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IN PRIMATES**

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SOME QUESTIONS ON PARAMETERS OF NEURAL EVOLUTION IN PRIMATES

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INTRODUCTION

This paper is purposely discursive and general. I am neither a palaeontologist nor a neuroanatomist, but a physical anthropologist trying to understand man's place in nature and his evolution. The more neuroanatomical literature I read, the more convinced I become that our understanding of the evolution of structure and behavior suffers from serious lack of thought regarding appropriate units of behavior and structure that can be brought together in a synthesis. My purpose, therefore, is to raise many questions rather than provide any answers. Accordingly, and as a starting point, I will attempt to question the utility of quantitative parameters of the nervous system and its evolution in Primates. Following a discussion of the limits of evidence and the rationale behind using quantitative parameters, I will suggest a few other approaches that might be given serious consideration by those in the neurological sciences with the necessary expertise and equipment.

Each primate species has its own peculiar assemblage and interdependent organization of anatomical structures and behavioral patterns derived through processes of evolutionary modification. Limb proportions, muscle masses, sensorimotor capabilities, and social behavior vary considerably both between and within major taxa, reflecting numerous strategies of adaptation to different lifeways and ecological surroundings. Saltatory hopping, vertical clinging, quadrupedalism, brachiation, and bipedalism are serviced by anatomical and behavioral complexes, ultimately requiring various degrees of nervous control and coordination.

The obverse side of this matter is that in spite of the specific variability there is still an underlying core of adaptive commonality derived through tens of millions of years of evolution and adaptation within an arboreal existence. The commonality side of these adaptations includes locomotion, prehensility, dependence on visual information, gregariousness, need for stimulation, curiosity, and a plasticity of behavior.

Although our knowledge of primate structures and behaviors has expanded enormously in the last two decades, even to the biochemical level, our appreciation of the nervous systems of different primates has hardly kept pace with these other areas. Aside from easily determined parameters such as absolute and relative brain size, or derived indices of cephalization, etc., there are few anatomical data that serve to relate primate brains to their varied adaptations in any specific manner. This applies particularly to those features of behavior (both social and sensorimotor, i.e., aggression, locomotion, prehensility) which are species-specific as against those of universal or near-universal distribution in the primate order. Primates have well-developed brains, reflected both in absolute and relative brain weights and are, of course, intelligent. They are capable of advanced degrees of prehension and general motor finesse (Tilney's 1928 "neokinesis"), and this is also reflected in the fiber tracts serving information input (particularly the visual system and lemniscal pathways) and output through the pyramids, organization of motor cortex, extrapyramidal system, and cerebellum. More general attributes

such as gregariousness, intragroup social binding, mother-offspring affect, etc., cannot as yet be related to the nervous structures of the primate vs other mammalian orders in any hierarchical, organized way. Of course, some of these commonalities, as well as some specifics, can be found in other mammalian orders, e.g. the carnivora.

At the present time, there is no comparative primate neurochemistry, and comparative neurophysiological studies relating to behavioral specifics are hardly common. Although neuroanatomical data for primates are more available, and are expanding, there are vast hiatuses. This is not, of course, a problem unique to primates. For example: what are the essential neural substrates responsible for the behavioral differences between a Siamese and an alley cat, or between a cocker spaniel and a basenji hound, or the grey Norway and black rat? Only recently have scientists published findings relating to neurochemical differences in strains of mice. Two large problem areas exist in trying to relate structural variations of the brain to behavioral patterns distinct at the species and generic taxon levels: (1) units of behavior, and (2) units of structure.

Brain morphology, either purely descriptive or quantitative, may not be the most appropriate level at which to discover meaningful relationships with the remaining bodily structures and behavioral patterns integrated in a taxon's adaptations. Still, one would expect this to be a reasonable starting point. In the bird class there is an enormous range of behavioral stereotypes, with but few clear relations to differences in neural structure. The same can be said for fish brains, aside from crude correlations between olfactory and visual correlates between, say, a carp and a trout. Wherein lies that magic level of structure(s) of nervous tissue that will allow a true synthesis between behavior and structure?

