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EVOLUTION, BEHAVIOR AND THE PREFRONTAL CORTEX

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Abstract. There are two distinct but equally important methods for studying behavioral evolution; one emphasizes the phylogenesis and adaptednes of behavior; the other seeks to discover general principles regarding processes and mechanisms of biological significance, without primary concern for historical (phylogenetic) considerations. Neuropsychologists have relied almost exclusively upon the second of these approaches. This paper argues that both orientations are required for a proper study of the evolution of the prefrontal cortex and its functions, and advocates an increased application of ethological principles and methods in comparative studies of prefrontal cortical functions.

Neuropsychologists typically investigate the functions of the prefrontal cortex in animals in much the same way as the comparative psychologists used to study the evolution of intelligence. Neuropsychologists, like traditional comparative psychologists, emphasize laboratory learning tasks and concentrate on studies of the immediate causation of behavior, to the neglect of questions concerning the adaptedness and the phylogeny of behavior.

The phylogenesis and adaptedness of behavior are, in contrast, problems of prime significance to the ethologists. Ethology has supplanted comparative psychology as the dominant theoretical orientation toward the study of animal behavior (Dewsbury, in press) because it provides a more comprehensive basis for investigating behavioral problems that are important in systematic biology. Ethology has, however, had only a limited influence on studies of prefrontal functions in animals. This paper is intended to show how ethology may contribute to our understanding of the evolution of the functions of the prefrontal cortex in mammals.

The species-specificity of behavior

Animal species have diverged and specialized to exploit unique ecological niches in ways that favor survival and reproduction. Each species has evolved a characteristic pattern of sensitivity and attention to particular stimuli, motor abilities, and discrete learning capacities to meet the demands of its normal physical and social environment.

The comparative neurological literature provides many examples of species-typical specialization in sensory functions. The auditory projection cortex in cats is greatly expanded compared to that of dogs, raccoons or primates. On the other hand, the cortical sensory representation of the forepaw is small in cats compared to raccoons, and the cortical visual system of cats is primitive and poorly developed by primate standards (Welker and Seidenstein 1959, Diamond and Hall 1969, Radinsky 1969).

Striking divergences in cortical sensory representation, correlated with species differences in habits and habitats, are observed within single lines of descent (Solnitzky and Harman 1946, Welker and Campos 1963, Radinsky 1968), while animals from different lines of descent develop similar sensory representations in response to similar ecological demands (Radinsky 1968, Diamond and Hall 1969).

Behavioral observations indicate that the learning abilities of animals are as specialized and as closely related to ecological factors as their sensory capacities are. Every species appears to have its own set of special learning abilities, each one evolved to facilitate adaptation to specific ecological and social requirements. Animals are now seen as "intelligent" in distinctly different ways that are often more highly correlated with ecological than phyletic variables (Warren, in press). Rhesus monkeys, for example, surpass cats and dolphins in the formation of visual discrimination learning sets, but are markedly inferior to dolphins in learning to emit vocal operants. Dolphins find their way about by echolocation, frequently under conditions of extremely limited visibility; their performance relative to monkeys on vocalization and visual discrimination tasks appears to reflect the importance of these processes in adaptation to their normal environment. Rhesus monkeys are also quite deficient compared to cats in learning auditory discrimination problems. This may plausibly be interpreted as indicating that nocturnal predators learn more readily than diurnal vegetarians to approach arbitrary sound sources. Animals generally learn quickly to associate stimuli and responses that are important for survival in their usual environment, and learn slowly or not at all when required to form associations that would prejudice survival in nature (Seligman 1970).

Comparative psychologists tried for more than 70 yr to devise a standard test of animal problem solving ability that would enable them to rank species along a dimension of "intelligence" in such a way as to reflect variations in brain size and complexity. They failed (Warren, in press), because natural selection acts directly upon *specific* learning capacities required for survival in a given species-typical context so that any particular standard test is inevitably more or less unsuitable for representatives of different species (Tinbergen 1951). The particularistic view of intelligence suggested by ethology is consonant with the results of factor analytic studies of learning by dogs (Scott and Fuller 1965), and with the great success of recent attempts to correlate specific symptoms of the frontal lobe syndrome with particular foci within the frontal granular cortex in rhesus monkeys (Butter 1969, Goldman and Rosvold 1970, Iversen and Mishkin 1970) and in the prefrontal cortex in dogs (Dąbrowska 1971). It also seems consistent with the multiplicity of specific gnostic units postulated by Konorski (1967).

