

BRAIN EVOLUTION AND COGNITION

Edited by

**GERHARD ROTH and
MARIO F. WULLIMANN**

University of Bremen, Brain Research Institute and Center for Cognitive Science,
Bremen, Federal Republic of Germany

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Introduction

PROBLEMS IN THE STUDY OF BRAIN EVOLUTION AND COGNITION

*Mario F. Wullimann and Gerhard Roth, University of Bremen,
Brain Research Institute and Center for Cognitive Science*

Why a book about the evolution of brains and their cognitive functions? Although the evolution of nervous systems and brains has been much investigated, it still is a debated and unsettled topic, as is the question about the relationship between brains and cognitive functions. Therefore, we organized an international symposium entitled “Brain Evolution and Cognition” at the University of Bremen in December, 1994. Many scientists followed our invitation to present their current ideas on that topic in Bremen. In the wake of that meeting, the plan emerged to publish a book, and almost everyone involved agreed to make a contribution. A few more authors not initially involved with the symposium were asked to join the book project (and they kindly agreed to do so) and so here we are at last.

In our introductory remarks to the symposium, the contributors were encouraged to search for answers to the following questions: Can one draw principles of brain evolution? Why did some brains become large and complex, and others small and simple and still others remained as they were for hundreds of millions of years? Where, how, and why did cognition evolve? Is there any definable relationship between cognitive functions and brain structures and function? What are the forces that drove the evolution of cognitive functions (external, internal, or both)?

Before we let the chapter authors provide answers to these questions, we discuss some problems in the study of brain evolution and cognition.

HANDICAPS IN THE SEARCH FOR AN EVOLUTIONARY HISTORY OF VERTEBRATE BRAINS

The case of horses is one of the finest examples of what paleozoology, paleobotany, paleoclimatology, and paleoecology can do in reconstructing the phylogeny and evolutionary history of a certain animal group (Carroll, 1988). The reason why there is so much more known on the evolution of horses than on the evolution of vertebrate brains is obvious: There is an almost complete fossil record in the case of horses. This primary source of information is missing in the case of brains and represents the first handicap for the search for an evolutionary history of brains. The only

paleontological information on fossil brains is available in the form of endocasts and has mostly been used in the context of brain weight/body weight analyses. Although this approach yields fascinating results in its own right—particularly in the primate and other mammalian cases (van Dongen, 1998; Jerison, this volume, Chapter 18)—it cannot go beyond the primary data and explain the emergence of particular cytoarchitectonic differences, let alone their related functional implications that arose in the course of vertebrate brain evolution. Unfortunately, as in the case of most soft organs, there is no paleontological record of the fine structure of brains. Thus, historical brain research is mostly left with neontological data from extant species and its analysis using the phyletic method. A second handicap becomes apparent when we look at the drastically different functional interpretations of, for example, the bird versus the mammalian brain that have been given during the past century based on comparative descriptive neuroanatomy. The sometimes breathtaking beauty of diverse histological and cytoarchitectonic patterns in various vertebrate brains (Nieuwenhuys et al., 1998) apparently has gone along with conflicting evolutionary explanations (i.e., these differences have an immense potential for divergent interpretation). Thus, it is clear that descriptive neuroanatomy alone is not a sufficient source for a stringent functional explanation of brain structures. One of the greatest problems in that respect has been that certain preconceived views—deeply rooted in the teleological preevolutionary concept of a *scala naturae* (i.e., nature's attempt at arriving stepwise to perfection going from lower to higher vertebrates)—were sought to be confirmed in the sometimes great apparent morphological differences in brain structure (e.g., between fishes and mammals). The idea was that of a successive addition of major brain parts and related increasingly complex functions going from fish to human in evolution (see critical reviews by Northcutt, 1981; Roth, 1994; Wullimann, 1997). Naturally, the study of behavior and cognition has been influenced by such preconceived notions coming from comparative neuroanatomy. However, research of the past three decades has increasingly shown that there are more commonalities in general brain organization and behavior of vertebrates than was previously believed.

