. By the time the brain evolved, the decussation of the visual fibers was complete. In order to execute coordinated avoidance responses in a bilaterally symmetrical body it was necessary for the organism to relay the visual impulses to the musculature of the same and opposite side—hence the recrossing of the motor system. As a result, decussations have been retained.

Another explanation by Cajal for the optic decussation is indicated in figure 3. The fields of vision, which are represented by the arrows, are reversed by the lens of the eye. The result is that the projection on the retina is inverted. If each eye is stimulated by only part of the field, then the panorama of the field in the brain will not be reproduced accurately if the optic pathways do not decussate (fig. 3A) and will if the optic pathways do decussate (fig. 3B). Ovio (1927), who disagrees with Cajal's interpretation, claims that the entire field is projected to each eye and hence the presence or absence of a decussation is immaterial (fig. 3C and D). However, in laterally directed eyes Cajal's figures are probably correct. Because the early forms in which the

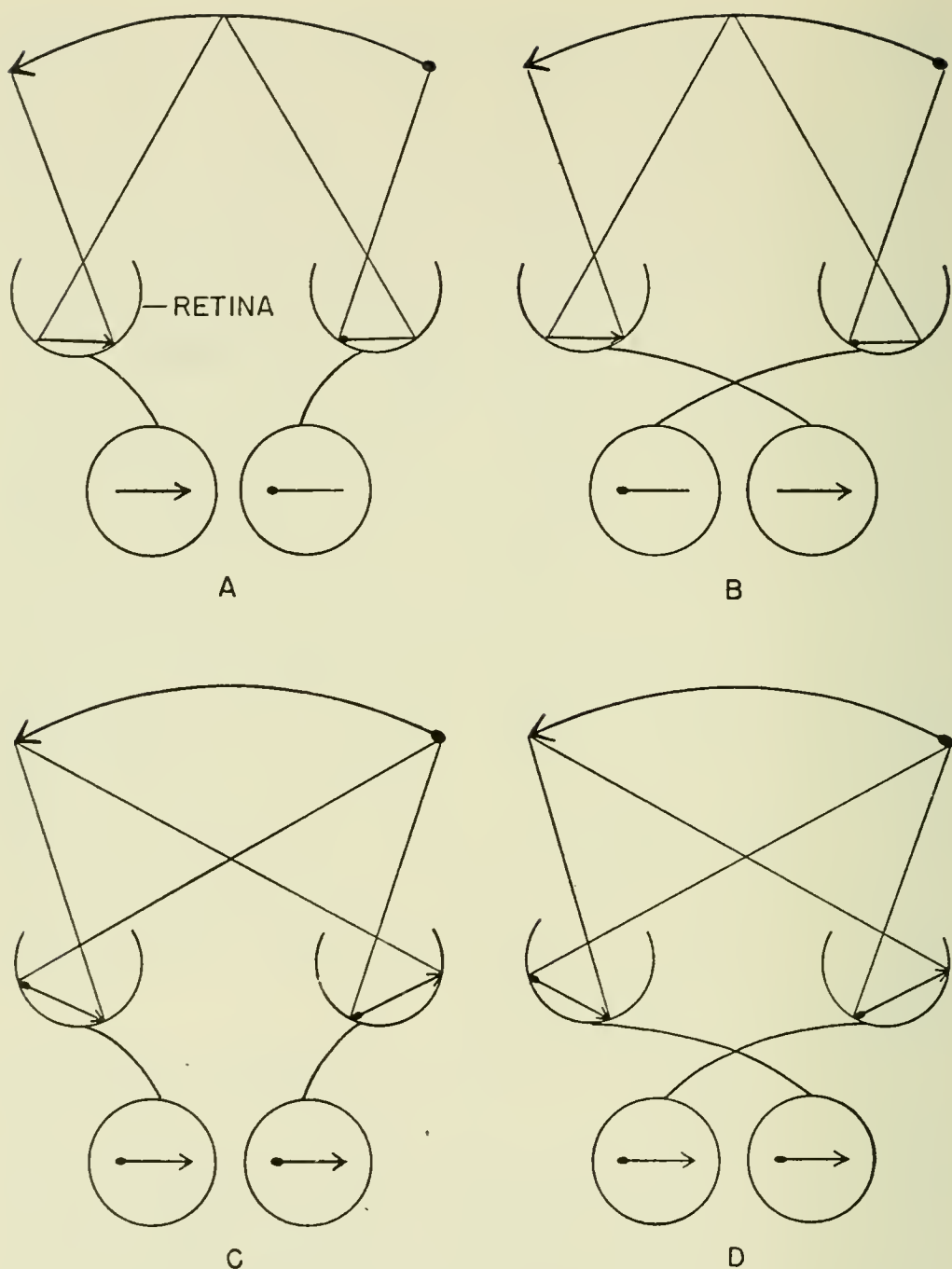


FIG. 3. Explanations for the original role of the optic chiasma in lower vertebrates. The arrow above each eye represents the field of vision (the panorama of the environment), and the arrow on the retina is the projection of the field inverted by the lens. A disparity of the projection of the panorama to the central nervous system exists if the optic pathways do not cross over (A) and no disparity exists if they cross over (B), according to Ramón y Cajal (1911). There is no disparity of the projections to the central nervous system, according to Ovio (1927), whether the optic pathways decussate (C) or not (D).

decussation arose are lost in antiquity, the experimental testing of these theories is impossible.

