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# *Group Report*
# *General Principles of Cortical Operation*

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## INTRODUCTION

The goal of our working group was to identify general principles of cortical operation. In our approach to this formidable problem, we decided to break it down into a series of questions dealing with cortical operations at different scales: first at the level of individual modules, then at the level of interactions among various modules within a cortical area, proceeding to a consideration of interareal interactions, and finally to a discussion of cortical maps, their principles of operation, and the abstractive, categorical operations beyond mapping. It was agreed at the outset that the true general principles of cortical organization were not likely to be revealed at this stage of our understanding, but that an airing of various points of view on these difficult questions combined with suggestions for future research questions and methodologies would be beneficial.

## INTRINSIC OPERATIONS

In attempting to define the intrinsic operations of a cortical module, it became clear that there were divergent viewpoints as to the appropriate size and nature of a module, and even whether such a module could be defined rigorously, given the differences (to be considered later) among and within cortical areas.

The question was initially posed as follows: suppose one slid an aperture with a diameter of 60 microns across the cortical surface, looking down through all cortical layers. Could one identify a consistent set of operations that were performed within such a module, and was this related to a consistent microstructure? This innocent statement led to much debate about the appropriateness of the scale of analysis. The areal dimensions of visual cortical hypercolumns, proposed by Hubel and Wiesel a decade earlier, are two orders of magnitude greater than that of the modules proposed here, and it was suggested that a module with these dimensions would be more appropriate. It was also suggested that the functions of a module would be incomprehensible without the lateral connections with which it was associated. In visual cortex, for instance, such interactions may participate in the generation of basic cortical properties such as orientation and direction selectivity. Similarly, the artificial separation of a module from its feedback pathways from higher areas was felt to be unwise. It was suggested that the generation of different cortical functions might best be examined with apertures of varying spatial scales, and even that the horizontally extended cortical layer rather than a cortical cylinder be defined as the basic module for study.

Support for the position that the smaller aperture described above was appropriate derived from two viewpoints: (a) that we were searching for the *minimal*, simplest, most basic set of operations performed by the cortex; and (b) that a cylinder of about this size and a depth of 2 mm represented a set of cortical cells with strong ontogenetic links (Rakic, this volume). In early cortical development, such a group can be shown to arise from the same ventricular germination zone, to migrate along the same path to the cortex, and early in development, before the full development of dendritic or axonal arbors, the cells can be observed stacked one upon another through the cortical thickness like a string of beads, with separations between adjacent groups. Experiments are in progress to determine whether all cells in such a module are derived from a common precursor. If one accepts the view that an elementary unit on this scale exists, then it has at least one simplifying effect, for it makes it understandable that the operational units observed in the waking, adult cortex may differ in size and dimensions in different areas of cortex, and even vary from time to time in a dynamic fashion. The incremental/decremental unit may well be one of these embryological units (Mountcastle 1979).

Despite a lack of consensus about the dimensions and nature of the module under discussion, an animated debate about the nature of the operations within it ensued. Perhaps the simplest and most minimal function of a cortical module derives from the fact that it has both inputs and outputs and as such relays information. Yet there is evidence that an important function of a cortical module beyond that of a simple relay lies in its ability to select its inputs or for an individual module to be selected by inputs. The notion that *selection* and *dynamic maintenance* of inputs were basic cortical processes derived support from "plasticity" experiments in both visual and somatosensory systems which show that the afferent input to a cortical module, whether it be from one eye or a patch of skin, can be altered by a variety of experimental manipulations. This idea was disputed by some who thought that such modifications told us little or nothing about the cortical circuit itself and really only changed the set of inputs being processed by the same circuit.

In seeking expressions to capture the essential operations of cortical modules, the influence of sensory coding experiments loomed large. The view that the basic cortical operation involved *cross-correlation* or other *filter* operations, *coincidence* or *alignment* in *time* and/or *space* appeared to be the dominant view. The abundant evidence that cortical neurons respond selectively to particular inputs while being relatively unaffected by other physical features of the stimulus supports the filter view. The diverse utility of spatial and temporal coincidence detection, which underlies neural mechanisms of orientation selectivity and stereopsis in vision, distance estimation, azimuthal location and target velocity in audition, and direction selectivity in somatosensation and other sense modalities supported the view that coincidence detection was of fundamental importance.

Another basic operation of cortex that was mentioned involved dynamic shaping of input, or contrast enhancement. This function was exemplified by the selective responses to the *relative* velocity of foreground and background motion in cat V1 and monkey V5 (MT) and by the ability of monkey V4 cells to "discount the illuminant" and respond to the color of the stimulus independent of the wavelength with which they were presented. It was felt, however, that these examples were likely to involve long-range intracortical interactions as well as operations intrinsic to a module, and so they might better be considered within the framework of inter- or intraareal interactions discussed below.

A more active view of the functions of the operation of the basic cortical module was evoked by the term "construction". This term emphasizes that stimulus properties like direction, speed of motion, color, and orientation are not explicitly represented on the receptor sheet and must be constructed in the cortex. This view contrasts with that of the passive feature extractor emphasized above.

