ENCEPHALIZATION OF MOTOR FUNCTIONS DURING THE EVOLUTION OF THE PRIMATE NERVOUS SYSTEM

J. F. FULTON, M.D.,

Laboratory of Physiology, Yale University School of Medicine,
New Haven

I. INTRODUCTION

I had the privilege of spending part of August and most of last September in the gracious and hospitable atmosphere of Scandinavia, and since the visit was more prolonged than I had anticipated I put my time to good use by studying and collecting the works of that great Swede, Carl von Linné.

You are no doubt aware that he introduced the term "Primate," and since I was eager to learn how his concept of the first order of mammals had developed during the course of his scientific life, I traced the order through the various editions of his *Systema naturae*. The order is recognized in the first edition of the *Systema*—published in 1735 when Linné was 27 years of age—but under the name "Anthropomorpha," although the structural characteristics are not clearly defined. He merely described "dentes primores 4. utrinqu: vel nulli." Pectoral mammae and several other specific structural details are mentioned in the second (1740) and sixth (1748) editions,[1] but "Anthropomorpha" is retained as the name of the order, and it is not till the celebrated tenth edition of *Systema naturae* (1758–59) that the word "Primates" makes its appearance. Linné placed emphasis upon teeth as a basis of classification and definition of a primate from the 10th edition runs somewhat as follows:

"A quadruped with four parallel incisors, single canines, two pectoral mammae, hands rather than paws, two complete clavicles and an arboreal habitat."

Linné included the bat in his original classification and his definition of the order would also have embraced many related forms, such as the flying lemurs, tree shrews, etc. The *Bradypus*, for example, were included in the first, second and sixth editions, but they were dropped from the Primates in the tenth edition and in the twelfth.[2] To the Linnean characteristics, one nowadays, in defining the primate, adds that it has five fingers and five toes, usually flat nails, the first and second digits being opposable; the thumb and hallux may be atrophic. Usually a single offspring is produced at birth in a completely helpless condition, but twinning occurs normally in some of the lower primates, and multiple birth may rarely occur in all forms.

---

[1] The only editions of *Systema naturae* prior to the tenth that Linné himself revised.

[2] The twelfth edition was in part revised by Linné, and was the last edition that he touched.

I cannot here go into Linné's subdivisions of the primates, but let me briefly remind you that one now recognizes three suborders of primate, the *Tarsioidea*, *Lemuroidea* and the *Pithecoidea*. Their characteristics are as follows:

Tarsioidea. The group of animals nearest the stem of the primate tree are believed to be the tarsioids which are represented by only one existing species, *Tarsius Storr.* Recent studies of Matthew (1928), Chester Stock (1938) and others, indicate that tarsioids similar to existing species were found in the middle Eocene, and that they flourished then in this hemisphere and in Europe, as well as in the Orient. At present they occur only in a limited part of Melanesia, namely the southern Philippines, the Celebes, Northern Borneo, the Malay peninsula, and possibly in some intermediate islands. Few, if any mammals, other than *Tarsius*, have survived from the middle Eocene and hence they must be regarded as among the oldest existing mammals—they are indeed "living fossils."

Interest in the comparative study of cerebral function prompted me two years ago to make a trip to the southern Philippines to study the *Tarsius* with a view to exploring the feasibility of transporting them to this country by air (Fulton, 1939). Tarsiers had not hitherto been brought either to America or to Europe, although the attempt had been made on several previous occasions. Too little was known of their feeding habits, and of their uncertain temperament. While in the Philippines I made the acquaintance of a retired army captain, Mr. Norman Cook, who, while stationed in the Davao Gulf in southern Mindanao, had succeeded in keeping tarsiers as pets and he passed on to me his notes concerning their feeding habits and other features of their natural history (see Cook, 1939; see also Lewis, 1939).