SILENT REVOLUTIONS EMERGING

Three events had a substantial effect on a new understanding of vertebrate brain evolution in the second part of the twentieth century. First, the explosive development of neurobiological methodology (e.g., the invention of many new investigative tools such as immunohistochemistry, neuronal tracing agents, improved extracellular and intracellular neurophysiology, and refined protocols for controlled behavioral studies) marked massive progress for various disciplines of the neurosciences. At the same time, the quantity and diversity of data available for comparative evolutionary brain studies has been tremendously enlarged, and the validity of interpretations has been improved. Second, the introduction of Hennigian cladistics (Hennig, 1966; Northcutt, 1984; compare Wullimann, this volume,

Chapter 1) into the comparative discussion as a tool for analyzing neural characters altered the way one deals with the interpretation of evolutionary change in brains (compare, for example, a treatise on the evolution of the mammalian isocortex by Northcutt and Kaas, 1995). Finally, the immense new input coming from developmental molecular genetic studies led to the discovery of many early active regulatory genes and developmental pathways that directly bear on the vertebrate brain *Bauplan* and continue to have a tremendous effect on evolutionary brain studies (Heinzeller and Welsch; Strausfeld; Wullimann, this volume, Chapters 2, 12, and 1, respectively).

THE AMNIOTE TELECEPHALON AS A CASE IN POINT

In browsing through many chapters of this book, it becomes clear that a central question in the discussion on vertebrate brain evolution is how the large and differentiated telencephalon of birds compares to that of mammals: Are there comparable structures and functions in their respective pallium and subpallium, and what, if any, is their common origin in phylogeny? There is a long and winding road of comparative neuroanatomy starting at the beginning of the twentieth century on that subject (nicely summarized by Striedter, 1997). However, by midcentury, the eminent American neurobiologist of that time, C. Judson Herrick, succinctly summarized the then accepted view (which became the traditional one for later decades) in 1956 in his book *The Evolution of Human Nature*: “The bird’s cerebral hemispheres are composed almost entirely of the enormously enlarged corpora striata, which are concerned almost exclusively with stereotyped reflex and instinctive behavior.” Thus, the suspected less well developed plasticity of behavior, learning capacity, and other cognitive abilities of birds compared to mammals was considered beautifully consistent with two neuroanatomical findings, the first one being that birds have a massive intraventricular telencephalic nuclear neural mass, the dorsoventricular ridge, resembling the relatively much smaller basal ganglia of mammals. Second, the situation seemed in reverse when the pallium (especially the isocortex or dorsal pallium) was considered: Birds have a rather small structure (Wulst) in comparison to the large isocortex of most mammals (Hofman; Nieuwenhuys; Schüz, this volume, Chapters 17, 6, and 16 respectively). However, views changed dramatically as new data became available on the intrinsic neurochemical, hodological, and neurophysiological organization of avian telencephalic areas during the 1960s. Harvey Karten, a pioneer of a new school of comparative neurobiology, proposed that most of the avian dorsoventricular ridge in fact functionally corresponds to isocortex of mammals and that the avian basal ganglia are equally represented by a limited territory at the base of the telencephalon, much like the situation in mammals (Karten, 1969; Shimizu, this volume, Chapter 5). This view is indeed more consistent with the mammal-like, fascinating learning and cognitive capabilities of the vocalizing African gray parrot Alex (Pepperberg, 1990). Cognitive abilities are partially equally well developed in pigeons (Delius, Siemann, Emmerton, and Xia; Macphail, both this volume, Chapters 15 and 13, respectively),

which even display a suite of critical anatomical, neurochemical, neurophysiological, and behavioral features together composing an equivalent to a prefrontal cortex of sorts (Güntürkün and Durstewitz, this volume, Chapter 14; compare also Wagner, this volume, Chapter 7, for the special case of the barn owl).