Perhaps the most provocative view of the essential cortical operation was that one did not exist. While a superficial examination of the cortex under a 60 micron aperture would reveal many commonalities among the zones of cortex studied, there would also be many differences and great variability among individual dendritic and axonal arbors, even within an individual area of cortex that appeared homogeneous with lower resolution views. The variation in detailed microanatomy may bespeak variation of function in individual modules. Additionally, it was suggested that the logical structure of a module's operation may vary across time, or as a function of behavioral state. Moreover, since there is good evidence that each module has outputs to other cortical areas, to subcortical systems, and within its own area, it is entirely possible that a different function is expressed at each output and even that each output subserves different functions at different times.

## SIMILARITIES AND DIFFERENCES BETWEEN MODULES WITHIN OR ACROSS CORTICAL AREAS

The question of constancy of operation was hampered by our inability to agree on what the basic operations were, but that did not stop us from searching for commonalities and divergences of structure and function as a function of cortical location.

A given module of cortex has many similarities to other modules regardless of its location. One finds a constant number of neurons in all cortical regions (except for the perverse VI), a constant proportion of inhibitory interneurons, and a relatively constant proportion of lateral intracortical inputs. In nearly all modules the number of fibers entering and leaving appears constant. The pyramidal cells of the deeper cortical layers are the source of output toward effector systems and for feedback pathways. Pyramidal cells of the upper layers output to other cortical areas, and inputs arrive in the middle layers.

In searching for variations among modules, we wanted to distinguish sharply differences in output that related to differing *inputs* from those relating to differences in the circuits. We were encouraged initially by reports indicating that it had proved possible to redirect visual inputs to the region of the cortex normally processing auditory input in both hamsters and ferrets. When these regions of cortex were studied, some units were found to display orientation selective receptive fields, a hallmark of visual cortex. This led to questions about whether the construction of orientation selectivity was indeed a fundamental property of cortical modules (there is evidence of orientation selectivity in somatosensory cortex as well), and what the auditory equivalent of orientation selectivity might be. It was pointed out, however, that in both the cat and rabbit there was evidence for orientation selectivity at the level of the retina, so that the presence of some degree of cortical orientation selectivity in the redirected projections may reflect a relatively simple relay function of the cortex, rather than a more interesting filtering or construction operation.

Continuing with the topic of orientation selectivity, interest was focused on the nature of the operations performed within the blob and interblob zones of striate cortex. Despite the fact that the modules in these zones differ in the nature and degree of orientation, wavelength, and spatial frequency selectivity, we could not attribute these differences to differing intrinsic circuitry since the areas received differing inputs as well. While there is no evidence for clear-cut structural differences in terms of number of types of elements within or outside the blobs, we were more taken by the evidence of neurotransmitter diversity between the blob and interblob zones. The increased density of glutamic acid decarboxylase activity within the blobs and that of neuropeptide Y immunoreactivity in the interblob regions was regarded as reasonable evidence for diversity, at least in terms of neurotransmitter parameters.

## ALTERATIONS OF MODULAR FUNCTIONS BY EXPERIENCE

Since the general subject of cortical plasticity was covered by another group, we restricted ourselves to consideration of alterations of cortical function involving changes in intrinsic circuitry rather than those involving inputs. As cited earlier, studies involving expansions of receptive fields, or capture of cortical territory by one or another input, were outside our view. We did, however, delineate a few examples of functional alterations of what we believed to be *cortical* properties by experience in adult animals. These included studies of eyeblink conditioning of motor cortical cells by Woody and his colleagues (Woody and Engel 1972), and also studies indicating that the degree of direction selectivity of an individual visual cortical cell could be altered by exposure to repetitive unidirectional stimulation (Marlin et al. 1987). Studies in trained monkeys have illustrated an important set of memory-related functions in the prefrontal and parietal cortex. In monkeys trained in tasks involving delayed alternation (Niki 1974), or delayed saccadic eye movements, populations of cortical neurons have been found which become active soon after the cue whose position must be memorized; they then remain active more or less continuously throughout the delay period. Neurons like these which have been studied by several members of our group may well carry the information which enables the animal to perform these memory tasks.

We also discussed examples in which abnormal early experience altered the properties of the cortical circuit. One clear example of this occurs in cats reared in stroboscopic illumination throughout early postnatal development. In these animals a specific visual cortical unit property, namely direction selectivity, is virtually abolished without substantially altering other aspects of cortical processing mechanisms (Cynader and Chernenko 1976).

These studies indicating the modifiability of cortical circuitry appealed to us, and they even prompted some of us to add memory and information storage to the list of basic cortical operations of cortical modules listed above. Yet even though these studies convincingly demonstrated changes in cortical unit properties as assessed electrophysiologically, the lack of anatomical and/or biochemical evidence that could be adduced and the lack of certainty of the role of both intra- and extracortical enabling inputs in these memory/adaptation processes made it clear how far we still are from understanding the ways in which experience affects the basic cortical circuit.

## OPERATIONS PERFORMED BY INTERCOLUMNAR INTRAAREAL INTERACTIONS

Cross-correlation studies of the strength of synaptic interactions between cells within small regions of visual or motor cortices suggest that a thalamic input evokes activity more strongly linked radially along a functionally or anatomically defined cortical column than horizontally between such columns (e.g., Toyama, this volume). Moreover, evidence indicates that important operations are performed within all studied cortical regions by local, horizontally directed axons, which serve to link neighboring columns in a highly organized fashion.