RATIONALE

Matters of Evidence

Before turning to a discussion of parameters and the primate nervous system, it is necessary to understand certain limitations of an evidential nature that constrain our study of the evolution of the primate brain. Strictly speaking, it is impossible actually to study the evolution of the primate brain. As I have discussed more fully elsewhere (1964, 1966a, 1968), neither comparative neuroanatomy of extant primates nor fossil endocasts are equal to the task. Contemporary primates are the present end products of their own lines of evolutionary development, and endocasts cannot provide information about internal brain organization, either for the cortex (density, dendritic branching, glial/neural ratios, cytoarchitectonic or functional organization) or the subcortical components so important in both sensorimotor and affective or emotional behavior. Our only hope, if we insist on strict empiricism, is nicely frozen, Frankensteinian remains of a series of fossil apes and men inbedded in blocks of tertiary and quaternary ice. Aside from these possible fantasies, we must rely on the indirect evidence from comparative neuroanatomy and behavior, and the fossil record of man including not only bones, but the tools, shelters, and butchered remains of other animals, since these are the only "fossilized behaviors" we will ever have.

I share the dominant view that man's behavioral specificities or differences cannot be reduced to any single parameter, whether it be mass size, frontal lobes, neuron number, infraparietal lobules, glial/neural ratios, or even base ratios of different RNA's in the neuron and glia. Behavior, whether specifically of discrete sensory or motor actions, aggression or submission, or cognitive activities such as

thinking, abstracting, language, etc., involves the interaction of many neural components, i.e., nuclei and fiber tracts, acting either simultaneously or in time intervals amounting to milliseconds. Behavior is the result of systems of neural tissues interacting through time. This hardly means that we are doomed to forego analytic study of the brain, meaning its components, since each contributes to the smooth action of molar behavior, which we can observe, and each correlates to some degree with the capabilities evidenced by the degree of behavioral efficiency, as in learning-to-learn phenomena and amount of cortex, or in fine manipulative skills and the pyramidal and extrapyramidal systems. It is uncertain, however, whether the crude morphological parameters we use are sufficient for understanding the neural basis of behavior, or whether we must move from parameters such as brain weight, encephalization coefficients, area of nuclei in cross section, volumes of nuclei, or glial/neural ratios, to more biochemically-based ones. My own bias is that the biochemically based parameters will correlate better with morphological parameters than with behavior. In any event, we have little, if any, good understanding of the nature of the brain differences which account for the behavioral differences in different animal taxa, particularly at lower levels of distinction (e.g., generic and specific).

One must assume then that by studying a comparative series and understanding the neural basis for behaviors in broad outline (e.g., amygdala and rage), and the interdependent variations between both variables, one can arrive at general formulations which can be applied to the indirect evidence from the fossil record, and work toward a logical synthesis of what man is and how he came to be. If this latter is our ultimate goal, we must appreciate fully the limits of approaches which cathect only on brain mass and not organization. We can no longer talk about brains evolving first or last, since such views constrain us to look at the evolutionary dynamics of our past in rigid ways (Holloway, 1968, in press). The only method of reconstruction is speculation, framed in such a way that the hypotheses are (1) concordant with our knowledge of neural structures and behavior, the fossil record, evolutionary theory, and genetics; (2) hypotheses derived from the above must be testable against further knowledge. If the propositions making up any theory cannot be tested against either the fossil record or structure-function relations, they are useless except as serendipitous probes. To put it another way: if we had a truly synthetic understanding of primate behavior, structure, and evolution, we should be able to do either of the following: (1) predict behavioral qualities (social and sensorimotor) from a description of the nervous system; (2) predict brain morphology from descriptive primate behavior. Obviously, we are a rather long way from effecting this kind of understanding, and if one thinks about our current knowledge of nonhuman primate nervous systems, can one find a basis to make a single behavioral prediction that is species-specific? Indeed, can such parameters be found?

Matters of Quantification

The usefulness of quantitative parameters naturally depends on the parameter chosen. Here, for the present, I would like to discuss quantification in very general terms. One logical reason for determining quantities is that one can compare the size of a structure between two forms. In general, what is big is important, and differentials in the size of a structure between related forms are crude indications of natural selection acting on behavioral units mediated by the structure. Although this is undoubtedly so obvious as to approach banality, increased sizes—whether of neuron numbers, volumes of tissue such as the cortex

and associated thalamic nuclei, or numbers of fiber tracts in the pyramids—all say something about selection pressures for behavior in the past and the kinds of environments faced by the animals in question. Increased sizes must eventually relate to more molecular events such as duration and/or rate of mitotic divisions, which in their turn depend on codes of amino acid sequences (codons) in DNA. We are certainly a long way from making empirical connections between molecular events such as genetic readout and our volumetric comparisons of neural nuclei.

