INFORMATION PROCESSING IN BIOLOGICAL SYSTEMS

Editors
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Chairman

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The Editors Dedicate this Volume
to the Memory of
Paul Adrien Maurice Dirac
(1902–1984)

PREFACE

This volume contains the greater part of the papers submitted to the Information Processing in Biology portion of the 1983 Orbis Scientiae, then dedicated to the eightieth year of Professor P.A.M. Dirac. Before the volume could be published, Professor Dirac passed away on October 20, 1984, thereby changing the dedication of this volume, and its companion, on High Energy Physics, to his everlasting memory.

The last Orbis Scientiae (as it was often in the past) was shared by two frontier fields - in this case by High Energy Physics and Information Processing in Biology, demonstrating the universality of scientific principles and goals. The interaction amongst scientists of diverse interests can only enhance the fruitfulness of their efforts. The editors take pride in the modest contribution of Orbis Scientiae towards this goal.

It is a pleasure to acknowledge the typing of these proceedings by Regelio Rodriguez and Helga Billings, and the customary excellent supervision by the latter. The efficient preparation and organization of the conference was due largely to the skill and dedication of Linda Scott. As in the past, Orbis Scientiae 1983 received nominal support from the United States Department of Energy and the National Science Foundation.

The Editors
Coral Gables, Florida
April, 1985

CONTENTS

INFORMATION PROCESSING IN THE CORTEX: THE ROLE OF SMALL ASSEMBLIES OF NEURONS*

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ABSTRACT

Arguments are given for the proposed major roles played in cortical function by small assemblies of as few as 30 neurons. Predictions include that the processing capabilities of the primary visual cortex are much greater than those discovered in the pioneering work of Hubel and Wiesel. Results from experiments recording response from cat primary visual cortex to time sequences of bar stimuli show dramatic phenomena.

I. INTRODUCTION AND ARGUMENTS FOR THE SMALL ASSEMBLY

A most important problem in understanding processing of sensory input in the mammalian cortex, as well as other tasks such as memory storage and recall, is the functional organization of groups of neurons. We have proposed[1] that there is a key mode of organization (similar to that of Mountcastle[2]) in the cortex characterized by small assemblies consisting of as few as 30 ("output" pyramidal) neurons (with perhaps a similar number of "local" interneurons). Major predictions are that cortical sensory processing involves flow of firing activity among assemblies as well as back and forth among

*Supported in part by the UCI Focused Research Program in Brain Function

different cortical areas, and that the "readout" or "coding" of sensory cortical neurons involves the detailed structure[3,4] of their spike trains and not simply the average firing response over some substantial time step (~ 50-100 ms). In particular, we predict that the processing capabilities of the primary visual cortex are much greater than those discovered in the classic, pioneering work of Hubel and Wiessel.[5] To examine these problems and test these predictions, we developed a new experimental approach using detailed time sequences of stimuli for the primary visual system (readily generalized to other visual areas of sensory systems[6]) which is powerful even when recording from one microelectrode. Our recent, preliminary results[7] from cat visual cortex are dramatic and demonstrate that this approach will provide a "laboratory" for studying cortical network behavior.

We begin by summarizing some of the arguments[1,2,4,8,9] for the small assembly. In essence, we examine the next scale size in cortical neuronal organization up from the single neuron. The concept of (large) assemblies of neurons providing the basis for (a) statistical reliability, (b) safety factor against local damage (e.g., ~ 10^4 neurons "die" daily in human cortex and are not replaced), (c) maintenance of firing activity for some fraction of a second in the network, and (d) enhanced signal to noise has a long history which includes important discussions by Lorente de Nó[10] and Hebb[11]. We propose that these assemblies have a minimum (depending on locus and function) of ~ 30 neurons which provide the basis for cooperative phenomena not present in the individual neurons.