The importance of both local and long corticocortical connections is demonstrated by experiments in which extensive destruction of thalamic projections has produced a reduction of only some 20–25% in the estimated number of intracortical synapses. The organization of local horizontal connections has been studied in a number of cortical regions by both punctate extracellular and intracellular injections of transported tracers. In most areas studied, punctate injections give rise to patches of anterograde and retrograde label interdigitated with unlabelled zones. Much of this evidence was discussed in detail, particularly for the visual cortex, by another group at this conference (see Gilbert et al., this volume). In both visual and somatosensorimotor cortices, approximately one half of the pyramidally shaped neurons give rise to horizontally-directed, collateral axons which extend for several hundred micra or even several millimeters (motor cortex) from the cell body; the presynaptic terminals of these axons are of the Type 1 category and are presumably excitatory. The connections made by one of these axons appear to be patchy: diffuse branchings and synaptic contacts are made at several points along the parent axon to cells apparently within selected, vertically oriented columns. GABAergic inhibitory neurons also give rise to horizontal projections. These extend for smaller distances and the spread of these axons appears different depending on their layer of origin. Thus, observed axon trajectories and types suggest an organization whereby longer excitatory projections from deeper–lying pyramidal cells within a column may distribute in selective, patchy fashion to surrounding functionally related columns and at these sites evoke local excitatory and, via GABAergic or other neurons, inhibitory actions. These laterally-directed circuits differ in their extent and density in different cortical areas and even within areas. The patches extend over a greater range in both V4 and in motor cortex than they do in VI. Within VI, connections involving the cytochrome oxidase blobs extend further than those involving the interblob zones. In cat VII, the patches are anisotropically distributed across the cortex, extending two to three times as far in one direction as in the other orthogonal direction (Matsubara et al. 1987).

Such circuits form a basis for important local, intercolumnar operations. But what is the nature of these operations, and what is the general functional importance of intercolumnar connections?

The very existence of topographic continuity in central sensory and motor maps suggests that important operations are performed by local circuits upon inputs received from, or outputs directed to, corresponding adjacent regions of peripheral receptor and effector surfaces. For example, it seems clear that intercolumnar inhibition, produced by local horizontal circuits, is the substrate for *contrast enhancement* in a number of sensory cortical areas, a process which preserves and indeed sharpens boundaries between stimulated and adjacent regions of the receptor surface. This sharpening process occurs at all stages of sensory systems and in cortex may extend to other properties including orientation selectivity, a notion reinforced by evidence that nearby patches in cat VII interconnect neurons with orthogonal orientation preferences (Matsubara et al. 1987). A similar circuit may, by the same operation, serve to *sharpen* selection of movement direction or patterns of muscular synergy. In the visual system an asymmetric, feed-forward inhibitory network may be the basis for detection of stimulus direction and a fundamentally similar, intercolumnar circuit may encode *stimulus direction* in area 1 of somatosensory cortex. In auditory cortex, intercolumnar inhibition may contribute to computation or sharpening of various topographically represented attributes of an auditory stimulus (Suga, this volume).

But what about local, horizontal excitatory processes? It is probable that such connections contribute to a strengthening of coincident or cooperative discharge by a set of columns with similar functions. There is evidence that horizontal, excitatory signals are directed from a particular orientation column in visual cortex to the supragranular layers within columns of similar orientation selectivity. Local excitatory interactions in V4 appear to be part of the process by which V4 units extract color information from reflectance. Local, excitatory interactions have also been demonstrated in the motor cortical regions which affect muscles acting at adjacent joints in the alert monkey (Kwan et al. 1987), muscles whose cooperative activity is fundamental to coordinated limb movement. Such circuits may also form the basis in other cortical areas for interconnecting columnar regions whose collective outputs produce definable behaviors. Rizzolatti's experiments (this volume) in the periarcuate motor-premotor area have shown, for example, that neurons relating to arm-hand and to mouth movements lie in close proximity. It is possible that local circuit, cooperative interactions between such neurons may contribute to relatively complex behaviors such as reaching, grasping, and ingesting food, without sole mediation by the longer corticocortical,

cortical-subcortical loops that have been presumed to underlie in entirety even simple behavioral acts. Additional anatomical studies and cross-correlations of unit discharge are needed in such regions in order to define further the operations performed by local intercolumnar or intraareal connections.

In a system characterized by a lateral spread of excitation, one inevitable casualty is topographic precision. We then considered the question of how we get precise percepts and movements from apparently broadly tuned neural substrates in the section on cortical maps.

## INTERAREAL CONNECTIONS AND THEIR FUNCTIONAL IMPLICATIONS

There is functional, anatomical, and biochemical evidence for the existence of a large number (on the order of 50–100) of separable neocortical areas. There is anatomical evidence showing that any given area is connected with up to two dozen other areas. Each area has its own unique set of connections, and these connections may be highly selective with regard to both sources and termination. For example, the elegant demonstrations of interdigitation between various inputs to monkey prefrontal cortex, cat auditory cortex, and to monkey V2 are evidence for the existence of precise *specificity* in interareal connections. We considered two extreme positions to characterize the relationship among cortical areas:

1) Cortical areas are part of a distributed reentrant interconnected system in which specific functions do not reside in individual areas, but instead reside in the distributed activity of these areas. Furthermore, only certain subsets of modules in a given area participate in any given distributed system.

