EVOLUTION OF THE PSYCHENCEPHALON

by Paul D. MacLean

Abstract. In evolving to its great size the human brain has retained the distinctive features and chemistry of three kinds of brains that reflect an ancestral relationship to reptiles, early mammals, and late mammals. It constitutes, so to speak, a psychencephalon comprised of three-brains-in-one, a triune brain. In the evolution from reptiles to mammals two key changes were the development of nursing and maternal care. Through the agency of "newer" parts of the brain a parental concern for family eventually generalizes not only to other members of the species but to the entire biosphere, a psychological development that amounts to the evolution of responsibility and what we call conscience. Given our freedom to decide "yes" or "no" on various issues, we need not look beyond the evolving family to find a reason for being, an ethic to live by.

Certain discoveries of the past fifty years have made it appear that the brain has some of the properties of a plant. Of particular note are recent findings of a growing number of substances that travel back and forth in nerve fibers somewhat like sap in a tree. It would almost seem that the ancients, with their notions about animal spirits flowing back and forth within neural tubes, were not so far off the track after all. Because of such findings one may today hear the brain referred to as a pulsating plant. Viewed analogously in such terms, animals could be regarded as plants which acquired the means of moving themselves around. Human beings have gone a step further and invented motorized land vehicles and airborne contrivances to extend and multiply contacts with presumed substantial beings and things in the external environment. One must say "presumed" because it is not at all

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clear how the brain, which regards itself as a gelatinous substance, has been able to derive a scale of hardness ranging from talc to diamond for objects perceived in the outside world. The communication and coding of signals within the gelatinous brain are imprecise and infinitely slow compared with the presumed instruments of precision used in the "hard sciences." Who is to say that the brain did not outsmart itself when it chose light as a yardstick? Is it possible that the seeming vastness of the universe is but an artifact of the mind? As measures, why not choose odors which seem to have no definite beginning and no definite end? As Helen Keller remarked, "Touch is in the object; smell is in the organ."

When, in addition to these considerations, we allow ourselves to reflect that the brain spends its life imprisoned within a bony shell, it drives home what basically lonely creatures we are. Analytic introspection suggests that the condition that accounts for our uniqueness as individuals and our feeling of individuality is the brain's dual source of information from the internal *private* world and the external *public* world. Signals to the brain from the world within are entirely private, whereas those originating in the outside world can be publicly experienced and compared. Little wonder that we keep trying to break out of our isolation and maintain contact with other beings and things in the outside world.

In the present review of the evolution of the brain and mind, it will be noted that we as members of the class of mammals seem to find the greatest warmth of companionship within the body of the human family. Yet even here we find a pervading feeling of isolation that seems to be goading us towards communication with beings in another world. For some in our midst, the peopled heaven of yesterday almost seems as if it could become a reality, waiting for a Noah's ark that is big enough and fast enough for transportation to eternal life in the cosmos.[1] They would regard the feverish human activity building up since the industrial revolution, the present surge in computer and other electronic technology, as an unconscious expression of humanity's drive to achieve lift-off. Their major concern would be that less futuristically minded souls might in the meantime resort to atomic weapons in an attempt to surpass others in plundering the world's resources. Regardless of such extreme eventualities, there is an immediate growing concern, as expressed in the present issue of *Zygon*, that all of us may be needlessly contributing to the defacing and irreversible ruination of our environment. Some economic doctors ascribe the deteriorating situation to a psychotic derangement of the collective mind, ironically manifest by the delusional fear that businesses and institutions must tumor-like continue to grow or else perish. Whatever the reasons, I will mention in the final discussion a psychological predisposition that could serve as a healthful, restraining influence, referring to the role of "social grooming" that is so typical of mammals, and particularly of human beings.

Attributes of the Psychencephalon

It has been known since the last century that the cerebral hemispheres are requisite for the spontaneous, directed activities of terrestrial vertebrates. As Sir David Ferrier observed, if a decerebrated animal "be left to itself, undisturbed by any form of external stimulus, it remains fixed and immovable on the same spot, and unless artificially fed, dies of starvation. . . ."[2] Subsequent experimentation has provided repeated confirmation that the neuraxis below the level of the hemispheres contains the neural apparatus required for posture and locomotion and the integrated bodily actions involved in self-preservation and procreation. Since the cerebral hemispheres are essential for psychological functions, they may be appropriately referred to as the psychencephalon.

A comparison of the brains of existing vertebrates, together with an examination of the fossil record, indicates that the human psychencephalon has evolved and expanded to its great size while retaining the features of three basic evolutionary formations that reflect an ancestral relationship to reptiles, early mammals, and recent mammals (see fig. 1). Radically different in structure and chemistry and in an evolutionary sense countless generations apart, the three formations constitute a hierarchy of three brains in one—a triune brain.[3] This situation suggests that our psychological and behavioral functions are under the joint direction of three quite different mentalities. There is the added complication that the two older formations do not have the capacity for verbal communication.

Just as the three basic evolutionary formations of the brain can be distinguished on the basis of their anatomy and chemistry, they can also be shown to account for certain different functions. In this brief account, I will deal successively with the protoreptilian, paleomammalian, and neomammalian formations.

The Protoreptilian Brain

Developments in histochemistry have been of great help in identifying corresponding parts of the brain in reptiles, birds, and mammals. In regard to the protoreptilian counterpart, two illustrations will suffice. As illustrated in figure 2, a Koelle stain for cholinesterase brings into sharp contrast the greater part of ganglionic structures that form the base of the forebrain in reptiles, birds, and mammals. With the application of the Falck-Hillarp histoflourescence technique the same

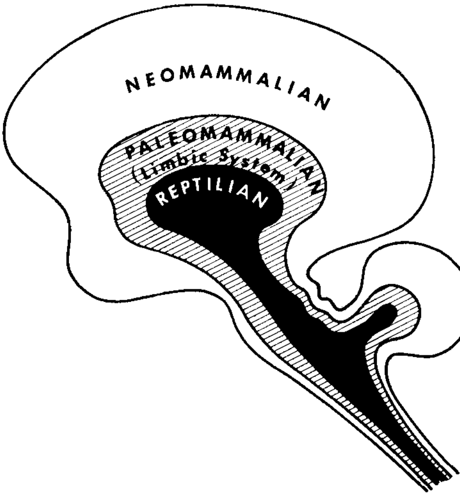

FIG. 1.—The triune brain. In its evolution the primate forebrain expands along the lines of three basic formations which anatomically and biochemically reflect an ancestral relationship, respectively, to reptiles, early mammals, and late mammals. The three formations are labeled at the level of the forebrain which may be regarded as the psychencephalon. (From P. D. MacLean, "The Brain in Relation to Empathy and Medical Education," *Journal of Nervous Mental Disease* 144 [1967]: 374-82.)