A second reason for such an interest in quantification is that it shows something about both the magnitude and direction of shifting reorganization of neural components in different primates. The quantitative data show that ape and monkey brains are not simply enlarged or smaller versions of each other, and that through their evolutionary developments each primate brain bears the stamp of specificity. As obvious as this might appear, there are still many students of evolution, particularly physical anthropologists, willing to use cranial capacity in fossils as evidence pro or con regarding language, tool-making, complexity of social organization, hunting ability, and evolutionary dynamics. To return to the subject of reorganization, Hopf and Kraus (1967) show that the volume of the thalamus increases in size as does the volume of the cortex in a range of primate species. The plot produced is log-log, showing an almost perfect 45° angle, with a correlation of better than .99. Internally, however, the thalamic nuclei do not uniformly show simple proportional increases related to cortical expansion alone, but nuclei such as the pulvinar, dorsomedial and lateral show striking increases the higher one goes in the scale, relating to particular cortical areas. This type of relationship also appears with the basal ganglia (particularly the caudate and putamen) and limbic nuclei and tracts.

PARAMETERS

In the broadest sense, a parameter is a number characterizing a population, a measure of some attribute or relationship of a structure or structures. The crudest parameters used for comparative purposes are absolute and relative brain weight or volume. Obviously, the amount of functioning nervous tissue available for an animal to utilize is a variable related to its behavior. Absolute and relative brain weights are parameters of such a variable as amount of functioning tissue and, as we know, these correlate only crudely with whatever parameters we choose to measure behavioral variables, such as length and extent of memory or intelligence. A considerable amount of energy has been directed toward the discovery of various mathematical relationships or indices which might better correlate mass relations of the brain to behavior and show man's neural supremacy. Although such attempts are clearly of value in demonstrating parallel evolution in diverse taxa toward more effective plasticity of behavior and pinpoint the enormous importance of cerebral cortex in primate evolution, they clarify little about actual evolutionary adaptations of a more specific nature. Two problems exist: (1) the ranges of variability of mass with no particular relationship to behavior within species (e.g. man); (2) mass parameters completely ignore reorganization among the nuclei and tracts that mediate specific behavioral variables. Behavioral differences, as between man and chimpanzee, for example, must rely on more than mass weight or volume. Microcephalics and nannocephalics (Lenneberg, 1967; Holloway, 1964, 1968) possess specifically human behavioral patterns with brain weights to be disdained by large-brained gorillas who remain nonhuman.

Another parameter often used to make correlations with behavior is neuron number (e.g., Gerard, 1963; Garn, 1963; Jerison, 1955, 1963). Although such a parameter may correlate with some measure(s) of behavioral complexity, it overlooks reorganizational changes in brain systems (e.g., Holloway, 1966b). It is very doubtful that differences in behavior between taxa can be reduced to neuron numbers until these numbers are further broken down in terms of numbers in precentral cortex related to the thumb, or interparietal lobule, etc. It is doubtful that even such a breaking down into finer functional units would work, considering the role of subcortical structures (e.g., ascending reticular formation, hippocampus, caudate, etc.) in cortically-mediated behavior. For example, there does exist the interesting possibility that healthy chimpanzees have more functionally operative neurons in their brains than do nannocephalics or certain microcephalics who maintain their human specificity of behavior. (This will depend, of course, on neural densities, size of cells and dendritic branching, and numbers and functional status of morphologically immature neurons.) In other words, volumes of brains and neuron numbers are unsuitable parameters for making anything but the most crude behavioral correlations; the same ones we have faced for the past hundred years.

A more specific parameter would be a real extent (per cent of total) of cerebral cortex involved in particular behavioral actions (e.g. area for hand, thumb, tongue, vision, etc.). Such data depend upon careful stimulation and recording of the cortex of anesthetized animals (Woolsey, Welker *et al.*). At the present time, there are no quantitative data published for primates based upon such techniques. Welt's (1962) review of this approach to primate behavior and cortical structure shows that there are significant differences among primates, although they have not been quantified as yet.

For example, in New World monkeys, there is considerable variation in extent of cortex which produces tail movements when stimulated, or which registers firing when the tail is stimulated. The tail area in cortical Sm I area is largest in those ceboids which possess a prehensile tail, and the distal portion projects to more cortex than the proximal segment, a situation paralleled by all the higher primates, the gibbon excepted, with respect to front and hind limbs. In squirrel and cebus monkeys, the tail area is larger than in Old World monkeys, yet smaller than for the spider monkey. Another interesting observation from Welt's studies is that the chimpanzee shows greater differentiation of digital movements than man upon cortical stimulation.* If the underlying assumption that expanded functional areas reflect evolutionary selection for such behavioral specifics is correct, such a parameter should relate to both naturalistic and laboratory studies of behavior, and should lead to fuller understanding of past evolutionary dynamics in the particular taxon's development, while permitting incorporation of data on modifying or monitoring subcortical systems, such as the basal ganglia, cerebellum and brain stem.