The classical access to neural circuitry has been through the use of the Golgi staining procedures which allow visualization of 1 to 5% of the elements present in tissue scarcely 0.1 mm thick. Figure 1a looks similar to a circuit wiring diagram. However, more realistic representations of neural connections are becoming available through the use of scanning electron microscopy (SEM), providing an incredible three-dimensional setting. In Figure 1b, the neurons,

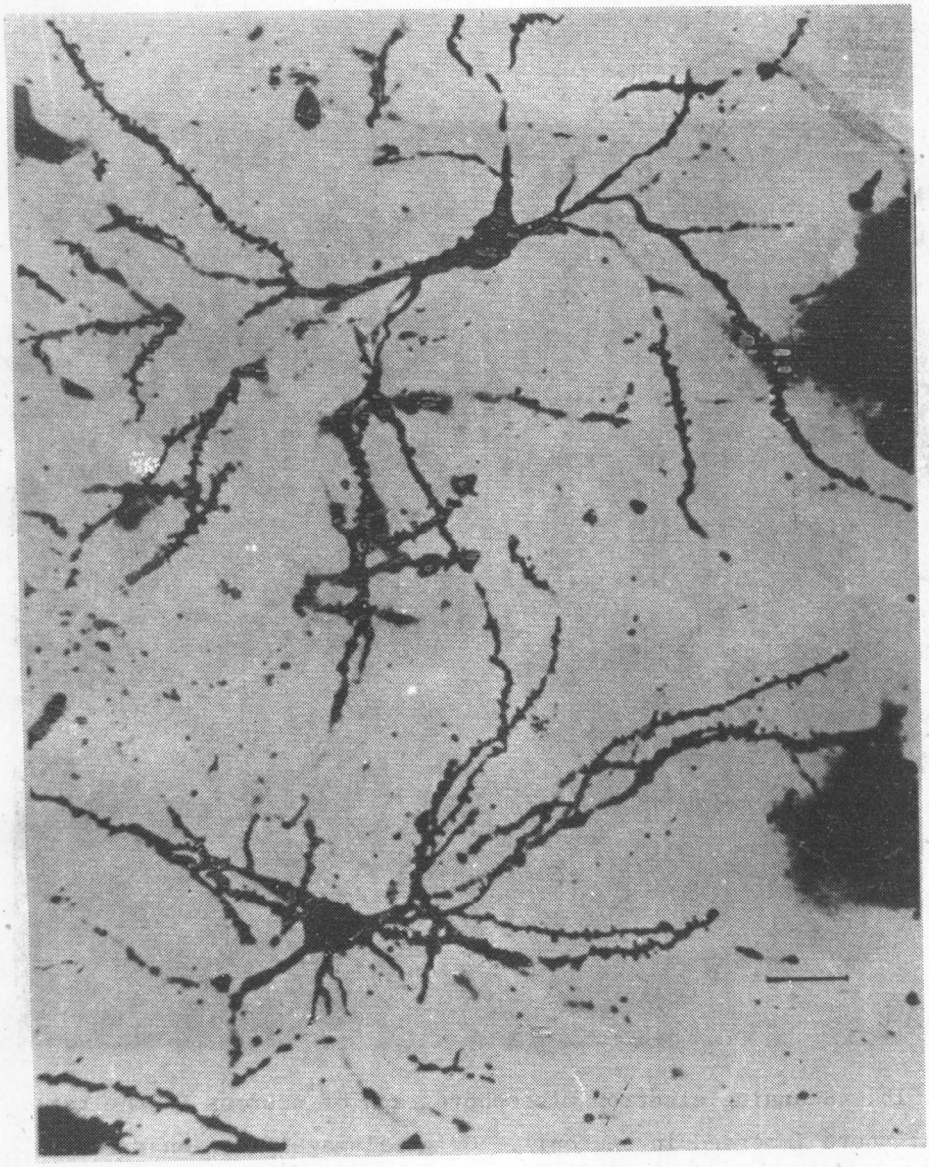

Fig. 1a. Golgi stained preparation of neurons in the human caudate nucleus showing cell bodies and segments of dendrites. Original magnification ×450.