structures shown in the figure glow a bright green because of the presence of dopamine, a neural sap that appears to be requisite for bringing into the play the total energies of the organism. These same structures are rich in serotonin and the recently discovered opiate receptors and endorphins.[4] In reptiles and birds these ganglionic structures lie beneath the dorsal medullary lamina and are identified as the olfactostriatum and paleostriatum (*paleostriatum augmentatum* and *paleostriatum primitivum*). In mammals these striatal (literally, striped) structures are referred to as the olfactostriatum and corpus striatum. The latter is comprised of the caudate nucleus and putamen which are inextricably bound to the globus pallidus and satellite collections of gray matter. Since there is no term that generally applies to the whole striatal complex, I will simply refer to it as the R-complex (reptilian complex).[5]

To someone not engaged in brain research, it might seem odd that after more than 150 years of investigation there has been no clear definition of the functions of the R-complex.[6] In clinical neurology the structures in question are usually referred to as the basal ganglia. Because of motor disorders that occur subsequent to disease of related ganglia in the thalamus and midbrain, the R-complex has been inferred to be primarily implicated in motor functions. Consequently, it has been traditional in textbooks and neurological teaching to dis-

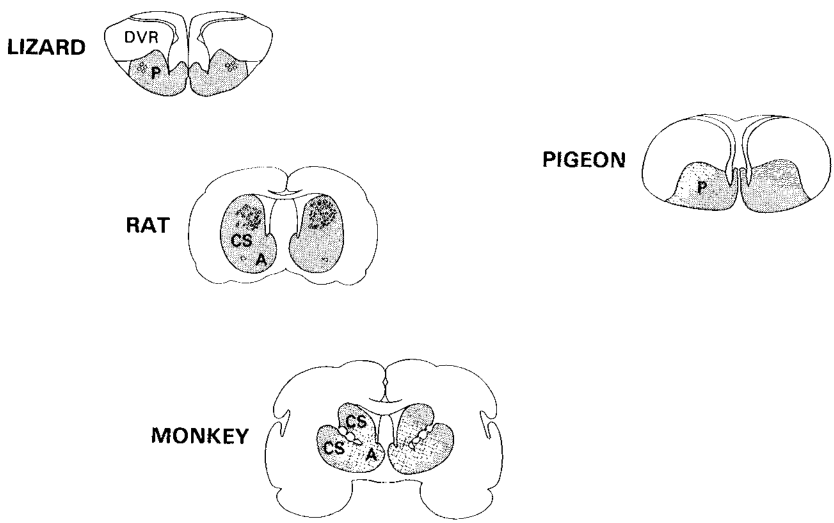

FIG. 2.—Picture obtained upon applying a stain for cholinesterase to brain sections of a lizard, rat, monkey, and pigeon. Combined with other evidence, the stain reveals that the striatal complex is a common denominator of the basal forebrain of terrestrial vertebrates. (Redrawn from A. Parent and A. Olivier, "Comparative Histochemical Study of the Corpus Striatum," *Journal für Hirnforschung* 12 [1970]: 75-81.)

cuss the R-complex as part of the motor system dominated by the motor cortex of the neocortex. This view has prevailed in spite of the recognition that large destructions of different parts of the R-complex may result in no notable motor deficit. Moreover, electrical stimulation of extensive parts of the R-complex results in no movement.

The Mammal-like Reptiles. For comparative research purposes, it is unfortunate that no existing reptiles are directly in line with mammals. Is it possible that any living form would provide an appropriate experimental substitute? If the reading of the fossil record is correct, the lineage of mammals can be traced back to the therapsids, the mammal-like reptiles. Long before the dinosaurs, they populated the world in profuse numbers. Two hundred and fifty million years ago when there was but one continent, Pangaea (fig. 3). They roamed every part of it, and today their remains are found on every continent. A few years ago fossils of mammal-like reptiles similar to those in the Karroo Beds of South Africa were found in Antarctica, which was once joined to Africa and formed part of the massive southern continent that Edward Suess called Gondwanaland.[7] Robert Broom calculated that the Karroo Beds hide the remains of more than 800 *billion* mammal-like reptiles.[8] There were two main varieties—carnivores and herbivores (fig. 4). Present day mammals derive from the carnivores. Some forms resembled dogs and wolves (fig. 5). In body carriage and structure of the jaws and teeth, the advanced forms closely approached the condition of mammals. Late in Triassic times the mammal-like reptiles mysteriously became extinct. What was the development of the brain in these animals? As yet there are no good endocranial casts of the most advanced mammal-like reptiles. Morphological considerations based on casts of less advanced mammal-like reptiles, indicate, along with other evidence, that the brains were not too unlike present day lizards.

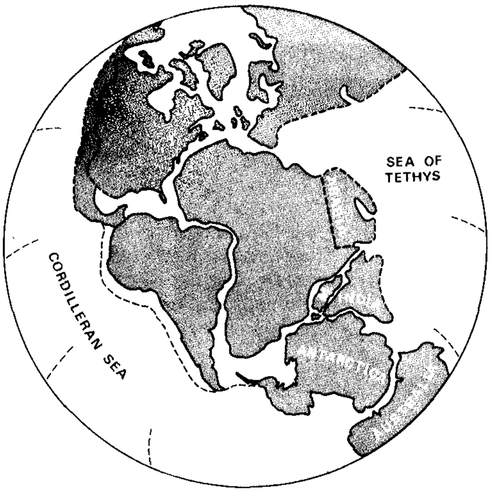

FIG. 3.—Pangaea. At the time of the earliest mammal-like reptiles the land masses forming most of the present continents appear to have been gathered together into one megacontinent known as Pangaea. The remains of mammal-like reptiles are found on every continent (see text). Note where India and Madagascar (M) were located. India has since moved through the Sea of Tethys and come to rest against the Himalayan Mountains. (Drawing based on a reconstruction by E. Irving, "Drift of the Major Continental Blocks since the Devonian," *Nature* 270 [1977]: 304-9; from P. D. MacLean, tentatively titled *The Triune Brain* [New York: Plenum Press, forthcoming].)