Returning to volumetric parameters: a welcome interest in regard to the exact quantitative organization of subsystems serving emotional behavior has been shown by Stephan and Andy (1966), Hopf (1965), Daitz (1953), and Powell and colleagues (1957) in the volumetric analysis of the limbic system. This data usually takes the form of volumetric reconstruction from areal measurements of

* As was pointed out during a discussion period at this conference (not included in this monograph), one must not ignore the peripheral structural differences between chimpanzee and man that show that the chimpanzee possess neither the musculature nor the arrangement of digits for fine manipulative skills that man does.

particular nuclei in cross section. As I discussed in my 1968 review, these kinds of data show very well that primate brains have become reorganized in the course of evolution. Closely similar indices are those of percentage of cross-sectional area taken up by particular nuclei or fiber tracts, as for example in Tilney's (1928) planimetric indices for the brain stem, or Solnitzky's (1946) data for cerebellar nuclei.

It may well turn out that these simple kinds of parameters will not correlate well with behavioral adaptations characterizing each species, except grossly at the motor and sensory levels. It is instructive, for example, to consider the following experimental results from Kitsikis (1968) on the suppression of arm movements in *Macaca* by caudate stimulation. Her experiments show that the threshold for suppression varies depending on the position of the arm and the degree of activity of proximal and distal extremities; i.e., the reticular formation, and probably cerebellar efferents to the midbrain will affect the threshold for suppressing arm movement through caudate stimulation. This kind of experimentation shows two things: (1) integrated systems of fibers, nuclei, and proprioceptive information of ongoing actions are essential to the quality and quantity of motor actions; (2) the performance of homologous actions can differ in various primates with similar quantities of particular nuclei or cortical configurations if other systems in the brain differ. Such possibilities could easily be studied by performing the same experiments on different primate species.

A similar problem area which might yield a few good correlations would be the limbic system and emotional behavior. From numerous studies on both ablation and stimulation of neural sites in the hypothalamus, septum, anterior and posterior thalamus, we are learning that there are complex inhibitive and facilitative interactions between these nuclei and the cortex in mediating aggressive responses (see Grossman, 1967 for review). There do not exist at present enough quantitative data on the limbic system to encourage even a crude correlation with our expanding knowledge of natural and laboratory behavior of primates.

Clark and Birch (1946) showed that testosterone injections did alter the dominance relationships between chimpanzees. In 1955, Mirsky showed that such injections apparently had no effect on rhesus macaques. Aside from the obvious fact that such studies deserve duplication and extension, these investigations suggest that there are threshold differences in aggressive behavior between chimpanzee and macaque. Could they be related to volumetric parameters of limbic nuclei? One can review the entire literature on primate aggressive behavior and, with the sole exception of Chance (1962), never find any reference to possible neural differences in limbic structure being related in an evolutionary context to social behavior. One problem is surely the question of simple volumetric data in behavioral correlation, and the other problem, of course, is the complexity of emotional behavior. That is, the various nuclei are numerous, and the behavioral correlates are to be associated with systems of nuclei and tracts rather than one or two nuclei (e.g. the amygdala), since all evidence (stimulation and ablative) shows an interaction between inhibitive and facilitative subsystems. Perhaps some additive parameter lumping together facilitative structures against inhibitive ones would be better suited for gross correlations with behavior.

On the other hand, the following example may help to illustrate why quantitative parameters, at least of the type so far employed, may be of no use in this question, notwithstanding the fact that social behaviors are too complex to find ready correlation with subcortical neural structures. The researches of MacLean and his colleagues (1962) have shown a system of positive stimulation sites in

cortex and subcortex for a penile erection display in squirrel monkeys. There are a number of points in the brain where this display will occur with stimulation, including regions of the posterior hypothalamus. Robinson and coworkers (1968) have recently tried similar procedures with macaques. They have been able to evoke penile erection by means of electrode stimulation. However, they do not get this reaction when stimulating posterior hypothalamic sites. As they have pointed out, penile display is an organized dominance pattern in squirrel monkeys, but not in macaques, which correlates with the absence of penile erection in the posterior hypothalamic stimulations, a region associated with aggressive behavior. At this more molecular level of behavior, one may seriously doubt whether any quantitative parameters could be found to provide a neurally-based substrate explanation for such behavioral differences between two members of the Anthro-poidea.

