

Dynamic Neuronal Operations within the Somatic Sensory Cortex

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INTRODUCTION

I emphasize in this review observations upon the dynamic neuronal operations within the somatic sensory cortex of primates. The aim is to derive from them some general principles of cortical operation. I shall summarize only briefly the large body of knowledge concerning “functional organization” of the somatic sensory cortex, but emphasize its importance for understanding cortical function.

It is appropriate first to indicate some concepts that pertain to brain and cortical function in general. Studies of connectivity between brain structures and of the functional properties of cortical neurons, largely made in sensory areas, have led to a new principle of brain organization: that of the unit module and the distributed system. The general idea is that major structures of the brain including the neocortex are composed of replicated neural circuits (for want of a better term, modules) that differ in intrinsic connectivity and processing modes between different major structures, but are similar within any single structure. The direction of neural processing within a cortical module (or column) is in the translaminal direction; processing in the tangential dimension of the cortex is limited in extent and is frequently disjunctive. Each module processes neural signals from its several inputs to its several outputs, imposing transforms determined by the general properties of the structure and its extrinsic connections (Mountcastle 1979).

Although much has been learned about intrinsic and extrinsic cortical connectivity, we cannot define in precise terms the functional operations in any small area of the neocortex. The interlocking subsets of modules in different structures may be distant from one another in space but they

compose precisely connected distributed systems. These facts pose a number of questions central to the field: What operation is executed in any small cortical area? Do operations differ along different channels within a single cortical module, or between modules in different cortical areas? Are the neural counterparts of perceptual and other higher functions instantiated in the dynamic activity in distributed systems; or, to what degree can they be localized to one area/structure or another?

This general idea encompasses another much older in the history of brain science: that of parallel processing. Parallel processing mechanisms vary from gross to minute levels within the somatic afferent system. Several pathways carry neural signals of somesthetic events from the periphery to the spinal cord and brain stem, and from thence to the forebrain. The ventrobasal complex of the thalamus projects upon both the first and second somatic cortical areas. There is parallel processing for different modalities of mechanoreception in different modular sets at each level of the system. One can readily imagine how processing may differ along channels that are initially quasi-parallel, and may lead to different output portals of a module, aimed at different targets in the nervous system and serving different functions. It is not readily apparent, however, how recombinations of the outputs of different parallel channels compose the central neural mechanisms of complex somesthetic perceptions such as stereognosis. Parsimony suggests that no single channel within the nervous system is redundant, even though some may appear more or less parallel and replicative from the level of entry to that of output.

FUNCTIONAL ORGANIZATION OF THE POSTCENTRAL GYRUS, SI

Structure and Connectivity

A somatic sensory area of cortex is one that receives a major afferent inflow from the somatic afferent system and whose neurons thus respond to somatic stimulation, and which can be shown on other grounds to play a role in somatic sensibility. The first and second somatic areas (SI and SII) qualify; several parietal areas posterior to SI are also somatic sensory in nature, but differ in character from SI and SII: the supplementary sensory area (SSA) of medial area 5, lateral area 5, and area 7b. I consider here only SI, which itself contains four cytoarchitectonic areas, from anterior to posterior areas 3b, 3a, 1 and 2, arranged in long, narrow mediolateral strips. Each has a distinctive cytoarchitecture and pattern of extrinsic connectivity, and neurons that differ in certain functional properties. Each area receives its specific thalamocortical inflow from sets of cellular modules (rods) of the ventrobasal complex (VB) of the thalamus, sets thought to be largely separate in

their cortical projections though partially intermingled in VB. Reciprocal projections between SI and VB are arranged in tightly localized relations between thalamic rod and cortical column (Jones et al. 1982). SI also receives ascending inflow from nuclei of the basilar forebrain, the central core of the brain stem, and the intralaminar nuclei of the thalamus, mainly the centrolateral nucleus. These systems are widely surmised to control the general excitability of the cerebral cortex.