In the evolution from reptiles to mammals, three key changes were the development of (1) a warm blooded condition, (2) nursing, and (3) parental care. Did the advanced mammal-like reptiles lay eggs; did they care for their young? Or like the offspring of today's giant Komodo dragons, did the young have to escape to the trees to avoid being cannibalized?[9]

In the evolution of mammals, vocalization and hearing became of utmost importance for maintaining parent-offspring relationships. Presumably vocal communication helped to assure contact among diminutive early mammals living in the dark floor of the forest. The

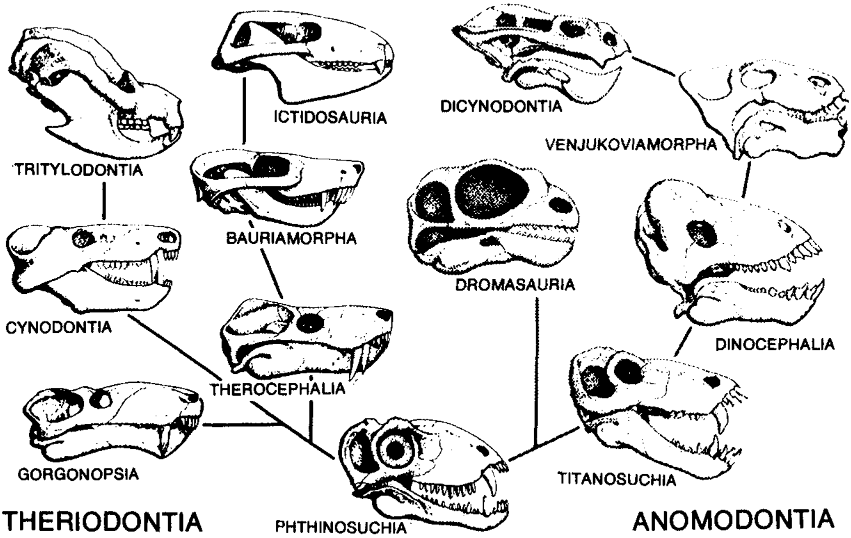

FIG. 4.—The "family tree" of therapsids. Romer considers the Phthinosuchia as the parent stock leading to two great groups of mammal-like reptiles—one, carnivorous and the other, herbivorous. Here the herbivorous line has been partly shaded out so as to focus attention on the two main lines of carnivores, either of which might have led to the mammals. (From A. S. Romer, *Vetebrate Paleontology* [Chicago: University of Chicago Press, 1966].)

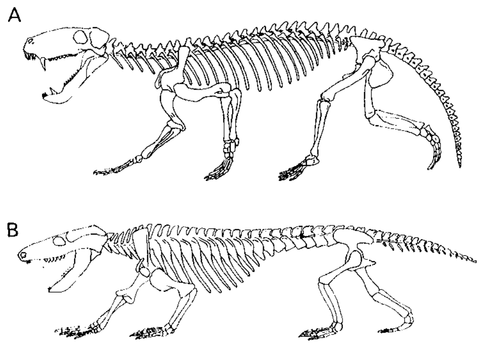

FIG. 5.—Examples of two carnivorous types of mammal-like reptiles. Note that the teeth and carriage of the body have a resemblance to the mammalian condition.

A. A gorgonopsian called *Lycaenops* because of its wolf-like appearance.

B. A cynodont named *Thrinaxodon*. The name Cynodontia for the mammal-like reptile of this type refers to their dog-like teeth. (Upper and lower figures, respectively, redrawn after A. S. Romer, *Vertebrate Paleontology* [Chicago: University of Chicago Press, 1966], and A. S. Brink, "Note on a New Skeleton of *Thrinaxodon liorhinus*," *Paleaeontologica Africiana* 6 [1958]: 15-22, with the difference that the jaws are shown agape.)

so-called "isolation call" characteristic of mammals is probably the most basic mammalian vocalization, serving to maintain maternal-offspring contact and familial affiliation.[10] Could the mammal-like reptiles hear and vocalize, or were they hard-of-hearing and mute like most existing lizards? In the advanced forms, two small bones of the jaw joint (the quadrate and articular) had become smaller, but were far from being transformed into the hammer and anvil of the mammalian middle ear.[11]

Reptilian Behavior. The so-called stem reptiles are considered to be the ancestors of the mammal-like reptiles. The bony structure of one of the stem reptiles was sufficiently lizard-like in appearance that one order is called *Varanosaurus*, the same name given to today's monitor lizards of which the Komodo dragon is one variety.[12] From an evolutionary standpoint, it is curious that ethologists have paid little attention to reptiles, focusing instead on fishes and birds. Of existing reptiles, lizards would probably bear the closest resemblance to the mammal-like reptiles, with the giant Komodo dragon perhaps being the best prototype.

In neurobehavioral work, as in other scientific pursuits, advances in knowledge depend partly on the recognition of similarities and differences. In analyzing the behavior of lizards one can identify more than twenty forms of behavior that are also characteristic of mammals (table 1). All such behavior can be further reduced to individual components out of which are formed distinctive constructs and sequences of constructs.[13] The sum total of all the building blocks of behavior and their various assemblages constitute the so-called behavioral profile, or ethogram, of an animal. Exclusive of verbal behavior, one recognizes in human beings and other terrestrial vertebrates two main aspects of the behavioral profile. For descriptive purposes they can be compared to the profiles of two main mountain ranges. In one range are the distinctive peaks representing the chain of activities in an animal's daily master routine and subroutines. In the other range are four main peaks and subpeaks corresponding to four main types of behavioral patterns (displays) used in prosematic communication. Prosematic, meaning rudimentary signaling, applies to any nonverbal signal—vocal, bodily, or chemical—used in communication.[14]

In lizards the four main types of communicative signaling are referred to as (1) signature; (2) challenge (territorial); (3) courtship, and (4) submissive (assentive) displays. These displays which variously incorporate static and dynamic modifiers may be illustrated by those of the common green anolis lizard (*Anolis carolinensis*) (commonly referred to as the American "chameleon") that we have used extensively in our neurobehavioral studies. Anolian displays have been described

