1. INTRODUCTION

Recent studies conducted principally in the somatosensory nervous system of primates have revealed that cortical maps are alterable as a function of experience in adults. The specific nature of this evident dynamism of cortical representations bears a series of important implications for consideration of the significance of features of sensory system organizations. In this report, we shall a) briefly summarize the basic conclusions drawn from these studies on the dynamics of cortical map structure, b) outline by example the results of studies from which these conclusions have been drawn, and c) then specifically consider some implications of these studies for our understanding of the significance of special organizational features of the auditory system.

2. CORTICAL FIELDS ARE DYNAMICALLY MAINTAINED AND ARE ALTERABLE IN ADULT PRIMATES

According to the dominant contemporary view of cortical organization, cortical representations are established early in life through a "critical period" before which there is a pruning of anatomical projections to a fixed, adult form. Cortical representations have been believed by most investigators to be static in adults, with their functional structure defined by a static projection system anatomy. That basic view of sensory system organization has been particularly reinforced by studies on the origins of ocular dominance columns within visual cortical fields (see Movshon and Van Sluyters, 1981; and Sherman and Spear, 1982 for review) and in studies of "barrels" representing individual vibrissae within the somatosensory cortex of rodents (see Kaas, et al., 1983 for review). In both of these carefully studied systems, alterations of ocular dominance column or barrel boundaries and structure are possible during the first days of postnatal life, for example by sensory deprivation. However, at later times no anatomical alteration of projections into these zones is seen. Thus, the neuroanatomical connections establish functional cortical maps early in life, and after that early stage (goes the current dominant view) substantial map alterations can not occur.

Recent studies conducted principally within the somatosensory projection system challenge that view. They reveal that: a) There is great individual variability in the details of representation of the skin surfaces in adult primates. This variability must, in part, be accounted for by the different individual tactile experiences of the animal. b) A rapid reorganization of cortical maps occur after peripheral nerve injury (Merzenich, et al., 1983a; Merzenich and Kaas, 1983) or digit amputation (Merzenich, et al., 1983b). Following such lesions, the representation of the skin surfaces in the bordering cortical map regions rapidly expand, to "reoccupy" the deprived cortical sector. By that reorganization, representations of surrounding skin surfaces are topographically enlarged. With that enlargement, there is a corresponding reduction in receptive field sizes, i.e., the expanded representations are finer-grained. c) This reorganization is progressive, and occupation of a deprived zone several millimeters across is initially completed in roughly 2-3 weeks (Merzenich, et al., 1983c). However, even after initial complete territorial "reoccupation", further substantial map changes are recorded, over time. d) There is also a rapid reorganization of cortical maps after indursion.
of a cortical lesion completely destroying the representation of a part of the body surface (Jenkins, et al., 1982). In this reorganization, all of the skin surfaces formerly represented within a small infarcted zone are later found to be represented in the cortical region surrounding it. With this reestablishment of representation, the mapping of skin surfaces formerly represented in this surrounding zone is degraded, i.e., is of a coarser grain. e) Substantial local alteration of cortical maps have been recorded following changes of the use of the hand in normal monkeys. Thus, for example, dramatic map alterations have been recorded in the cortical representation of a finger struck several thousand times/day for several months in a bar-press task. Almost equally remarkable changes were seen in the patterns of representation of surrounding skin surfaces (W. Jenkins, M. Merzenich, J. Zook, and M. Stryker, unpublished observations).

These studies indicate that the detail of cortical maps is established by use, and is alterable throughout life. They have established a series of "rules" on the reorganization process which indicate, in part, the nature and purposes of this alterability. Those rules (see Merzenich, et al., 1983c; 1983d) include:

a) During the course of map alteration, map topography is continuously maintained.

b) During map alteration, the normal overlap "rule" (percentage overlap of receptive fields is a nearly linear function of cortical distance, and the distance over which fields no longer overlap is roughly constant at 500-600 microns) defined by Sur and colleagues (1980) is at least roughly maintained.

c) There is apparently a distance limit to map reorganization. In Area 3b (the somatosensory konicortex) it is roughly 600 microns. That is, a given skin surface site can be represented anywhere over a zone roughly 1200 in diameter, with the actual site of representation defined by the monkey's functional use of his skin surfaces over the long term.

It is almost certain that temporal coincidence or sequencing of inputs and levels of temporally appropriate activity constitute the basis of the dynamic maintenance and alteration of these maps (see Merzenich, et al., 1983d; Edelman and Finkel, 1983). The reason is simple: There are no other realistic alternatives. Since the original postulation of Hebb (1949), there have been several proposed models of how cortical maps might be created (the issue has usually been addressed as a developmental one) by such response correlations (e.g., see Malsburg, 1973; Swindale, 1980; 1982; Willshaw and Malsburg, 1976).

We have hypothesized that map alterations by use constitute the basis of acquisition of skill, and have drawn several correlates between observed map changes and the neurological consequences of corresponding lesions (see Merzenich, et al., 1983b; 1983d). Our results are consistent with a "group selection" theory for pattern recognition, formally proposed by Edelman (1978; 1982).

![Fig. 1. Maps of hand surface representations within cortical Area 3b in a normal adult owl monkey (A), and 64 days after amputation of digit 3 (B). Representational areas of dorsal hand surfaces are shaded. The cortical zone originally representing digit 3 is outlined by a dotted line in B. Receptive fields defined for neurons in microelectrode penetrations into the former digit 3 representational zone in the second map (dots in B) were on adjacent skin surfaces on digits 2, 4 and palmar pads; all are drawn in C](image-url)