2) Cortical areas are characterized by functional specialization, and their interconnections can be viewed as part of an information or output processing chain.

While recognizing that neither of these propositions was likely to be exclusively correct, we nonetheless attempted to adduce evidence that would support one or the other. Support for the first proposition was derived from studies of trained animals performing behavioral tasks involving eye or arm movements.

From these studies it has become clear that:

1) A large number of cortical areas become active during even the simplest of movement tasks;

2) The same areas appear to participate in several distinct circuits relating to different tasks, which may involve different relative activation of the areas;

3) All of motor cortical areas can project to downstream effector systems,

albeit with different segmental and laminar distributions; and

4) Action initiation cannot be shown to be associated with any individual cortical area such as motor cortex or with a single subcortical structure such as the basal ganglia, the cerebellum, or brain stem motor nuclei.

The evidence for conjoint activation of motor areas cannot be readily accounted for in terms of a chain becoming active in sequence. Recordings have been made from cortical neurons in a variety of areas while a monkey performs a visually directed reaching movement. It has been consistently found that there is broad overlap in timing among the areas examined. This is consistent with a distributed reentrant network. Nonetheless, some important tendencies for functional specificity have emerged from such studies. There is a tendency for the earliest cortical activity associated with a centrally initiated or voluntary movement to occur at sites both rostral and caudal to, but remote from, the central sulcus. During visually guided reaching movements, for example, activity clearly related to the impending movement is perhaps first detectable in area 7 of the posterior parietal lobe (Mountcastle et al. 1975) and in the postarcuate premotor cortex which is linked reciprocally with this region (Kubota and Hamada, 1978; Humphrey 1979; Rizzolatti and Gentilucci, this volume). Within cortical area 2 and the rostral primary motor cortex, motor output neurons receiving somatosensory input primarily from joint receptors next begin to discharge (Lemon and Porter 1976; Fetz et al 1980; Lamour et al, 1980; Wise and Tanji 1981). By virtue of such input from joint and other deep receptors, these cells are in a unique position to specify the initial postural conditions upon which the movement is based, and thus to specify appropriate movement direction. Next to discharge, often *after* movement onset, are neurons located close to the central fissure, neurons within caudal area 4 of the motor, and within area 3b of the first somatosensory cortex; these cells are sensitive to joint/cutaneous or cutaneous inputs, respectively, from the moving limb or body part (Lamour et al. 1980; Fetz et al. 1980; Fetz and Soso 1980; Evarts and Fromm 1981; Wise and Tanji 1981). Such a separation of neuronal properties in terms of timing of movement-related discharge and form of somatosensory input has suggested that tissue anterior and posterior to the central fissure may be part of two general networks: one for movement initiation on the basis of visual and joint position cues (located farther from the fissure), and another for movement guidance and termination on the basis of joint position and cutaneous inputs (located nearer to the central fissure) (see Humphrey 1983 for a discussion of this concept). Those in favor of some functional specificity for each cortical motor and premotor area emphasized, however, that while specific areas may be coactivated in various tasks, the degree of activation may be quite unequal and each cortical zone may perform a somewhat separate role in the initiation and control of movement. This view departs slightly from a strict concept of distributed networks, where differing cortical zones may be part of the same functional system, with similar roles in the control of movement.

Strong evidence for functional specialization of different cortical areas emerged from studies of visual and auditory processing mechanisms. Anatomical studies of monkey cortex (Zeki, this volume; show that the cytochrome oxidase blobs of VI, which contain predominantly wavelength rather than orientation selective cells, are connected with the thin cytochrome oxidase stripes of V2, which in turn project to V4. The interblob zones of layers 2 and 3, which contain orientation but not wavelength selective cells, project specifically to the interstripes of V2. The cells in layer 4B project to V3 and also to V5. In V2, the functional segregation seems to be maintained. Thin stripes contain wavelength selective and broad-band cells, but few if any orientation selective cells. Directionally selective cells, though relatively few in number, are found in thick stripes only, and it is these stripes that project selectively to V5 and also to V3. Wavelength selective cells are not found in the thick stripes.

This evidence complements and reinforces earlier evidence for functional specialization in the prestriate visual cortex. Altogether, the evidence shows the cortical separation of visual submodalities related to color, form, and motion, and that each submodality is not the preserve of a single area or pathway, but of several. Thus the motion pathway includes layer 4B of V1, the thick stripes of V2, areas V5, V5A, V6, and the parietal areas. The color pathway includes the blobs of layers 2 and 3 of VI, the thin stripes and interstripes of V2, the V4 complex, and the inferotemporal areas. The "form" pathway includes the interblobs of V1, the interstripes of V2 and possibly V3A. Form may also be represented in V4 in that orientation selective cells are found there, but it is difficult to separate form from color, and whether the information on form implicit in the responses of cells in V4 is the same and used in the same way as that reaching, e.g., V3A, remains to be seen.