Among other things Captain Cook's notes indicated that tarsiers would eat only living food, and, as had long been suspected, he found that they were primarily insect-eating. Profiting by this information, I succeeded in keeping a number of specimens alive and transported one by Clipper back to Honolulu, but in the old clippers odds were against one because livestock had to be carried in unheated baggage compartments which at 12,000 feet frequently fell to a subfreezing temperature. I made arrangements, however, with an enthusiastic young naturalist named John Eckman to bring back some specimens by boat and these arrived in November, 1938. A pair, male and female, have survived for eighteen months in my laboratory (Catchpole and Fulton, 1939).[3] These are, I believe, the first tarsiers to be maintained in captivity outside of Melanesia. The male is just becoming sexually mature; the female's sex cycles have been closely studied, but she did not reproduce. It is of some interest that this specimen of *Tarsius* has proved to have quite regular 26 day cycles (oestrus).

The morphological characteristics of the tarsioids indicate that they occupy a place of transition between the insectivores and the primates. Hence, a study of their brain from the structural as well as from the

---

[3]Both animals died quite suddenly of filarial infestation in June and July, 1940. some twenty months after reaching this country.

functional standpoint is of the greatest possible interest (see Woollard, 1925, 1935; also Woodward *et al.*, 1919).

Lemuroidea. An offshoot of the primate stem is found in the lemurs, galagos, pottos, aye-ayes of Central Africa and Madagascar which answer to Linné's definition of a primate. They are less significant from the point of view of the primate evolution than are the tarsioids, because they probably represent an offshoot considerably distant from the base of the primate tree. However, they are more available than are the tarsioids and exist in a great many species.

Pithecoidea. An enormous branch of the order of primates is grouped under the pithecoids which include two large divisions (i) the Old World Monkeys (catarrhines) including all the apes and man and (ii) the New World Monkeys (platyrrhines). Hence, from the point of view of comparative study of the brain, the suborder Pithecoidea includes those forms to which attention is ordinarily directed. The grouping within the three suborders is indicated in the following table:

ORDER I: PRIMATES

I. TARSIOIDEA, a rare insect-eating primate which has changed little since Eocene times and exists in only one Genus: *Tarsius* Storr (several species or varieties). They are nearer the base of the primate stem than any other extant form.

II. LEMUROIDEA, a lowly offshoot of the primate stem, with tarsioid affinities, exist in four families:
   1. *Lemuridea*................Lemurs.
   2. *Lorisidea*................Loris, Potto.
   3. *Galagidea*................Galago ("Bush-baby").
   4. *Daubentonudea*............"Aye-aye."

III. PITHECOIDEA, an enormous group including Old World (*Catarrhini*) and New World (*Platyrrhini*) monkeys, the anthropoid apes and man, divided in six families:

MONKEYS

(*Platyrrhini*)
   1. *Hapalidae*................Marmoset.
   2. *Cebidae*.................Ring-tail, Spider, Woolly, Howler.

(*Catarrhini*)
   3. *Cercopithecidae*...........Langur, Four-fingered, Green and Red Military Monkey, Macaque, Japanese Ape, Baboon, Mandrill.

ANTHROPOID APES AND MAN

(*Catarrhini*)
   4. *Hylobatidae*..............Gibbon.
   5. *Pongidae*................Orang-utan, Chimpanzee, Gorilla.
   6. *Hominidae*..............Man (only one existing species).

II. THE COMPARATIVE APPROACH

Marshall Hall (1833) insisted that the nervous system is to be regarded as a group of segmental reflex arcs which had become functionally interrelated in the course of evolutionary development, the headward segments having become dominant over the segments more

caudally situated. The most conspicuous feature in the evolution of the brain, especially of primates, lies in the growing dominance of the cerebral cortex over all lower levels of nervous function.

Evidence of this dominance has been inferred from the increased complexity of the anatomical matrix in man and chimpanzee, as compared with pithecoid monkeys and lemuroids; but complexity of the matrix has of itself little meaning in the absence of functional analysis. From the response to *stimulation* important indications have been obtained concerning functional complexity. The exposed brain of various animals had been stimulated in 1800 by Aldini (1804), during the controversy which followed the discovery of animal electricity (1791), but the motor area as such was not disclosed. The German neurologist, Hitzig (1874), was the earliest to stimulate the motor area of the monkey and to compare his results with those obtained in the dog, but he did not compare the monkey with other primate forms. An abortive attempt in this direction was made by Beevor and Horsley in 1890, but the first systematic comparison of monkey, orang, chimpanzee and gorilla, was made by Sherrington and his collaborators between 1892 and 1917 (see especially Leyton and Sherrington, 1917). Cushing (1909) and Foerster (1936) later extended corresponding studies on responsiveness to electrical stimulation to the human brain (see also Penfield and Boldrey, 1937).