In all non-mammalian vertebrates (fishes, amphibians, reptiles, and birds) all the fibers of the optic nerve cross over in the optic chiasma. On this basis we may conclude that the total decussation of optic fibers in the optic chiasma is a heritage character that was probably established in the early vertebrates and has persisted in all non-mammals.

In most mammals some of the visual nerve fibers passing through the optic chiasma are uncrossed (Polyak, 1957). The number of uncrossed fibers varies from none in the primitive primate *Tupaia* (a tree shrew) to almost one-half of all optic fibers in man and higher primates. There are only a few, if any, uncrossed optic fibers in the Cetacea, insectivores, and rodents. Approximately one-twentieth of the fibers are uncrossed in the rat, one-sixth to one-eighth uncrossed in the horse, one-fifth uncrossed in the common opossum, one-fourth uncrossed in the dog and Australian bushy tailed opossum, one-third uncrossed in the cat, and one-half uncrossed in the higher primates and man (fig. 4). This character of having both crossed and uncrossed fibers in the optic chiasma resides exclusively in mammals and is called the Law of Newton, Müller, and Gudden (Walls, 1942). The uncrossed components are the axones of retinal ganglionic cells on the temporal (lateral) side of the retina (fig. 4). This is the area of the retina that receives its photic stimulation from the environment in front of the animal. Further analysis indicates that a close relation exists between the degree of frontality of the eyes and the proportion of uncrossed fibers. The animals with the most laterally placed eyes have from none to a few uncrossed fibers, and the animals with frontally directed eyes have the greatest proportion of uncrossed fibers. In brief, the number of uncrossed fibers is related to the size of the field of vision where there is overlap between the two eyes. The conclu-

sion is that the uncrossed components are an expression of adaptive radiation correlated to the degree of frontality of the eyes. It is highly possible that no uncrossed components were present in the optic chiasma of the basic mammalian stock. Hence the uncrossed components arose independently in the different mammalian orders.

The presence of both crossed and uncrossed fibers in the optic chiasma and optic tract (fig. 4) has parallels in other afferent (sensory) systems in man—for example, the auditory system and the vestibular system. In the auditory pathways, the crossing over occurs in the trapezoid body, which is in a way the equivalent to the optic chiasma, while the crossed (predominant number) and uncrossed fibers form

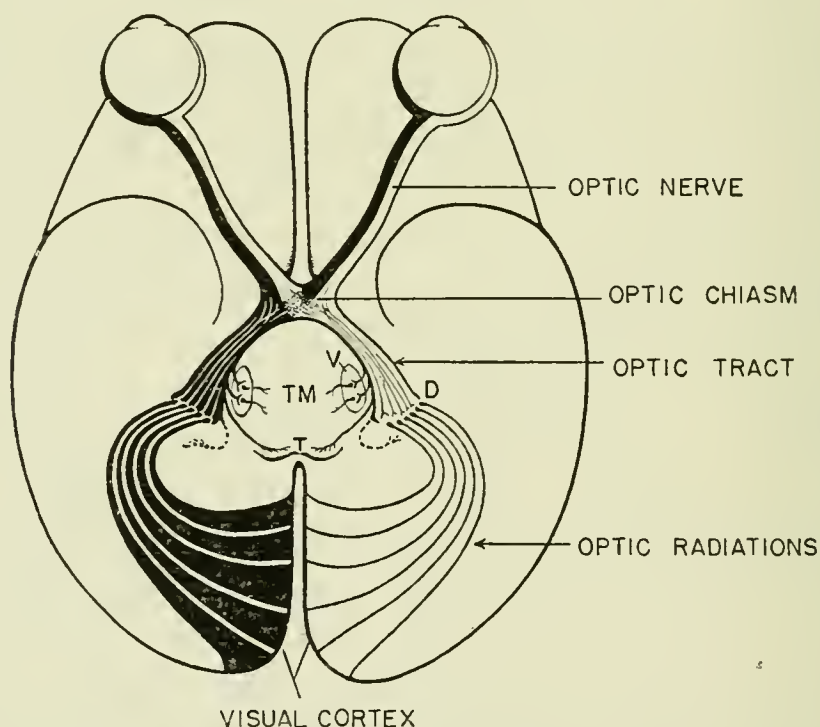


FIG. 4. Diagram of human visual system. Note that the fibers originating from the lateral (outer) half of each eye do not cross over in the optic chiasma, whereas the fibers originating from the medial (inner) half of each eye cross over in the optic chiasma. Because the lens inverts the fields of vision, the image that projects to the lateral halves of the eye comes from the fields in front of the eye. *Abbreviations:* D, dorsal division of lateral geniculate body; T, tectum of midbrain (specifically, superior colliculus); TM, tegmentum of midbrain; V, ventral division of lateral geniculate body. See text for explanation; figure adapted from Polyak (1957).