Electrophysiological studies of the mustached bat (Suga, this volume) also provide strong evidence for extreme functional specificity of auditory processing mechanisms. Individual areas contain neurons specialized for extracting information about target range, target velocity, or target location. Each auditory area appears highly specialized for the analysis of an individual information-bearing parameter.

Evidence of recovery, or lack thereof, after injury provided grist for both sides of the distributed system/functional specialization division. That lesions of V5 (MT) caused precise deficits in motion perception supports the view of functional specificity, but the rapid recovery from many of these deficits seems to indicate that other areas can take over this function with relative ease. Many examples of recovery of function after motor system injuries could be adduced, and while some of these may reflect intraareal compensatory mechanisms of the sort described by Merzenich (this volume), some involving total destruction of individual areas were more difficult to refute. However, it was pointed out that many lesions of both motor and sensory systems can produce permanent and specific effects. Striking examples involve the cases of patients who, following specific lesions outside the primary visual cortex, suffer not a global scotoma, but rather a specific submodality defect. Lesions have produced specific defects in color vision, sparing the perception of form, motion, and depth; and in other cases, specific defects in motion perception sparing the other visual submodalities. The overall weight of the evidence thus appeared to clearly favor the concept of functional specificity, at least in areas closer to the sensory processing side of the cortex.

## MAPS AND THEIR MEANING

A striking characteristic of cortical areas is that they appear to contain maps of one sort or another. We set out to define and discuss the various types of maps in the cortex, to understand the advantages and disadvantages of multiple maps, and to consider the problem of how information might be read out from representations like those already studied in the cortex.

### Sensory or Motor Maps

Maps of the sensory or effector sheet were the first to be discovered within the cortex, and some of us have become a bit blasé about their function. Yet it should be emphasized that even primary cortical maps are rarely a faithful representation of their input. The Cartesian coordinate representation of the visual field in the primate LGN is transformed into a log-polar mapping in VI (Schwartz 1977); the representation of vertical and horizontal visual space, which is similar in the LGN, differs by a factor of two or three in cat V2 (Cynader et al. 1987). In different areas within the bat auditory cortex, the representation of different parts of the basilar membrane can vary dramatically, as can the relative magnification factor for central and peripheral visual fields in the various extrastriate areas. In addition, different maps seem to display differing degrees of precision in their representation of the sensory or effector sheet. Indeed, it was suggested that as long as sensory or effector topographic order remained within a map it signified that further processing had yet to be done.

We considered the advantages of several small maps, as opposed to one large map that would encompass the functions of these multiple areas. We agreed that difficulties would arise for processing mechanisms with only one map because it would become difficult to represent all of the information-bearing parameters that needed to be processed within the structure next to each other, to still maintain topographic fidelity, and to enable reasonably short range connections, shown earlier to be important for lateral inhibitory and synergistic functions, to operate effectively and with the temporal precision required for a coincidence-detecting system. Moreover, it was pointed out that different functions appeared to require different degrees of topographic precision and unequal representations of parts of the sensory or motor sheet. The problem is clearly exemplified by the importance of extended lateral interactions for color but not for form vision. Knowledge of the color of a surface involves knowledge not only of the wavelength of the stimulated patch of retina, but also of the wavelengths in an extended surround area. This may provide the rationale for the greater lateral spread of connections involving blob zones than among interblob zones in VI. This is an exception to the general rule that the intracortical connections are constant in extent throughout a cortical area. If many different functions, each with different requirements, had to coexist in a single cortical map, then the consistency of operating principles within an area would be lost. However, it was pointed out that, despite the difficulties noted above, it was common particularly in primary sensory cortices for *several* variables to be mapped recurrently across the surface within a single topographic map, and that this was one of the fundamental properties of columnar organization.

## Computational Maps

While the above discussion concentrates on maps related to the periphery, there is impressive evidence derived from the mustached bat auditory system (Suga, this volume), that different types of information-bearing parameters (IBPs) characterizing biologically important sensory signals are represented in separate areas of the sensory cortex. When variations of an IBP are biologically important, different values of the IBP are mapped and systematically represented within this separate area. Some examples of IBPs in the auditory system include echo-delay, interaural time and amplitude differences, FM rate and depth, and AM rate and depth.

An IBP for one species may not be an IBP for another species, and an identical IBP may carry different types of information for different species. Therefore, the functional organization of the sensory cortex can be different among species according to differences in their species-specific sensory signals and species-specific behavior. Furthermore, it can be different among sexes and individuals within the same species when they are concerned with different values of IBPs. Computational maps representing IBPs need to have little or no topographic order, at least as defined with regard to the sensory epithelial sheet. Instead, their essential order is observed in the pattern of representation of the information-bearing parameters for which they are specialized. Segregation and separate mapping of different IBPs appears to be a basic solution employed by the neocortex in processing sensory signals. Each of the separate areas representing different IBPs is interconnected with other areas. In fact, the outputs of computational maps can be combined to form a still higher order map, such as an auditory space map in the owl inferior colliculus or the frequency versus amplitude map in the mustached bat. The upper limit for combination of such maps has not yet been defined. Several advantages in signal processing emerge from such computational maps: (a) a map facilitates identification of values of IBPs and reduces the problem of identification of IBP to that of localization in a map; (b) lateral inhibition can easily be employed to increase the selectivity of neurons; and (c) the sensorimotor interface is facilitated.