Another functional approach, more revealing than that of electrical stimulation, lies in comparative study of the effects of ablation of corresponding areas of the brain in different primate forms. It was David Ferrier (1875) who first proved in the monkey that if a region excitable for the arm is removed the arm becomes paralyzed. Leyton and Sherrington (1917) made a similar observation in the chimpanzee, and they imply that paralysis was more profound relatively in the chimpanzee than in the monkey when a homologous area was removed; no emphasis, however, was placed upon the more enduring character of the paralysis in anthropoid as compared with monkey.

In recent studies begun late in 1930 with Allen D. Keller (Fulton and Keller, 1932) and since continued over a period of ten years with a series of collaborators, we have had opportunity to make a systematic comparative study of the effects both of stimulating and of ablation of some forty different species of primates, beginning with pottos, galagos and marmosets, and extending through old and new world pithecoid monkeys, four orangs and some 80 chimpanzees. More than two thousand pithecoid monkeys have been used in the course of the study.

Evidence of Encephalization

The most primitive nervous system, even that of the earthworm, is organized in terms of functional levels, and it is obvious that the more headward levels are dominant over the more caudal segments. The extent of this dominance, however, varies widely in different species, and it is for this reason that much importance is attached to the comparative physiology of the central nervous system. Such comparative studies have progressed in two important directions: (i) analysis of the gradual encephalization of function, and (ii) investigation in a given

form of functional localization in the cerebral hemisphere. The last phase of the problem will be touched upon at the end of this discourse.

Motor systems. An illustration of differing degrees of dominance of the headward segments is found by comparison of cat with monkey. The cat (or dog) after removal of its cerebral hemispheres exhibits essentially normal locomotor movements; it is able to walk and to maintain itself upright against the force of gravity. An adult pithecoid monkey, however, when it loses its cerebral hemispheres, never regains its ability to walk; in other words, the control of locomotor movement has, in these primate forms, become almost completely taken over by the cerebral cortex. Locomotor function has become, as we asy, "encephalized."

There are certain relatively constant features of organization of the brain in all primate forms. The first is the position of the motor and sensory areas. In pithecoids the cerebral hemisphere is divided by a fissure, usually referred to as the "central sulcus," which separates the rostral (motor) from the caudal (sensory) portion of the hemisphere. In some of the Lemuroids there is a small dorsal sulcus that sometimes unites with sulcus rectus to form a primitive central sulcus (Connolly, 1936, p. 307). In *Tarsius* the hemisphere is usually quite smooth, but occasionally in *Tarsius*, as in the marmosets, there is a slight indentation coinciding with the posterior margin of the motor area (Woollard, 1925). The posterior division of the cerebral hemisphere, *i. e.*, the part lying caudal to the central sulcus, is primarily sensory in function and receives the great sensory projections from the thalamus and from lower spinal levels. The frontal lobes constitute the anterior portion of the hemispheres and include all tissue lying rostral to the central sulcus. This part of the hemisphere is primarily motor in function, but it also has a vast assemblage of interneurons which increase enormously in extent as one ascends the primate scale. The fore part of the frontal lobe is made up almost entirely of interneurons, and the region itself is referred to as the "frontal association areas." They are primarily concerned with higher intellectual functions, *i. e.*, memory and the capacity to plan for future action.

How does one know that the brains of chimpanzee and man are more encephalized than those of pithecoid monkeys, lemuroids and tarsiers? A suggestion comes from stimulation of the frontal lobes. The motor area of a tarsier has never been stimulated—the animal is still too rare and too precious—but I have stimulated pottos and galagos, which belong to the lemuroids, and also marmosets, and there are, in addition, several reports of stimulation of prosimiae in the literature (Volsch, 1906; Mott and Halliburton, 1908). It is strikingly true that only the most stereotyped movement patterns can be evoked from the central cortex of these primitive primates, whereas in chimpanzee and man highly discrete movements of individual fingers, corner of the mouth, the eyelids, the vocal cords and other individualized movement patterns can be evoked on cortical stimulation. Moreover, in man and chimpanzee there is a mosaic of sharply circumscribed foci controlling these specialized movements; while in the lemuroids the distribution of excitable points is homologous, but excitable foci are much less individualized.

