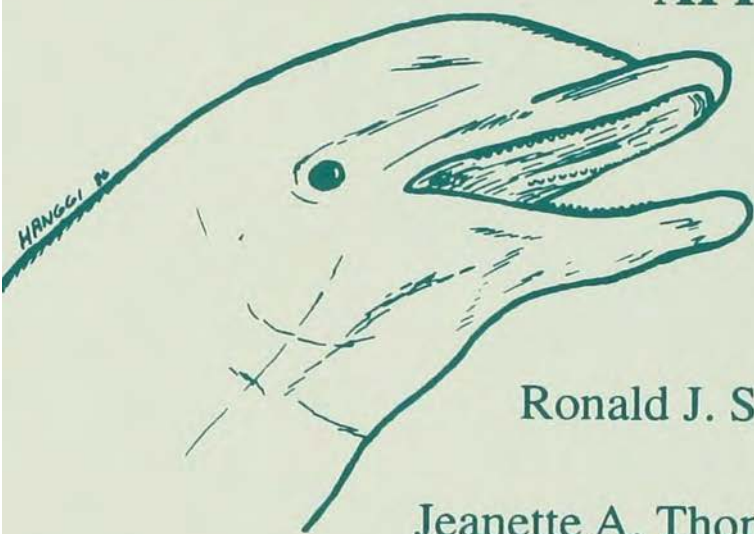


**DOLPHIN COGNITION  
AND BEHAVIOR:  
A COMPARATIVE  
APPROACH**



Edited by

Ronald J. Schusterman

Jeanette A. Thomas

Forrest G. Wood





# **Dolphin Cognition and Behavior: A Comparative Approach**

# COMPARATIVE COGNITION AND NEUROSCIENCE

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# **DOLPHIN COGNITION AND BEHAVIOR: A COMPARATIVE APPROACH**

**Edited by**

**RONALD J. SCHUSTERMAN**

*California State University, Hayward, and  
University of California, Santa Cruz*

**JEANETTE A. THOMAS**

*Hubbs Marine Research Institute, San Diego*

**FORREST G. WOOD**

*Naval Ocean Systems Center, San Diego*



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# Foreword

The conference on dolphin cognition and behavior held at the Hubbs Marine Research Institute at Sea World in June, 1983 led to a stimulating and productive exchange of data and ideas. I am sure I speak for all the participants in thanking the organizers and sponsors for making this possible. The resulting papers (which are far too numerous and diverse for any meaningful review here) include both first-hand reports of dolphin behavior strongly suggesting cognition, and reviews of experiments with other animals whose abilities are relevant and helpful to those planning further investigations of dolphin mentality. While parrots and apes are obviously very different from cetaceans, the eye-opening discoveries made in the past few years about their apparently intentional communication provide significant comparisons with the emerging picture of cognition in dolphins and other marine mammals. It is obvious that dolphins' behavior is complex and versatile. Despite the lack of hands they can learn to carry out a variety of manipulative tasks. Complex communicative exchanges take place under natural conditions, and in captivity they can learn to understand a variety of visual and acoustic signals.

A highly significant but neglected question is whether dolphins are consciously aware of what they are doing. To many people the versatility and complexity of their behavior makes it obvious that they must often be acting intentionally, with some understanding of the likely results of their behavior. For example, dolphins are often kept together in small groups from which only one is trained to perform a complex set of maneuvers to entertain the public. In some cases when the trained animal is removed, another immediately performs the complex actions without prior experience or practice (Herman 1980). Perhaps one dolphin can learn the gymnastic tricks of another without thinking about

them, but it seems more likely that such an observing companion is consciously aware of what the trained dolphin is doing and how he might perform if given the opportunity.

On the other hand, it has become customary for behavioral scientists to ignore the question of animal consciousness, and some even minimize the significance of human thoughts and feelings. Although overt behavior is easier to observe, this does not mean that subjective, conscious mental experiences are nonexistent or unimportant. One can never prove with absolute and logical certainty that another person or animal is consciously thinking; but such extreme standards of proof are seldom if ever required in other areas of science. Given the obvious reality and importance of our own thoughts and feelings, together with the similarity of basic elements that make up all central nervous systems, it is at least as difficult to prove the nonexistence of mental experiences in dolphins, apes, or other animals as to establish their presence.

If and when dolphins do experience conscious thoughts, it may well be adaptive to communicate them to their companions. The coordination of social interactions is surely facilitated by exchange of information about any thoughts and feelings that may be important to the participants. Therefore the interpretation of their communicative signals may well be a long step towards literally reading the minds of dolphins. While it is possible that all dolphin behavior is comparable to the large fraction of our own behavior that goes on without conscious awareness, conscious thinking may be the most economical and efficient way to deal with complex and constantly changing situations, as I have suggested elsewhere (Griffin 1984). This is why it is so important to learn just what the communicative capabilities of dolphins really are.

It has been widely held that animal communication conveys only relatively crude emotional states aroused in the communicator by the immediate stimulus situation. But recent studies of primates both under natural conditions (reviewed in a symposium edited by Harré & Reynolds, 1984), and in captivity (reviewed by Ristau & Robbins, 1982), show that they sometimes communicate semantic information. This may include information about objects and events that are not currently available to stimulate the communicating animals. This is why the data presented in Herman's chapter in this volume are especially significant. Dolphins can learn to comprehend messages from their trainers about objects not visible or otherwise detectable at the time the message is received. As the lingering taboos of behaviorism are relaxed, it seems likely that investigators of other animals will begin to inquire how extensive this sort of communication may be.

One of the most important attributes of human language is what George Miller (1967) appropriately described as "combinatorial productivity." This means the addition of new and important meaning by rule-governed combinations of words, ordinarily into sentences. Until recently this seemed to be a unique human accomplishment. But Herman demonstrates that dolphins can learn to comprehend relationships encoded in sentence-like sets of commands. It remains to

be seen whether they can also learn to produce rule-governed messages, but an ability to understand and respond appropriately to messages whose meaning requires comprehension of the rules as well as of the individual elements is certainly an important step in the direction of combinatorial productivity in animal communication.

In the thoughtful discussion of Herman's experiments at the conference, it was pointed out that we scientists whose native language is English tend to assume that grammatical rules providing combinatorial productivity must necessarily involve word order or the temporal sequence of other signals. This type of rule is easy to manipulate experimentally, but it is by no means universal among human languages. Many languages use inflection of key words to convey grammatical relationships, such as which noun is actor or object and who performs a certain action. The fact that this sort of grammatical rule is so widespread might mean that it is in some ways a simpler and perhaps even an easier way to combine words meaningfully. Would apes, parrots, dolphins or other animals learn more readily to communicate with combinatorial productivity if the rules involved modifications of signals rather than their temporal order? This notion was one of many potentially fruitful ideas that took shape during the conference, and readers of the following chapters will find abundant and comparable food for thought.

*Donald R. Griffin*  
*The Rockefeller University*

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# ACKNOWLEDGMENTS

From October 3–5, 1980, Hubbs Marine Research Institute in San Diego hosted a workshop entitled “Potentials for Research on Cognition in Dolphins and Human-Dolphin Communication.” About 15 scientists discussed problems in characterizing the perceptual world of dolphins, comparative learning capacities of dolphins and chimpanzees, the significance of brain size in relation to intelligence, and training methodologies in dolphins. At that time the need to address these topics at a larger conference was established.

On July 6–8, 1983, about 30 scientists from many disciplines within the broad areas of the brain and behavioral sciences participated in a conference called “Dolphin Cognition and Behavior: Comparative and Ecological Aspects.” The conference was hosted by Hubbs Marine Research Institute. Robert Buhr organized the conference with assistance by William E. Evans, Ronald J. Schusterman, and Forrest G. Wood. This book is based to a large extent on papers given at the conference or generated as a result of discussion at the conference.

Both meetings were funded by the Office of Naval Research under the Oceanic Biology Program. Dr. Bernard J. Zahuranec and Dr. Donald Woodward from the Office of Naval Research provided valuable assistance in organizing and participating in the meetings.

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# **Dolphin Cognition and Behavior: A Comparative Approach**





# BRAIN AND SENSES OF DOLPHINS

Theodore H. Bullock

Cetaceans present unique opportunities for new insights into the mammalian brain—the highest achievement of evolution. Some species possess the greatest brains in nature, at least in respect to size. The brains are remarkably specialized in many ways, compared to those of other mammals. They have been evolving separately from other mammals for a long time. Their cognitive achievements, although not yet fully assessed, their special sensory capacities, acoustic signaling, songs, and other behavioral features add reasons that the correlates in brain anatomy, physiology, and chemistry should be studied for clues to understanding how brains mediate cognition and behavior.

In spite of these strong reasons and the great interest in dolphins and whales, their brains are relatively little studied and our knowledge lags well behind that for other orders of mammals. Extraordinary difficulties lie in the path of investigation of cetaceans, even of anatomy. The overriding difficulty is scarcity of material and access permitting the use of modern methods. A quite proper reluctance to sacrifice specimens of these magnificent species has almost completely prevented the use of the most revealing modern techniques of experimental anatomy for tracing connections by allowing the living nerve cell to distribute substances it takes up into all its axonal and dendritic processes—methods

which provide the main body of information for establishing homologies and functional interrelations of parts of the brain in other mammals.

The same factors, plus some reluctance even to record physiological activity in the brain of cetaceans with chronically implanted electrodes in the alert and cooperating animal—by the same techniques used on humans for many years for the benefit of the patient—have kept the progress of this branch of research down to a handful of papers. In both anatomical and physiological approaches it is vastly more difficult to learn something about cetacean brains than about those of the great apes.