TABLE 1

SPECIAL FORMS OF BASIC BEHAVIOR

1 SELECTION AND PREPARATION OF HOMESITE ┐
2 ESTABLISHMENT OF TERRITORY │ DOMAIN
3 USE OF HOME RANGE ┘
4 SHOWING PLACE-PREFERENCES
5 TRAIL MAKING
6 MARKING OF TERRITORY
7 PATROLLING TERRITORY
8 RITUALISTIC DISPLAY IN DEFENSE OF TERRITORY, COMMONLY INVOLVING THE USE OF COLORATION AND ADORNMENTS
9 FORMALIZED INTRASPECIFIC FIGHTING IN DEFENSE OF TERRITORY
10 TRIUMPHAL DISPLAY IN SUCCESSFUL DEFENSE
11 ASSUMPTION OF DISTINCTIVE POSTURES AND COLORATION IN SIGNALING SURRENDER
12 USE OF DEFECATION POSTS
13 FORAGING
14 HUNTING
15 HOMING
16 HOARDING
17 FORMATION OF SOCIAL GROUPS
18 ESTABLISHMENT OF SOCIAL HIERARCHY BY RITUALISTIC DISPLAY AND OTHER MEANS
19 GREETING
20 GROOMING
21 COURTSHIP, WITH DISPLAYS USING COLORATION AND ADORNMENTS
22 MATING
23 BREEDING AND, IN ISOLATED INSTANCES, ATTENDING OFFSPRING
24 FLOCKING
25 MIGRATION

in detail by B. Greenberg and G. K. Noble.[15] As diagrammed in figure 6, the signature display consists simply of three to five combined head nods and pushups together with a brief extension of a crimson colored throat fan occurring after the second head nod. Signature displays seem to reflect a kind of self-assertion that comes into play in both nonsocial and social contexts. Among members of a group, the signature display appears to serve as a form of recognition. Challenge displays are of two types (distant and near) and are used chiefly by territorial males in establishing territory, maintaining dominance within a social group, and fending off invaders. The challenge display includes the dynamic components of the signature display combined with a number of static modifiers which, like many athletic uniforms, makes the subject appear larger in size. The courtship display begins

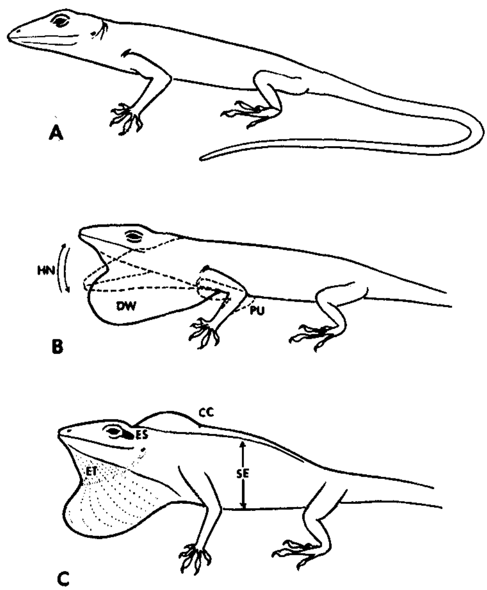

FIG. 6.—Features of the signature and challenge displays of the common green anolis lizard (*Anolis carolinensis*).

A. The usual attentive posture.

B. Diagrammatics of the signature (assertion) display. The signature display consists of three to five head nods (HN) and pushups (PU) along with an extension of the dewlap (DW). The broken lines indicate the excursion of the head and flexion of forelimbs during pushups. Note absence of static modifiers.

C. Diagnostic features of the challenge display of adult male lizards. In addition to the dynamic components of the signature display, the challenge display has several static modifiers. The first to appear are the extended throat (ET) and sagittal expansion (SE), followed by an elevation of the nuchal and dorsal crests (CC). A darkly pigmented eyespot (ES) may appear after two to three minutes. See text for further details. (From N. Greenberg, P. D. MacLean, and J. L. Ferguson, "Role of the Paleostriatum in Species-typical Display Behavior of the Lizard Anolis carolinensis," *Brain Research* 172 [1979]: 229-41.)

with the signature display followed by a number of head nods and an approach towards the female with a prancing strut. The anolian submissive display is characterized by four slight up and down motions of the head. It is performed by members of either sex and of all ages.

Neurobehavioral Studies. In our initial behavioral studies on lizards we focused on the challenge displays because they can be reliably induced in two adult territorial males. In the attempt to identify brain mechanisms underlying this display, we have used the green anolis lizard. Since the optic nerves of this species are almost entirely crossed (fig. 7), we can place a lesion in only one hemisphere of the brain and then test the animal's behavior with either eye covered. In this way we avoid the possible complication of interfering with their ability to maintain an adequate bodily temperature for being active. As schematically indicated in figure 7, we found that it was only with hemispheric lesions largely confined to the R-complex (marked with an "X") that interfered with the expression of the challenge display. Although capable of climbing, jumping, and catching crickets, the experimental animal showed no interest in the rival lizard when looking with the eye projecting to the injured hemisphere. But when

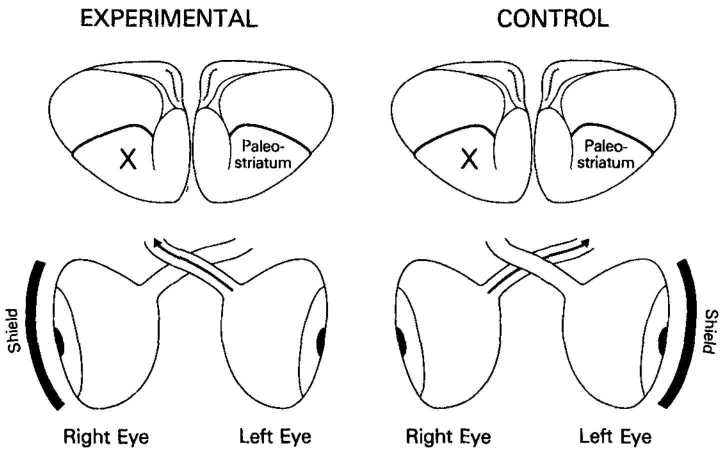

FIG. 7.—Schematic of procedure for obtaining control and experimental observations in the same brain-damaged lizard. In neurobehavioral research on lizards, it is important to minimize the possibility of interfering with the regulation of the body temperature. Since the optic nerves are almost completely crossed in the anolis lizard, the conditions are provided for destroying nerve tissue in one hemisphere (e.g., at site "X") and then testing the animal with either eye covered by a shield. Under control conditions (right side of figure), the lizard gives its usual distant challenge display upon seeing a rival territorial lizard with the eye projecting to the normal hemisphere. Although capable of seeing, there is a negative response when looking with the eye projecting to the hemisphere with part of the paleostriatum destroyed (left side of figure). Lesions elsewhere in the hemisphere are without effect. (From P. D. MacLean, tentatively titled *The Triune Brain* [New York: Plenum Press, forthcoming].)

allowed to see the rival with the eye leading to the undamaged hemisphere, there was an evocation of the full challenge display.[16]