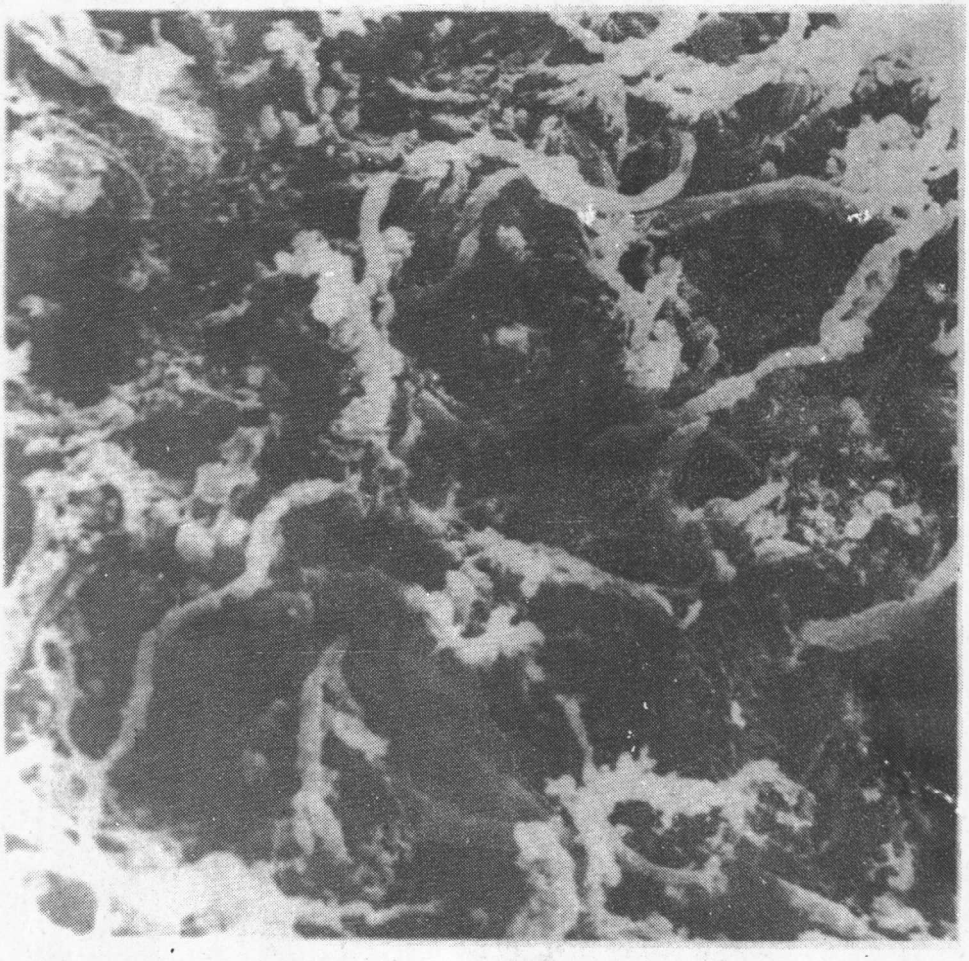

Fig. 1b. Scanning electron microphotograph of neurons in the rat spinal cord immersed in neuropil. Original magnification ×2000. These photographs are from the lab of A. B. Scheibel (Ref. 1).