the lateral lemniscus, the equivalent to the optic tract. The data on the relative number of crossed and uncrossed fibers of the lateral lemniscus in other animals are virtually unknown (owing to inherent technical difficulties), so that it is not possible to make even a tentative statement of the phylogenetic history of the relative proportions of crossed and uncrossed components. The vestibular pathways within the central nervous system are also composed of both crossed and uncrossed components.

Regeneration of the optic nerve

The quality of the regeneration of the optic nerve is of comparative neurological interest. When a nerve of the peripheral nervous system of an adult vertebrate is transected, regeneration of the severed fibers may occur, with good function recovery. This does not apply to the severed nerve fibers of the central nervous system of some vertebrates. With the optic nerve as an example of a fiber tract of the central nervous system, let us take a synoptic view of its regenerative potential in some vertebrates. Among the technical reasons why the optic nerve is classified as a central nervous system tract are the absence of neurilemma (Schwann) cells, the presence of meningeal sheaths (pia-arachnoid sheath and dura mater) investing the nerve, and the fact that its nerve fibers are of the second order.

The optic system in teleost fishes (five marine and two fresh-water species from five different families) has the capacity to regenerate and to restore vision after the optic nerve is completely transected (Sperry, 1955). Data on the quality of regeneration of the optic nerve in any cyclostomate and cartilaginous fishes are not available.

When the optic nerves of frogs and salamanders are severed, excellent regeneration and visual recovery occur—possibly exceeding those in the teleosts. The plasticity of regeneration of the optic system in the frog is illustrated

by an experiment by Sperry (1951). A normal frog or a frog with regenerated optic nerves (following transection) was able to capture a flying fly with the tongue by the visuomotor coordination of body, head, and tongue. A frog with regenerated optic nerves in which the eyes were rotated through 180 degrees at the time of transection was unable to capture a flying fly. Its visuomotor coordination was directed to the right instead of the left (or vice versa).

The paucity of data on the regeneration of the optic nerve in birds and reptiles is such that no preliminary statement can be made concerning the regenerative potential in these two classes of vertebrates.

If the optic nerve of man and other mammals is transected, its fibers degenerate and do not regenerate, even if the blood supply remains intact (Polyak, 1957). Some fibers of the central nervous system of adult mammals will regenerate following their transection and will regain their electrophysiological properties (several papers in Windle, 1955), but unequivocal functional return has not been demonstrated.

The phylogenetic implications of the regeneration of the central nervous system are speculative, as the problem has been investigated in only three of the seven living vertebrate classes. A cautious conclusion can be made that in the mammals the potentiality for regeneration is present in at least some fibers of the central nervous system. It is possible that the poor regeneration in the mammalian central nervous system is not due primarily to the lack of an inherent regenerative capacity of its nerve cells, an old heritage, but rather to other factors that prevent, inhibit, or block regeneration.

Tectum of the midbrain

In the midbrain is located the tectum, an important central station of the visual system (fig. 4). This structure is

the chief central end station for "psychic" vision and visual reflexes in the inframammalian classes of vertebrates and in some "lower" mammals.

In man and "higher" mammals, the "visual" tectum (superior colliculus) is associated mainly with the light reflex (pupillary constriction) and accommodation (figs. 4 and 5). The phylogenetic path taken by the primates and man is essentially one in which the psychic aspects of visualization shift from the tectum to the cerebral hemispheres by what is known as encephalization (migration of functions to higher levels). The result is that (1) the tectum becomes smaller and retains the centers for light and accommodation reflexes, (2) a shift occurs in the relative sizes of the dorsal division and ventral division of the lateral geniculate body of the thalamus (fig. 4), and (3) the cerebral cortex assumes paramount significance (figs. 2, 4).

Encephalization

A living animal that in its way stands near the start of the road of encephalization is *Tupaia*, a Malayan tree shrew that is classifiable as an intermediate form between the insectivores and the lemurs. *Tupaia* may be considered to represent a key form at the base of the primate stock—a living fossil.

Tupaia resembles the inframammals by having (1) an optic chiasma that contains only crossed fibers, (2) a tectum that is the dominating mechanism in the optic reflex arcs and in the visual psychic perception, and (3) a large ventral division of the lateral geniculate body. *Tupaia* foreshadows the higher primates by having (1) a dorsal division of the lateral geniculate body and (2) a visual cerebral cortex which is but slightly differentiated.