Whales and dolphins which are taken in the course of the still extant commercial operations are wasted as far as research use is concerned because, in addition to other factors, the cost of bringing scientists and their tools to the surviving but doomed animals is beyond the research funds of the competent people. The opportunities due to these remaining fisheries, hopefully soon to be abolished, should not be wasted. Without encouraging the fisheries in any way, humane research upon doomed or dying animals should be greatly accelerated before it is too late, in the interest not only of human welfare, which this knowledge would surely benefit, but of a real appreciation of the cetaceans themselves.

Chapters in this section demonstrate that some significant results can be obtained in spite of the difficulties. Occasional opportunities arise to preserve a brain freshly and suitably, at least for the older, classical stains. More rare are the qualified anatomists who will devote the time necessary to work up and examine such material and see it through to publication. Peter Morgane and his coauthors are among these few; they have made the most of long and laboriously collected, well-fixed brains of many species. They provide here the most advanced analysis to date, including cell anatomy based on staining by the Golgi method, of the degree of evolutionary achievement of the dolphin cortex, reaching rather surprising conclusions from the point of view of prevailing views based upon inadequate and premature anatomy.

A small number of electrophysiological recording experiments have been done, beginning in the early 60s on anesthetized, mostly doomed animals, in Japan and the U.S.S.R., and on chronically implanted animals in the U.S. and the U.S.S.R. Most recently the technique has been used, based upon standard clinical methods, of recording from outside the skull, in the "far field," averaging hundreds of responses over several minutes. S. H. Ridgway reviews the short latency, relatively more stimulus-bound responses, as well as studies revealing a unique pattern of sleeping. D. L. Woods and coauthors report a preliminary study showing that long latency electrical waves can be found when a dolphin is presumably engaged in cognitive processes of a moderately high level, hence that this active and promising field of research on humans can be extended to cetaceans.

Behavioral evidence is the main grist for the next two chapters which review particularly the sensory capacities. P. Nachtigall compares vision, hearing and

the chemical senses among marine mammals, pinnipedes and otters as well as cetaceans. C. S. Johnson examines more closely the evidence on hearing in the best studied dolphin and its specialized form used in echolocation.

The net result of these five chapters is to reinforce our appreciation of the need for further study of the capacities and of the morphological, physiological and, it should be added, the chemical correlates of cognition and behavior in these remarkable mammals, among other reasons because they have independently evolved so different a brain from most mammalian orders.

# 1

# Evolutionary Morphology of the Dolphin Brain

P. J. Morgane

*Worcester Foundation for Experimental Biology*

M. S. Jacobs

*New York University Dental Center*

Albert Galaburda

*Harvard Medical School and Beth Israel Hospital*

## INTRODUCTION

Studies of the cetacean brain are expected to shed considerable light on mammalian brain evolution and, in particular, on how the brain has adapted to markedly differing environments, such as between land and water. To date, although there have been numerous studies on different aspects of cetacean brain anatomy, what has been lacking is integration of this information with that available from studies of evolutionary neuroanatomy. Relative to this, the cetacean brain has historically often been given special status based on its size and fissural complexity rather than on the microscopic appearance of the cortical formations comprising its main divisions.

Before considering the status of the dolphin brain, it should be noted that development and formation of the neocortex of mammals and reptiles took place in a land environment, which shows much more diurnal and seasonal variation than does an aqueous environment. The cetaceans are a major Order of mammals showing a complete secondary return to an aqueous medium. Genetically related to all terrestrial mammals, the cetaceans are of particular evolutionary value and uniqueness, since they have adapted themselves to activity in an aqueous medium according to evolutionary laws characteristic of the whales alone. In doing so they exemplify the potential possibilities of environmental changes on the structural organization of the brain, in particular, the great adaptability of the cortical

formations of the cerebral hemispheres. In this regard, analysis of comparative anatomical material reveals that the most important morphologic changes that occur in the mammalian nervous system in the process of evolution can be demonstrated primarily in the telencephalon and, especially, in the cortical formations (Filimonoff, 1949).

Development of the chordate nervous system has followed the path of a progressive development of rostral regions in relation to the caudal ones. It is the development of cortical areas and especially of the neocortex that is of particular

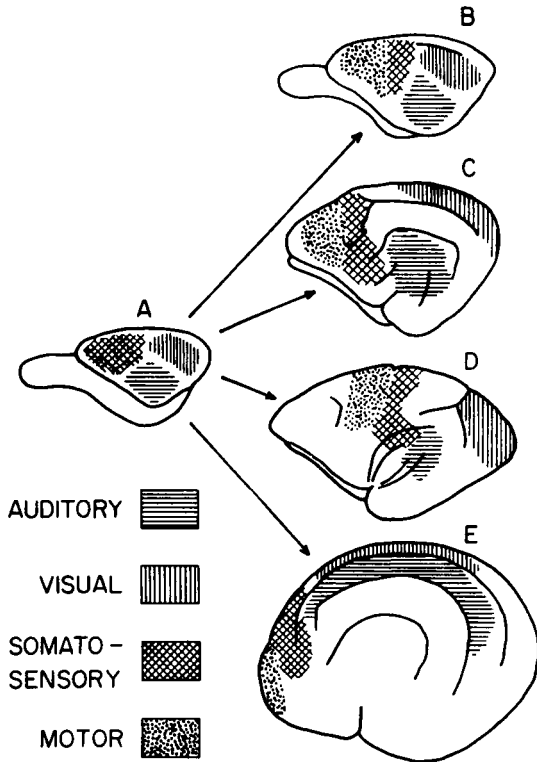


FIG. 1.1. Schema showing sensorimotor areas projected onto the brain surface in a variety of mammals. The brain of the hypothetical common ancestor or "initial" type is indicated in A. In this regard, we view the hedgehog brain as a possible model of the brain of the initial ancestor of mammals. The representations of sensorimotor areas are shown in B: rabbit; C: cat; D: rhesus monkey and E: dolphin brain. Note in the dolphin the displacement of the visual and auditory areas onto the dorsolateral convexity of the hemisphere and the lack of intervening cortex between visual and auditory areas and between visual-auditory areas and sensorimotor areas (as indicated by electrophysiological mapping studies of Ladygina et al., 1978).

interest. Filimonoff's fundamental studies (1947, 1949) have made it possible to visualize the hypothetical original type of the mammalian cortex and has provided support for morphological regularities of departures from this original or "initial" type of cortical organization (Fig. 1.1). Of these departures from the prototype, the primate type of cortex has so far been studied most thoroughly. This type is characteristic of monkeys and man who have primitive Insectivora at the root of their phylogenetic tree. In evolution the departure from primitive Carnivora belonging to the group of Creodonta, an extinct suborder of the order of Carnivora, has received the least study. This group has often been proposed as including modern Orders of Ungulata, Carnivora, Pinnipedia, and Cetacea. However, Gingerich, Wells, Russell and Ibrahim Shah (1983) have evidence that whales may have evolved from a family of archaic ungulates called Condylarthra and entered the shallow seas in the early Eocene Period (approximately 60 million years ago). They completely adapted themselves to the new conditions and appear to have preserved characteristic features of the original structure of the brain of primitive mammals in greater measure than have the land animals. At the same time the cetaceans were in a position to develop specific features of adaptation not characteristic of land mammals. Thus, studies of the cetacean brain structure make it possible to move closer to solving some of the most important problems of evolution of the mammalian brain.

## SUBDIVISIONS OF THE CORTICAL FORMATIONS

Before elaborating and discussing the basis of our subdivision of the cetacean brain it is essential to review some of the basic principles of Filimonoff (1947, 1949) dealing with what he terms a rational division of the cerebral cortex. Using these concepts we can better interpret the organization of the dolphin brain as revealed by our recent studies.

Filimonoff (1949) emphasized that the study of comparative anatomical data is essential to unraveling the problems of a rational classification of cortical formations. Such a classification represents one of the basic tasks of architectonic analysis of the cerebral cortex as a morphological discipline proper as well as a discipline of considerable value in the solution of the problems of localization of function.

In the classification of Filimonoff various types of cortical formations can be identified. The *paleocortex* (semicortex or cortex semi-separatus) is phylogenetically and ontogenetically the most ancient type of cortex and is characterized by an incomplete separation of the cortical lamina from the subcortical cellular aggregates. The *archicortex* or old cortex is characterized by a cortical lamina which has already become fully separated from the subcortex. It is, however, considerably less complex in its structure than that of the final stage of cortical evolution, the *neocortex*. Via so-called transitional cortex the archicortex

passes into the lower level of the intermediate or periarchicortex (the pre-subicular and entorhinal areas), whereas the neocortical lamina passes into the upper level of the latter (superlamination). As noted, the *intermediate cortex*, separating the ancient and old cortex from the new cortex, is divided correspondingly into two major zones which are termed peripaleocortical and periarchicortical formations (Fig. 1.2). It is emphasized that the new, ancient, and old cortex, sharply differing from each other in terms of cellular organization and stratification during the process of development, as well as in the adult organism, are not directly adjacent but are separated from each other by transitional areas which cannot be related either to the new, old, or ancient cortex and which we can single out, on this basis, as special areas which are termed the intermediate cortex.