Several generalizations can be drawn from knowledge of the corticocortical connections of SI (for review, see Jones 1984):

- 1) area 3b projects upon adjacent areas 1 and 2, and receives only a faint projection in return from area 1—area 3b is to a certain extent a feed forward element in the cortical circuitry;

- 2) successively more posterior areas of the parietal lobe are reciprocally linked with successively more anterior areas of the frontal lobe;

- 3) the SSA receives projections from all SI areas, projects to areas 4 and 6, and is reciprocally linked with area 5 and the supplementary motor area (SMA);

- 4) the SMA receives from areas 1 and 2, and is reciprocally linked with areas 4 and 5 and with the SSA; and

- 5) SI and SII are each linked reciprocally with homologous areas of the contralateral hemisphere; in addition, SI projects upon contralateral SII.

The terminals of commissural and ipsilateral corticocortical axons project to areas of SI that are arranged in columns of 0.5–1.0 mm dimension, separated by zones of nearly equal size in which terminals are much less dense (Jones 1981). Terminal density also waxes and wanes along the mediolateral bands. Retrograde/antegrade labeling experiments show that the cells of origin of commissural fibers are located mainly in the columnar zones that receive commissural terminals. This modular, disjunctive distribution of sources and sinks appears to hold for other extrinsic connections of SI, and indeed for many other areas of the neocortex as well (Goldman-Rakic and Schwartz 1982), but whether it is universal is unknown. The generalization emerging from these studies is that the total set of modules of an otherwise uniform cytoarchitectural area is fractionated into subsets, and that each subset entertains an incomplete sample of the total set of extrinsic connections of the area.

Studies of the last decade have provided a mass of information concerning the neuronal and synaptic organization of the neocortex. This includes the morphology of cortical neurons, the distribution of their axonal and dendritic trees, the nature of the synaptic terminals they emit and receive, the identity of their synaptic transmitter agents, and the laminar location of the origins and terminations of extrinsic connections. The findings are rapidly leading to a flow diagram of the intracortical circuits. This subject will be summarized in other chapters of this volume.

Columnar Organization of the Somatic Sensory Cortex

The columnar organization of the neocortex has now been documented in a host of anatomical and physiological studies, in sensory, motor, and association areas, in a variety of mammalian species and a number of experimental conditions, including that of the waking, behaving monkey (for reviews, Mountcastle 1979, 1984). The general principles are simple: the predominant flow of neuronal activity in the cerebral cortex occurs along neuronal chains linked in the translaminal dimension of the cortex; the spread of activity in the tangential dimension is severely limited; neurons in these vertical chains exhibit a certain set of functional properties in common; modules (columns) whose neurons have different sets of properties are interdigitated in the X-Y dimension of the cortex. The result is that several variables can be mapped in an intermittently recursive manner within a single two-dimensional topographic map. The evidence for SI is that microelectrode penetrations made normal to the pial surface encounter neurons in each successive cortical layer that have similar properties of place, modality, dynamic response characteristics, and abstracted features (Mountcastle 1957; Powell and Mountcastle 1959). Microelectrode penetrations made tangential to the pial surface move through blocks of tissue (200–500 μm) within which neurons with similar properties are observed, but encounter sharp transitions in neuronal properties as the electrode passes from one column to the next. The concept of columnar organization is dynamic; the columnar defining properties are determined partly by the projected properties of the afferent inflow, such as place and modality, and partly by intracolumnar processing mechanisms, such as abstracted or reconstructed properties like directionality. The degree to which either dominates columnar definition varies greatly from one neocortical region to another, and it is only in regions of koniocortex like 3b that static properties are so clearly the predominant defining characteristics.

What might be the smallest operational unit within the neocortex? The answer may come from studies of the ontogenetic development of the neocortex, summarized by Rakic in another chapter of this volume. Briefly, the neocortex is constructed from inside to outside by the successive migration of neurons from the proliferative epithelium of the ventricular zone of the neural tube to the developing cortical plate. Moreover, each small unit of proliferative epithelium generates a group of cells that come to lie in a narrow cylinder extending from the pia to the white matter. A strict topological relation is maintained between the germinal units of the ventricular zone and these embryogenic units of the neocortex. There is no evidence that the neurons of these units migrate in the tangential dimension of the neocortex, although of course their dendritic and axonic processes do so. Is it possible that such an elementary unit of 30–60 μm tangential

dimension ever functions as such in the adult cortex? The presence of narrow columns or bands of cells with particular orientation sensitivities in area 17 suggests that this might indeed be so. Moreover, mapping of the postcentral gyrus in the monkey before and after transection and re-suture of the median nerve, and re-innervation of the glabrous skin of the hand, revealed basic columnar units not significantly larger than the embryogenic units described above (Kaas et al. 1981).