dendrites, axons and glia appear strewn almost at random. (note that the input synaptic connections, ~ 10^4 per neuron, on the neurons and their dendrites cannot be seen at this scale). It is with this new visual insight gained from the SEM that we review the role of small assemblies of neurons in brain function. Although none of the arguments is more than qualitative or suggestive, their diverse origin (theoretical, anatomical and physiological) and combined weight is substantial:

i) Poststimulus histograms (PSH). Consider the presentation of a "meaningful" stimulus to an animal that then has some "repeatable" behavioral response. It is well known that, although the spike train response of a single cortical neuron is not reproducible[12], the PSH or (experiment) averaged response of a single neuron to many presentations (roughly 10 to 40) of the stimulus to the animal is "reproducible". If this widely used PSH is to have physiological significance, we expect the firing response of a "network" containing the individual neuron to be repeatable because the behavioral correlates to a single stimulus presentation are repeatable (as in the eye-blink paradigm of Thompson[12]). We assume that the network is divided into assemblies of neurons defined, as in Fig. 2, so that the firing response (to a single stimulus presentation) of the assembly averaged across the localized group of neurons in it would be the same as the PSH of a single neuron (of a given type) in the assembly. This definition for the assembly directly relates the number of constituent neurons to the number of presentations necessary to achieve a "reliable" PSH, i.e., roughly 10 to 40.

ii) Dendritic bundles. The presence of dendritic bundles (see the SEM picture in Fig. 3) has been well established anatomically in a number of neuronal systems throughout the mammalian nervous system by the work of many investigators.[13] Dendritic bundles are groups of dendrite shafts which course in very close apposition, typically, from 1 μ apart to direct membrane apposition. With wide variation, most bundles include 10-30 dendrites with bundle diameters

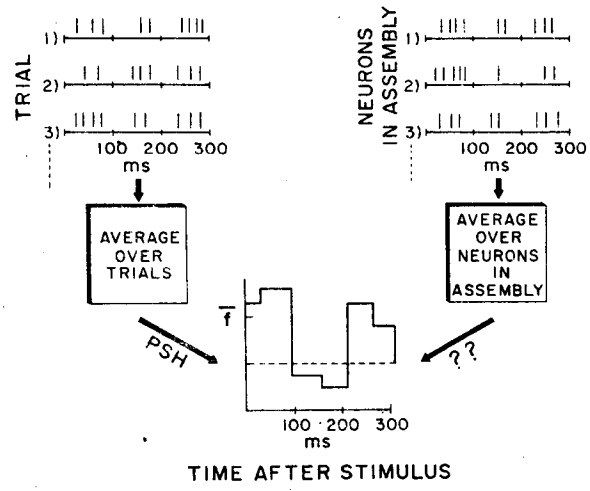

Fig. 2. Schematic drawing illustrating our definition of an assembly of neurons. The spatial average across neurons in the assembly for one trial is assumed equal to (denoted by question marks) the average for different experimental trials or poststimulus histogram (PSH) for each individual neuron in the assembly. The upper left part of the drawing represents the spike train responses of a typical cortical neuron to repeated brief "meaningful" stimulus to the animal. They vary from experimental (numbered) trial to trial. However, the average $\bar{f}$ over trials or PSH (~ 10 to 40 trials) in the lower center is "reproducible". The dashed line represents the background activity of this cell. The "size" of the time bins and the relevant "levels" of average firing $\bar{f}$ will probably vary from region to region in the cortex. The upper right part of the drawing illustrates the spike train responses of the individual (numbered) neurons in the assembly to one stimulus presentation.

of roughly 40 μ and a distance between bundles (in cortex) of ~ 60 μ. Although few direct physiological experiments have been carried out to determine their role, these bundles are unquestionably important fundamental units in brain function. We infer this, for example, from extensive work on bundles development showing[14] that, in many regions, they are not present at birth. These anatomic units are clearly of the appropriate size to be the basis for the assemblies defined in i) and due to their close membrane apposition, could carry out the direct electrical averaging needed for the theoretical assemblies (also see iv)).