The evidence of encephalization becomes much more impressive, however, from study of the effects of isolated ablation of those areas in the frontal lobe which an excitation gave movement, *e. g.*, of the leg. If the leg area is removed, the leg itself becomes paralyzed. *The extent and duration of the paralysis, however, varies widely in different forms.* It was mentioned that a cat, after complete removal of the hemispheres, is able, after a period of several hours, to walk about as if nothing serious had happened. The galago, potto and marmoset behave much as would a cat, although they exhibit a somewhat more enduring paresis. Mott and Halliburton (1908) were also struck by the slight character of the paresis following motor area ablation in the lemur. On removal of the leg area of a galago or potto, the leg shows obvious weakness for a few days, but power is regained after a period of time and the animal ultimately progresses as if nothing had happened. Pithecoid monkeys, such as the macaque, exhibit a profound paralysis when the foot area is removed, but recovery gradually occurs and after a few months the animal may move its foot almost normally in ordinary locomotor movements (see Fulton and Keller, 1932); signs of weakness, however, persist indefinitely in circumstances of fatigue, for even six months or a year after destruction of the leg area an animal will begin to drag its affected foot after a fatiguing chase. Hence, the mechanism governing foot movements are sufficiently encephalized in the macaque monkey to give some degree of *permanent* deficit when the foot area is removed. The baboon is considerably more affected than a monkey, and the gibbon lies clearly between the baboon and chimpanzee in intensity of its cortical paresis. Turning to chimpanzee and man, a far more profound paralysis results than in pithecoids or in the gibbon, when the foot area is ablated, *i. e.*, both chimpanzee and man exhibit a permanent and readily recognized motor deficit when the foot area of the frontal lobe is destroyed.[4]

If one compares the hand instead of the foot, the difference between species is even more striking, for a human being whose arm area has been destroyed, can never again use his fingers for the fine movements essential to play the piano, or even to button a shirt. Monkeys, on the other hand, although they do not ordinarily play the piano, exhibit other exquisitely delicate movements of the fingers and these show far less ultimate impairment following a lesion of the arm area than those of chimpanzee and man. Hence, we are led to conclude that the patterns of skilled movements are more highly encephalized in man and ape than in monkey.

In passing, it is interesting to note that control of movements of the tail in certain prehensiled tailed South American monkeys is so completely encephalized that when the tail areas are removed bilaterally, the tail itself becomes permanently and completely paralyzed, exhibiting only a spastic prehensility similar to the condition of spasticity encountered among primates after decerebration (Fulton and Dusser de Barenne, 1933). Human tails occur atavistically and some have been motile, implying cortical representation (Ross Harrison, 1901).

---

[4]These comparisons, especially among the prosimia, are based upon unpublished observations. For the pithecoid monkey, baboon, gibbon and chimpanzee, see Fulton and Keller, 1932.

Sensory systems. One may cite many parallels in the sensory sphere of similar encephalization of function. One of the most striking is that of the visual system. In fish, the optic system appears to be without significant connection with the forebrain and removal of the cerebral hemisphere causes no obvious impairment of vision, although behavioural disturbances are said to follow (G. K. Noble, unpublished). According to Schrader (1889), much the same is true of reptiles and birds. However, in rodents, particularly rabbit and rat, the visual cortex becomes encephalized; if the occipital lobes are removed, pattern vision is impaired, but the capacity to discriminate between differing intensities of light still remains unaffected (Lashley, 1932). Marquis (1932, 1938) has shown that dogs appear for a time completely blind after removal of the occipital lobes, but that brightness discrimination eventually returns with little or no impairment, while object vision is entirely destroyed. In monkeys object vision and brightness discrimination disappear entirely; a considerable degree of brightness returns (Malmo, unpublished). Man is rendered completely and permanently blind by extensive injury of occipital lobes, and he regains no consciousness whatsoever of light when this part of this cerebral hemisphere has been destroyed.

The encephalization of other categories of sensory functions follow a parallel schema, notably in somatic sensation in relation to the parietal lobes (see Ruch, 1935, and Ruch, Fulton and German, 1938).