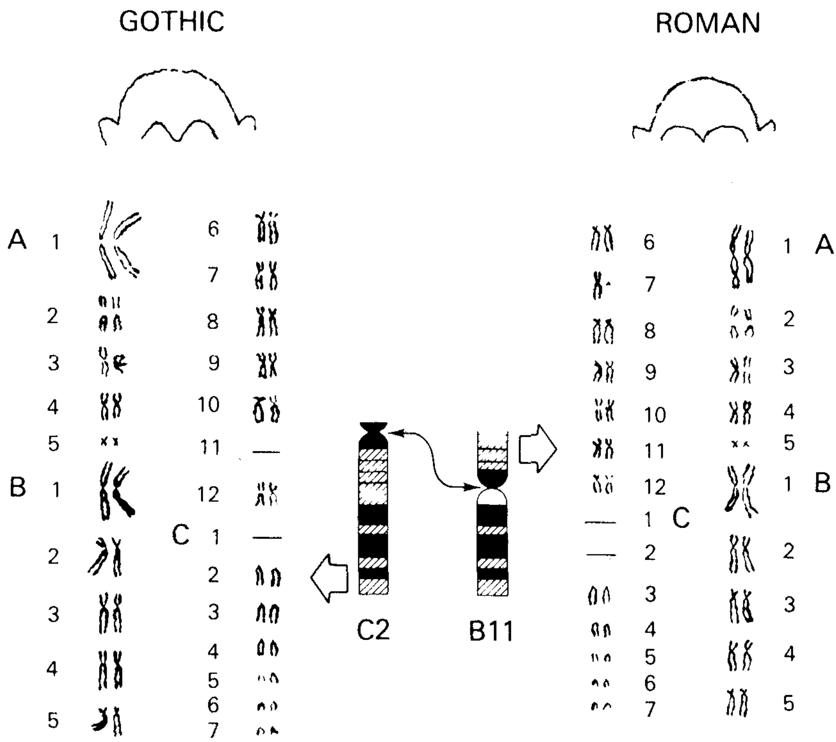

FIG. 8.—Contrasting ocular patches of so-called gothic- and roman-type monkeys (shown diagrammatically in left and right upper parts of figure). Only the gothic-type monkeys will display consistently to their reflections in a mirror. In addition to differences in appearance and behavior, these two varieties of squirrel monkeys have minor karyotypic differences. Their forty-four chromosomes can be classified into three groups (A, B, and C) on the basis of the length and position of the centromeres. As illustrated by the enlargement at the center of the figure, N. S. F. Ma and co-workers postulate that the difference between the gothic-type monkey from Columbia and the roman-type from Peru is owing to a pericentric inversion of the B11-C2 chromosomes. Regarding geographic factors, the authors speculate that "differences in the number of acrocentric chromosomes in *Saimiri* may be due to individual migration followed by recombination and selection." (Entirely redrawn after N. S. F. Ma, T. C. Jones, R. W. Thorington, and R. W. Cooper, "Chromosome Banding Patterns in Squirrel Monkeys [*Saimiri Sciureus*]," *Journal of Medical Primatology* 3 [1974]: 120-37; from P. D. MacLean, tentatively titled *The Triune Brain* [New York: Plenum Press, forthcoming].)

In a study continuing since 1961, I have observed the effects of brain lesions on the display behavior of squirrel monkeys. Like lizards, squirrel monkeys have the four main forms of displays mentioned above. In both the aggressive (challenge) and courtship displays, the dominant male approaches the other animal, vocalizes, and directs the erect phallus towards the other animal. The "signature" display of one subspecies incorporates the features of the courtship and challenge displays. This display may be used as a form of greeting. Curiously enough, members of this subspecies will regularly perform the greeting display upon seeing their reflections in a mirror. As diagrammed in figure 8, we refer to the mirror-displaying animal as the gothic type because the ocular patch (top left of figure) forms a peak over the eye like a gothic arch. The so-called roman type monkeys with the round arch (top right) are not interested in mirrors, although they perform the other kinds of displays including the aggressive, courtship, and submissive displays.

Because it allows a control of several variables, I have used the mirror display test as a model for detecting what parts of the brain are implicated in prosematic communication. In observations on more than 120 monkeys, I have found that the medial pallidal segment of the R-complex represents a region of convergence of neural mechanisms essential for the expression of the mirror display. Electrocoagulation of this region or of its projecting pathways may either eliminate or result in a fragmentation of the display.[17]

Comment in Relation to Human Behavior. The results of these experiments indicate that in animals as diverse as lizards and monkeys, the R-complex plays a basic role in displays used in social communication. By inference, they also indicate that the R-complex is essential for conspecific recognition through the performance of like-kinds of behavior. The performance of like-kinds of behavior for which I use the term "isopraxis" is what typifies a species.[18]

Isopraxis is one of six important interoperative behaviors seen in reptiles and higher forms (table II). Without defining them, I shall simply point out that the listed behaviors find expression in such human activities as the performance of daily routines and subroutines; adherence to fashions (both social and scientific); responding to partial representations whether alive or inanimate; repetitious, obsessive-compulsive acts; slavish conformance to old ways of doing things; obeisance to precedent as in legal and other matters; ceremonial reenactments; and all manner of deception.

I mention these proclivities because one finds it frequently stated that all human behavior is learned.[19] If that is so, one might ask why is it that in spite of the high degree of human intelligence and culturally learned behavior, human beings continue to do all the ordinary things that animals do? Here we need consider but one curious example. There appear to be some carry-overs from animal to human displays that are so subtle that they have escaped even the notice of expert ethologists, making it seem all the more remarkable that, if as claimed,

TABLE 2

GENERAL ("INTEROPERATIVE") FORMS OF BASIC BEHAVIOR

1 ROUTINIZING

2 ISOPRAXIC

3 TROPISTIC

4 REPETITIOUS

5 REENACTMENT

6 DECEPTIVE

"everything human beings do as human beings they have had to learn from other human beings."[20] The subtlety pertains to the close-in challenge display of territorial lizards. In the close-in display lacertilians rise up on all fours and present themselves sideways while stepping in a stilted, staccato manner that makes them appear off balance. Some rodents perform a similar broadside display, but it happens so rapidly that observers may fail to notice it. As S. A. Barnett has observed, two rats in a confrontation rise up with all four limbs extended, the back arched, and the flank turned toward the opponent. While in this posture each moves around the other "with short, mincing steps, still presenting his flank."[21] I had been unaware that the "challenge" display of two adult, rival gorillas incorporated lacertilian features until I saw Dian Fossey at one of our laboratory seminars perform what she refers to as the "parallel display" of two silverbacks.[22] When she mimicked their sideways presentation and their walking with stilted, awkward steps, one was immediately reminded of the close-in display of certain lizards. In the case of chimpanzees, Jane Goodall has described a bipedal swagger which appears to correspond to the strutting display of the gorilla.[23] Her description calls to mind the posture and movements of a Japanese wrestler.