The clear identification of the intermediate cortex as one of the basic cortical types together with the ancient, old and neocortex, corresponds to Filimonoff's earlier formulated concept of intermediate cortical formations which is one of the basic principles in interpreting development of the cerebral cortex. In dealing with cortical formations strongly differing from each other either structurally or genetically, there is always found between them these intermediate formations, the structure of which represents a certain transition of basic formations from one

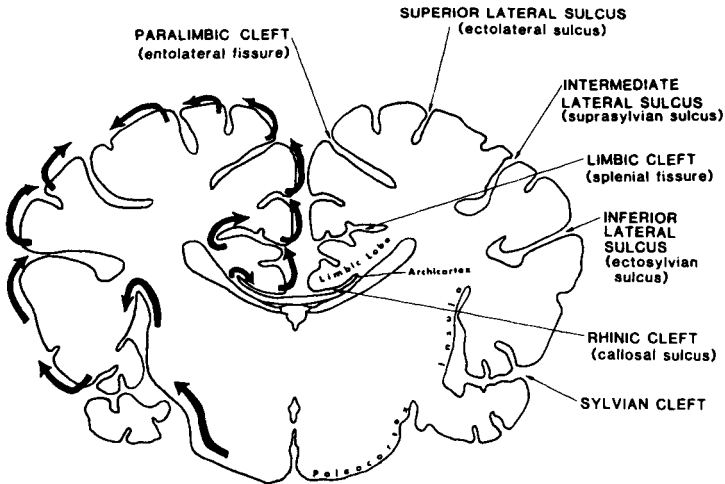


FIG. 1.2. Schema of dolphin brain (frontal section) indicating Evolutional directional trends of cortical growth outwards from two primitive cortical moieties, archicortex medially and paleocortex laterally. The different cortical fields extending outward from the primitive cortical moieties represent successive waves of circumferential architectonic differentiation in evolution (also see Fig. 1.3). The arrows represent directions of cortical differentiation outward from primitive cortices in Evolution.

to the other, although these may remain under these circumstances sharply and linearly separated from one another. Importantly, by means of this principle, we can establish basically the subdivision of cortical zones into areas and the areas into individual cortical fields. The comparative anatomical study of architectonic structures in the mammalian Orders show that there are always present, without exception, the same basic zones which can be singled out by studies of ontogenetic material and that also here the principle of intermediate formations is of basic importance. In accordance with this principle, within the whole mammalian Class the neocortex is separated along its entire length from the paleo- and archicortex by the intermediate cortex.

In summary, the cerebral cortex is thus divisible into five principal zones: ancient cortex (paleocortex), old cortex (archicortex), intermediate cortex (peripaleocortex and periarthicortex), and the new cortex (neocortex). As the basic studies of Filimonoff (1947, 1949) demonstrate, the concept of intermediate or transitional cortical formations can be regarded as one of the leading principles underlying processes of cerebral cortex formation and, correspondingly, it serves as the basis for division of the cortex into its fundamental areas and into more functional structural units.

In studying the evolution of the cerebral cortex, analysis of the development of the ancient and old cortical areas and of the intermediate cortical areas which separate them from the new cortex is of particular interest. Neocortex appears in phylogenesis in typical form only in the mammalian Class (Filimonoff, 1949). Here it plays a greater role the further we get away from the initial forms of animals, i.e., from those archetypal forms (see Fig. 1.1) which are of particularly great importance to the understanding of the entire evolutionary process. At the same time, only within the limits of the ancient, old, and intermediate cortices can we find precise homologies of their component structural units which provides for their correct quantitative evaluation. This latter is absolutely essential to the elucidation of the dynamics of evolution of the cerebral cortex, to the correct characterization of changes which are taking place, and to the determination of directions in which these changes occur.

It is possible, by studies of corresponding data, to express in definite terms the structural characteristics, based on quantitative and topographic correlations, of the cerebral cortex in the representatives of various Orders of the mammalian Class. A comparison of these formulas with those characterizing the so-called initial type, which can be constructed on the basis of the studies of ontogenetic material, permits approaches to the solution of the problem concerning the degree of proximity of individual investigated structural types of the cerebral cortex to the initial type. Using these approaches will permit solution of the problem concerning the presence or absence in each investigated type of various features deviating from the initial type as well as the trend of corresponding deviations. The solution of these problems also provides us with the data needed to evaluate the ways and means of cerebral cortical evolution within the mammalian Class.



In the evaluation of the essence of individual features characterizing the cerebral cortical structure in a given Order, of basic significance is their comparison with features which characterize this structure in the so-called "initial" type (see Fig. 1.1). At present, the true initial type does not exist in nature but a certain idea of it can be obtained on the basis of embryogenetic studies, though only in a general way and in a somewhat conjectural sense. A comparison of any investigated species with this archetype shows that high degrees of deviation from the initial type may be limited to specific individual features and appear as a sharp contrast against the basic features which are closer to those of the initial type. This sharp contrast may attest, to a greater or lesser extent, to the primitive character of the cortical structure of the corresponding brain as a whole. On the other hand, even in cases of high organization of the cerebral cortex, against a basic background of deviating features, individual characteristics inherent in the initial type may similarly appear as a sharp contrast.

The simultaneous presence, in cases with a primitive and in cases with a complex organization of the cerebral cortex, of characteristics which deviate from the initial type, as well as features which are similar to it, attests to a certain independence of the evolution of various features from each other. At the same time, this diversity attests to the highly important role of idioadaptations in the evolution of the cerebral cortex, i.e., adjustments to specific environmental conditions. In this regard, it is important to stress that cortical formations, due to their extreme plasticity, react particularly strongly by means of changes in structure to environmental changes. They react under these conditions by showing modifications of a differentiated nature, i.e., modifications involving not the cortex as a whole but mostly in special cellular groups in various combinations, corresponding to alterations in various environmental conditions of existence.

### CONCEPTS OF NEOCORTICAL EVOLUTION: APPLICATION TO STUDIES OF ARCHITECTURE OF THE CETACEAN CEREBRAL CORTEX

In considering the evolution of the brain it is of paramount importance to determine both the extent and direction of evolutionary development of the different cortical formations. By studying the direction of differentiation outward from the archicortical and paleocortical cortices into the limbic and insular cortices and, thence, into the paralimbic and parinsular cortices and, finally, into highly specialized motor and sensory cores (primary cortex), we may be able to better establish the directionality of evolutionary changes in the brain and perhaps determine the extent to which evolution has taken place in the specific cortical formations. We have been applying just such approaches recently to a study of the evolutionary anatomy of the whale brain. These studies clearly show the importance of understanding the underlying morphogenetic sequences in order to phylogenetically reconstruct the cortical formations.

Before interpreting the organization of the cortical formations of the dolphin brain based on our recent studies, we need first to stress several points in relation to cortical growth and development. These principles have been elaborated in considerable detail by Sanides in a series of studies (1970, 1972) and we have applied them to the analysis of the cerebral cortex of the dolphin. The essence of these principles can be summarized as follows: The limbic lobe is a derivative of archicortex while the insular cortex is a derivative of paleocortex. This principle of the basically "dual" nature of neocortex means that there are two neocortical moieties, one differentiated in stages away from the hippocampus and the other in stages away from the piriform cortex. Thus, there are successive waves of circumferential cortical differentiations away from both archicortex and pal-

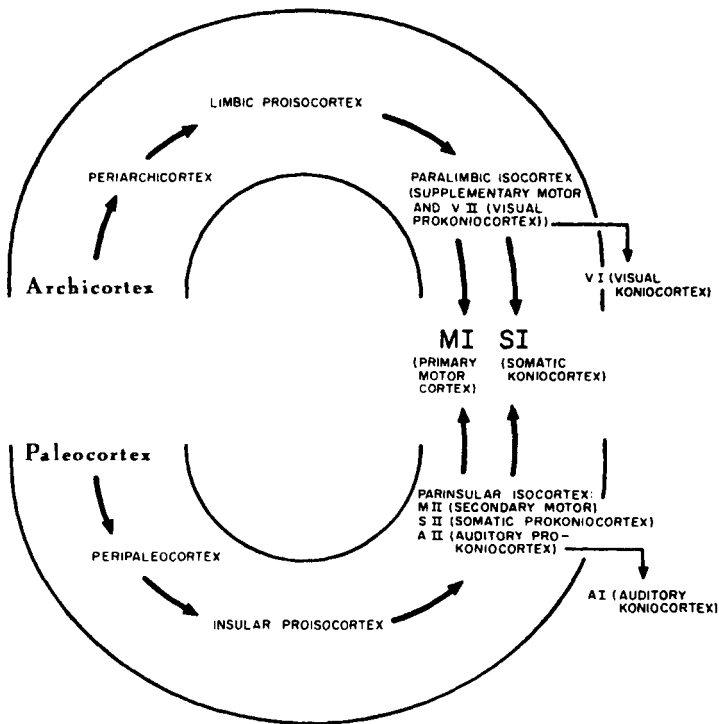


FIG. 1.3. Schema indicating directional trends of growth of cerebral cortex outward from archicortex and paleocortex through several cortical growth ring stages. This schema shows all four cortical growth rings extending outward from each primitive cortical moiety culminating in most mammalian species in the fourth cortical growth ring represented by Motor I (primary motor cortex, MI), Somatosensory I (primary sensory cortex, SI), Auditory I (primary auditory cortex, AI), and Visual I (primary visual cortex, VI). In the convexity cortex of the dolphin we find no evidence of the fourth cortical growth ring, the leading edge of cortical differentiation in the dolphin cortex being represented by the paralimbic and parinsular isocortices.

ecortex (Figs. 1.2 and 1.3) that result in the formation of two different moieties of neocortex. These outwardly extending cortical formations have been referred to as "growth rings" of the neocortex (Sanides 1970, 1972). These studies of evolutionary direction of cortical differentiation shed considerable light on how the brain is organized and constitute basic approaches to tracing the evolution of, and eventually defining, the mammalian neocortex. This approach has so far been used as a tool for tracing differential trends of evolutionary significance in a series of primates and lower mammals (Sanides 1970, 1972), and we are now for the first time beginning to apply such approaches to studies of the organization of the whale brain. In our recent work (Morgane, Jacobs & Galaburda, 1985) we began to elaborate a concept of neocortical evolution in the dolphin (*Tursiops truncatus*) by histological analysis of successive growth rings of cerebral cortex in this species using both Nissl and Golgi material. In our earlier studies, using primarily cytoarchitectonic analysis, we have described the paleocortex (Jacobs, Morgane & McFarland, 1971), and archicortex (Jacobs, McFarland & Morgane, 1979), whereas in later studies on the limbic lobe (Morgane, McFarland & Jacobs, 1982) and the insular formation (Jacobs, Galaburda, McFarland, & Morgane, 1984) we have stressed the quantitative approach to cortical cytoarchitecture.