Encephalization has two anatomical aspects because in evolution the thalamic nuclei and the cerebral cortex are functionally closely related, especially as the lateral genicu-

late body relays the optic impulses to the primary projection areas of the cerebral cortex. Hence encephalization can be subdivided into diencephalization (lateral geniculate body is a nucleus of the thalamus which is a division of the diencephalon) and into corticalization (refers to cerebral cortex). Although we are discussing the optic system at this time, this concept also applies to other sensory systems such as the auditory system and the general sensations of pain, temperature, and touch in their various manifestations. These systems during phylogeny are also associated with an increasing functional role of the thalamus and the cerebral cortex.

The ventral division (pregeniculate nucleus) of the lateral geniculate body is relatively large in inframammals and in "lower" mammals, including *Tupaia*. In the higher primates this ventral division is quite small. This division is concerned with motor reflexes, for it relays impulses to the midbrain tegmentum (fig. 4). This mechanism predates the thalamo-cortical connections (Herrick, 1948).

The dorsal division of the lateral geniculate body (fig. 6) is not only small in *Tupaia* but has only three laminae of cells. In the lemurs the division is larger and has the typical "higher" primate pattern of six laminae. This stratification of the geniculate body is associated with the perfection of the primate visual system.

A concept that may have phylogenetic validity was suggested by Herrick (1948) on the basis of some comparative neurological data. In the "lower" forms such as urodeles, the optic terminals are widely dispersed to many structures of the brain stem and the explanation of this spread "is to be sought on motor side of arc." In the "higher" forms there is segregation of the optic terminals until in the primates the psychic visual pathways (retina to lateral geniculate body to cerebral cortex) relay in a point to point projection, and, as stated by Clark (1943), "there is no possibility

that these impulses can be disturbed and modified 'en route.' . . . The cerebral cortex receives retinal impulses in a remarkably pure and unadulterated form."

Corticalization is associated with the acuity and higher faculties of sight in the mammals. The primitive mammalian soricid shrews have no visual cortex, while *Tupaia* has a cortical area that is not the typical visual (striated) cortex. The lemurs and true monkeys have a cyto-architecturally definable striated cortex which is located mainly on the lateral surface of the occipital lobe. In the "higher" monkeys, great apes, and man, this striated cortex gradually becomes located primarily on the medial surface of the occipital lobe (figs. 4 and 6). This medial "migration" is actually an accommodation to the increasing size of the cerebral hemispheres in the primates and is not a true migration.

From a functional viewpoint, corticalization is associated with the transference of visual perception from the tectum to the cerebrum. In the rabbit and rat encephalization has proceeded so that lesions of the tectum give no visual defects (Ghiselli, 1937), but the transference is not completely corticalized, for a rat with the visual cortex ablated loses pattern vision but is not blind. The ablation of the striated area in the cat, dog, or monkey results in an animal that has no object vision but can still perceive light and dark (Marquis, 1935; Klüver, 1941). They are aware of shadows passed over the eyes. The chimpanzee and man have no light perception when the striated cortex is totally lost.

The principle of encephalization also applies to other sensory systems as well. In man corticalization has not progressed so far in the general senses as in the visual sense. Cortical loss does not completely abolish pain sensation, for example. The crude general senses (pain, temperature) are largely subcortical sensations, and acute senses (weight discrimination, stereognostic capacity) are cortical sensations.

An increase in corticalization has taken place in the phylogenetic sequence of monkey, great apes, and man.

THE PYRAMIDAL SYSTEM

The pyramidal (corticospinal) system is a motor tract that projects from a large area of the cerebral cortex, passes through the pyramid of the medulla, and terminates in the spinal cord (fig. 2). It has a role in the performance of skilled movements. As the tract is present only in mammals, it is phylogenetically a new tract.

In this discussion, I am omitting any reference to the relation of the pyramidal tracts to the supplemental motor areas, to the secondary motor areas, and to afferent input. Instead I wish to concentrate on only one point—an interpretation that explains the variability in the extent and location of this motor tract as an expression of adaptive radiation.

The following information is reviewed by Lassek (1954). There are wide anatomical variations in different mammals as to the position, length, cross sectional area, and fiber count of this tract. A constant feature is its identical course in the brain stem (fig. 5).

Short pyramidal tracts are presumed to be present (Marchi technique) in such diverse mammals as the opossum (Order Marsupialia), rabbit (Order Lagomorpha), guinea pig (Order Rodentia), pangolin (Order Photidota), bat (Order Chiroptera), mole, hedgehog (Order Insectivora), sheep (Order Artiodactyla), and mule (Order Perissodactyla). The tract extends the entire length of the cord in the rat and mouse (Order Rodentia), cat and dog (Order Carnivora), and monkeys, apes, and man (Order Primates). The tract is located in the posterior funiculus in most rodents, in the anterior funiculus in the mole and hedgehog, and primarily in the lateral funiculi in carnivores and primates (fig. 5).

