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Development of Cortical Sensory Maps

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Abstract. A number of observations support the conclusion that crude topographic features of cortical maps can develop without instructions from the receptor sheet, but that such instructions play an important role in forming map detail, lamination and modular organization patterns, and neuron response characteristics. The peripheral receptor sheet appears to instruct by providing correlations in axon activity patterns based on proximity and receptor transducing properties. Higher order neurons in cortical maps and higher order maps are also subject to the influences of correlated activity created by central computations. In addition, variations in prenatal and postnatal conditions change correlation patterns over time. The potential for map modification is reduced over the developmental sequence, but the possibility for local modifications remain throughout life. Higher order maps, by maturing later, are more subject to postnatal influences.

INTRODUCTION

Most of neocortex in both primitive and advanced mammals consists of various numbers of systematic representations of the arrays of peripheral receptors (Kaas 1987). The details of these "maps" of sensory receptor sheets are variable across the multiple maps of the same receptor sheet within an individual, variable for the maps of homologous fields across individuals of a single species, and variable for the maps of the homologous field across species. Yet, major features are so consistent that a given map typically can be identified as a particular field in a particular species, and homologous maps across species have characteristic organizations (e.g., Kaas 1983). The organizations of the adult maps, of course, depend on developmental sequences. It may be reasonable to suppose from these observations that many of the consistent features of cortical maps are "hard wired" and subject to genetic programs that are little influenced by perturbations in the prenatal and postnatal environments. Indeed, the longstanding and now classical theory for the development of sensory maps, the chemospecificity theory of Sperry (1963), has no role for experience and other factors that could be considered in the realm of "self-organizing." However, the variability that occurs in cortical maps, especially that within a species (see Merzenich et al. 1987), suggests that the map organization is subject to environmental influences (see Kaas 1987). Moreover, the importance of environmental factors in its development has been demonstrated by a number of experimental observations. Thus, it now seems necessary to postulate that neural activity patterns, initiated in the peripheral receptor sheet and subject to consistencies and variations in the prenatal and postnatal environments, play a substantial role in generating patterns of organization in cortical maps. Indeed, the new touchstone appears to be the Hebbian synapse and the significance of receptor–initiated correlated activity in maintaining and reinforcing central synapses. Within this broad framework of considering an interaction of hard wired and self-organizing factors, this review presents a series of general, empirically supported principles of map development, followed by a discussion of the implications of these principles for understanding the mechanisms of map development. The major features of cortical maps that pose developmental questions are topographic order, modular organization, and neuron response characteristics. Because of the extent of the experimental observations, this review concentrates on the development of topographic order.

GENERAL PRINCIPLES

1. Crude topographic features of cortical maps can develop without instruction from the receptor sheet. The activity or state of the peripheral receptor sheet appears to be unimportant for the development of at least crude topology in cortical maps. The most convincing evidence stems from genetically eyeless (anophthalmic) mice where the missing retina cannot instruct the development of cortical maps. While the question of how visual cortex represents the retina or visual space cannot be addressed in these mice, one can ask whether the connections between the thalamus and cortex are normal. The answer is that thalamocortical connections are at least crudely normal in topological organization (e.g., Kaiserman-Abramof et al. 1980). Because the studies employed relatively imprecise anatomical methods, it is not clear if the connection pattern has normal or degraded fidelity (however, see below).

Related evidence from the effects of damage to peripheral afferents is also consistent with the conclusion that at least crudely normal topological patterns of thalamocortical projections do not depend on the state of the receptor array. Dawson and Killackey (1985) have shown that when connections between the ventroposterior nucleus and primary somatosensory cortex, S-I, first emerge shortly after birth in rats, the pattern of connections corresponds to the normal topographical pattern. Because these thalamocortical connections are established before the brainstem and thalamic components of the somatosensory relay appear to be functional, Dawson and Killackey argue that topographic order in the thalamocortical pattern develops independently of a "template" in the periphery. Similarly, topographic patterns of geniculocortical connections develop after early removal of retinal afferents (Guillery et al. 1985; Rakic and Williams 1986; Rakic, this volume). Again, the anatomical experiments fail to provide much information on the precision of the thalamocortical patterns.

2. Detailed cortical maps can develop prenatally without the benefit of postnatal experience. In some mammals, primary sensory representations have an organization that is quite adult-like at or near the time of birth. Evidence comes from both the somatosensory and visual systems. In an early study, Rubel (1971) compared microelectrode maps of primary somatosensory cortex in newborn and adult cats and concluded that the maps at the two ages are highly similar in somatotopic organization. In addition, neurons in S-I at both ages were found to be similarly responsive to light touch and the bending of hairs and have receptive fields of comparable relative size. More recently, Krubitzer and Kaas (unpublished observations) have used microelectrodes to map somatosensory cortex of newborn and older monkeys. In newborn marmosets and squirrel monkeys, neurons in "S-I proper" (area 3b) were responsive to light tactile stimuli, and receptive field sizes approximated those of adult monkeys. More importantly, the somatotopic organization of the area was not notably different from that in adult monkeys. Finally, the barrel field of S-I of mice, where a morphologically distinct "barrel" of cells represents each mystacial vibrissa, has a normal organization when it first emerges several days after birth (see Cooper and Steindler 1986). The organization of visual cortex and the properties of neurons in visual cortex have been investigated in newborn sheep (see Kennedy et al. 1983 for review). In newborn lambs, retinotopic organizations of primary and secondary cortex, though not extensively investigated, appear to be normal and many neuron response properties appear to be mature. However, there are few binocular cells, and orientation and direction selective cells are less common.