### Growth Rings of the Neocortex

The concept of growth rings of the neocortex, based on circumferentially changing characteristics of the cortex from more primitive cortices outward toward the convexity can be described as follows: The first stage of a laminated cortex is the two-strata periarchicortex medially and peripaleocortex laterally which, together, comprise the periallocortex. This periallocortex represents the first incipiently laminated cortex and is the first growth ring of neocortex (see Fig. 1.3). The periallocortex is thus considered the first step of neocortical evolution or what we term the primary stage of neocortex. The second growth ring, which is the proisocortex of the limbic lobe medially and insular cortex laterally, appears outside of the first growth ring. The third growth ring is formed also of two moieties, a paralimbic one medially and parinsular one laterally. These are the sites of additional, so-called secondary and supplemental sensory and motor representations (Fig. 1.3). The fourth or last stage of cortical evolution comprises, in the case of sensory cortex, special cores of koniocortex appearing within the sensory regions. In this last stage of cortical evolution koniocortex appears as a core rather than a ring within the cortical sensory regions. In the case of motor cortex the area gigantopyramidalis appears. The principle to keep in mind is that the gradations originating from phylogenetically older cortices determine the structure of more recent cortices and, therefore, they appear to represent directions of cortical differentiation during evolution.

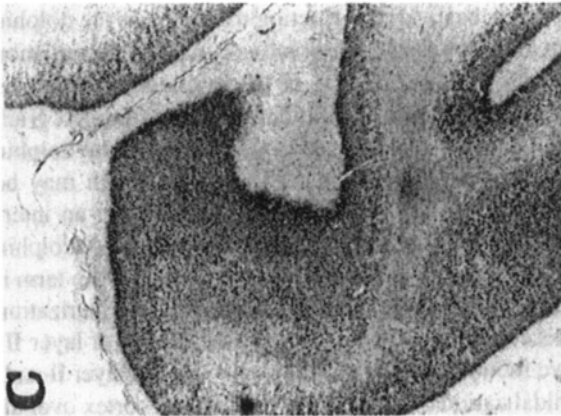
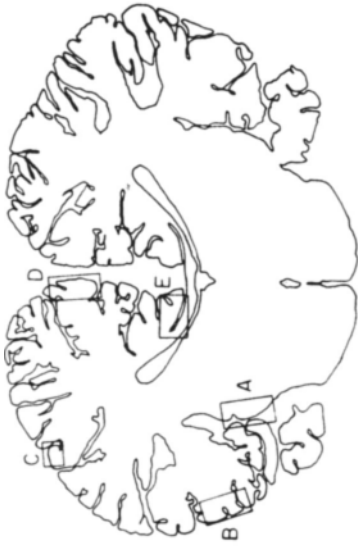
## Features of Progressive Cortical Differentiation

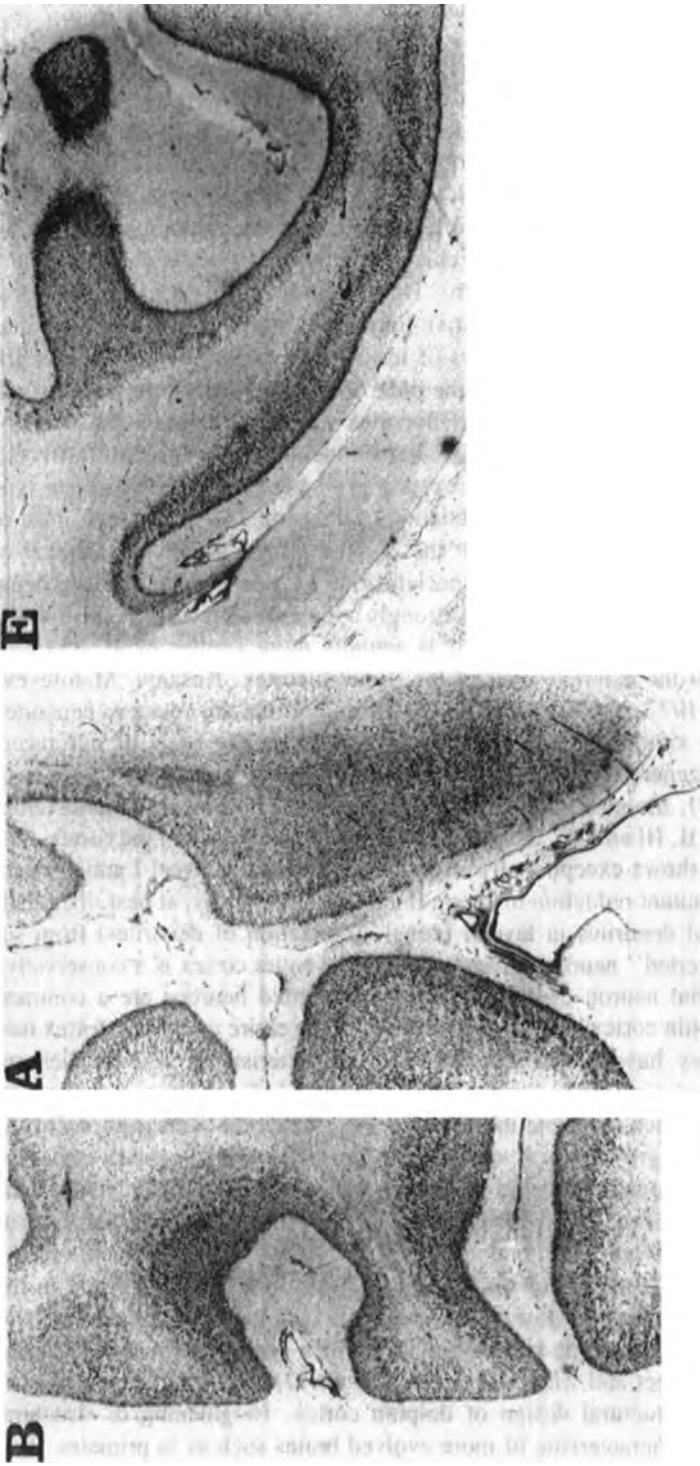
It is important first to summarize various features which form the basis of progressive cortical differentiation. These features relate to the continuing trends we see in animals with more highly evolved brains and represent changes that have occurred in the brain in progressing from lower mammalian forms to higher forms such as primates, including man.

The major prevailing trends in progressive cortical differentiation are: (1.) A shift in emphasis from the inner (layers V and VI) to the outer (layers II, III and IV) strata of the cortex, i.e., greater development of the outer layers. The most advanced stage of cortex is one with high granularization and showing an extero-pyramidal character, i.e., there is diminishment of band-like layer V (a "limbic" feature) associated with an increase in cell number, particularly in the outer pyramidal layer III and, especially, a relative increase in lamina IIIc cells; (2.) A stepwise appearance of granular cells, this stepwise granularization or stellarization process being a main trend in higher neocortical evolution. In this process there is emergence of an incipient inner granular layer IV, via a dysgranular stage in which granule cells are intermingled with small pyramidal cells. Overall, in progressive cortical evolution there is an increase in number of Golgi type II granular neurons relative to type I pyramidal neurons. Granule cells actually make their first appearance in the limbic and insular proisocortices; (3.) An overall thickening of cortex with special development and sublamination of the upper cortical laminae; (4.) A clear accentuation of lamination and; (5.) Extensive development of the basal dendritic skirt, this basal arborization of dendrites being a major progressive feature of pallial neuron evolution.