Even learning theorists have begun to recognize that models which provide a satisfactory account of learning in some species may not apply to other species. Thus Sutherland and Mackintosh (1971) concede that their two-stage attention theory of discrimination learning, which is quite successful in its treatment of discrimination learning by rats and nonmammalian vertebrates, can not accommodate the results obtained in tests of the theory with cats (Hirayoshi and Warren 1967) and monkeys (Warren 1966).

The contemporary views of the evolution of behavior indicates that it is unwise to concentrate research on the functions of the prefrontal cortex upon a few species, observed in a limited number of experimental situations. The results of frontal ablations are measured by changes in species-specific behaviors. Only by studying many species in a variety of situations can we hope to differentiate specific and general lesion effects and to establish unequivocal similarities across species. Even those who are not primarily interested in evolutionary phenomena must concern themselves with this problem, since it must be faced in estimating the species-generality of facts and teories and their possible extrapolation to man.

In the past we have often assumed that frontal injuries would occasion similar changes in the behavior of different species of mammals. This assumption may be invalid. We ought to be prepared, perhaps even to expect, to find different results from frontal lesions in different species, and to entertain scepticism concerning apparently similar effects until they have been shown to be robust, replicable and based upon qualitatively similar behavior in normal animals of the species that are compared. A great deal more caution in generalizing findings across taxa is in order, and an urgent need for comparing different ecotypes within the same family or order to define the legitimate range of generalization is evident.

The adaptedness of behavior mediated by prefrontal cortex

An important emphasis in ethological research is the experimental investigation of the selective advantage that accrues to a group of animals as the result of their manifesting a specific pattern of behavior. A classic example is Tinbergen's work (1951) on egg shell removal by black-headed gulls which is summarized in Hinde (1970). This response takes only about half a minute a year, yet Tinbergen has shown that it is an important component of an elaborate system of behavioral defenses against predation.

We can be confident that the prefrontal cortex did not evolve to enable animals to learn delayed response problems in the WGTA. Until quite recently, however, there was little information available concerning the basic biological question: What are the functions of the behavior mediated by the prefrontal cortex in adapting animals to their usual environment?

It is now clear that destruction of the frontal granular cortex has a profound effect upon the social behavior of rhesus monkeys. Observations of captive animals in the laboratory indicate that frontal monkeys are less aggressive and more fearful and withdrawn than normal and operated controls, yet more likely to emit threatening or aggressive responses under inappropriate conditions than controls (Brody and Rosvold 1952, Batuyev 1959, Butter et al. 1970, Deets et al. 1970, Snyder 1970).

Even more severe deficiencies are seen when rhesus monkeys with frontal decortications are studied under more natural conditions in the field. Adult monkeys that were trapped and subjected to frontal ablations and then released close to their social group failed to rejoin the group and remained solitary. Females with infants ignored or rejected their young in the laboratory after prefrontal removals and deserted them upon release in the field. The frontals also showed a marked reduction in the frequency of threat gestures, facial expressions and vocalizations in their social interactions (Myers, this Symposium). Similar changes have been reported to occur in monkeys with anterior temporal or amygdala lesions (Dicks et al. 1969, Myers and Swett 1970), but neither temporal nor amygdala lesions produce hyperactivity. Rhesus monkeys with lesions in the cingulate cortex failed, in contrast, to show changes in the pattern of social interactions with conspecifics in the laboratory or in the wild. The cingulate preparations did, however, manifest an increase in aggression toward humans while recovering from surgery in the laboratory (Myers, this Symposium).

These observations suggest a preliminary answer to our question regarding the adaptive functions of the behavior mediated by the prefrontal cortex in rhesus monkeys. Rhesus macaques live in permanent social groups and are poorly equipped to survive as isolates. The frontal granular cortex is apparently an important component of a neural system essential for normal species-specific social behavior in this species. It seems reasonable then to hypothesize that an important selection pressure leading to the elaboration of the prefrontal cortex was the advantage resulting from more complex and highly coordinated social behavior.