The mapping function. It has been known for nearly a century that the body surface is represented in the contralateral postcentral gyrus of primates by an orderly sequence running from the caudal regions medially to the face laterally. This general pattern was established by the methods of clinical Neuroscience, and was greatly elaborated after the evoked potential method was introduced in the mid-1930s. Application of the single neuron analysis method in mapping studies has revealed that the body is represented separately and completely in each of the four cytoarchitectural areas of the postcentral gyrus, in SII and the SSA, and perhaps less precisely in areas 5 and 7a (for reviews see Woolsey 1981; Kaas 1983). Several general principles have emerged from mapping experiments using the single neuron method:

- 1) The four postcentral representations fit precisely the four strip-like cytoarchitectural areas of SI, areas 3a, 3b, 1, and 2. The details of the representations differ within the four patterns, but they correspond to the medial to lateral sequence of body parts.

- 2) These representations are somatotopic, not segmental, in nature. Although adjacent peripheral parts are generally represented in adjacent cortical loci, there are exceptions, so that the map of the body cannot be related to the representational map in the cortex by any simple translational rule.

- 3) The areas of cortex devoted to particular body parts differ in different animals of the same species, which raises the question whether they are modified by epigenetic experience.

- 4) Matched body parts such as the hand or digits are represented in patterns that progress, reverse, and retrace as the site of recording approaches and crosses the boundaries between the four cytoarchitectural areas of SI (Kaas et al. 1981). This is the best evidence supporting the multiple representation concept. A major problem hovers beyond details: why maps at all? Given the modular organization of sensory systems and neocortex and the precise and specific connections linking selected sets of modules in one area with sets in another, one can imagine orderly central neuronal processing of sensory inflow if maps did not exist! Yet maps abound. There are at least eight maps of the body and more than a dozen of the visual field in the neocortex of the macaque monkey. This emphasizes an old and

still unsolved question: what efficiencies and what adaptive advantages pertain to the facts of adjacency?; i.e., that neighboring loci in peripheral sensory sheets are generally represented in neighboring loci in the cerebral cortex.

Place Properties of Postcentral Neurons

The receptive field (RF) of a SI cutaneous neuron is that area of skin within which natural stimuli activate the cell. The RFs of 3b cells are continuous, with a single boundary, and contralateral except for those in the peri- and intra-oral regions, where some are bilateral. The intensity of response to standard test stimuli varies from a maximum near the center of the field to a minimum at its edges. The excitatory RFs of 3b neurons are commonly overlaid by inhibitory RFs. When the latter are larger or eccentrically placed relative to the former, surround or lateral inhibition results. This pattern appears more commonly in area 1 than in 3b, and more on hairy than on glabrous skin. In-field inhibition is always more powerful than surround inhibition. Body parts with the greatest somesthetic acuity and the densest peripheral innervation are greatly magnified in the cortical map. The areal magnification factor varies, e.g., by a factor of more than 100 between the glabrous skin of the hand and the hairy skin of the trunk. RFs sizes are linearly proportional to the inverse magnification factor in both 3b and 1; magnification differs slightly between these two areas, so that the area 1 map is somewhat less precise than that in area 3b (Sur et al. 1980). Area 3a receives almost exclusively cortically projected afferent input from deep tissues, joints and muscles, but the somatotopic arrangement in 3a is generally similar to that of 3b. Area 2 is also dominated by projections from deep tissues, but it receives a sufficient relayed projection from cutaneous afferents to reveal there a third representation of the body surface, perhaps in a less precise map than in either area 1 or 3b. The properties of postcentral neurons increase in complexity with transition from area 3b to area 1 to area 2 (Darian-Smith et al. 1982; Iwamura et al. 1982).

It is now clear that the place properties of SI neurons are maintained dynamically. RFs can be altered by drugs that influence synaptic security, and—as described below—by changes in the nature of peripheral sensory inflow.