iii) Mountcastle's irreducible processing unit. As detailed by Mountcastle,[2] there are many data demonstrating that the cortex is organized functionally into columns of roughly 500 μ diameter (and 2000 μ in depth) consisting of ~ 10^3 - 10^4 vertically arranged (perpendicular to the cortical surface), heavily interconnected neurons (see, e.g. Fig. 1 of Lund[15]). The column is defined by its inputs from the thalamus and its patterns of functional response. For example, all the neurons in the column of the primary visual cortex shown (in the highly idealized model) in Fig. 4 respond maximally to stimuli presented in the same locus in the visual field. In his organizational principle for the functioning of the neocortex, Mountcastle[2] regards the columns as the basic processing networks (with interactions among columns). Each column consists of irreducibly small processing units: minicolumns of neurons, roughly 40 μ in diameter. The minicolumns are then wired together into columns or networks having the capability of performing its appropriate, quite sophisticated, processing or memory tasks by being able to exhibit sophisticated, dynamic firing patterns persisting for some fraction of a second. The best studied, most highly organized sensory regions are the areas of the visual cortex (see Fig. 5). In particular, many properties of the primary visual cortex have been determined in the pioneering work of Hubel and Wiesel.[5] The highly idealized model of a column in Fig. 4 is divided into minicolumns