The relevance of this hypothesis to other mammalian species is uncertain. It is interesting to note, however, that even in cats, a relatively unsocial species, frontal animals are less aggressive and less successful in competition for food than normal controls (Warren 1964), and more indifferent toward humans (Warren et al., this Symposium).

The experiments which demonstrated the participation of the prefrontal cortex in the regulation of social behavior in monkeys and cats illustrate an important point. Observations of the spontaneous behavior of animals with lesions in the prefrontal cortex toward conspecifics, models and humans yield important information that could not be obtained in testing individual subjects in formal learning tasks.

Phylogenetic comparisons

Although the theory of evolution provides an ordering principle in all fields of biological research, evolution presents so many facets, so many worthwhile objects of investigation, that different sorts of biological scientists approach evolutionary problems in quite different ways. A major concern of the ethologists, for example, is the study of closely related forms, species within the same genus or family, in order to determine phylogenetic relationships. In this work, primary emphasis is placed upon identification of homologous characters in allied forms to determine phylogenetic relations among the forms and the historical origins of the characters in question (Lorenz 1950).

Students of the prefrontal cortex have, in contrast, largely ignored questions about phylogeny in their research. We know almost nothing of the phylogeny of the prefrontal cortex and its functions in any line of mammalian descent. Experiments with rats, cats, dogs and rhesus monkeys permit no inferences concerning phylogeny since "rats were never ancestral to cats nor were cats to primates; rather each represents a different evolutionary lineage. Therefore, from the point of view of the phylogenesis of primate characteristics, the rat-cat-monkey comparison is meaningless" (Hodos and Campbell 1969, p. 341), and "there is no more point in regarding New World monkeys as representative of man's ancestors than there is in regarding rats as representing the ancestors of cats" (Hodos 1970, p. 30).

A few neuropsychologists have begun to study species differences in the effects of neural lesions from a phylogenetic standpoint, comparing either closely related forms or species that constitute a quasi-evolutionary sequence. A quasi-evolutionary sequence (Hodos and Campbell 1969) consists of a series of animals within a common lineage that includes the available living descendents of groups which were ancestral to more advanced forms, as in Masterton, Heffner and Ravizza's (1969) comparison of auditory sensitivity in opossums, hedgehogs, tree shrews, bushbabies, macaques, chimpanzees and humans.

Phylogenetically oriented lesion experiments have yielded some rather unexpected results. The effects of lesions in a number of telencephalic sites upon maternal behavior in rats and mice were investigated by Thomas, Hostetter and Barker (1968) and suggest a type of interspecific double dissociation. Lesions in the dorsal limbic cortex, but not in the septum have devastating effects on maternal behavior in rats. The converse pattern is found in mice; septal lesions produce a profound defect in maternal behavior while cingulate lesions have only very slight effects in mice. In addition, mice with septal lesions fail to manifest the rage syndrome characteristic of rats with septal lesions (Carlson and Thomas 1968). These observations indicate that brain-behavior relations may vary markedly among species with grossly similar brain morphology.

Destruction of the amygdala produces different effects upon the behavior of different species of monkeys. Adult vervets (*Cercopithecus aethiops*) manifest a prolonged anorexia but do not become hypersexual after amygdalectomy. Amygdalectomized rhesus monkeys are hypersexual but show no severe disturbance in feeding behavior (Kling et al. 1969, Kling et al. 1970). Species differences in the effects of amygdalectomy have even been observed within the same monkey genus. Amygdalectomies occasion a less profund loss of positive social behaviors in *Macaca speciosa* than in either *M. mulatta* or *M. ira.* This disparity may be correlated with the higher frequency of grooming and contact behavior in intact *M. speciosa* (Kling and Cornell 1971).

In contrast to these results indicative of substantial variations among fairly similar forms in the neural control of behavior, Ward and Masterton (1970) examined the effects of destroying the visual cortex in tree shrews and failed to obtain clear evidence that such lesions produce effects markedly different from those observed in monkeys, apes or men. Their findings are difficult to reconcile with the notion of a gradual encorticalization of visual functions in primate evolution.