As in the case of lizards, the stilted, staccato steps seen in the displays of the great apes seem to carry the message of a series of exclamation marks, calling to mind the goosestep of a military parade and its similarity in profile to the *Schrägstellung* gait of a Komodo dragon (fig. 9). Among different species, the sideways presentation and stilted, staccato steps have such an uncanny resemblance that it would almost seem that the challenge display had been genetically packaged and handed up the phylogenetic tree of mammals.

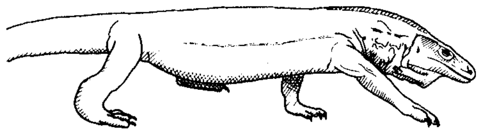

FIG. 9.—Display of a Komodo dragon. The close-in agonistic display of an adult Komodo dragon is similar to that of an appeasement display of a juvenile shown here. The animal walks slowly in a stiff-legged, stilted manner. The angle of the right forelimb in this picture is reminiscent of the goose step. Note three static modifiers seen in other lizards—namely, elevated roach (nuchal and dorsal crests), extension of gular fold, and sagittal expansion. (From W. Auffenberg, "Social and Feeding Behavior in *Varanus komodoensis*," in *The Behavior and Neurology of Lizards*, ed. N. Greenberg and P. D. MacLean, Department of Health, Education, and Welfare Publication No. [ADM] 77-491 [Washington, D.C.: U.S. Government Printing Office, 1978], pp. 301-31.)

THE PALEOMAMMALIAN BRAIN (LIMBIC SYSTEM)

Earlier in speaking of lizards, I mentioned the adult cannibalism of their young. With the evolution of mammals, it was as though there had come into being a primal commandment against cannibalism. Also of momentous significance in mammalian evolution is the development of greatly improved audiovocal communication and protracted parental care. Indeed, one might say that the history of the evolution of mammals is to a large extent the history of the evolution of the family.

If judged by existing reptiles, the extinct forms leading up to mammals would have had only a rudimentary cortex. In the lost transitional forms between mammal-like reptiles and mammals, it is believed that the primitive cortex ballooned out and became further differentiated. The cortex presumably provides the organism a greater capacity to learn on the basis of current experience. This function in turn depends on the ability to retain the memory of a present experience and to compare it with past experiences.

As illustrated in figure 10, most of the phylogenetically old cortex is found in a large convolution which Paul Broca called the great limbic lobe because it surrounds the brain stem.[24] In 1952 I suggested the term limbic system as a designation for the limbic cortex and structures of the brain stem with which it has primary connections.[25] In its totality the limbic system represents an inheritance from early mammals—hence the expression paleomammalian brain.

Functions of Limbic Subdivisions. Somewhat like a great metropolis, the limbic populations of nerve cells fall into a number of districts. In the brain map of figure 11 the three main cortical subdivisions of the limbic system are identified respectively by overlying small numerals 1, 2, and 3. As diagrammed the first two subdivisions are closely

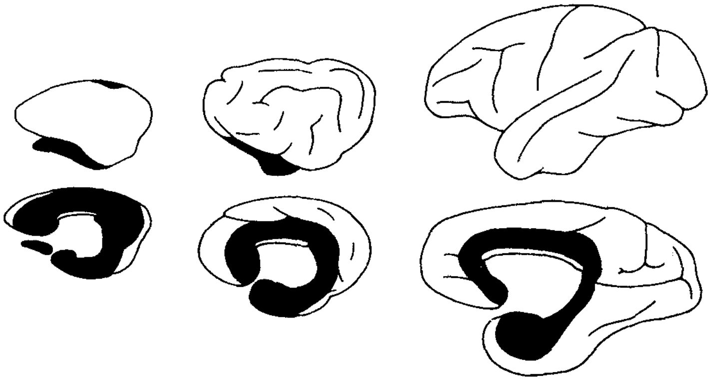

FIG. 10.—The cortex of the paleomammalian brain (limbic system). Largely contained in the limbic lobe of Broca (shaded) the evolutionary old cortex appears as a common denominator in the brains of all mammals. The cortex of the neomammalian brain (shown in white) mushrooms late in evolution. (After P. D. MacLean, "Studies on Limbic System 'Visceral Brain' and Their Bearing on Psychosomatic Problems," in *Recent Developments in Psychosomatic Medicine*, ed. E. Wittkower and R. Cleghorn [London: Pitman & Sons, 1951], pp. 101-25.)

associated with the olfactory apparatus. The population of nerve cells in the first subdivision has been shown to be concerned with activities insuring self-preservation—namely, feeding, fighting, and self-protection. The second subdivision has proved to be involved in primal sexual functions and sociosexual expression subserving procreation.[26] The intimate interrelationship between oral and sexual functions in this part of the brain can be attributed to the strong mutual interconnections of the two subdivisions with the olfactory apparatus which spearheaded the evolution of the forebrain and which plays a primary role in both feeding and mating, as well as in the fighting that may precede.

As indicated in figure 11 the main pathway of the third subdivision bypasses the olfactory apparatus. According to some authorities there is no rudimentary counterpart of the third subdivision in the brains of reptiles.[27] Although well developed in all mammals, this subdivision shows progressive expansion in higher primates, reaching its greatest development in the human brain. Our studies of twenty years ago revealed that parts of the third division are involved in primal sexual functions.[28] As will be further explained below, there is also evidence that this division is involved in maternal behavior and in play.[29]

Global Functions of the Limbic System. The clinical study of psychomotor epilepsy provides the best evidence that the limbic system is involved in emotional experience and expression. Scarring of

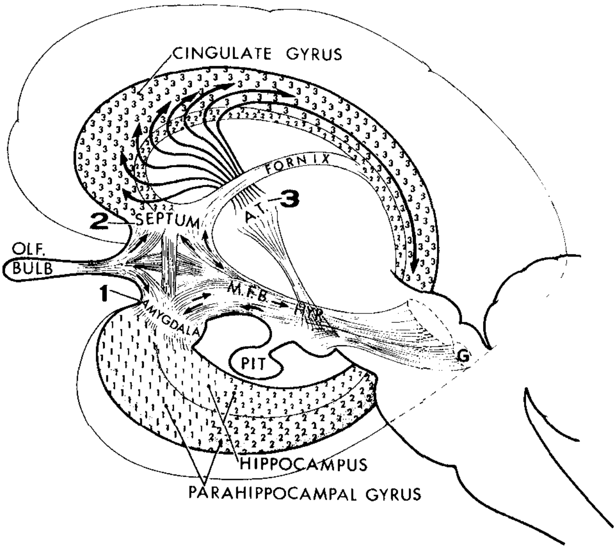

FIG. 11.—A brain map of three main subdivisions of the limbic system and their major pathways identified by the overlying numbers. See text for summary of their respective functions. Abbreviations: AT, anterior thalamic nuclei; HYP, hypothalamus; MFB, medial forebrain bundle; PIT, pituitary; G, dorsal and ventral tegmental nuclei of Gudden; OLF, olfactory. (After P. D. MacLean, "A Triune Concept of the Brain and Behavior," in *The Hincks Memorial Lectures*, ed. T. Boag and D. Campbell [Toronto: University of Toronto Press, 1973], pp. 6-66.)