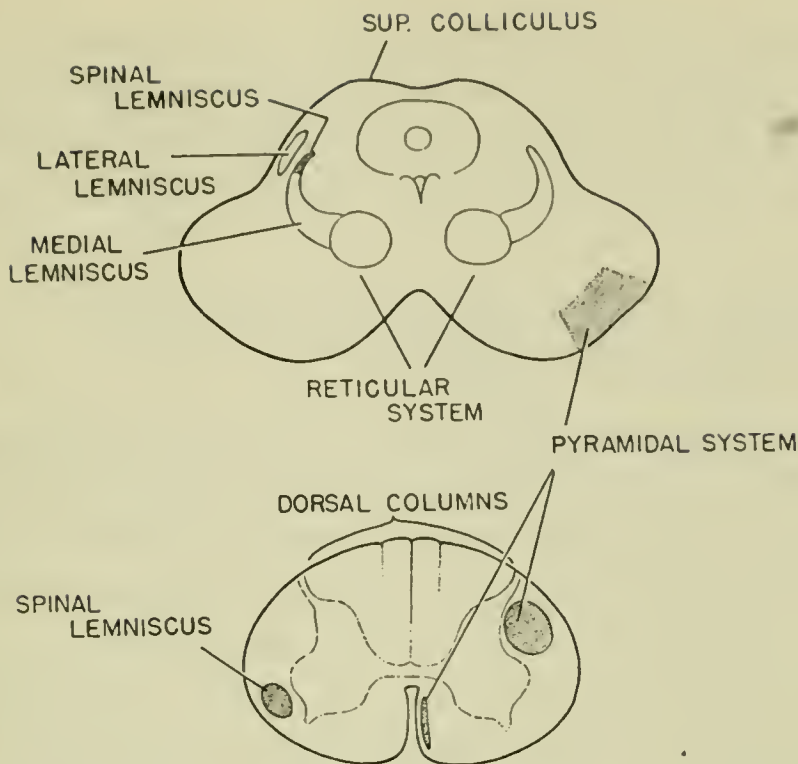


FIG. 5. Cross sections of the human mesencephalon and the spinal cord (lower figure) to illustrate the location of several structures. The upper part of each figure is the dorsal aspect. The lemniscal systems include the spinal lemniscus (pain, temperature, and light touch, also called spinothalamic tracts), the medial lemniscus and dorsal columns (touch and proprioception), and the lateral lemniscus (audition). Part of the reticular system is located in the midbrain. The superior colliculus is associated with the light reflex.

According to Lassek (1954) no correlation exists between the number of fibers present in this system with the size or the weight of an animal or to the ability of mammals to perform skilled movements. It is likely that more data will be forthcoming on various anatomical aspects of this system in many mammals when some of the newer experimental techniques, such as the Nauta-Gygax method, are applied.

To find a phylogenetic interpretation for these and other data on this diverse series of living mammals, Lassek uses phrases such as "as we go up the phylogenetic scale."

A more logical interpretation is that its variability in extent and location in the spinal cord of different mammals is another expression of the principle of adaptive radiation. In view of the fact that each mammalian order has an inde-

pendent origin in the Paleocene, it is likely that from a common location in the brain stem of the early mammals the pyramidal system expressed itself independently in the various orders of mammals during their subsequent evolution.

THE RETICULAR SYSTEM AND THE LEMNISCAL SYSTEMS

The phylogenetically old integrator of the central nervous system is known as the reticular system (figs. 2 and 5). It is present throughout the neuraxis—spinal cord, brain stem, and cerebral cortex. Some parts of it are called the reticular formation or the central reticular core.

The lemniscal systems include some of the long tracts of the central nervous system (fig. 5). A lemniscus is generally considered to be an ascending tract, with its nucleus of origin in the spinal cord or lower brain stem and its terminus in the brain stem and thalamus, and as transmitting a sensory modality or several related sensory modalities (Herrick and Bishop, 1958). A case could be made for broadening the definition and concept of the lemniscal systems to include all long tracts that are now excluded, including those to and from the cerebellum and motor tracts such as the pyramidal tract.

The reticular system may be characterized as the multi-neuronal, multisynaptic, diffuse, non-specific, and phylogenetically old system. The lemniscal systems may be characterized as the oligoneuronal, oligosynaptic, compactly organized, specific, and phylogenetically relatively new systems.

Let us quickly interpret these terms. A multineuronal, multisynaptic, and diffuse system implies that relatively many nerve cells (neurones) and synapses are diffusely organized and interposed between the site of the initial stimulus and the site of terminus. Although the neuro-anatom-

ical organization appears as a reticular network under the microscope, the reticular system has well-organized patterns (Scheibel and Scheibel, 1958). An oligoneuronal, oligosynaptic, and compactly organized system implies that relatively few nerve cells, relatively few synapses, and a compact bundle organization are present in each unit of these systems. The lemniscal systems are specific in that their ascending pathways conduct impulses of specific modalities of the senses—pain, temperature, touch, vibratory sense, audition, and so forth (fig. 5). The non-specific character of the reticular system is associated with the concept that the ascending portion of the system is important in exerting a generalized influence on the cortex, with the resulting arousal or wakefulness (Magoun, 1958). The stimulus is not of a specific modality, although the specific pathways do send collateral fibers into the reticular system.