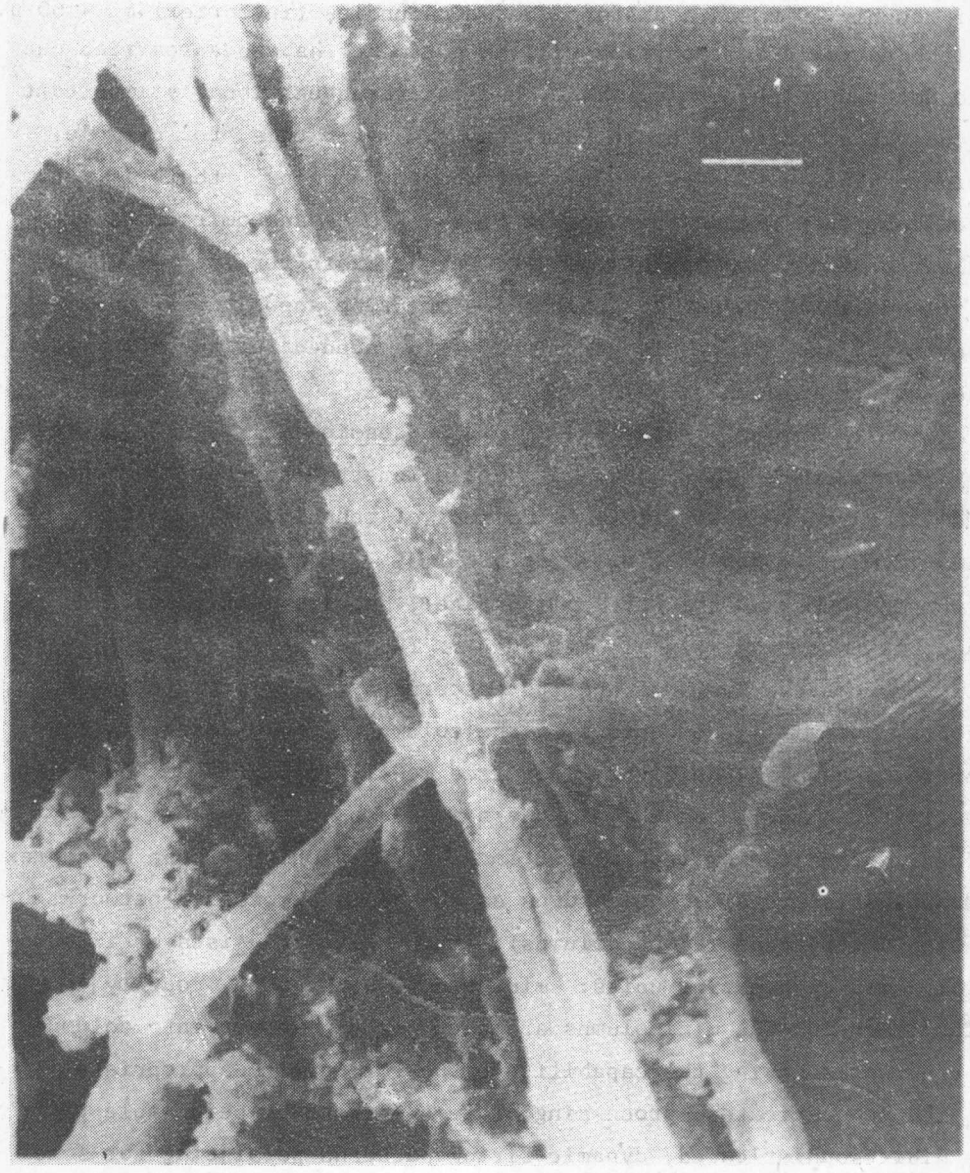

Fig. 3. Scanning electron microphotograph of a dendrite bundle in the spinal cord of the rat. The bundle appears to contain five to seven dendrite shafts, with elements entering or leaving along the course of the bundle. Axons and neuroglia are also in contact with the outer surfaces of the complex. Original magnification ×4000. Scale bar 10 μ. From the lab of A.B. Scheibel (Ref. 1).

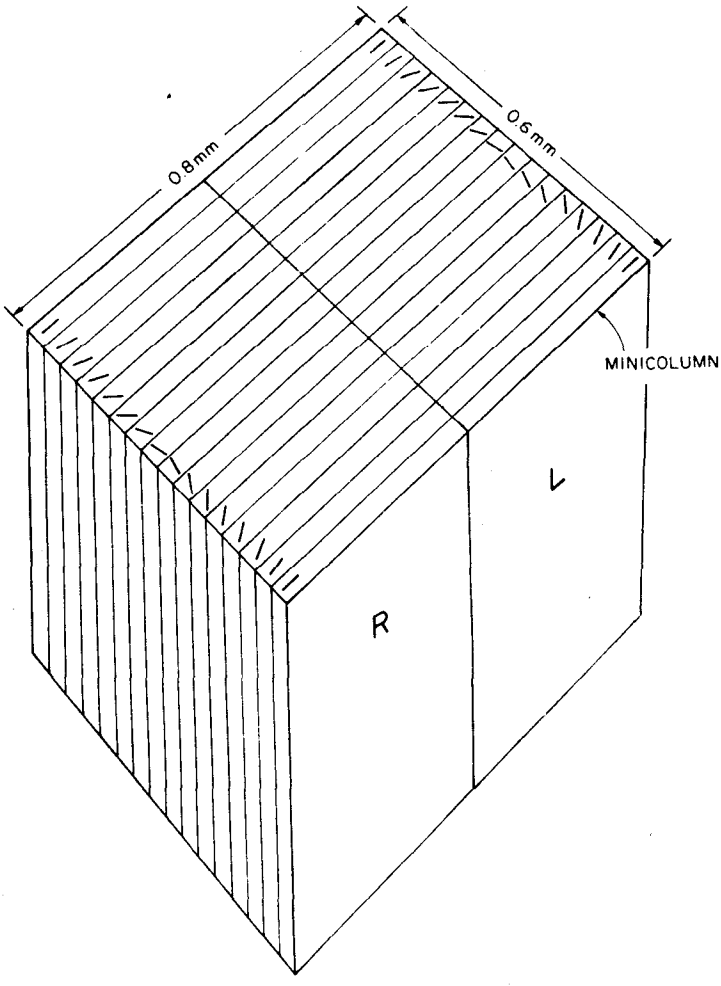

Fig. 4. Idealized model of a column in the primary visual cortex with each minicolumn labeled by orientation (denoted by bar) and ocular dominance. The firing response of the neurons in a particular minicolumn is maximal to bar light stimuli presented in the orientations indicated and to the left (L) or (R) eye.