When one approaches a given function of the human brain from the comparative standpoint by studying the particular function in a series of animals extending from tarsier and the lemurs up through the monkeys and the great apes, one can "extrapolate" quite accurately and predict how man will defer in regard to this particular function.

So much then for the principle of encephalization. Clinical neurologists often remark: "Well, you are working on cats and monkeys and your results are, of course, not applicable to the human being." My reply to this is generally somewhat direct, namely, that, if one approaches human function from a comparative standpoint far more basic light can be thrown upon it than by concentrated studies carried out on man himself without reference to his forebears in the evolutionary scale. A study of the monkey is also quite meaningless so far as the rest of the animal kingdom is concerned, unless a given function in one species is compared with the corresponding studies on forms occupying differing positions in the animal scale. The comparative approach to the human brain explains why it functions as it does.

III. FUNCTIONAL LOCALIZATION IN THE FRONTAL LOBES

The greater part of the cerebral cortex is made up of six primary layers of cells, but each layer has a different *cellular architecture*. The frontal lobes are subdivided on the basis of cytoarchitecture into a number of structurally discrete fields to which Korbinian Brodmann (1909), the Armenian histologist, gave an erratic series of numerical designations. Thus, the motor area—which on stimulation causes movement of skeletal muscles—is known as area 4; the adjacent premotor region as area 6; another area which on stimulation moves the

eyes is numbered 8, etc. The map in Fig. 2 gives these numerical designations as modified by Dusser de Barenne; the capital letters L, F and A denote respectively Leg, Face and Arm, so that area L.4 is the leg area and A.6 the part of the premotor area concerned with the arm, etc.

(Motor fields (Areas 4 and 6)

The excitable characteristics of these areas has already been described, *i. e.*, a mosaic of discrete foci can readily be demonstrated. When these areas are ablated in monkeys or chimpanzees, an enduring paralysis occurs; indeed, if areas 4 and 6 (including leg, arm and face) are destroyed bilaterally in an adult monkey, the animal is as gravely paralyzed as when both cerebral hemispheres are removed (Bieber and Fulton, 1938). This means not only that the motor functions are encephalized to this surprising extent in higher primate forms, but it also indicates that they are *localized* to a given rather small area within the cerebral hemisphere. This localization is far less discrete in the lemuroids than in the pithecoids.

In the adult pithecoid the functional localization of motor patterns is so complete that enduring volitional paralysis follows bilateral ablation of particular regions. But this is not true of young animals of the same species. You are familiar with the biological concept that ontogeny tends to repeat phylogeny, *i. e.*, that embryological development is on its broad outline a recapitulation of evolutionary history. It is undoubtedly, therefore, a fact of prime importance that when the motor and premotor areas are removed from monkeys shortly after birth, as has been done in the recent studies of Dr. Margaret Kennard (1938), the baby pithecoids behave much as do *adult* galagos and pottos after a similar lesion, *i. e.*, they have only slight motor paralysis. However, as these baby macaques grow older, signs of deficit begin to appear; but they never become as grave as the paralyses which follow a corresponding ablation in an adult animal. There exists in the infant nervous system of a pithecoid monkey, greater capacity to reorganize its functional localization, *and the pithecoid infant behaves as if it were an adult lemuroid.*

Dr. Kennard is much interested at the moment in attempting to discover what part of the nervous system is responsible for integrating movement patterns of her normal infant macaques. The basal ganglia undoubtedly play an important role; but during the first six months of life their function is gradually taken over by the cerebral cortex. In these young animals, therefore, as in the human infant, the evolutionary process of encephalization proceeds under our very eyes.

Considerations of space forbid more detailed discussion of the other cytoarchitectural areas of the cerebral cortex, but in the case of all those which have been fully investigated a corresponding increase of functional discreteness has been established as the primate scale is ascended. In the tarsioids and lemuroids the cerebral cortex is smooth and only the major fissures—such as the Sylvian—can be identified; the boundaries of lemuroids are more indefinite functionally and anatomically than in the pithecoids. The insectivors and rodents have a similarly smooth cortex with even less discreteness of functional localization, and this has no doubt been responsible for a modern error among

experimental psychologists who, until very recently, have insisted in the equipotentiality of all regions of the cortex. In so far as "learning" is concerned there may be a basis for their contention—and this is true of man as well as animals—but when one scrutinizes the great sensory and motor functions of the primate forebrain the concept of equipotentiality is not only one of harmony with every known fact of comparative neurophysiology, but it is in addition naive and misleading.