An organization similar to that just outlined for sensory systems seems to also exist within the motor system. Multiple cortical areas exist for the control of arm-hand movements (Muakkassa and Strick 1979), even within the primary or MI motor cortex (Humphrey 1986). While highly interconnected, each of these systems has a unique set of inputs and independent projections to the spinal cord and to the brain stem (Schell and Strick 1984; Martino and Strick 1987). Yet, it is likely that the behavioral conditions under which each system is more active, and the particular influences which each exerts on arm-hand movements, differ significantly. The arm and hand are "represented", for example, within the supplementary motor and postarcuate premotor areas, yet the major motor functions of the two areas are distinguishable. Activity within the supplementary motor area appears to be most related to activation of axial and limb musculature in organized movement synergies, where coordination and sequencing of proximal (axial) and distal limb muscle activity (bilaterally) are important (cf. Humphrey 1979; Brinkman and Porter 1979; Wiesendanger 1981). Activity within the postarcuate premotor area, however, appears clearly related to coordinated arm-hand movements toward objects in the extrapersonal space which will be brought into contact with the mouth, such as reaching for, grasping, and ingesting food (Rizzolatti, this volume). Within the precentral motor cortex, the multiple representations of arm and hand allow for the possibility of limb control on the basis of different somatosensory cues (e.g. Strick and Preston 1978), for synergistic control of neighboring joints during voluntary movements about particular joints (Kwan et al. 1978; Humphrey 1986), or for separate control, through antagonist co-contractions, of the mechanical impedance of the various joints within the limb (Humphrey and Reed 1983). Thus the multiple motor representations within the cortex appear to differ in significant ways, and to provide for partially independent control of the same body parts in manners that depend upon (a) particular behavioral goals; (b) the sensory stimuli that guide movement; (c) the muscle synergies that are necessary for particular movement patterns; and (d) the mechanical impedance of the musculoskeletal system through which central motor structures must deal with external objects. Future research will reveal more clearly the particular motor-behavioral variables "computed" by or "represented" within these cortical zones, the ways in which these computations are performed in conjunction with intraspinal circuitry, and their unique contributions to the control of movement and posture. Additional research is also needed to determine the extent to which these neuronal operations are modifiable by experience, as suggested by the provocative "plastic" changes in the details of representation within sensorimotor cortical areas of the type reported by Merzenich et al. (this

Thus, while sensory epithelial maps represent the entire sensory sheet, computational maps appear to represent an extracted or constructed variable. In addition to the examples cited above, in the auditory system of the mustached bat and barn owl, other examples in the motor system include the representation of saccade direction across the primate frontal eye fields (Bruce, this volume) and the representation of motor direction across motor cortex (Georgopoulos, unpublished preliminary observations).

## Readout from Maps

In considering the outputs of computational maps such as those described above, and even of maps of sensory or motor sheets, the problem arises as to how the information contained within such maps can be read out. In most cases where it has been studied, the precision of the behavior of the entire organism exceeds, often by an order of magnitude, the performance of individual neurons within the map. Neurons can also be tuned to *several* parameters, yet broad or multiple-parameter tuning among individual neurons is not necessarily indicative of loss of accuracy in coding. Coarse coding using overlapping and large receptive fields can yield a precise readout, since the pattern of activity of the overall population will change with small changes in the coded variable. Likewise, a center of mass computation on the activity of a population of coarsely coded neurons will extract information with high precision. This may explain why fine motor outputs emerge from a population of motor cortex units with broad tuning. The problem with this sort of coarse coding technique is not that it cannot precisely represent the value of a single variable, but that it has difficulty resolving two closely arranged variables. Perhaps this is one of the reasons why computational maps often seem specialized to construct, compute, or select a *single* answer—such as a target range, a direction of saccade, or an arm movement. Mechanisms of selective attention may be useful to limit the number of variables that have access to such coarsely coded areas.

## Beyond Topography

While each of the areas described above was characterized by a map with regard to some parameter or another, and each represented that parameter with some degree of topographic fidelity, there appear to be examples of areas in which the representation of information-bearing parameters in relation to the sensory sheet is superficially disorganized. One such example is area 7A of the poster parietal cortex studied by Andersen (this volume). Cells in this area code location in craniotopic coordinates, but their firing rate is dependent on eye position. Eye-position independent coding of spatial position is not specified at a single cell level, but rather may be encoded in a distributed fashion. A layered network model trained to localize position in space from eye and retinal position signals produces receptive field properties in the network units which are quite similar to the receptive field properties actually observed in posterior parietal neurons. This model suggests that the parietal lobe is learning associations between eye position and retinal inputs. The network does not contain a topographic map in its units' receptive field positions, as appears to be the case among parietal neurons. Rather, the readout of distributed code is embedded in the structure of the learned synaptic weights of the connections. The spatial receptive fields of both parietal neurons and network units are very large, yet the readout of these distributed codes in both cases is very precise for spatial position.