However, as convincing as the neuroanatomical similarities and functional correspondences might be, the question of whether or not they are homologous rests on data to be gained in taxa outside birds and mammals (Northcutt and Kaas, 1995). Only a comparative evaluation, including an outgroup comparison, will eventually tell us which characters might be considered ancestral for amniotes and which are derived for birds or mammals. Not unexpectedly, the situation is complex. Clearly, the avian telencephalic morphotype (i.e., dorsoventricular ridge versus isocortex) is present in other sauropsids (Ulinski, 1983), and many of the diagnostic features that led to the recognition of basic pallial regions, such as a medial (hippocampus; Rehkämper, Frahm, and Mann, this volume, Chapter 9), lateral (olfactory) and dorsal pallium (isocortex), as well as of subpallial divisions (e.g., septum, caudatoputamen, pallidum), are seen in nonavian sauropsids as well (Butler and Hodos, 1996). Although many forebrain features typical of amniotes are recognized meanwhile in anamniotes as well (Wullimann, 1997; Demski and Beaver, this volume, Chapter 10), the search for the ancestral amniote condition remains a matter of controversy. On the motor side (basal ganglia), recent investigations point to a detailed correspondence of structure and function between the amniote and the amphibian brain (Marin et al., 1998; ten Donkelaar, this volume, Chapter 3). However, the ancestral condition for sensory and integrative systems is less well established, and there may be many independently derived features, such as dominance and detailed functional properties of visual subsystems in the bird and mammalian cases (Hodos and Butler, this volume, Chapter 4). An eminent problem for a comparative analysis is that amphibians—the outgroup of sauropsids and mammals—are paedomorphic in their brain morphology to various degrees and might not reliably be used for establishing the ancestral tetrapod condition (Roth et al., 1993; Roth and Wake, this volume, Chapter 8).

A third event that revived comparative neurobiology recently is the new alliance between molecular developmental and evolutionary studies. Many early active regulatory genes and developmental pathways clearly are common to all bilaterian animals and their brains even outside the vertebrates (for a critical review of the relationship between genes and brain phenotype, see Wullimann, this volume, Chapter 1). There are equally amazing correspondences between invertebrate and vertebrate brains on the anatomical (Strausfeld, this volume, Chapter 12) and the behavioral level (Menzel, Giurfa, Gerber, and Hellstern, this volume, Chapter 11). To return to the vertebrate range, early regulatory gene expression patterns led to the proposition of a new (neuromeric) model of the vertebrate brain *Bauplan* (Puelles and Rubenstein, 1993) that has proven to be highly fruitful in a number of evolutionary questions. In particular, early forebrain gene expression patterns shed new light on the evolution of the amniote brain, challenging Karten's theory outlined previously: The dorsoventricular ridge may be homologous to part of the mammalian amygdala and claustrum rather than to isocortex (Puelles et al., 1999), as similarly proposed based on neural circuitry before (Bruce and Neary, 1995; compare Shimizu, this volume, Chapter 5).

Some of the discussed pervasive similarities between different vertebrate brains (and even between all bilaterian brains) should not be misunderstood to advocate a generality of animal brain organization. A true comparative neurobiology will finally explain not only the commonalities but also the various specializations of vertebrate brains (Nieuwenhuys et al., 1998). The search for the evolutionary emergence of those vertebrate nervous structures subserving complex behavior, including cognition, is far from being completed and the discussion about it continues. The present book lends vivid testimony to that notion.

A SPECIAL POSITION FOR HUMANS?

In traditional Western thinking, humans are situated well above the animal kingdom; they have qualities and capabilities that are either unique or greatly exceed those found in animals. However, during the nineteenth century, it became undeniable that at least with regard to their anatomy, human beings are representatives of one out of many evolutionary lines in the sense that in every aspect of their body they are vertebrates, mammals, primates, and great apes. This certainly was a shocking conclusion: Human beings are animals.

At the same time, most biologists (Charles Darwin being among the notable exceptions) continued to believe that at least with respect to spiritual or cognitive abilities, humans are still far superior to animals: Only humans have mind and consciousness, only humans can think and plan. However, unless these abilities were assumed to be supernatural qualities, they had to be derived from properties of the brain. Thus, a necessary conclusion was that—unlike the rest of the body—the human brain had unique properties in comparison to other vertebrate brains. Many candidates for such unique properties have been discussed, including the absolute or relative size of the entire brain, of the cerebral cortex, of the prefrontal cortex, the possession of speech centers, and the degree of lateralization.