The functional approach to the evolution of the primate brain has thus given clarity and precision to doctrines which in the past have been based largely upon inferences drawn from morphological studies.

REFERENCES

Aldini, G. Essai theorique et experimental sur le galvanisme. Paris, 1804. x, 398 pp., 4 pl.

Beevor, C. E., and Horsley, V. A record of the results obtained by electrical excitation of the so-called motor cortex and internal capsule in an orang-outang (*Simia satyrus*). Philos. Trans., 1890, **181 B**: 129–158.

Bieber, I., and Fulton, J. F. The relation of the cerebral cortex to the grasp reflex and to the postural and righting reflexes. Arch. Neurol. Psychiat., Chicago, 1938, **39**: 435–454.

Brodmann, K. Vergleichende Lokalisationslehre der Grosshirnrinde in ihren Prinzipien dargestellt auf Grund des Zellenbaues. Leipzig, J. A. Barth, 1909; reprinted, 1925, xii, 324 pp.

Catchpole, H. R., and Fulton, J. F. Tarsiers in captivity. Nature, 1939, **144**: 514.

Clark, W. E. LeGros. Notes on the living tarsier (*Tarsius spectrum*). Proc. Zool. Soc. Lond., 1924, 217–223.

Clark, W. E. LeGros. Early forerunners of man. A morphological study of the evolutionary origin of the primates. London, Balliere, Tindall and Cox, 1934, xvi, 296 pp.

Connolly, C. J. The fissural pattern of the primate brain. Amer. J. Phys. Anthrop., 1936, **21**: 302–422.

Connolly, C. J. Development of the cerebral sulci. Amer. J. Phys. Anthrop., 1940, **26**: 113–149.

Cook, Norman. Notes on a group of tarsiers in captivity. J. Mammol., 1939, **20**: 173–178.

Cushing, H. A note upon the faradic stimulation of the postcentral gyrus in conscious patients. Brain, 1909, **32**: 44–53.

Dusser de Barenne, J. G., and McCulloch, W. S. Functional organization in the sensory cortex of the monkey (*Macaca mulatta*). J. Neurophysiol., 1938, **1**: 69–85.

Ferrier, D. The Croonian Lecture. Experiments on the brain of monkeys (second series). Philos. Trans., 1875, **165**: 433–488.

Ferrier, D. The functions of the brain. London, Smith Elder and Co., 1876, xv, 323 pp.

Foerster, O. The motor cortex in man in the light of Hughlings Jackson's doctrines. Brain, 1936, **59**: 135–159.

Fulton, J. F., and Dusser de Barenne, J. G. The representation of the tail in the motor cortex of primates, with special reference to spider monkeys. J. cell. comp. Physiol., 1933, **2**: 399–426.

Fulton, J. F., and Keller, A. D. The sign of Babinski. A study of the evolution of cortical dominance in primates. Springfield, Ill., Charles C. Thomas, 1932, xv, 165 pp.

Grunbaum, A. S. F., and Sherrington, C. S. Observations on the physiology of the cerebral cortex of some of the higher apes. Proc. Roy. Soc., 1901, **69**: 206–209.

Hall, M. On the reflex function of the medulla oblongata and medulla spinalis. Philos. Trans., 1833, **123**: 635–665.

Harrison, R. G. On the occurrence of tails in man, with a description of the case reported by Doctor Watson. Proc. Ass. Amer. Anat., 1901, **14**: 141–148.

Hilgard, E. R., and Marquis, D. G. Conditioning and learning. New York, D. Appleton-Century Co., 1940, xii, 429 pp.

Hitzig, G. Untersuchungen uber das Gehirn. Berlin, A. Hirschwald, 1874, vi, 276 pp.

Kennard, Margaret A. Alteration in response to visual stimuli following lesions of frontal lobe in monkeys. Arch. Neurol. Psychiat., Chicago, 1939, **41**: 1153–1165.