## Features of Conservative Cortical Differentiation

Our recent Golgi studies have shown that the dolphin brain displays primarily features of conservative cortical differentiation. These will, therefore, be summarized and briefly discussed as a basis for interpreting the status of the dolphin brain. Some of the major prevailing trends in conservative cortical differentiation are: (1) Agranularization or what we term priority of the agranularity principle: The dolphin cortex is largely of the agranular type and there is a limited granularization trend seen over the entire cortex of the dolphin brain. In the dolphin there appears to be only an incipient development of layer IV which may be considered a primitive cortical feature and is, by definition, a sign of an intermediate-type cortex. Since layer IV is barely identifiable over the entire dolphin cortex and still has immature pyramidal cells in it from adjacent layers we term it "dysgranular" which represents the weakest degree of incipient granularization of the cerebral cortex; (2) Accentuation and strong pyramidalization of layer II. In the dolphin cortex, we have found a strong pyramidal character of layer II and, for that matter, strong pyramidalization of all layers of the dolphin cortex over all





**FIG. 1.4.** Basic schema of frontal section of dolphin brain with boxes indicated where histological sections (A, B, C, D, E) were examined extending ventrally from paleocortical formations (A) around the convexity (B and C) and onto medial surface (D) to the archicortical formations (E). Note strong accentuation of layer II of cortex over the entire convexity (cresyl violet preparations, approximately X9.5).

areas so far examined. Thus, Golgi type I neurons clearly predominate relative to type II neurons in all cortical laminae. Layer II is also strongly accentuated over the entire cortical formation of the dolphin brain (see Fig. 1.4). An accentuated layer II in the convexity cortex is considered largely a protoneocortical (periallocortical and proisocortical) mark expressing the originally prevailing layer I input of the axodendritic type. This effectively means the cortex in the dolphin is entirely covered over with a paleo-archicortical type of organization which represents a primitive architectonic feature. Thus, the horizontal fibers of the cortex, to which a highly organized associative function is ascribed, are located in man in the phylogenetically recent layers of the cortex, predominantly in layer III, whereas in the dolphin they are in the older and functionally primitive layer I. This latter is a characteristic of periallocortex in other mammals. Most of the cells in layer II in the dolphin brain are transitional pyramidal or multiform cells which are larger than granules. The presence of transitional intermediate type neurons is evidence of weak differentiation of the cortex. In this regard, most of the pyramids we have examined in the dolphin cortex are of the atypical or indeterminate type. This lack of specialization of neurons, with most being transitional or immature in type, is a strongly conservative feature in the dolphin brain. The pyramidalization layer II is actually quite similar in its structural organization to the external layer of the periarchicortex. Kesarev, Malofeyeva and Trykova (1977), in particular, have pointed out that the cetacean neocortex has numerous similarities to periarchicortex and, on the basis of our recent findings, we generally concur with this analysis; (3) Strong development of layers I and VI, the more primitive layers of cortex, along with underdevelopment of layers II, III and IV, the phylogenetically newer layers of the cortex. The dolphin brain shows exceptionally strong development of layers I and VI with some concomitant reduction of layers II and III. Layer IV is, at best, incipient. (4) Widespread dendrites in layer I (zonal arborization of dendrites) from so-called "extraverted" neurons in layer II over the entire cortex is a conservative feature of pallial neuron evolution. These extraverted neurons are a common feature of dolphin cortex and are prominent over the entire convexity cortex (see Fig. 1.5). They have apical dendrites that characteristically divide dichotomously at varied wide angles and terminate in layer I. Since these "extraverted neurons" very much resemble those of the superficial cell condensations of the first and second growth rings of the neocortex (the periallocortex and proisocortex) we recognize them as ancient type cortical neurons. In reality, the extreme example of the extraverted type goes back even to the amphibian level of brain evolution before a cerebral cortex has developed (see Fig. 1.6). In the cerebral cortex of most mammals this type of neuron is preserved only in the primitive allocortices, the most typical cell of its type being the granule cells of the dentate gyrus; (5) Little areal variability which can be characterized as the "uniformity" effect and which Kesarev et al. (1977) term a monotonous character or single structural design of dolphin cortex. Heightening of structural heterogeneity is characteristic of more evolved brains such as in primates. This

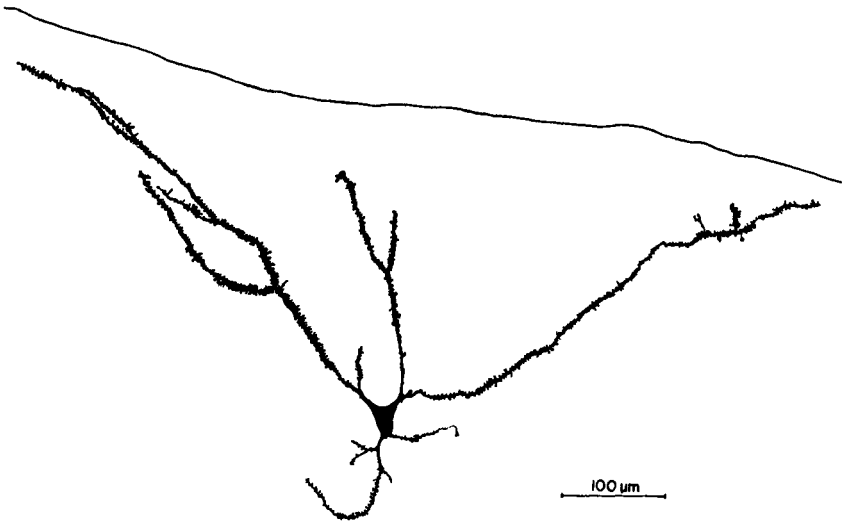


FIG. 1.5. Camera lucida drawing of cell of bandlike layer II in convexity cortex of dolphin brain. Accentuated layer II consists of polymorphic cells of the overall pyramidal type which are darkly staining and larger than granule cells. The peculiar "extraverted" character of these cells is revealed primarily by the Golgi method. The cells in layer II in dolphin convexity cortex have a well-developed dendritic pattern which is not found in isocortical laminae of the rat or cat, but is found in convexity cortex of hedgehog and bat brains (Sanides, 1972). These wide angle tufted cells in the convexity cortex are mostly atypical pyramidal cells with a short apical shaft from which dendrites spread widely into layer I or show direct widespreading of apical dendrites from the perikaryon into lamina I. In all of these cells the under-developed basilar dendrites never have reached development or spread like the apical dendrites. There is extensive overlapping of the external dendritic fields of the accentuated layer II cells within the zonal layer, the perikaryon of layer II cells appearing shaped by the extraversion and wide dendritic spread. As is known, extraversion in the allocortical and periallocortical formations is an expression of the fact that the zonal layer still represents the main afferent and association plexus of the cortex. This arrangement is a conservative feature agreeing with the observation in the hedgehog brain that thalamic terminations reach the zonal layer. The pial surface of the cortex is represented by the wavy line above the neuron.

homogeneous appearance of wide areas of the cortical formations of the dolphin brain is a decided feature of dolphin cortex in Nissl material we have examined (Morgane et al., 1980, 1982; Jacobs et al., 1984). The projectional regions of the cortex in cetaceans appear to directly interlock with each other and do not appear to be widely separated by associative regions, as in most other mammals. These projectional areas of the cortex in cetaceans are, however, arranged in the very same order as in the hypothetical ancestor of mammals (see Fig. 1.1): the visual region is retromedial, the auditory region is lateral and the somatosensorimotor area is rostral; (6) Arcuate pattern of main sulci and gyri on the lateral convexity



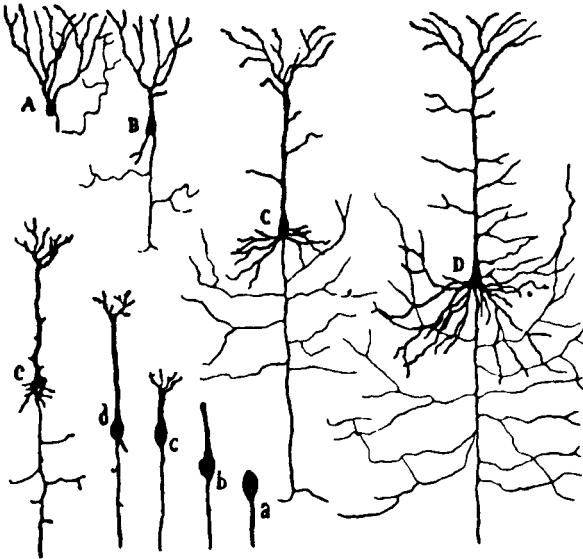


FIG. 1.6. Schema from Ramon y Cajal showing phylogenetic trends of development of pallial neurons in A (frog), B (lizard), C (mouse) and D (man). Note how this phylogenetic trend is paralleled by the ontogenesis of a pyramidal neuron of the mouse (a-e). From: S. Ramon y Cajal: *Histologie du système nerveux de l'homme et des vertébrés*, Paris, Maloine, 1909. Note the striking resemblance of cortical cells in frog (A) and lizard (B) brains to the extraverted neurons (Fig. 1.5) seen in layer II on the convexity cortex of the dolphin brain.

of the hemisphere suggestive of the pattern seen in carnivores and ungulates. This is a distinct feature of all cetacean brains we have examined; (7) Co-existence of progressive and conservative characters in the brain, so-called "mosaic" evolution of the brain. Kesarev (1970, 1975) has emphasized that dolphin cortex is of a special character exhibiting combinations of features of very high and primitive organization, though the progressive features he referred to mostly relate to the expanse of cortex and extensive gyrification rather than to specific intrinsic, histological features; (8) Generally indistinct areal boundaries. This is the usual feature in the dolphin cortex as seen in our studies and those of Kesarev (1970, 1975) and Kesarev et al. (1977); (9) Generally poor lamination over the entire cortical surface. This is particularly related to an incipient layer IV which is characteristic of all whale brains we have so far examined.