Although none of the experiments just cited deal with the prefrontal cortex, they strongly suggest that investigators concerned with this part of the brain would do well to emulate their colleagues in ethology and neuropsychology in determining the variation in the behavioral effects of frontal lesions which occurs within closely related species and in quasi-evolutionary series.

Neuropsychologists are trained in medicine or psychology, fields in which a nonhistorical experimental orientation prevails. It is tempting to speculate that this accounts for their neglect of phyletic questions as well as their frequent use of the concept of homology in an ahistorical manner.

Campbell and Hodos (1970) have contributed substantially to the clarification of the concept of homology in neuroanatomy. They point out that the term homology has been defined in two different ways, in terms of (i) inheritance from common ancestry, and (ii) structural correspondence. They make the reasonable suggestion that communication with other biologists would be enhanced if neuroanatomists used homology in the historical sense only, and advocate acceptance of the following disjunctive terminology.

"Homology: Structures and other entities are homologous when they could, in principle, be traced back through a genealogical series to a stipulated common ancestral precursor, irrespective of morphological similarity".

"Homoplasy: Structures or entities that are morphologically similar but that cannot, in principle, be traced back to a stipulated common precursor are homoplastic".

The prefrontal cortex in common laboratory animals is certainly not homoplastic. Both cats and dogs lack the strongly granular fourth lamina characteristic of primates (Akert 1964). Anterograde degeneration studies show that the mediodorsal thalamic nucleus projects to two regions in the rostral cortex of rats, yet these regions may be ablated without producing retrograde degeneration in the mediodorsal nucleus (Leonard 1969).

In regard to homologies, Akert (1964) found evidence of a similar topological order in the projections of major divisions of the mediodorsal nucleus to restricted areas of the prefrontal cortex in cats, dogs, squirrel monkeys and rhesus monkeys. Largely on the basis of this structural correspondence, he concluded that the frontal areas involved were homologous in the four species compared.

Today we are rather more aware of how common parallelism and convergence are in evolution and how frequently they produce resemblances not found in common ancestors. Although the following examples do not relate directly to the prefrontal cortex, they seem apposite in this context.

1. Studies of the endocasts of fossil brains indicate that the cruciate sulcus, a major landmark in the sulcal pattern of almost all carnivores, appeared quite late and independently in the evolution of felids, canids and other families of carnivores (Radinsky 1968, 1969). Thus, despite its near ubiquity in the order, we are not entitled to regard the cruciate sulcus in different carnivore lineages as a homologous characteristic.

2. Old World and New World monkeys evolved from prosimian ancestors that lacked the simian sulcal pattern. Both monkey stocks subsequently and independently developed a central and arcuate sulcal complex in the frontal lobe. Sanides (1970) finds considerable differences in the location of the central sulcus in relation to the motor and somatosensory areas in his architectonic studies of platyrrhine and catarrhine monkeys, and regards the similar sulcal pattern in these groups as an instance of convergence or parallelism, rather than homology.

3. The organization of the visual cortex is quite similar in cats and squirrels. Microelectrode studies indicate that both species have three visual areas, V_I, V_{II} and V_{III}, which correspond to architectonically distinctive areas 17, 18 and 19 respectively. Hall, Kaas, Killackey and Diamond (1971) explicitly discount the possibility that this pattern of organization in the visual cortex of cats and squirrels is homologous, however, since they can find no trace of V_{III} in hedgehogs, the closest living approximation to a common ancestor of squirrels and cats.

None of these illustrations impugn Akert's (1964) claim that the frontal cortices of dogs, cats, rhesus monkeys and squirrel monkeys are homologous. But they do strongly suggest that his case wants strengthening by data obtained from relatively unmodified descendants of ancestral forms, hedgehogs for the whole set, and tree shrews and prosimians for the monkeys.

The comparative study of processes and mechanisms

The preceding argument stressed differences among species to show that neuropsychologists should concern themselves with the species-specificity, phylogenesis and adaptedness of behavior. It was not intended to deny or to obscure the fact that there are many important neuropsychological similarities among mammals, as the following few examples testify.