The obvious conclusion from these studies is that sensory maps can be very adult-like, even in the details of the represenations, at the time of birth. While the organizations of these primary maps may depend on instructions from the periphery, they develop in great detail without the benefit of sensory stimulation in the postnatal environment.

3. The peripheral receptor sheet instructs the cortical map. Several years ago, Hendrick Van Der Loos and Josef Dörfl (1978) posed the intriguing

question, "Does the skin tell the somatosensory cortex how to construct a map of the periphery?" The existence of instructions from the receptor sheet would help explain the close relationships between peripheral receptor densities and cortical magnification factors consistently noted in early to recent mapping studies. More compelling evidence comes from the observation that the receptor sheet and the cortical map vary in a matched manner among individuals of the same species. As is well known, the precise organization of the barrel field of primary somatosensory cortex of rats, mice, and several other rodents is apparent in tangentially cut brain sections stained for cells, because a cluster or barrel of neurons is distinct for each whisker in the muzzle of the face. Normally, the number and arrangement of mystacial vibrissae are highly consistent within a species. Individuals do vary, however, in occasionally having one or more extra or fewer whiskers, and when this happens the cortex always has a matched pattern of "barrels." While it remains possible that a genetic factor encodes both changes in the number of whiskers and the number of cortical "barrels" (plus brainstem and thalamic "barrels"), Van Der Loos and Dörfl (1978) argued that it is much more reasonable to suppose that the early developing arrangement of receptors and afferents in the skin tells the cortex how to construct the details of the map.

Related studies in the visual system are well known. When an eye is removed or disadvantaged in developing mammals that normally have ocular dominance columns as adults, the representation of the normal eye expands to occupy most or all of the map in primary cortex (see below). Some of the observations on the organization of visual cortex in the "Boston" type of Siamese cats are also consistent with the concept of instructions from the periphery (see Kaas and Guillery 1973 for review). In Siamese cats, a region of central retina that normally projects to the ipsilateral lateral geniculate nucleus is misdirected to the contralateral lateral geniculate nucleus, in effect producing an enlarged receptor sheet for the crossed retinogeniculate projections. In some (Boston type), but not all (Midwestern type), Siamese cats, the topological pattern of the geniculostriate projection is altered to produce a single retinotopic cortical map of the enlarged contralateral retinogeniculate projection.

The overall conclusion is that cortex at early stages of development is capable of "correcting" mismatches with the periphery and creating a new and better match. Such a matching of central maps to the peripheral receptor sheet has been termed "system-matching" by Gaze and Keating (1972).

4. Influences from the peripheral receptor sheet constrain the terminal arbors of input axons and thereby fine-tune map organization. Jenson and Killackey (1987) have recently addressed the issue of what happens to the development of the terminal arbors of thalamocortical axons when the influence of the periphery is removed. Inputs from the mystacial vibrissal pad in rats were disrupted on the day of birth by cutting the infraorbital

branch of the trigeminal nerve. The terminal arbors of individual thalamocortical afferents in the barrel field of S-I were examined after the lesioned rats became adults. Cutting the infraorbital nerve at birth disrupted the normal clustering of afferents into barrels. In addition, terminal arbors of thalamocortical afferents were larger but less dense in any local region, and had greater overlap with more distantly entering axons. Because normal arbors form a more compact, densely branched plexus, the number of synapses per arbor may not differ in normal and experimental animals. However, the regions of cortex innervated by the abnormal arbors were clearly greater than in normal rats, suggesting that a major influence of inputs from the peripheral receptor sheet is to reduce arbor size, thereby creating smaller receptive fields and probably more detailed topographic maps.

5. Normal relays to cortical maps may have enlarged representations when "competing" relays are "disadvantaged" during development. A number of experiments on visual cortex of cats and monkeys have led to the general view that different inputs compete for cortical space, and that inputs with normal activity patterns will replace inputs with reduced or impaired activity patterns (see Hubel et al. 1977; Stryker 1982). More specifically, removing one eye or altering the vision of one eye by suturing the eyelids early in development can result in an enlarged representation of the normal eye in primary cortex at the expense of the representation of the removed or deprived eye (Hubel et al. 1977; Rakic 1981). The change can be measured both physiologically and anatomically in that more cells and cortical territory are activated by the normal eye, and the arbors of geniculostriate axons are more massive for the normal eye. A related observation in Midwestern Siamese cats is that both the reduced ipsilateral and abnormal contralateral retinogeniculate pathways lose cortical territory to the normal contralateral pathway (see Kaas and Guillery 1973). Apparently the projection from the termporal retina, which is continuous in normal cats but disrupted into an abnormal contralaterally projecting component and a normal ipsilaterally projecting component in Midwestern Siamese cats, fails to compete with the relay of the fully retinotopic relay from the nasal retina.