The reticular system is old phylogenetically in that it is present in all the living vertebrates, while the lemniscal systems are more prominent in the higher vertebrates (Herrick and Bishop, 1958).

In a broad sense the afferent pathways of the reticular system include the ascending reticular pathways (Nauta and Kuypers, 1958) and the efferent (motor) pathways, including the extrapyramidal system (reticulospinal tracts). In the salamander (Herrick, 1948; Herrick and Bishop, 1958; Kappers, Huber, and Crosby, 1936) are found several lemniscal systems in which the segregation of the functional systems is incipient. They are associated with cutaneous sensibility, low-grade auditory and vestibular proprioceptive fibers, and proprioceptive function (dorsal spinal lemniscus, lateral lemniscus, visceral-gustatory lemniscus, and others).

In the mammals, especially primates, the lemnisci are prominent and compact. These mammalian lemnisci are probably derivatives of lemnisci similar to those present in the salamander and have been modified by the addition of

more fibers and more refined modalities. In man these tracts include the spinal lemniscus (pain and temperature), dorsal columns (tractus gracilis, tractus cuneatus), medial lemniscus (touch, proprioception), and lateral lemniscus (audition). (See fig. 5.) These tracts as well as the pyramidal tract in a sense bypass the reticular core (Bishop, 1958).

The relation of the reticular system and lemniscal systems to the heritage of the human brain is significant. In 1934 Herrick summarized the significance of the neuropil in the evolution of cerebral structure. The neuropil is the dense felt-work of fibers in the central nervous system—in other words, the network of the reticular formation. “The neuropil is the mother tissue from which have been derived both the specialized centers and tracts which execute the refined movements of the local reflexes and the more general web which binds these local activities together and integrates the behavior.” A plausible concept is that the diffuse neuropil (reticular formation) is probably the primordial network, while the long compact tracts have been formed by a concentration and functional modification of neuropil fibers during evolution. The nuclear patterns (cell bodies of nerve cells) of the brain-stem reticular formation have phylogenetic implications. The small reticular cells are more numerous in the mammals than in lower forms. This morphological evidence supports a concept of the “greater” functional significance of the reticular system in mammals as compared to lower forms. Special nuclear groupings of the reticular cells are found in all vertebrate classes, with the possible exception of the Amphibia. These nuclei are formed as a response to the influence of various stimuli (neurobiotaxis), for during phylogeny and ontogeny these cells frequently migrate to and concentrate in other portions of the brain stem (Kappers, Huber, and Crosby, 1936). This suggests that the nuclear patterns of the larger cells express an adaptive radiation related to functional

requirements. The general patterns of nuclear organization are discussed by Kappers, Huber, and Crosby (1936), Olszewski and Baxter (1954), and Noback (1959).

Another indication of an ancient heritage in the human brain is found in the descending tract of the trigeminal nerve (pain and temperature from head), the tractus solitarius (taste and visceral senses), and the descending vestibular tracts. These tracts, which are formed by the root axons of some cranial nerves, descend in the brain stem of mammals. After synapsing many of these systems ascend to higher levels. In the salamander, for example, the root fibers of the afferent cranial nerves bifurcate into ascending branches and descending branches (Herrick, 1948). In mammals and man the descending tracts just noted are probably the retention of the descending branches found in the ancestral vertebrates. Incidentally, the intrinsic neurones of the reticular system in mammals have axons that bifurcate into long ascending branches and long descending branches (Scheibel and Scheibel, 1958).

Although the lemniscal systems are well developed in man and the primates, the large extent of the reticular system in these forms indicates that the integrative function of the latter system is probably not subordinated during evolution. The prominent lemniscal systems in man and the primates are associated functionally with more refined modalities and anatomically by some myelination (Herrick and Bishop, 1958). One consequence of phylogeny of the primates especially has been the shift from the generalized stereotyped activity of the "lower" vertebrates to more emphasis on skilled non-stereotyped activities. The lemniscal systems play a role in this phylogenetic trend in the primates.

THE CEREBRAL CORTEX

The human cerebral cortex is probably the most intricate and complex structure in the animal kingdom. It is respon-

sible for our biased anthropomorphic thinking. I can discuss here a few facets of this structure.

The cerebral cortex of mammals is divisible into the paleocortex, archicortex, and neocortex (figs. 2 and 6). A discussion of synonymous and subsidiary terminology, which abounds in the literature, is beyond the scope of the present paper.