Modality Properties of Postcentral Neurons

Postcentral neurons are specific for modality; i.e., they respond differentially to the features of peripheral stimuli encoded by one or another set of primary afferent fibers. This definition of “modality” is not always congruent with that used in sensory Psychophysics. Suprathreshold convergence in the

system must occur within, not between, modality types. Whether this specificity is, like that for place, maintained by dynamic mechanisms is unknown. Three classes of SI neurons relating to the glabrous skin of the hand have now been identified (Mountcastle et al. 1969): those relating to the rapidly adapting first order (Meissner) mechanoreceptive afferents; those to the slowly adapting (Merkel) mechanoreceptive afferents; and those to Pacinian afferents. A large class of SI neurons is activated by joint rotation, another by muscle stretch. Neurons of different modality types are segregated into modules, within which neurons in all layers are of the same type. Modules of different modality types are interdigitated in the cortex, but the distribution of modules of different modality types differs between the areas of the postcentral gyrus.

The large majority of the modules of area 3a contain neurons related to deep afferents, some from joints and some from muscles; a few cutaneous modules occur in the region of representation of the digits. Area 3b contains modules of both slowly and rapidly adapting cutaneous neurons; within each somatotopic unit these are regularly alternated, providing an example of the principle of intermittently recursive mapping of more than two (and in principle many) variables to the two dimensions of the cortical surface (Sur et al. 1984). The cutaneous neurons of 3b rarely show directional properties. In area 1, the majority but not all of the modules contain RA cutaneous neurons; these cells are more commonly sensitive to the directions of stimuli moving across the skin than are area 3b cells. Area 1 contains modules of neurons responsive to Pacinian input. Modules of cells responding to stimulation of deep tissues occur but are uncommon in areas 3b and 1; but they dominate area 2, particularly those with neurons responding to joint rotation.

It is obvious from this description that the afferent inputs to the four SI areas differ in modality composition. Whether this implies that the qualitative nature of intracortical processing mechanisms differs in the four areas is unknown, nor have we any inkling of how the outputs of these areas are used together to construct the neural counterparts of meaningful perceptions of the many somatic sensory events evoked by combination of signals in two or more modality classes of primary afferent fibers.

The Modifiability of Microconnectivity and the Reorganization of Cortical Somatotopic Maps

Changes in peripheral afferent input produced by denervation, nerve block, or amputation of a part alters the effectiveness of remaining central connections so that central neurons acquire new, adjacently displaced RFs (Wall and Egger 1971; Paul et al. 1972). These changes appear quickly after nerve block and disappear with its removal; they may progress during long

term denervations and may occur at any synaptic level in the somatic system. The acute effect suggests a selective shift in the effective subset of synaptic terminals upon a cell from one previously dominant to an overlapping one which becomes effective after removal of the first. The cellular-molecular mechanisms of this shift are unknown.

Merzenich, Kaas and their colleagues (Merzenich et al. 1983a, b; 1984) have developed the method of micro-mapping the postcentral somatotopic maps before and at a series of intervals up to months after peripheral nerve transection or digit amputation. Their experiments have produced the following results:

1) The detailed topography of the maps differs between individuals of the same species, age and sex.

2) Several weeks after median nerve section without reinnervation, neurons in the deprived area of cortex acquire new RFs that lie in regions of skin innervated by the ulnar and radial nerves. This reorganization progresses over many months. It is a central not a peripheral event. The end result is a reorganization such that no unresponsive cortex remains.

3) The new representations in the deprived areas are themselves somatotopic in nature.

4) Similar results are produced by amputation of a digit. When two adjacent digits are removed, occupation of the deprived cortical area is never complete. Thus the distance over which occupation can move in the tangential dimension of the cortex is 5–600 μm —about the width of the cortical distribution of the synaptic terminals of a single thalamocortical axon.

The general hypothesis generated by these results is that although the “hard-wired” anatomical substrate determines the gross cortical map, the detailed topography is generated, maintained and changed by dynamic processes operating on a connective microstructure that is degenerate in nature.