## RECENT STUDIES OF CETACEAN CORTEX

In the past most workers seem to have been overcome by the vast expansion of the cortex in the whale brain, particularly the convexity, so-called "associa-

tion," cortex. Our recent studies, using Golgi material, indicate that the dolphin brain has not reached the definitive final evolutionary stage of cortical development represented by the primary sensory and primary motor cortex. Thus, we find no hypergranular cores (koniocortex) in the dolphin and no evidence of primary motor cortex. Accentuated layer II, with many dendrites of extraverted neurons extending into layer I, is characteristic of the entire convexity cortex in the dolphin brain. In earlier evolutionary stages, before the primary motor and primary sensory cortices are elaborated, the paralimbic and parinsular representations are still contiguous. Our preliminary findings indicate that this contiguity of paralimbic and parinsular cortices appears to be the situation in the dolphin brain. The hedgehogs, which are survivors of the Paleocene epoch when archaic mammals were dominant, did not reach the stage of primary sensory and motor cortex evolution (Sanides, 1970, 1972). Whales are thought to have returned to water some 70–90 million years ago (Kesarev et al., 1977) and, related to this,

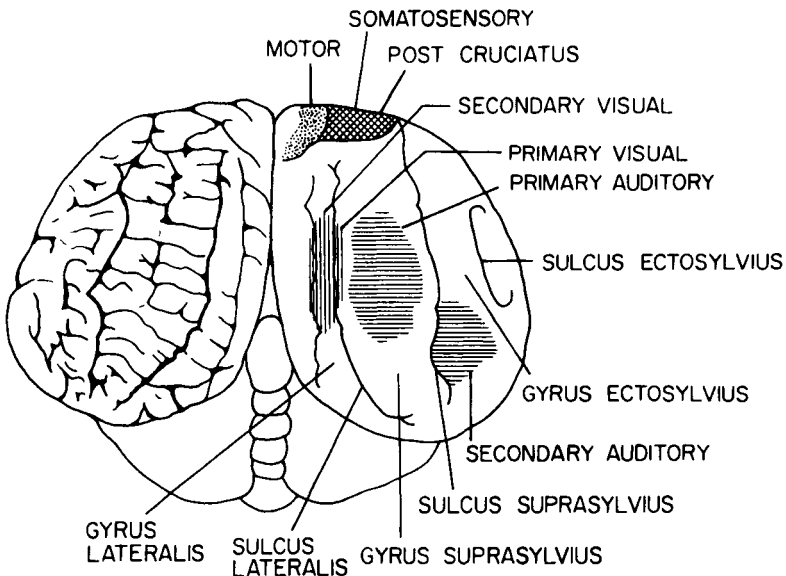
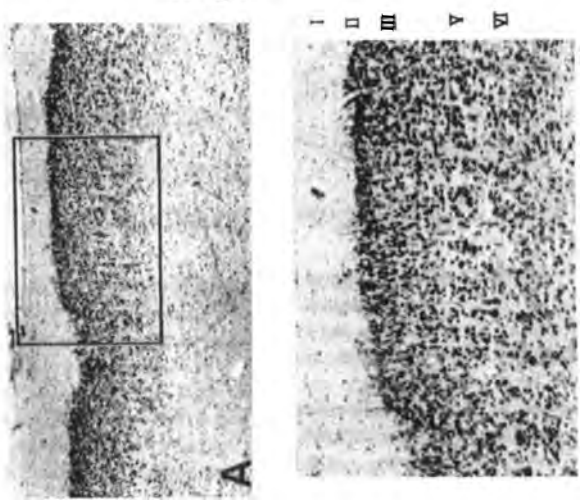
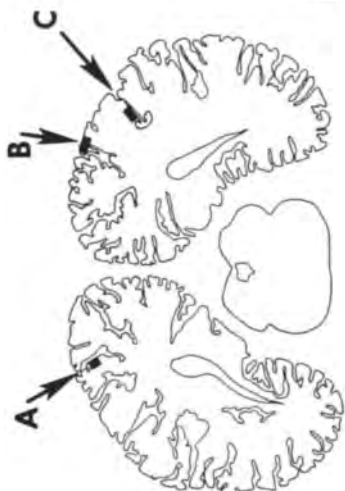
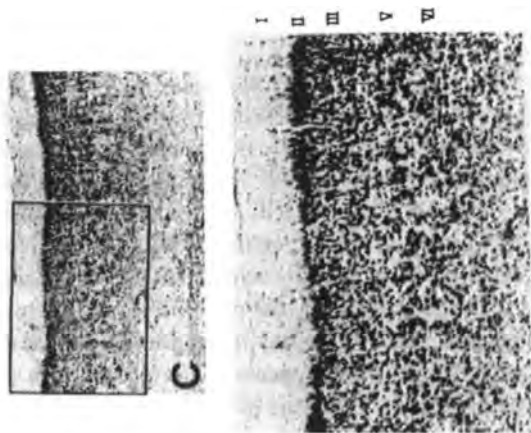
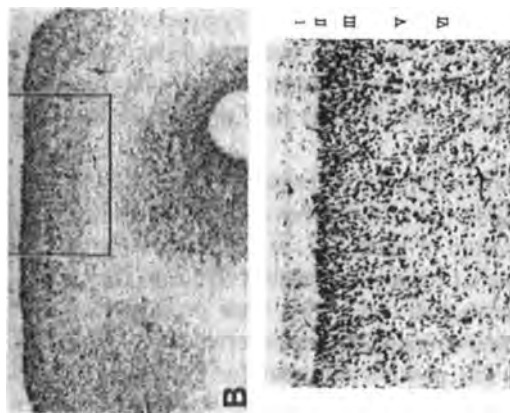


FIG. 1.7. Map of electrophysiological localization in dolphin brain described by Sokolov et al. (1972). In these studies they claimed to be able to distinguish primary from secondary auditory and visual areas as shown in the map. In this figure, redrawn from the earlier Sokolov et al. (1972) work, areas of nonresponsive cortex between the auditory and visual areas, as well as between the somatosensory and motor areas, is indicated. This differs somewhat from the later Russian work (Sokolov et al., 1978) indicating that these various areas are in close proximity with little intervening cortex. This latter would agree more with the concept of the "initial" type brain shown in Fig. 1.1E.



**FIG. 18.** Cytoarchitectonic organization of the cortex of the suprasylvian gyrus of *Tursiops truncatus* shown at three locations: (A) along the medial wall of the gyrus forming the external bank of the lateral sulcus, (B) on the free surface of the gyrus and (C) on the lateral wall of the gyrus forming the medial bank of the suprasylvian sulcus. The locations of these cortical fields (A, B, C) are shown by arrows on the orienting section outline. The higher magnifications of cortical areas represented by A, B and C (below each) show the cytoarchitectonic details. The suprasylvian cortex is extremely thin ( $0.97 \pm .03$  mm) and the percentage ratio of the width of its layers (I:II:III:V:VI) is 31:7:32:12:18, indicating dominance of layer III in the cortical plate (cortical plate = layers II+III+V+VI). The suprasylvian cortex is densely cellular (cortical cell density =  $36,300 \pm 2,800$  neurons/mm<sup>3</sup>), far denser than the cortices we have previously quantified in the limbic lobe (Morgane et al., 1982) and insula (Jacobs et al., 1984). The laminar packing density of neurons in the cortical plate exhibits a decreasing density gradient from layer II through layer V (laminar density, L.D., layer II =  $103,400$  cells/mm<sup>3</sup>; L.D. layer IIIa =  $91,400$  cells/mm<sup>3</sup>; L.D. layer IIIb =  $61,400$  cells/mm<sup>3</sup>; L.D. layer IIIc =  $47,600$  cells/mm<sup>3</sup>; L.D. layer Va =  $39,300$  cells/mm<sup>3</sup>; L.D. layer Vb =  $26,200$  cells/mm<sup>3</sup>; L.D. layer VIa =  $38,700$  cells/mm<sup>3</sup>, and L.D. layer Vb =  $21,200$  cells/mm<sup>3</sup>). The predominant cell type throughout the cortex has a transitional pyramidal shape, with only approximately 11% of the neurons examined in Nissl preparations appearing to be stellate cells. Subsequent Golgi studies have verified this. The majority of these are scattered among the pyramids of layer III, especially in layer IIIc. A typical layer IV containing stellate cells, present in most land mammals, is not seen in the dolphin. Although the cortical plate is composed chiefly of small pyramidal-type cells throughout, variations in cell size are present in the different horizontal layers. The mean size dimensions (major cell axis by minor cell axis) of neurons in the various layers exhibit a narrow range. The predominant size of the pyramidal cell population is small superficially in the cortex (layer I =  $13.4 \mu$  by  $9.2 \mu$ , layer II =  $13.8 \mu$  by  $9.0 \mu$ , layer IIIa =  $13.2 \mu$  by  $8.8 \mu$ , layer IIIb =  $12.8 \mu$  by  $10.2 \mu$ ). At deeper levels of the cortex, however, the mean size of pyramidal cells increases (layer IIIc =  $15.6 \mu$  by  $11.8 \mu$ , layer Va =  $15.0 \mu$  by  $10.2 \mu$ , layer Vb =  $15.8 \mu$  by  $11.0 \mu$ , layer VIa =  $15.2 \mu$  by  $11.0 \mu$ , layer VIb =  $14.2 \mu$  by  $10.0 \mu$ ). The difference between mean sizes of the pyramids of layers IIIc and Va is not significant ( $P < 0.70$ ) indicating an equipyramidal type cortical organization. The small population of stellate cells throughout the cortex remains essentially unchanged in size, with mean sizes in the different layers ranging only from  $9.2 \mu$  by  $9.0 \mu$  in layer II to  $10.8 \mu$  by  $10.2 \mu$  in layer VIa. From the medial wall of the suprasylvian gyrus (A) to the free surface (B) and, thence, to the lateral wall of the gyrus (C), layers II and III become increasingly more compact and the borders shared by layers III and V become more difficult to distinguish. Decreasing clarity of the III-V border results from the appearance of scattered pyramidal and some stellate-type neurons in layer IIIc and the equipyramidal relationship existing between layers IIIc and Va. The size relationship between pyramids of layer IIIc and Va reflects whether a particular cortex is oriented toward motor (emphasis on layer V pyramids) or a sensory-association (emphasis on layer IIIc pyramids) type of organization. At this general location in the lateral edge of the suprasylvian gyrus the shortest latency evoked responses of neurons to sound (click) stimuli have been elicited, indicating this to be the site of the primary auditory cortex in the dolphin (Ladygina et al., 1978). The equipyramidal relationship between layer IIIc and Va present in suprasylvian cortex of dolphins contrasts with the strongly extempopyramidal relationship present in primary sensory and association cortices of land mammals. It is apparent that in the evolution of the cetacean auditory