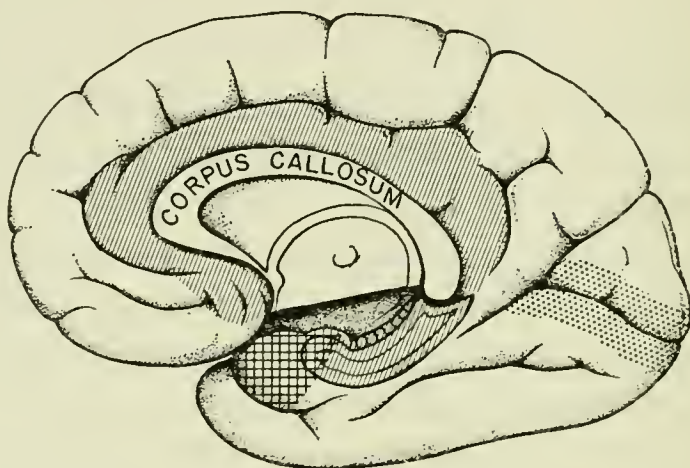


FIG. 6. Medial surface of human cerebral hemisphere. Outlines of the archicortex (parallel lines), the paleocortex (cross hatched), and the neocortex (unshaded) are suggested. The archicortex above the corpus callosum is called the mesocortex. A portion of the archicortex is exposed by a partial dissection. The visual fibers from the lateral geniculate body are projected to the visual cortex (stippled).

The paleocortex and the archicortex are present to a greater or lesser degree in all living vertebrates. In the primates, they form a ring around the diencephalon and corpus callosum. Together they are referred to as the rhinencephalon (smell brain), the limbic lobe of Broca, visceral brain, or the allocortex. In a word, it is the old cortex with a history of over 400,000,000 years. It persists in man, and although it is overshadowed by the large neocortex, the allocortex has considerable size, especially the archicortex. Its basic function, which is only superficially understood today, is in the realm of smell, emotion, and visceral autonomic activity.

The paleocortex is associated with smell, and its stimula-

tion in the intact cat evokes actions related to feeding, sniffing, chewing, and salivation. The archicortex (specifically hippocampus) is not related to smell, as is indicated by the fact that it is present in such mammals as the anosmic dolphin and whale. In 1937 Papez implicated this structure and others in this region as the central mechanism for emotional expression. On the basis of stimulation and ablation experiments by Klüver and Bucy (1939) and others in cats and monkeys, the relation of these regions to some phases of emotion is on a firm footing. When the hippocampus was stimulated an animal showed signs of fear, anger, or fury, and its facial expression was transformed to one of attention, surprise, anxiety, or bewilderment. When the temporal lobe and hippocampus were ablated bilaterally in monkeys and cats (Klüver-Bucy syndrome), wild and vicious animals were transformed into tame and fearless animals. Such monkeys would touch snakes that would normally have produced intense fright and terror. The heritage of this old cortex persists in man and affects our daily lives.

The neocortex makes its initial appearance in the reptiles (Crosby, 1917; Kappers, Huber, and Crosby, 1936), but it is in the mammals that the neocortex blossoms out as a dominant structure of the brain. Small-brained mammals have smooth cortices (lissencephalic brains) and large-brained mammals have cortices with gyri and sulci (gyrencephalic brains). The presence of gyri and sulci, fissuration, is explained by Baillarger's law of folding compensation. Fissuration is a method by which a large brain retains the balance between the volume of the cerebral cortex and that of the subcortical cerebral structures. To increase its volume, the cortex expands in area as the square (not by greater thickness), while the subcortical structures expand as the cube. The differences in the linearity of the sulci are, in part, related to the size of the brain. As the brains in a "phylogenetic" series increase in size, the linear contours

of the sulci on the cerebral surface change. Within the primate order the small-brained lemurs have a series of longitudinally oriented sulci, and the medium-sized brains of the monkeys have a series of transverse and arcuate-shaped sulci (Tilney and Riley, 1928). The large brains of the great apes and man have a complex fissural pattern.

Many orders have animals with cerebral sulci and gyri—all large-brained animals including elephant, horse, cow, whale, cat, and man. No completely gyrencephalic order of mammals exists, as all orders arose from small-brained lissencephalic animals (Edinger, 1948). The early fossil horse (*Eohippus*) and the primitive living primates have smooth cortices. The implication is that the game of trying to compare fissures in different orders such as the ansate coronal sulcus in the cat with the central sulcus in primates has doubtful significance. Comparing functional cortical areas in animals of different orders is defensible. There is a general relation between body size and brain size, especially in related mammals. The brain size in turn has a relation to degree of fissuration. Although this relation holds, it is not absolute. Edinger (1948) has demonstrated that, in the Eocene horses, a slight increase in body size was accompanied by a large increase in brain size. In the Oligocene horses, on the other hand, the increase in body size was accompanied by only a slight increase in brain size.

