Neurobiology of Neocortex
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Introduction

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The cerebral neocortex is the crowning achievement of brain evolution and the key neural structure subserving higher brain functions including human intellectual capabilities. The stunning complexity of cortical organization as revealed by early neuroanatomical techniques has long dissuaded neuroscientists from devoting their skills to a detailed analysis of neocortex. The investigation of simple model systems appeared to be the more promising strategy for unravelling the neural basis of behavior. However, over the last two decades refinement of neurobiological techniques has led to a renaissance of research activities aimed at the analysis of cortical organization.

Research on the neocortex has advanced system by system. Initially, it was confined essentially to sensory and motor areas; however, to date virtually all cortical regions, including multimodal association areas and prefrontal cortex, are the subject of intense investigation. Rules and principles have been defined in each area, but usually with reference only to the system under consideration. Thus, despite the accumulation of an impressive data base, we have yet to achieve a universal theory of cortical organization: a theory which would account not only for general principles of organization within particular areas, but also for cooperative interactions between different cortical regions. Considering the relatively high degree of uniformity in the structural and functional organization of neocortical areas, we believe that such a theory is attainable if sufficient and concerted attention is paid to cross-system generalities.

The purpose of this Workshop was to work toward this goal by making the problem explicit and by challenging system specialists to become more

eclectic in their interests, to exchange information about various systems, and to evaluate the already impressive list of common properties among cytoarchitectonically and functionally distinct areas of the cortex. The rapid development of new and ever more sophisticated research methods has made the mammalian neocortex more accessible to scientific scrutiny, as well as leading to numerous rapidly growing and highly specialized method-oriented subfields. This renders communication between various disciplines increasingly difficult. This Dahlem Workshop therefore attempted to provide the basis for communication not only between experts working in different regions of the neocortex, but also between representatives of the various technique-oriented subfields: neuroanatomy, biochemistry, physiology, genetics, immunology, psychology and systems theory. The format of a Dahlem Workshop, which favors intensive discussion within small but overlapping groups, was particularly well adapted for this undertaking.

Following the constraints imposed by the rules of the meeting, we defined four subtopics for focused discussion:

1) the phylogenetic evolution and the ontogenetic development of neocortical structures;
2) the structural and biochemical organization of cortical networks;
3) the functional organization of cortical processes both within and between particular areas; and
4) the relationship between system properties ad higher nervous functions, such as those assessed with neuropsychological and behavioral testing.

The discussion of these four topics was prepared for by a number of devoted background papers, and the outcome of the discussions of the panels has been summarized in four group reports.

The first group, which discussed the phylogenetic and the ontogenetic development of cortical structures, departed from the implicit hypothesis that the cortical organization, because of its puzzling complexity, can be fully understood only if the developmental rules leading to this complexity are known. Moreover, we hoped that insights into the mechanisms of developmental malleability and use-dependent neuronal plasticity might provide a key to understanding the adaptive processes in the adult neocortex. These are of particular importance since it is believed that they are involved in memory, learning, and also in the restoration of functions after lesions. These discussions touched upon the issue of the role of innate and environmental factors in shaping neuronal connectivity. Further subjects of considerable interest were the areal parcellations of cortex and the heterogeneous organizations of maps in the various sensory and motor systems.

The group concentrating on the structural and biochemical organization of neocortex screened the rapidly growing data on intracortical connectivity, local synaptic organization, transmitter systems, and membrane properties of cortical neurons. The group attempted to arrive at general principles of cortical organization, such as laminar patterns and columnar arrangements and, at the same time, made an effort to relate the long-known cytoarchitectonic features of various cortical areas to differences in internal organization. Further, it was considered necessary to examine the extent to which the growing evidence on the pharmacological and biophysical heterogeneity of cortical neurons requires revision of current concepts of the integrative capabilities of individual nerve cells.

The group discussing the functional organization of the neocortex placed emphasis upon the electrophysiological analysis of single cell responses in different cortical areas. The goal was to identify, across the various sensory modalities, common principles of feature extraction and encoding. The recent discovery of multiple sensory representations within the same modality, and the evidence of multiple reciprocal connections between the areas, raised the primordial questions of whether cortical operations must be considered parallel or serial processes, and whether particular constellations of features are encoded by the activity of individual neurons or by the joint activation of cooperatively coupled cell assemblies. However, the interest and competence of this group covered not only sensory processes, but predisposed it to also deal with problems of motor programming, pattern generation, and cross-modal associative functions.

These latter aspects were also central topics of the fourth group, which concentrated primarily on integrative functions of the cortical mantle. It was realized that phenomena such as state-dependent changes of cortical functions, selective attention, and selection of actions according to internally generated priorities, cannot be understood unless cortical operations are considered as a whole and in relation to subcortical centers. Thus, the group undertook the review of available knowledge on ascending central core-projections, which are thought to exert a modulatory action on cortical functions. Furthermore, it was expected that consideration of data emerging from brain imaging techniques, and from neuropsychological studies in patients with circumscribed cortical lesions, might provide valuable insights into the organization of these integrative functions. Particular emphasis was placed on single cell data obtained from cortical structures in awake animals performing specific tasks. These data are considered indispensable for the understanding of integrative cortical functions both in sensory and motor domains.

We are aware that the material provided in this book does not cover all aspects of contemporary research on neocortex. We also realize that the

background papers, whose purpose was primarily to serve as the basis for and to stimulate the discussions, cannot replace text books. We are quite confident, however, that the group reports in conjunction with the background papers reflect the present state of the art in a multifaceted way. In particular, we seem to have achieved a rather complete identification of questions that need to be answered and of methodological problems that need to be resolved in the near future.