the temporal limbic and neighboring cortex as the result of various causes has the effect of creating unpredictable bioelectrical storms that have a tendency to spread within parts or all of the limbic system. During the aura, which represents the beginning of a storm, the patient's mind lights up with vivid emotional feelings that range all the way from intense fear to ecstasy. Significantly a storm may also spark eureka-type feelings like those associated with discovery or free-floating feelings of belief or conviction regarding what is real, true, and important.[30] The last mentioned manifestations have profound epistemological implications.[31] A "primitive" mind providing feelings of what is real, true, and important may be adequate for judging the authenticity of food or mate, but where do we stand if we must depend on that same mind for belief in our ideas, concepts, and theories?

There is also clinical evidence that the limbic system plays an important role in the memory of current happenings. It is one of the wonders of the brain that limbic storms tend to spread in and be confined to the limbic system. During such storms an individual may carry out very complicated behavior and have no memory of it afterwards. One might say that victims of limbic epilepsy behave like disembodied spirits.

Chronic localized discharges in the limbic system may result in symptoms resembling those of schizophrenia and other psychoses. It is believed that the beneficial effects of some psychotropic drugs are due to a rather specific action on the R-complex and limbic system.

The Basic Animality

Before a brief consideration of the "neomammalian brain," it is pertinent to ask what an animal would be like with only the R-complex and limbic system. In such animals as rats and hamsters, it is possible by experimental intervention at the time of birth to prevent the development of the neocortex and its connections. We have found that hamsters growing up without the neocortex show every form of hamster-typical behavior.[32] They appear to grow and develop normally. They go through their daily routines like their control litter mates. They develop play behavior at the appropriate time. They mate and breed and rear their young.

Most significantly, if such animals are also deprived of tissue including the cortex of the third subdivision of the limbic system, they do not play, while females show deficits in maternal behavior.[33] It was as though these animals had regressed towards a reptilian condition.

In summary, the results show that the two older evolutionary formations of the brain are capable, along with the rest of the neuraxis, of giving expression to most forms of species-typical behavior, while the evolutionary newer parts of the limbic system appear necessary for the full expression of maternal behavior and the capacity for play. It merits reemphasis that three cardinal behavioral advances in the evolution from reptiles to mammals are nursing, parental care, and play.

The Neomammalian Brain

To credit the two older evolutionary formations of the psychencephalon with providing the underpinnings of basic behavior is not to downplay the importance of the neocortex. With respect to human beings nothing is more neurologically certain than that the neocortex provides the neural substrate for language and speech and that we owe to it the infinite variety of ways in which we can express ourselves. The neocortex mushrooms progressively in higher mammals (cf. fig. 10) and reaches its greatest development in human beings.

It is a remarkable feature of the neocortex that it evolves primarily in relation to systems receiving information from the external world—namely, the exteroceptive visual, auditory, and somatic systems. It was as though it were designed to serve as a more "objective" intelligence in coping with the external environment.

Handedness and Speech. In the available space it is impossible to touch upon the protean functions identified with neocortical systems. From the standpoint of primate evolution it would be particularly pertinent to consider the factors that have accounted for the tie-in of vocalization with handedness and speech. It is a subject, however, that invariably ends up on the shoals of speculation. Take for example the question as to why most human beings are right-handed—a condition which, according to artifacts of prehistory, has existed for thousands of years.[34] As a caveat in regard to the complexity of the problem it is to be noted that a predisposition to "rightness" in some form exists among some snails, flatfish, and other animals. Elsewhere I have speculated about the evolution of handedness, starting with Thomas Carlyle's "primitive warfare theory" and giving it a new twist in connection with Raymond Dart's osteodontokeratic culture.[35] Given the inherited predisposition to right-handedness, one can develop an explanation of the cerebral dominance of speech, first noting how it would be neurologically advantageous for a midline organ of speech such as the tongue with its bilateral innervation to receive its commands from a single hemisphere.[36] The representation of speech in the left hemisphere would provide the quickest and most effective means of coordinating speech and right-handed action. It is evident how under conditions of group hunting or of internecine strife split-second timing in enunciating a directional signal might make the difference between life and death. The same neurological economy with respect to cerebral dominance would apply to a written language because, whenever the idea first struck to jot things down, the right hand was ready and waiting!

Neurologically it has been considered a great waste that the nondominant hemisphere sits idly by without ever mastering a language. In the light of computer technology, I have suggested that there may be other compensations for this seeming deficiency. With computers an insufficiency of "memory" presents a continuing hindrance to achieving solutions to complicated problems. One might propose that nature, in placing linguistic functions in one hemisphere, "killed two birds with one stone—putting the midline organ, the tongue, under a single command and freeing the nondominant hemisphere to be used for a greatly expanded memory."[37] There is evidence that the nondominant hemisphere plays a role in the registration of memories.[38]

Transcendent Speech. In an evolutionary sense the "isolation call" is probably the oldest and most basic of mammalian vocalizations, serving to maintain maternal-offspring contact as well as contact with other members of the same species. In squirrel monkeys we have found that gray matter at the very core of the forebrain (posterior periventricular gray) appears to be essential for the production of these calls.[39] This gray matter receives part of its connections from a cortical area of the third limbic subdivision in which electrical stimulation results in affective vocalizations, including the isolation call.[40] In view of the questioned ability of vocalization in reptiles ancestral to mammals, it is of interest that upon electrical stimulation of the subhuman mammalian telencephalon vocalization can be elicited only from limbic structures. The vocalization required for speech appears to have required a quantum jump to the neocortex. Electrical stimulation of the so-called four speech areas interferes with speech but does not produce speech.[41]

It is a curious circumstance that the human brain attained its large size thousands of years before there was a language of words. And it is just as curious that it has been only two thousand years since human beings first saw the "sunya" (the empty space, the "zero," existing between the fingers) that has since afforded a workable language of numbers.[42] With the soaring developments in modern communication, who is to say what other languages, what metalanguages, what transcendent speech may still be in the making?