However, even that view has been questioned by modern comparative and evolutionary neurobiology. The human brain appears to be a “typical” primate brain, and while in some respects (e.g., degree of encephalization) it exceeds most, if not all, other animals, no fundamental gap is apparent between the brains of nonhuman animals and *Homo sapiens*. Furthermore, in many lines of invertebrate and vertebrate animals, anatomically and functionally complex and large brains have evolved independently. Thus, the human brain is not even unique in that respect. If we stick to the assumption that the cognitive or spiritual abilities of humans derive from brain properties, three explanations remain: (1) The exact properties that are the basis for unique abilities of the human brain have not yet been discovered; (2) these abilities originate from a special combination of brain properties that taken by themselves are not unique; and (3) there are no unique cognitive or spiritual abilities of humans.

WHAT IS COGNITION?

The term cognition has a long and diverse tradition in philosophy and psychology. Until recent times, this term was often restricted to perceptual, mental, emotional, and volitional states as far as these were connected to awareness and consciousness. Later, the term cognition has been applied to all those psychological functions that exceed simple stimulus-response relationships (D.O. Hebb) and/or refer to the acquisition or generation of meaning (E.C. Tolman). According to a much-cited definition by Ulric Neisser, cognition “refers to all processes by which the sensory input is transformed, reduced, elaborated, stored, recovered and used” (Neisser, 1967). In terms of cognitive psychology, this includes faculties such as pattern recognition, attention, short- and long-term memory, the representation and organization of knowledge (visual images, categorization, semantic organization, etc.), and complex cognitive skills such as language, comprehension and memory for text, problem solving, expertise and creativity, and decision making (Reed, 1996).

In another much-read textbook of cognitive psychology by Anderson (1990), cognition—as the target of cognitive psychology—is identified with the “nature of human intelligence and how people think” and at the same time with “information processing.” Of course, the latter interpretation is too narrow and not very useful in the context of comparative neuroscience. First, it is unclear, what is meant by “human intelligence,” and it is even more unclear what could be meant by “information processing.” There is no logically satisfactory distinction between information processing in the sense of signal processing and in the sense of processing and generation of meaning. While there is a well-elaborated information theory for the former (e.g., that developed by Shannon and Weaver; 1949), no such theory exists for the latter. This is most regrettable, because what brains do is not just processing of neural signals, but the generation of meaningful states. One of the greatest challenges of cognitive sciences is the establishment of such a theory of meaning.

It is likewise clear that cognitive psychology concentrates exclusively on human cognitive functions and largely ignores the question of cognitive functions in nonhuman animals. Historically, most authors either believed that there are no cognitive functions in animals at all or that they are beyond consideration. However, in cognitive psychology, cognitive functions were not restricted to states characterized by awareness and consciousness. This approach was an important step forward when compared to a more philosophical understanding of cognition as “highest mental states” necessarily involving consciousness. The recent establishment of the field of cognitive neuroscience is best exemplified by the voluminous book edited by Michael Gazzaniga (1995). However, the book does not give an explicit definition of the term cognition, but the titles of book chapters are largely identical with those of Reed’s (1996) book, (i.e., Sensory Systems, Strategies and Planning, Attention, Memory, Language, Thought and Imagery, Emotion and Consciousness). Since a substantial amount of data presented in these chapters come from animal experiments—mostly from primates and other mammals, with some data from birds and amphibians—it is indirectly implied that cognition is something that is found in animals as well.

Accordingly, in this book the term cognition is used in a wide sense to designate brain functions that exclude only primary sensory and motor functions, autonomic brain functions, reflexes and reflexlike stereotyped behavior. Cognition thus includes such diverse functions as perception, learning, memory, imagination, thinking, expecting, and planning, be they accompanied by consciousness or not. From this follows that cognition is not necessarily restricted to human beings, nor does it presuppose the existence of consciousness.

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