It is indeed possible to eliminate species differences in the performance of operant responses on partial reinforcement schedules, if one selects stimuli, responses and reinforcers to fit the characteristics of the species studied (Skinner 1957). Efforts to demonstrate fundamental differences on simple or moderately complex learning tasks between monkeys and nonprimate mammals have been largely unsuccessful (Warren 1965, Warren in press). Mammals resemble one another in that they surpass nonmammalian forms in the capacity to compensate for distorted sensory inputs and for transposition of nerves and muscles (Taub 1968). The basic pattern of somatosensory and motor cortical representation is constant in mammals (Woolsey 1958). Mammals with lesions in the prefrontal cortex are impaired in performance on delayed response, even though the magnitude of the impairment varies over species (Warren et al., this Symposium).

Such communalities form the basis for a second sort of comparative study, which is as important and profitable as the phylogenetic approach advocated by the ethologists: the investigation of adaptive processes and their biological bases in different sorts of animals, without primary regard to their taxonomic classification (Simpson 1958, Diamond and Chow 1962, Hodos and Campbell 1969, Hodos 1970, Mayr 1970).

"There is another sense of 'comparative' which is as much a part of the Darwinian tradition as the meaning favored by Lorenz. We are speaking of the use of different forms of life to arrive at an understanding of physiological mechanisms. An early example of this method is Harvey's investigation of the function of the heart. In establishing that the blood is transferred by the heart from veins to arteries, Harvey used the fish as a model. In the absence of a secondary circulation to the lungs, the passageway from veins to arteries is apparent. Harvey argued that the pulmonary circulation in mammals had obscured our realization that the function of the heart is the same in all vertebrates". (Diamond and Chow 1962, p. 174).

Young (1965) explains his choice of octopus as the subject for his research on the neural basis of learning and memory in similar terms. "The memory of mammals involves a complex set of centres and it yields a correspondingly detailed record of events in the world around. It is perhaps partly for this reason that attempts to understand it have had limited success. It is too complicated for us. In other biological fields comparative study has allowed elucidation of principles, which have then been applied to mammals ... Also, incidentally, mammalian brains are too big ... It may be, however, that there is a limit of simplicity of the nervous system below which it is not convenient to study memory, even if it is there. An animal such as a planarian, in which the nervous system has few distinct 'parts' and whose plan of organization is diffuse (and incidentally not yet understood) is not an attractive proposition, at least with current knowledge". (Young 1965, p. 289–290).

In general, the goal of this kind of comparative research is to discover how behavioral and neural mechanisms work in relatively simple or otherwise favorable cases, in the hope of discovering principles that can be validly extrapolated to other species. Species differences are not ignored but exploited to elucidate a problem, as when neurophysiologists study the neural activity of the squid's giant nerve fibers or the lobster's cardiac ganglion, or when they investigate "conditioning" in the abdominal ganglion of *Aplysia* and avoidance learning by isolated ganglia in cockroaches. Sometimes a species is selected for simple convenience, as when Schneider (1967) chose hamsters for his work on subcortical visual mechanisms because the superior colliculus is more easily accessible in hamsters than other mammals.

Further illustrations and definitions are inappropriate for this audience. Yet one must add that principles must be shown empirically to apply to animals representing diverse lineages and different sorts of ecological specializations before they can be accepted as truly general. In this context we can think of no better model than the research on the sensori-motor system in mammals by Woolsey and his associates. The available evidence suggests that there may be wider interspecific variations in the functions of the frontolimbic system than in the sensory motor system, however, and calls for a similarly sustained and systematic attack in this field.

CONCLUSION

Neuropsychologists have developed powerful techniques for the precise analysis of behavior in normal and brain injured animals under controlled laboratory conditions; many functions can not be studied in any other way, for example, visual discrimination performance by monkeys deprived of the striate cortex (Humphrey 1970). Neuropsychologists have concentrated almost exclusively upon the search for general principles regarding the neural mechanisms of behavior, however, and tended to ignore interspecies variability, the phylogeny and the adaptedness of behavior. Ethology has rightly stressed the study of these phenomena and become the predominant orientation in the field of animal behavior. But it would be foolish to maintain that either orientation is superior or inferior in other respects. Neuropsychology and ethology are different but essentially complementary approaches. Both can make important contributions to a synthetic science of animal behavior (Hinde 1970). The goal of this paper was to suggest that a similar synthesis is possible and desirable in research on the functions of the prefrontal cortex and in other areas of brain research.

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