These observations have important implications for normal cortical function: (a) A normal dynamic mechanism maintains specificity for place. Can this be true also for modality specificity? (b) Map modification is a normal event, and the maps in each individual may reflect his unique sensory experience; and (c) Modifiability is not confined to a critical period in development, but may occur at any time in life. It is the microstructure that can be changed, and it is within the microstructure that the detailed dynamic activity of sensory systems, and of the brain more generally considered, is played out.

DYNAMIC NEURAL OPERATIONS IN SOMESTHESIS

The term “dynamic” refers in the present context to the temporal and spatial distributions in central neural populations of the activity set in motion by

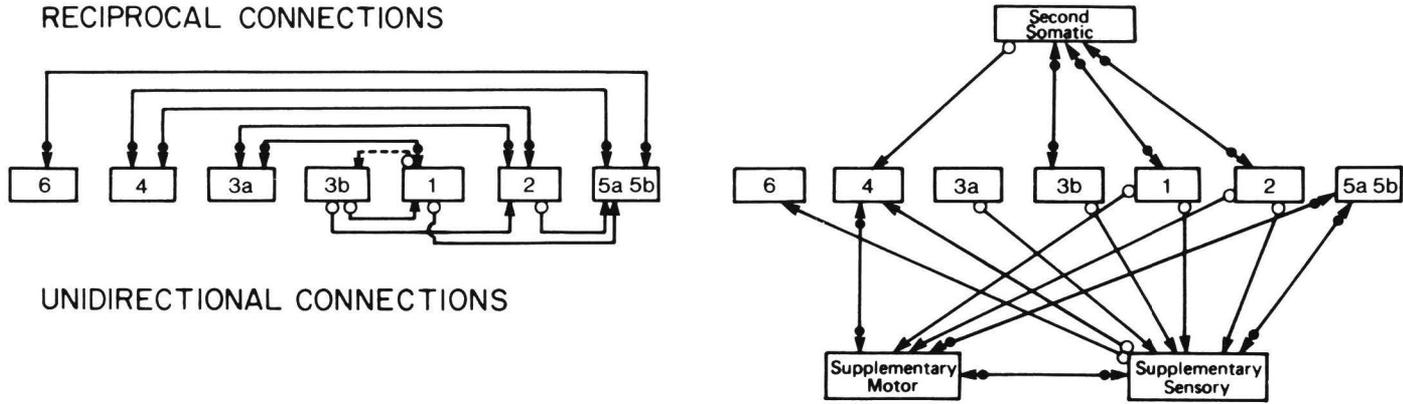


Fig. 1—Diagrams to summarize the cortical connections of sensory and motor cortices in monkeys. The dashed line for the connection on the left indicates a suggested but still uncertain projection from area 1 to area 3b. At right, open circles and solid arrowheads: unidirectional projections; solid circles and lines with double arrowheads: reciprocal connections. (From Mountcastle 1984)

sensory stimuli, activity varying on a time scale of tenths of seconds. Some questions of interest are these:

- 1) How are stimulus attributes encoded in the ensemble patterns of activity of cortical neurons?
- 2) How are those patterns modified by intracortical operations, and what transform of them is projected into distributed systems and leads to perception?
- 3) Do the intracortical mechanisms preserve or recode more efficiently the temporal and spatial properties of sensory stimuli?
- 4) Do these recodings differ at different output portals of postcentral modules?
- 5) What is the meaning of somesthetic perception of the precise signals for place and mode observed for postcentral neurons?
- 6) What neural mechanism provides a base for the recognition of and discrimination between somesthetic stimuli that differ in spatial and temporal patterns?
- 7) How do general control systems influence neuronal processing in somatic cortical areas?

Studies of tactile, flutter-vibration, and somesthetic spatial perception have yielded some understanding of dynamic cortical operations in these mechanoreceptive senses. These studies begin with measurements of the sensory capacity of man and monkey in identical reaction-time paradigms. Observations are then made of cortical neuronal activity in monkeys during their sensory performance. When the sensory capacities of the two primates are similar, it is inferred that neural operations like those observed in the monkey cortex are likely to occur in the human cortex under similar circumstances.