cortex differentiation has occurred in a different manner from that in land mammals, the latter involving the proliferation of large numbers of stellate cells and elaboration of layer IV (granularization). In view of the paucity of stellate cells in certain extant insectivores which may have had ancestors phylogenetically closer to those of modern cetaceans, cortical differentiation and specialization in the dolphin appears to have depended upon changes in existing populations of modified pyramidal cells. In the case of the auditory cortex, as indicated by our quantitative data, cortical specialization is associated in the dolphin not only with a greatly increased cell density, particularly in layers II and III and by an overall decrease in pyramidal cell size, but also by the appearance of larger pyramids in the deeper layers of the cortex, beginning with layer IIIc. The hyperpyramidalization occurring in the dolphin auditory cortex appears to parallel the various parameters of hypergranularization present in the auditory and other sensory cortices of most terrestrial mammals in which, in addition to increased cell density of layer IV, greatly increased numbers of stellate cells also appear in layers II and III. It would appear that in evolution of the dolphin, the region of cerebral cortex identified electrophysiologically as primary auditory cortex became specialized in a different way than in terrestrial mammals. In the aquatic environment auditory cortex of dolphin has been densely populated chiefly with transitional pyramidal cells that exhibit a decreased density gradient from superficial to deep levels of the cortical plate. The relative absence of neurons of stellate type and lack of typical layer IV further support the hypothesis that cortical specialization has occurred in a different manner in the dolphin. All fields illustrated stained by cresyl violet. Survey fields A,B,C, approximately 15.7X, enlargements 35.4X.

also apparently did not reach the final stage of sensory and motor cortex evolution. Actually, the general resemblance of the structural organization of the cetacean type cortex to the so-called "original architectonics" of the neocortex of primitive mammals (Creodonta) makes it possible to suggest that granularity of the neocortex of land mammals developed much later than at the time at which the ancestors of the Cetacea had already descended into the sea. The comparative studies of Sanides (1970, 1972) in insectivores and bats suggest that the formation of the koniocortices, as well as of the area gigantopyramidalis, i.e., the latest steps in sensory and motor cortex evolution, occurred in somewhat advanced mammals about 50 million years ago in the Eocene epoch with the rise of modern Orders and Suborders of mammals. By this time the whales had long since returned to the sea.

It should be emphasized that expansion and differentiation of neocortex has proceeded independently in the major mammalian lines of descent. The whales, having left terrestrial life many million of years ago, at about the same time as the Chiroptera, seem to reflect in their present neocortical structure the conservative features of those early mammalian stages that were perhaps preserved because of the decisive lack of further somatic sensory experience of land life for both groups of animals. Lacking this possible stimulus for higher neocortical differentiation, the neocortical evolution in the whales may, therefore have taken

a different path leading, among other things, to the enormous surface spread of the neocortex, compensating or even hypercompensating in this manner for the reduced level of cortical differentiation.

We have only recently been able to acquire adequate Golgi impregnated material of dolphin brain suitable for studies of the various types of neuron families in the different cortical areas and for analysis of the architecture of their dendritic processes. Of particular importance is that our preliminary Golgi analyses of several types of cortical formations (growth rings), including convexity cortex, is not, by any of the criteria described above, indicative of progressive cortical differentiation of the dolphin brain. In the case of the dolphin brain, in particular, and the whale brain, in general, we have observed that: (1) the cortex is highly agranular; (2) layer II consists largely of transitional pyramidal cells, particularly extraverted neurons with wide dendritic ramifications in layer I; and (3) layer IV, if seen, lacks typical granule cells and contains only poorly differentiated or immature pyramidal-type neurons.

In contrast to primates where lateral integration is so well known, convexity cortex in whales, like in carnivores, has not been adequately defined cytoarchitecturally or by Golgi analysis of cell structure and dendritic characteristics. Interestingly, in the convexity cortex of the dolphin there is no dominant development of layer IIIc pyramids which is a hallmark of association cortex in man and primates. On the other hand, there is some evidence from studies of the thalamus that there might be a prominent elaboration of association cortices in dolphin brain. Thus, the lateral, posterior and pulvinar complexes, which project to posterior association cortex in all known species, are large in dolphin (Kruger, 1959). Based on development of the thalamus, association or "intrinsic" cortical fields should be extensive in the cetacean brain. However, regardless of the status of association type cortex, we emphasize, as has Sanides (1970, 1972) that association does not appear to be the leading edge of cortical evolution.

Kesarev et al. (1977) and others in the Russian school prefer to term the entire cetacean cortex as *proisocortex*, i.e., not true neocortex. We generally disagree with this conclusion, preferring to think in terms of successive rings of cortical differentiation with the second and third growth rings (insulo-limbic and parinsular-paralimbic cortex, respectively) representing earlier types of true neocortex. This parinsular-paralimbic cortex appears to comprise most of the convexity cortex in the dolphin. Thus, our findings to date indicate that the final stage of neocortical evolution as seen in most land mammals has not apparently been reached in the dolphin brain. In these terms, the dolphin brain, therefore, exhibits many similarities to the brain growth ring development seen in hedgehogs, and, in some ways, in bats. As already noted, the hedgehog brain may possibly be viewed as a model of the brain of the initial ancestor of mammals. In this regard, our recent Golgi studies have also shown, as is the case in the hedgehog and bat cortex, a strong development of extraverted neurons in layer II over the entire cortex of the dolphin brain. An accentuated layer II in the cortex is

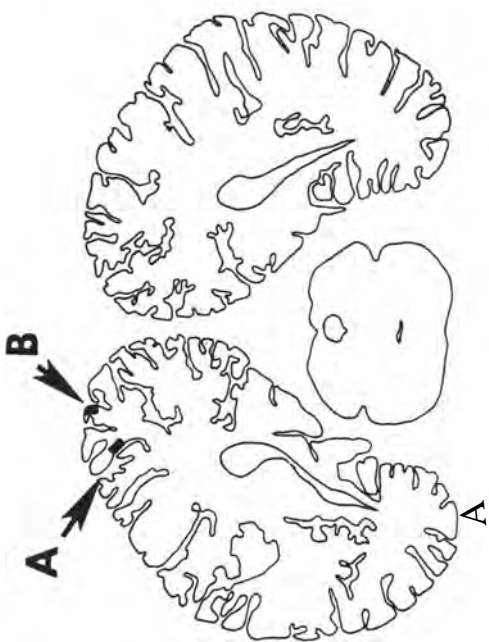
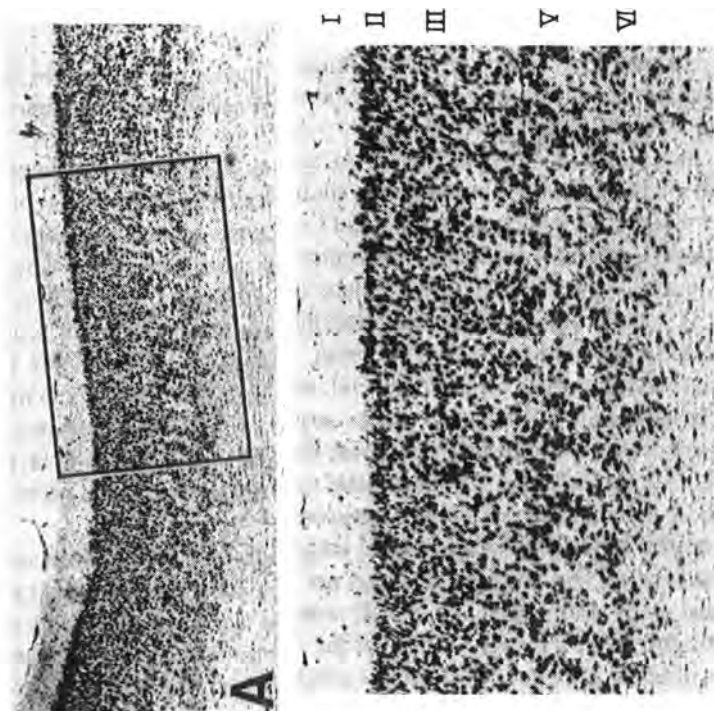
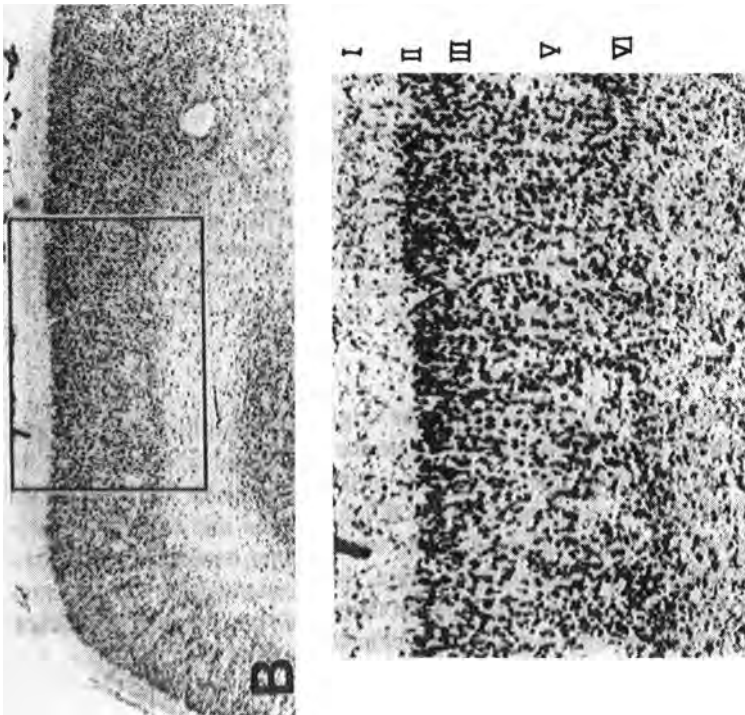