That one form of transcendent speech is in the making we may be quite sure. It found one of its earliest and clearest expressions two thousand years ago in the golden rule. Mention was made that with the evolution of the neocortex there was a predominant representation of the exteroceptive systems. As though an essential ingredient had been left out, a new sector of cortex appears in the neomammalian brain that ties in with interoceptive systems. The location of the cortical development in question becomes apparent by contrasting the low brow of a Neanderthal skull and the recently evolved high brow of a Cro-Magnon skull (fig. 12). Underneath the high brow is a greatly expanded sector of cortex that appears to be the only portion of the neocortex that establishes a strong communicative link with the internal world. This once speculative statement can now be said with some conviction because recently we have shown in monkeys that more than twenty-five percent of the cells of the medial dorsal nucleus are activated by the vagus nerve—the great visceral nerve.[43] The medial dorsal nucleus is the main nucleus projecting to the prefrontal cortex.

Clinically there are indications that the expansion of the prefrontal cortex affords an increased capacity to relate internal and external experience and thus to identify one's inner feelings with those of other beings. The prefrontal cortex is also recognized clinically to play a fundamental role in relating past, present, and future in regard to

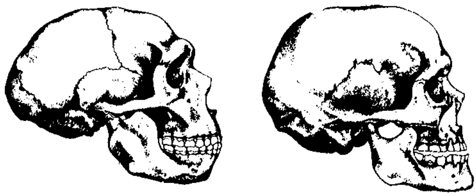

FIG. 12.—Contrasting profiles of Neanderthal and Cro-Magnon skulls. See text regarding suggested implications. (From A. S. Romer, *Vertebrate Paleontology* [Chicago: University of Chicago Press, 1966].)

"looking ahead" and making possible both anticipation and planning. Presumably it is through its connections with the medial dorsal nucleus that it obtains the "insight" required for the foresight to plan for the needs of others as well as the self. In the flowering of our medical heritage we have lived to see the evolution of such historically unique institutions as the World Health Organization and the National Institutes of Health dedicated to the alleviation of suffering, not only of human beings everywhere, but, hopefully, of all living things. Such developments must be regarded as a 180° turnabout from what has been a reptile-eat-reptile and dog-eat-dog world.

The concern for all living things also extends, by definition, to plant life and the nurturing environment. The concern mentioned in the introduction about the ruination of our environment would melt away if we kept remembering and reinforcing one of our natural mammalian tendencies and did not allow ourselves to regress to the reptilian level of our being. In pointing out behavioral differences between reptiles and mammals, I did not mention a significant distinction in regard to grooming. Reptiles have a built-in form of grooming; they simply shed their skins. Mammals, on the contrary, must actively and continually groom themselves in order to maintain a healthy integument. Mammals are also significantly different from birds, not because they groom instead of preen, but rather because in family or otherwise affiliated groups they engage in social grooming. But more than that, they practice cultural grooming, as expressed by their gardens, parks, monuments, architecture, and promotion of the fine arts.

One of the first signs of a sick animal is a failure to groom properly. Hence a healthy appearing integument is a reflection of an animal's condition to the very core, an observation counter to the claim that beauty is only skin deep. The same remarks could apply to human societies under conditions of epidemic disease, famine, war, or other dire stress, including the alleged psychological affliction mentioned in the introduction. In the case of nations at war, for example, houses go unpainted, repairs are not made, parks and playgrounds deteriorate, public buildings become shabby, and so on. It was as though under such conditions there was a regression towards a reptilian state, but without the primordial biological mechanisms of repair as a replacement for active grooming.

These and other considerations that could be mentioned suggest that except for matters concerning family and language, the limbic cortex and neocortex, respectively, have few wired-in programs for coping with situations involving large numbers of individuals. The adoption of a family way of life appears to have placed the mammal in a psychological bind with respect to crowds. As J. B. Calhoun has emphasized, harmonious mammalian family groups do not exceed an average number of twelve.[44] And as Garrett Hardin points out, there also seem to be conceptual limits to the number of individuals for whom the "collective" human family can assume responsibility.[45]

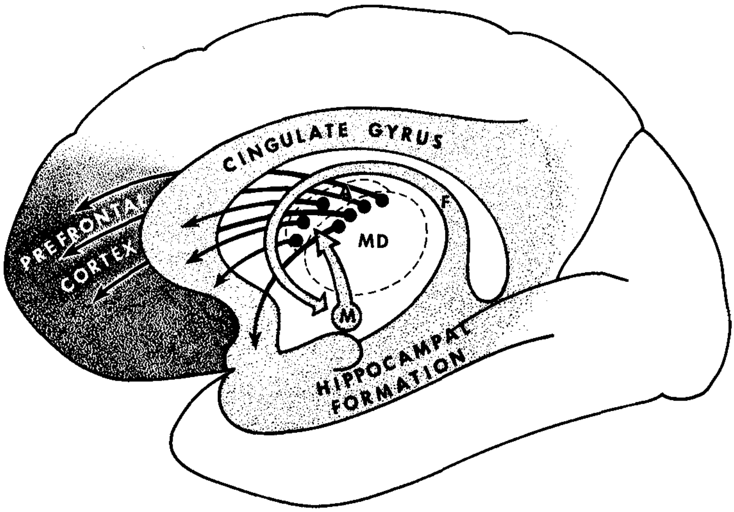

FIG. 13.—A limbic-prefrontal connection. The diagram indicates how the limbic system (light stipple) and its third subdivision is anatomically related to the prefrontal cortex through the third pathway shown in figure 11. Abbreviations: F, fornix; M, mammillary bodies of hypothalamus; MD, medial dorsal nucleus; A, anterior thalamic nuclei. (From P. D. MacLean, "A Triune Concept of the Brain and Behavior," in the *Hincks Memorial Lectures*, ed. T. Boag and D. Campbell [Toronto: University of Toronto Press, 1973], pp. 6-66.)

Is there, then, no way out of the family bind? Significantly, the prefrontal cortex is intimately geared in with the third great subdivision that has been found to be implicated in parental behavior, play, and affective vocalizations, including the isolation call (fig. 13). Mention was made earlier of the importance of the evolution of audiovocal communication for maintaining maternal-offspring relationships. Separation of offspring from the mother is calamitous. We can discern in this situation the evolutionary roots of unity of the family, unity of the clan, unity of larger societies, as well as the emotional intensity of feelings attending separation and, in its most acute form, the utter isolation of death. *Pari passu* with the evolution of those massive parts of the brain under consideration, a parental concern for the young generalizes to other members of the species, a psychological development that amounts to a progression from a sense of responsibility to what we call conscience. With good reason we can lift our eyes to these great reaches of the brain for a world-wide solution to current problems and those beyond. Given the human capacity to recognize gradations of "yes" and "no" on various issues and to decide empathically, one need hardly look beyond the evolving family to find a reason for being, an ethic to steer by.

NOTES

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