Cortical Neuronal Mechanisms in the Detection and Rating of Tactile Stimuli

The three major classes of mechanoreceptive afferent fibers innervating the glabrous skin of the hand are linked selectively to postcentral neurons with similar properties, sets of cortical neurons themselves grouped selectively in cortical columns. It has now been shown by direct recording that a single or a few impulses in a single afferent fiber of a conscious human may evoke a sensation (Torebjork et al. 1984). This is thought to depend upon the remarkable temporal and spatial amplification of input that occurs in the somatic system, particularly at the cortical level. Even the briefest local stimulus to the hand evokes a repetitive train of impulses in a large population of cortical neurons. How the particular location of that active population in SI cortex leads to the perception of the location of the stimulus remains an enigma.

Afferent inhibition plays an important role in limiting the spatial spread of populations of cortical neurons activated by sensory stimuli. Inhibition is not projected from one level of the somatic system to the next, but is generated at each by local circuit action. It may be exerted by local feed-forward or feedback circuits. Thalamic and cortical neurons are related to superimposed excitatory and inhibitory receptive fields; the latter are frequently larger than the former, so that both in-field and surround inhibition results. Afferent inhibition will clearly limit the spatial spread of the cortical population activated by a sensory stimulus, and thus contribute to stimulus contrast and spatial discrimination.

Humans working in the subjective magnitude estimation task rate brief mechanical stimuli delivered to the glabrous skin of their hands as linear functions of stimulus intensity. Only the SA afferents innervating the glabrous skin of primates have the range of response to account for this human capacity to discriminate between and to rate stimuli over a range of two mm of skin indentation. SA fibers innervating the monkey hand respond to stimuli of different intensities with a linear increase in frequency of discharge (Mountcastle et al. 1966); the related SA neurons of the monkey's postcentral gyrus respond similarly (Mountcastle 1984). Studies of human SA fibers have also shown a linear relation for the response of SA fibers innervating the hand. These studies of peripheral fiber responses in man and monkey, of postcentral neuronal responses in the monkey, and the magnitude estimation measures in man support the hypothesis that the observer's estimate of the intensity of peripheral somesthetic stimuli is determined by the transfer function at the peripheral transduction level. Thus further neural operations intervening between that input and behavioral output must in sum be linear, for the attribute of stimulus intensity. This generality is supported by many similar observations in the somatic and other sensory systems. They infer that neural operations in a sensory area like SI are capable of retaining a linear relation between the impulse frequency from input to output, or imposing a transformational code that preserves that relation.

The term "feature extraction" is used to refer to the selective sensitivity of central neurons to a particular combination of afferent signals which depicts a stimulus attribute not specifically encoded by any single set of primary afferent fibers, but which is reconstructed from combinations (Werner 1974). Studies of thousands of first-order fibers innervating primate hands have revealed none that provided neural signals of the directions of stimuli moving across the skin. Yet some neurons of SI cortex are sensitive to direction. Such cells are relatively rare in 3b, but more common in areas 1 and 2 where they tend to occur in columns in which the optimal direction of stimulus movement is a columnar defining characteristic. This directional sensitivity of cortical neurons is thought to be produced by an active

inhibitory process evoked by the moving stimuli, more powerful in the off than in the on direction (Gardner and Constanzo 1980).

Cortical Mechanisms in Flutter-Vibration: Temporal Dynamics

The mechanoreceptive sense of flutter-vibration is dual in nature, for the quality of the subjective experience differs with stimulus frequency. Sinusoids in the range of 5 to 50–60 Hz evoke a fluttering sensation localized to the zone of stimulation; higher frequencies (60–400 Hz) evoke the poorly localized hum we all call vibration; and sinusoids above 500–600 Hz are sensed as stationary. These two senses are served respectively by two sets of mechanoreceptive afferents innervating the skin of the hand: the rapidly adapting (RA) Meissner afferents flutter, the Pacinian afferents vibration. Detection and frequency discrimination thresholds are set by the tuning thresholds of these afferent fibers; i.e., the stimulus amplitude evoking one impulse per cycle (LaMotte and Mountcastle 1975). Humans and macaque monkeys working in similar reaction-time paradigms have identical thresholds over the same frequency ranges and the same capacity to discriminate stimulus frequencies and amplitudes.