This point of view provoked considerable discussion, with some skepticism of the ideas outlined above and with the suggestion that what was really needed was a concerted effort to find the actual topographic map in this structure. Still, the enchanting possibility of being able to derive *learned* order from superficial chaos suggested that the principle of distributed coding had some general validity and may prove a useful tool for understanding the functions of other structures whose topographic properties are currently obscure.

## Some General Problems and Solutions

Our perspective on the basic cortical operations thus far has been that of anatomists, physiologists, and behavioral scientists. Yet the cortex is a system, and since some members of our group were experts in systems theoretical approaches to neural function, our ideas were enriched by their contributions.

The problems involved in the analysis of cortical organization can be expressed in several ways. From a computational viewpoint they can be broken down to: (a) data acquisition and preprocessing; (b) control and interpretation; (c) construction of internal models (representations) of the outer world; and (d) implementation of behavior by different effectors (arms, legs, and speech production).

If K is the perceivable dimension of the external world, N the dimension of the usable internal state, and M the dimension of the effector system then, depending on the task, K and M are both much larger than N. This means we have both strong convergence on the internal state and high divergence for communication by speech and behavior. Consequently, data compression and effective use of memory have to be implemented.

A basic problem common to (a), (b) and (c) above is how to reduce the amount of data (not information) reaching the internal model because, in spite of massive parallel processing, it is too large to be processed in an adequate time (e.g., orientation in a three-dimensional environment). The dimension of the internal representation (N) must be low, variable, and task-dependent so that we can use it to choose appropriate behavior and to control data acquisition (feedback) by segmentation (in vision: looking at the right place at the right time). Three approaches are used in the implementation: (a) extensive use of the past (the whole negative time axis is used); (b) a common data format (at least in the cortex); and (c) the use of strategies (local and global optimizations, abstractions, etc.).

Currently, the most feasible experimental possibilities revolve around the question of the structure of a common data format. For instance, the anatomically monotonous structure of the cortex could be an implementation of such a format. Elements of this structure are: (a) lateral inhibition and facilitation; (b) topographical mapping; (c) functional mapping; (d) feedback; (e) organization of task–dependent hierarchies; and (f) cooperation between subsystems by means of synchronization.

Points b) and c) seem to be essential for cortical information processing and could be cleared up in the near future. These structures instantiate parallel processing, adaptation to a simple geometrical operator (e.g., the pyramidal cell), and variable combination of dynamic parameters by layered or discrete structures. This method of data processing can be used to code both the "grandmother cell" (pattern matching by correlation for fast responses) as well as "basic situations" that can be combined into complex ones.

The capabilities of maps are underestimated if they are interpreted as being only simple computational tricks. The generation of motor patterns is a good example showing that functional maps should not be interpreted only as systems for transforming coordinates and combining distinct parameters; rather, they also provide movement in a natural environment: a task of formidable complexity involving data compression, model construction, and generation of behavior.

These ideas point out that while we have made considerable progress in the past decades and even more during this meeting, we still have a long way to go in our understanding of cortical function.

## EPILOGUE

In the final sessions of our group, we looked toward the future, asking what directions should be taken and what tools we need in order to take them. Several of us expressed frustration that the methods we had available to us were insufficient to study and capture the essential processes by which the cortex functioned. In brief, we lack ways to study the activity of widely distributed populations of interacting neurons in a behaving organism. Some present and future techniques which may bridge this gap include remote measures of brain structure and metabolism as exemplified by PET and NMR scans. Improvements can be confidently expected in the development of voltage–sensitive dyes and the magnetic recording techniques which may enable detailed probes of deep as well as surface structures. The dramatic revolutions in molecular biologic techniques promise us a host of new ways to produce chemically specific monitoring, labelling, or inactivation of selected brain regions. Some or all of these techniques may help us in our efforts to solve the mystery of cortical operations.

On the other hand, some of us emphasized that the problems we faced were as likely to be conceptual as methodological. Schoenberg's comment that "there is still a lot of good music to be written in the key of C major" reminded us that a great deal of progress has been and continues to be made with our current methods. Further progress in understanding the basic operations of cortex may well come not simply from new techniques, but from closer coordination between neuroscientists and psychophysicists dealing with both the sensory and motor systems, and from studies of the actions and geometry of our musculature. Interactions with systems theorists, cognitive scientists, and computer scientists will also be valuable. The insights from these disciplines have as yet imperfectly permeated an increasingly reductionist neurobiology of cortex, and the reformulation of the problems of the basic cortical operations with the assistance of concepts derived from these disciplines may be of lasting value.

## REFERENCES

Brinkman, C., and Porter, R. 1979. Supplementary motor area in the monkey: activity of neurons during performance of a learned motor task. *J. Neurophysiol.* **42**: 681–709.

Cynader, M., and Chernenko, G. 1976. Abolition of direction selectivity in the visual cortex of the cat. *Science* **193**: 504–505.

Cynader, M.; Swindale, N.V.; and Matsubara, J.A. 1987. Functional topography in cat area 18. *J. Neurosci.* **7**: 1401–1413.

Evarts, E.V., and Fromm, G. 1981. Transcortical reflexes and servo control of movement. *Can. J. Physiol. Pharmacol.* **59**: 757–765.