FIG. 1.9. Organization of the cortex of the lateral gyrus in *Tursiops truncatus* as illustrated in two cortical fields: (A) in the external wall of the lateral gyrus forming the medial bank of the lateral sulcus, and (B) near the free surface of the gyrus. The locations of cortical fields A and B are shown by arrows on the orienting drawing. Boxes outlining portions of cortex on A and B are shown in accompanying photomicrographs (below each) at higher magnification. The cortices of both the lateral wall and free surface have an essentially similar cytoarchitectonic organization. Although the cortex is thin ( $1.14 \pm .01$  mm), it is slightly ( $0.17$  mm), but significantly ( $P = <.001$ ), thicker than that of the suprasylvian gyrus ( $0.97 \pm .03$  mm). In common with the suprasylvian gyrus, cortical layer III of the lateral gyrus percentagewise is also the broadest layer of the cortical plate (cortex other than layer I). The percentage ratio of the width of the cortical layers in the lateral gyrus (I:II:III:V:VI) is 20:7:37:15:21, indicating again the strong likelihood that this cortex is dominated by afferent rather than efferent cortical mechanisms. The cortical plate in the lateral gyrus is especially compact at the level of layers II and III and consists, as in the case of the suprasylvian gyrus, chiefly of small cells mostly of transitional pyramidal type that range in size from  $9.2$   $\mu$ m by  $8.4$   $\mu$ m to  $17.6$   $\mu$ m by  $11.8$   $\mu$ m. The overall cortical cell density is slightly higher ( $37,500 \pm 1,800$  neurons/mm<sup>3</sup>) than that of the suprasylvian gyrus, but the difference between the means is not significant ( $P < 0.70$ ). The same decreasing gradient pattern of laminar densities from layer II through layer V, present in the suprasylvian gyrus, is also present in the lateral gyrus (laminar density, L.D., layer II =  $105,000$  cells/mm<sup>3</sup>; L.D. layer IIIa =  $75,400$  cells/mm<sup>3</sup>; L.D. layer IIIb =  $54,500$  cells/mm<sup>3</sup>; L.D. layer IIIc =  $43,500$  cells/mm<sup>3</sup>; L.D. layer Va =  $35,800$  cells/mm<sup>3</sup>; L.D. layer Vb =  $20,000$  cells/mm<sup>3</sup>; L.D. layer VIa =  $33,100$  cells/mm<sup>3</sup>; and L.D. layer VIb =  $16,700$  cells/mm<sup>3</sup>). Throughout the cortex of the lateral gyrus the great majority of cells are modified pyramids that appear somewhat immature or transitional in nature. Approximately 13% of the neurons appear to be stellate cells and, as in the suprasylvian cortex, these cells are located mainly in layer III, especially IIIc. Obviously, the final classification of these cells cannot be made except in Golgi analysis. The cells in layer IIIc that may be of stellate type, however, are scattered among the more numerous pyramidal cells and are present neither in sufficient





numbers or concentrations to be considered as a distinct layer such as the internal granular layer of terrestrial mammals though we are continuing to study this issue. Considering the overall small size of neurons throughout the cortex, it is of interest that neurons of pyramidal type exhibit broader ranges of mean sizes (from 11.8 to 17.6  $\mu\text{m}$  by from 7.6  $\mu\text{m}$  to 11.8  $\mu\text{m}$ ) than do the stellate cells (from 9.2 to 12.2  $\mu\text{m}$  by from 8.4 to 11.2  $\mu\text{m}$ ). Moreover, a statistical comparison of pyramidal cell size in the cortex reveals that the pyramids of layers IIIb, IIIc and Va are significantly larger than those of layers II and IIIa, with P values being from 0.05 to less than 0.001 (layer I = 12.2  $\mu\text{m}$  by 7.6  $\mu\text{m}$ , layer II = 11.8  $\mu\text{m}$  by 8.2  $\mu\text{m}$ , layer IIIa = 13.4  $\mu\text{m}$  by 10.0  $\mu\text{m}$ , layer IIIb = 15.4  $\mu\text{m}$  by 10.0  $\mu\text{m}$ , IIIc = 15.8  $\mu\text{m}$  by 11.4  $\mu\text{m}$ , layer Va = 17.6  $\mu\text{m}$  by 11.8  $\mu\text{m}$ , layer Vb = 14.6  $\mu\text{m}$  by 10.6  $\mu\text{m}$ , layer VIa = 12.6  $\mu\text{m}$  by 8.8  $\mu\text{m}$ , and layer VIb = 15.2  $\mu\text{m}$  by 10.8  $\mu\text{m}$ ). It is important to point out, however, that there is no statistically significant size difference between layer IIIc and Va pyramids ( $P < .30$ ) indicating that, like the suprasylvian region, the cortex of the lateral gyrus has an equopyramidal type organization. In view of their similar equopyramidal organization, it is significant that most of the lateral gyrus has been shown to give rise to multiple evoked responses to light flashes (Ladygina et al., 1978). In general, the cortical cytoarchitecture of the lateral gyrus repeats the patterns present in the suprasylvian gyrus. Thus, as in the case of auditory cortex the visual cortex of the dolphin is essentially microcellular, hyperpyramidalized, agranular and is characterized by extremely dense layers II, IIIa and b, and an equopyramidal organization. Nevertheless, in spite of overall similarities, morphometric differences, especially involving layers III and V, are present and reflect organizational and functional differences between the two adjacent cortical regions. It is of additional interest that the cortex extending onto the medial surface of the hemisphere beyond the lateral gyrus in the dolphin, and comprising part of the medial occipital area (Kesarev et al., 1977), has been partially included in the visual projection zone by Ladygina et al (1978) based on limited electrophysiological evidence with exploring electrodes. In Loyez myelin material we have traced fibers from the lateral geniculate nucleus to this medial cortex which in *Tursiops* covers a prominent oval shaped lobule. As in the lateral gyrus, the cortex of the oval lobule is thin ( $1.2 \pm .05 \text{ mm}$ ) and the percent ratio of width of its layers (I,II,III,V,VI) is 13:5:32:22:28, again indicating the dominance of layer III. Although a number of architectonic differences from the lateral gyrus can be demonstrated morphometrically the overall cortical architecture of the oval lobule is of the same fundamental type as that of lateral and suprasylvian gyri. Both fields of lateral gyrus shown are stained by cresyl violet. Survey fields approximately 20X, enlargements approximately 50X.

clearly a protoneocortical mark indicating the originally prevailing layer I input of the axodendritic type. Of course, the extreme thickness of layer I and its strong content of horizontal fibers does not, in itself, serve as conclusive evidence of a phylogenetic closeness between dolphin brain and brains of insectivores. However, considered along with the many other conservative features we and others have defined in the dolphin brain, the accumulated evidence in no way points to signs of progressive evolution of the whale brain or to any evidence that the final cortical growth rings have developed in these brains.

## ELECTROPHYSIOLOGICAL MAPPING STUDIES OF THE CETACEAN BRAIN

With regard to the relative size and positions of specific types of cortex on the convexity of the brain in whales little is presently known. Sokolov, Ladygina and Supin (1972) and Ladygina, Mass and Supin (1978) have carried out a series of electrophysiological mapping studies on convexity cortex of the dolphin and a map summarizing their findings is shown in Figs. 1.1E, and 1.7. They have even claimed, on the basis of evoked potential work, to have been able to define both primary and secondary auditory and visual cortex in the dolphin (see Fig. 1.7). We have followed up this work with a cytoarchitectonic analysis of these same areas and, to date, have not on these grounds been able to demonstrate any koniocortices indicative of primary sensory cortex. In Figs. 1.8 and 1.9 we indicate the cytoarchitecture of similar cortical fields mapped by the Russians (as shown in Fig. 1.7). We are presently carrying out Golgi analyses of these same formations and, to date, these have revealed in these areas extremely extraverted neurons of accentuated layer II with dendrites extending at wide angles into accentuated layer I (see Fig. 1.5). Our Golgi analyses indicate that layer II is composed largely of immature-type pyramidal neurons with strong development of apical branches into layer I and poorly developed basilar dendrites. In general, our evidence to date in no way distinguishes a primary sensory cortical area on the convexity of the hemisphere. It appears that the parinsular/paralimbic type cortices we have identified as forming the main mass of convexity cortex may contain the equivalents of secondary sensory-motor areas, though none of these are clearly definable by cytoarchitectonic or Golgi analyses.

### SUMMARY

The whale cortex does not appear to have developed the last or phylogenetically latest stage of cortical evolution characteristic of primates and many other mammals. It is possible that hypergranular cores (koniocortex) and area gigantopyramidalis developed about 50 million years ago in land mammals, whereas whales returned to water some 70–90 million years ago before granularization of the cortex occurred. The leading stage in cortical differentiation in whales seem to be the paralimbic-parinsular stage which is the most primitive of somatomotor representation. It is obvious that Golgi studies combined with evolutionary and ontogenetic analyses, along with physiological approaches, are needed to shed further light on fundamental cortical types and their extent in the whale brain. Though the whale brain has taken a different course of evolution it retains all conservative characters seen in primitive terrestrial and aerial forms such as hedgehogs and bats. Given that the whale returned to water many million of

years ago as a totally aquatic mammal, continued studies of the cetacean brain may help in the understanding of mammalian brain evolution in general and the effects of environment on cortical development.

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