Kennard, Margaret A. The relation of age to motor impairment in man and subhuman primates. Arch. Neurol. Psychiat., Chicago, 1940, **40**: 377–397.

Lashley, K. S. Studies of cerebral function in learning. XI. The behavior of the rat in latch box situations. The mechanism of vision. XII. Nervous structures concerned in the acquisition and retention of habits based on reactions to light. Comp. Psychol. Mongr., 1935, **11** (no. 52), 79 pp.

Leyton, A. S. F., and **Sherrington, C. S.** Observations on the excitable cortex of the chimpanzee, orang-utan and gorilla. Quart. J. exp. Physiol., 1917, **11**: 135–222.

Linné, C. von. Systema naturae, sive regna tria naturae systematica proposita per classes, ordines, genera, et species. (1st ed.) Leyden, T. Haak, 1735, 14 fol.

Linné, C. von. Systema naturae per regna tria naturae secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. . . . 2 vol. (10th ed.) Stockholm, L. Salvius, 1758–59.

Malmo, R. B. Effects of removal of the visual cortex on brightness discrimination and spectral brightness distribution in the rhesus monkey. Dissertation, Yale University, 1940.

Marquis, D. G. Effects of removal of the visual cortex in mammals, with observations on the retention of light discrimination in dogs. Res. Publ. Ass. nerv. ment. Dis., 1934, **13**: 558–592.

Marquis, D. G. Phylogenetic interpretation of the functions of the visual cortex. Arch. Neurol. Psychiat., Chicago, 1935, **33**: 807–815.

Matthew, W. D. The evolution of mammals in the Eocene. Proc. zool. Soc. Lond., 1928, 947–985.

Mott, F. W., and **Kelley, Agnes M.** Complete survey of the cell lamination of the cerebral cortex of the lemur. Proc. Roy. Soc., 1908, **80 B**: 488–506.

Mott, F. W., Schuster, E., and **Halliburton, W. D.** Cortical lamination and localisation in the brain of the marmoset. Proc. Roy. Soc., 1910, **82 B**: 124–134.

Penfield, W. G., and **Boldrey, E.** Somatic motor and sensory representation in the cerebral cortex of man as studied by electrical stimulation. Brain, 1937, **60**:389–443.

Ruch, T. C., Fulton, J. F., and **German, W. J.** Sensory discrimination in monkey, chimpanzee and man after lesions of the parietal lobe. Arch. Neurol. Psychiat., Chicago, 1938, **39**: 919–937.

Ruch, T. C. Cortical localization of somatic sensibility. The effect of precentral, postcentral and posterior parietal lesions upon the performance of monkeys, trained to discriminate weights. Res. Publ. Ass. nerv. ment. Dis., 1935, **15**: 289–330.

Schrader, M. E. G. Zur Physiologie des Vogelhirns. Pflug. Arch. ges. Physiol., 1889, **44**: 175–238.

Sherrington, C. S. Notes on the arrangement of motor fibres in the lumbro-sacral plexus. J. Physiol., 1892, **13**: 621–772.

Stock, Chester. An Eocene primate from California. Proc. Nat. Acad. Sci. Wash., 1933, **19**: 954–959.

Stock, Chester. A second Eocene primate from California. Proc. Nat. Acad. Sci. Wash., 1934, **20**: 150–154.

Volsch, M. Ein Rindenreizungsversuch an einem Halbaffen. Mschr. Psychiat. Neurol., 1906, **20**: 470–471.

Vogt, C., and **Vogt, O.** Sitz und Wesen der Krankheiten im Lichte der topistischen Hirnforschung und des Variierens der Tiere. J. Psychol. Neurol., Lpz., 1936, **47**: 237–238.

Woodward, A. S., Smith, G. Elliott, Hill, J. P., Wood-Jones, F., Pocock, R. I., Cunningham, J. T., Mitchell, P. C., and **MacBride, E. W.** Discussion on the zoological position and affinities of *Tarsius*. Proc. zool. Soc. Lond., 1919, **19**: 465–498, 1 pl.

Woollard, H. H. The cortical lamination of *Tarsius*. J. Anat., Lond., 1925, **60**: 86–105.

Woollard, H. H. The anatomy of Tarsius spectrum. Proc. zool. Soc. Lond., 1935, 1071–1184.