During phylogeny the new parts of the brain, such as the neocortex, have become more prominent as compared to the older parts, such as the small allocortex. "However, such phylogenetic changes as have been analyzed appear to follow simple laws of relative growth so far as rates are concerned and can usually be correlated, by rather elementary mathematical procedures [small allometric growth curves], with the over-all size of the brain" (Harman, 1957). Ontogenetically this also applies to the growth of parts of the human brain (Noback and Moss, 1956).

In the phylogeny of the human brain from the insectivores (the basic mammalian order), a number of trends are apparent. The living insectivores are characterized as small-brained mammals with a relatively large allocortex, a relatively small neocortex, a visual integrating mechanism in the tectum, and a stereotyped motor response. As we progress "up the scale" of primates (lemurs, monkeys, anthropoid apes, and man) there is a progression of changes. The allocortex becomes relatively smaller and the neocortex relatively larger. In neocortical evolution, psychic perception and interpretation of vision are encephalized. This is correlated with the importance of vision, for in the primates visual discrimination is associated with the lively exploratory drives and its associated coordination with the useful hand. At the other end of the cerebrum is the prefrontal lobe cortex. Primates are socially inclined and have family bands and bonds. The prefrontal lobe plays its role in this area, for, in man, many of our social values and drives hinge on this area. It is here that a balance is struck between caution and uninhibited expression and the fact that ultimate goals are fabricated. It is the region of the day of the prefrontal lobotomy (Mettler, 1955).

In the phylogeny of the primate cortex, there is a progressive shift as the stereotyped motor activities of the more primitive mammals are modified by the ascendancy in the neocortex of influences that result in some release from stereotyped movements. The relative freedom of the hand with its opposable thumb is but one example. The pyramidal system is one mechanism in this release.

The nerve cell is the morphological substrate of the cortex or any other structure. A significant fact is that the cerebral cortex of mammals has a characteristic cellular pattern despite variations in cell number, cell form, and size. "What remains constant is the arrangement of the plexuses of dendritic and axonal branches, i.e. of the synaptic articulations

through which nerve impulses are transmitted" (Lorente de Nó, 1949). The cellular elements added, in the "higher" mammals, especially man, are tremendous numbers of cells with short axons (intracortical cells). Quoting again from Lorente de Nó, "Cajal assumed that the large number of cells with short axons was the anatomical expression of the delicacy of function of the brain of man. At present this assumption is almost a statement of fact."

SUMMARY

1. The brains of the vertebrates display a remarkable diversity of structure and of function. It is probably the most plastic structure in the animal kingdom.

2. The heritage of the long phylogenetic history of the vertebrate brain resides in the fabric of the structural and functional components of the human brain. (a) The nerve fibers that cross over in the optic chiasma have their counterparts in all the vertebrates. This old heritage goes back over 400,000,000 years. (b) The uncrossed nerve fibers in the optic chiasma are found only in the mammals. This new heritage goes back probably less than 60,000,000 years. (c) The coordinating mechanisms associated with the reflex patterns of the eye persist in the tectum of the human mid-brain—an old heritage. On the other hand, the substrates for visual perception have shifted to the lateral geniculate body and cerebral cortex (encephalization)—a newer heritage. (d) The pyramidal system, which plays a significant role in the motor activity of the human hand with its opposable thumb, is found only in mammals—a newer heritage.

3. The integrating mechanisms of our basic drives such as sleep and emotion reside in the reticular system and the allocortex of man. These mainsprings have a long phylogenetic history—an old heritage.

4. The cellular substrates of the long lemniscal systems,

concerned with specific sensory modalities, and the neo-cortex—newer heritages—are probably derived from the older multineuronal reticular system.

5. An expression of the interaction between the “old” cortex and the “new” cortex occurs in certain epileptic seizures in a man who passes through a state of confusion (paleocortex) and has a moment of speech difficulty (neo-cortex).

6. The concept of adaptive radiation is demonstrated by diversity of certain structures in the nervous system. Three examples in the mammalian brain include: (a) The number of uncrossed fibers in the optic chiasma is not related to the phylogenetic position of the animal but rather to the degree of frontality of the eyes. (b) The variability in the location and extent of the pyramidal system in the spinal cord in different forms can be readily explained as a system evolving from a common base but expressing itself in a different way in each order. (c) The fissural patterns in the cortex of different orders of mammals arose independently of one another because all orders arose from smooth-brained (lissencephalic) animals.

7. Nature is not static. Although man’s evolution of the past 200,000 or so years has been due primarily to the aids of civilization (Shapiro, 1957), the human brain, if man survives, will probably continually change over the millions of years to come. This past seems to attest to this concept.

8. The stanza of William King Gregory (1951) in his book “Evolution Emerging” is apropos:

“But who can tell the span or know the limits
In Time’s equation of the Past and Future?
What! will the players quit, with coin in hand,
Tipping the cosmic table in their anger?
’Tis idle to imagine, they’ll stay in,
‘Law’ against ‘chance,’ so spin the wheel again!”

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