At the more microscopic level, there are parameters such as cell size, neural density, glial/neural ratios, amount of dendritic branching and dendritic spine counts. With reference to the primates, data exist for only the first three parameters, but do not relate in any specific way to behavior except overall complexity (Holloway, 1967) of behavior, since they do correlate well with brain size (e.g., Shariff, 1953; Tower, 1954; Rensch, 1959). Friede's (1963) data on the microscopic structure of the cerebellum show that there is a considerable difference between man and macaque in the ratio of neuroglial cells to one Purkinje cell. In man the ratio is 44:1, in monkey, 17:1. Yet the volume of a single Purkinje cell is larger in macaque than in man, whereas the packing density of neuroglial cells in the molecular layer of macaque is less than in man. This relationship is the reverse of what one sees in the cerebral cortex. The physiological meaning of these differences is not known, and no data of a similar nature have been published on pongids. Whether such figures might reflect greater functional demands upon the cerebellar interplay in posture and manipulative excellence in man is open to speculation. Still, the usefulness of these parameters is at least threefold: (1) they are useful in describing cortical reorganization, (2) they are necessary preludes to biochemical analyses, and (3) they are manipulable through application of hormones and environmental stimulation (e.g., see Eayrs, 1959; Clendinnen & Eayrs, 1961; Diamond *et al.*, 1964; Holloway, 1966). Taken alone, i.e., without reference to the rest of neural organization, these parameters are of little value, relating only to behavior efficiency or maze scores. Aside from Shariff (1953) and Tower (1954), there are very few reliable data for different primates. To date, there is no published study of dendritic branching in any primate other than man (Schade *et al.*, 1962). Connectivity among neural elements is surely an important factor in behavioral plasticity and efficiency, provided such data are integrated with other neural parameters for those structures which subserve motivation, arousal, inhibition, facilitation, etc. When Haug's data are reviewed, the allowances made for the use of diseased animals, the glial/neuron ratios follow a definite trend. Glial cells are capable of multiple mitotic divisions; neurons are not. We do not know how many genetic loci may be involved in glial differentiation, but a logical case can be made for carefully considering these elements as important in primate evolution, since essentially more genetic loci would be involved for the action of natural selection on neural-glial interaction in behavior.

The above discussions cover most of the morphological neurological parameters found in the literature, but are hardly exhaustive. It should be obvious that such data are of considerable interest to anyone trying to follow evolutionary

dynamics for different taxa. Such data have relevance not only to this pursuit, but also to the development of more molecular parameters at physiological and biochemical levels. Here, there are no comparative data aside from Goodman's (1964) work showing different protein bands for heart lactic dehydrogenases between major primate taxa. This observation correlates with the fact that the heart type of LDH is related to oxidative metabolism and increases as one ascends the phylogenetic scale. So far, these do not relate in any particular way with behavior, but do correlate in a rough way with degree of placentation.

The following questions might be asked as illustrations of how well informed we are in regard to physiological and biochemical units and behavior: (1) Are there threshold differences based on neurochemical variables among different primates for the inhibition and facilitation of various limbic structures? (2) What differences exist between medial, lateral, anterior, and posterior sections of various primate hypothalami in terms of sensitivity to extero- and interoceptive influences of both a neural and hormonal nature? Are there, for example, differences between arboreal and terrestrial primates that show great variation in sexual dimorphism and aggressiveness? (3) Are there neurotransmitter differences in different primate species? (4) If evolution can be characterized as selection for different sequences in amino acids and protein chains, or arrangement of codons along DNA strands, should not these be determinable in brain cells? (5) If, as Hyden's (1962) works show, there are differences in nucleotide base ratios in both neurons and surrounding glial cells in different nuclei of the same species and the same nuclei of different species, shouldn't we be able to find them in primate brains too? (6) If, as Geschwind (1965) suggests, the inferior parietal lobule is unique to man's brain and language behavior, does it not follow that there must exist some biochemical code which determines this specificity?

I raise these questions for two reasons: first, that they may help to direct some needed research, and secondly, that they may serve as examples for other kinds of parameters which may eventually be of importance in understanding both behavioral and neural evolutionary changes in primates.

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