Fetz, E.E.; Finocchio, D.; Baker, M.A.; and Soso, M.J. 1980. Sensory and motor responses of precentral cells during comparable active and passive movements. *J. Neurophysiol.* **43**: 1070–1089.

Humphrey, D.R. 1979. On the cortical control of visually directed reaching: contributions by non-precentral motor areas. In: Posture and Movement, eds. R. Talbott and D.R. Humphrey, pp. 51–112. New York: Raven Press.

Humphrey, D.R. 1983. Corticospinal systems and their control by premotor cortex, basal ganglia and cerebellum. In: The Clinical Neurosciences. Vol. 5. Neurobiology, eds. R.N. Rosenberg and W.D. Willis, pp. 547–587. New York: Churchill Livingstone.

Humphrey, D.R., and Reed, D.J. 1983. Separate cortical systems for the control of joint movement and joint stiffness: reciprocal and coactivation of antagonist muscles. In: Motor Control Mechanisms in Health and Disease, ed. J. Desmedt. *Adv. Neurol.* **39**: 347–372.

Humphrey, D.R. 1986. Representation of movements and muscles within the primate precentral motor cortex: historical and current perspectives. *Fed. Proc.* **45**: 2687–2699.

Kubota, K., and Hamada, I. 1978. Visual tracking and neuron activity in the post-arcuate area in monkeys. *J. Physiol. (Paris)* **74**: 297–312.

Kwan, H.C.; MacKay, W.A.; Murphy, J.T.; and Wong, Y.V. 1978. Spatial organization of precentral cortex in awake primates. II. Motor outputs. *J. Neurophysiol.* **41**: 1120–1131.

Kwan, H.C.; Murphy, John T.; and Wong, Y.C. 1987. Interaction between neurons in precentral cortical zones controlling different joints. *Brain Res.* **400**: 259–269.

Lamour, Y.; Jenning, V.A.; and Solis, H. 1980. Functional characteristics and segregation of cutaneous and non-cutaneous neurons in monkey precentral motor cortex. *Soc. Neurosci. Abst.* **6**: 158.

Lemon, R.N., and Porter, R. 1976. Afferent input to movement related precentral neurons in conscious monkeys. *Proc. R. Soc. Lond. (Biol.)* **194**: 313–339.

Marlin, S.G.; Hasan, S.J.; and Cynader, M.S. 1987. Direction selective adaptation in simple and complex cells in cat striate cortex. *J. Neurophysiol.*, in press.

Martin, A.M., and Strick, P.L. 1987. Corticospinal projections originate from the arcuate premotor area. *Brain Res.* **404**: 307–312.

Matsubara, J.A.; Cynader, M.; and Swindale, N.V. 1987. Anatomical and physiological properties of the intrinsic connections in cat area 18. *J. Neurosci.* **7**: 1428–1446.

Mountcastle, V.B.; Lynch, J.C.; Georgopoulos, A.; Sakata, H.; and Acuna, C. 1975. Posterior parietal association cortex of the monkey. Command functions for operations within extrapersonal space. *J. Neurophysiol.* **38**: 871–908.

Mountcastle, V.B. 1979. An organizing principle for cerebral function: the unit module and the distributed system. In: The Neurosciences: Fourth Study Program, eds. F.O. Schmitt and F.G. Worden, pp. 21–42. Cambridge, MA: MIT Press.

Muakkassa, K.F., and Strick, P.L. 1979. Frontal lobe inputs to primate motor cortex: evidence for four somatotopically organized "premotor" areas. *Brain Res.* **177**: 176–182.

Niki, H. 1974. Differential activity of prefrontal units during right and left delayed response trials. *Brain Res.* **70**: 346–349.

Schell, G.R., and Strick, P.L. 1984. The origin of thalamic inputs to the arcuate premotor and supplementary motor areas. *J. Neurosci.* **4**: 539–560.

Schwartz, E.L. 1977. Spatial mapping in the primate sensory projection: analytic structure and relevance to perception. *Biol. Cybern.* **25**: 181–194.

Soso, M.J., and Fetz, E.E. 1980. Responses of identified cells in postcentral cortex of awake monkeys during comparable active and passive movements. *J. Neurophysiol.* **43**: 1090–1110.

Strick, P.L., and Preston, J.B. 1978. Sorting of somatosensory information in primate motor cortex. *Brain Rs.* **156**: 364–368.

Wiesendanger, M. 1981. Organization of secondary motor areas of cerebral cortex. In: Handbook of Physiology. Section I. The Nervous System. Vol. 2. Motor Control. ed. V.B. Brooks, pp. 1121–1147. Bethesda, MD: American Physiological Society.

Wise, S.P., and Tanji, J. 1981. Neuronal responses in sensorimotor cortex to ramp displacements and maintained positions imposed on hindlimb of the unanesthetized monkey. *J. Neurophysiol.* **45**: 482–491.

Woody, C.D., and Engel, J. 1972. Changes in unit activity and threshold to electrical microstimulation at coronal-precruciate cortex of cat with classical conditioning of different facial movements. *J. Neurophysiol.* **35**: 717–726.