Two classes of postcentral neurons replicate the response properties of the RA Meissner and Pacinian first-order afferent fibers. The slowly adapting peripheral fibers (Merkel) and the set of cortical neurons upon which they project are relatively insensitive to all but very low frequency stimuli. The RA postcentral neurons of the monkey that appear to transmit the signals essential for the sense of flutter have been studied in a number of experimental conditions, including that of the waking, behaving monkey (Mountcastle et al. 1969; for review, see Mountcastle 1984). The interest of the results in the present context is that they reveal some of the dynamic, temporal aspects of intracortical processing and cortical neuronal encoding. Postcentral RA neurons are sensitive to low frequency mechanical sinusoids delivered to their RFs, and respond with trains of impulses ordered periodically in time at the stimulus frequency. The cortical neural code differs from the one impulse/cycle code in the synaptically related RA primary afferents. A strong periodicity appears in the impulse discharge pattern of cortical RA neurons, for each stimulus frequency within the range of flutter sensation, and at stimulus amplitudes adequate to evoke tuned entrainment of peripheral fibers and conscious perceptions in monkeys and humans. The serial, dependent nature of the neural code in cortical RA neurons is readily apparent in expectation density or autocorrelation functions, and is destroyed after a random shuffle of impulse interval sequences.

The periodicity hypothesis was tested further by comparing the capacity of humans to discriminate between stimulus frequencies, measured in the

context of decision theory, with the cortical neuronal activity evoked in monkeys by similar stimuli. The “underlying sensory events” assumed in decision theory were equated with the human subjects’ estimates of stimulus cycle lengths. The d' values—the variabilities of the presumed underlying sensory events—obtained for human subjects were linear values of stimulus cycle lengths. These variabilities covaried with those of the evoked cortical neuronal activity, and both with stimulus cycle length. This infers that it is the variability of the cortical neuronal periodicity that leads to the observer’s uncertainty in estimating the length of stimulus periods. Indeed, a further inference is that the periodicity of impulse discharge in the set of cortical RA neurons is, in this case, the essential neural substrate leading to the perception of stimulus frequency.

Cortical Mechanisms in Form Perception: The Population Problem

Much of what we have learned in recent years about cortical neuronal representations of sensory stimuli has come from use of the method of single neuron analysis, particularly when applied in waking, behaving monkeys. It is obvious, however, that information concerning spatially distributed stimulus attributes is embedded in patterns of activity in populations of cortical neurons. Until now it has been necessary to attack this problem by post-hoc population reconstruction. In this method the experimenter manipulates the spatial position of the stimulus from trial to trial in such a way that the single cortical neuron under study is made, on successive trials, to occupy slightly different spatial positions in the population of cortical neurons activated by the stimulus. Then, on the reciprocal interpretation, the population occupied by the stimulus at one peripheral locus on one particular trial is reconstructed. Spectacular success has been achieved with this method by K.O. Johnson and his colleagues in studies of how stimuli with the spatial complexity of letters of the alphabet are represented in the primary afferent signals evoked by them (Johnson, K.O., personal communication). These investigators have now adapted these methods to study of the responses of postcentral neurons in waking monkeys to letter stimuli.

It is generally assumed that high-resolution tactile form recognition such as that of letters is based upon a peripheral input that is a quasi-isomorphic image of the stimulus, but that at successively higher levels of the nervous system transformations will yield less or even nonisomorphic images that achieve greater efficiency and flexibility in the use of central neural networks. Johnson et al. (personal communication) have discovered the following:

- 1) The neural representations of letters in the responding populations of first-order fibers are strongly isomorphic for both SA and RA mechanoreceptive afferent fibers innervating the monkey’s hand.

2) Letter representations derived from the responses of cortical SA and QA neurons, in both areas 3b and 1, are much less isomorphic than are those in first order fibers, although still recognizable upon visual inspection.

3) Application of a number of discrimination indices led to a counter-intuitive result; namely, that the representations at the cortical level, while less isomorphic than those at the peripheral input level, are more highly differentiated and thus more readily discriminable than are those of peripheral fibers. These findings implicate that the pattern at the level of the primary sensory cortex of the postcentral gyrus has already undergone a partial transformation with loss of isomorphism but preservation of discriminability. It is believed that this is the first requirement for a neural mechanism of recognition.

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