6. Normal inputs to maps may not achieve full size in the adult representations if "competing" inputs are removed before the arbors of thalamocortical axons develop normal or exuberant sizes. The usual expectation for developing maps is that reducing the activity in one input results in another input acquiring more cortical space. However, it is important to stress that another basically opposite outcome can occur. The removal of one input can result in a remaining input failing to achieve normal growth and cortical territory. The evidence for this second result is limited, but the possibility needs to be considered in studies of altered development and incorporated into theories of development.

The evidence that an apparently "advantaged" input to cortex may fail to achieve its full, normal representation comes from studies of Wall and Cusick (1986) on the representation of the hindpaw in S-I of rats reared with incompletely innervated hindpaws. In normal rats, the hindpaw skin is innervated by low threshold mechanosensory fibers from the saphenous and sciatic nerves, and inputs from these nerves are represented next to each other in a partially overlapping fashion in S-I cortex. In adults, the full extent of the overlap can be demonstrated by cutting one or the other of the two nerves. When the sciatic nerve is cut, the part of S-I activated by the saphenous nerve expands over a time course of 1–2 days, presumably by potentiating previously ineffective synapses, to occupy part of the sciatic nerve territory. The experimentally expanded representation of the saphenous nerve can be considered the full cortical territory (hidden plus obvious) of the saphenous nerve in normal adults. When the sciatic nerve is cut on the day of birth and prevented from regenerating, the normal growth of the relay of the saphenous nerve into the sciatic nerve cortical territory does not occur. Somewhat surprisingly, the representation of the saphenous nerve in these rats, reared to adults without "competition" from the sciatic nerve, occupies less than one-third the cortical space of the saphenous nerve in adult denervates. However, after the rats are a few days old, cutting the sciatic nerve does not lead to a result significantly different from that produced by cutting the nerve in adults.

The explanation for this unexpected result is uncertain. At the time of sciatic nerve section in day-old rats, the thalamocortical axons are still in the white matter, but are just about to invade cortex. Obviously, such axons would not have the fully extended axon arbors of later stages of development. It appears that removing a potentially competitive influence at this stage can result not in expansion into the free territory, but rather failure to grow, possibly due to the removal of some trophic influence, but also possibly due to the removal of other axons, which creates more synaptic space within the initial arbor.

7. Abnormal inputs to cortical maps can achieve some aspects of normal organization. The interesting experiments of Frost, Schneider, and coworkers have demonstrated the possibility of inducing sensory projections from other sources to abnormally terminate in developing thalamic nuclei deprived of their normal source of activation (see Frost and Metin 1985 for review). For example, visual inputs from the retina can be induced to densely innervate the auditory and somatosensory thalamus by reducing the central targets of the retina by ablating visual cortex and removing ascending auditory and somatosensory inputs to the auditory thalamus. To some extent these abnormal terminations of retinal inputs appear to be experimentally induced new connections, and to some extent they appear to be preserved and enhanced developmentally exuberant connections which normally would

have been lost. When similar lesions were made in newborn ferrets and microelectrode recording were later obtained from the ferrets as adults, neurons in auditory cortex were responsive to visual stimuli (Sur and Garraghty 1986). In addition, receptive field sizes and neuron response properties appeared to be "qualitatively similar" to those of one class (W-cells) normally found in visual cortex. Finally, nearby visual cells in auditory cortex typically had nearby receptive fields, suggesting the existence of at least remnants of retinotopic organization. Similarly, placing such lesions in newborn hamsters and recording in adults demonstrated that both S-I and S-II were responsive to visual stimuli (Frost and Metin 1985). Neurons in S-I and S-II had well defined receptive fields, and both S-I and S-II demonstrated some retinotopic organization. These experiments suggest that the rules of self-organization in cortical maps are not completely specific to each field but are, at least in part, individualized by the varying nature of the sensory inputs.

8. Reorganizations of developing and adult maps can be similar. A number of experiments have demonstrated that sensory maps in adult mammals have a remarkable ability to reorganize when the significance of inputs is altered (see Merzenich et al., this volume; see also Kaas et al. 1983). Most of these experiments involve nerve manipulations in the somatosensory system of normal monkeys. Briefly, cutting or crushing the median nerve of the hand deprives about half of the glabrous skin of the hand of innervation, which removes the normal source of activation for nearly half of the orderly map of the hand in area 3b (S-I proper) of parietal cortex. This cortex soon (hours to weeks) acquires responsiveness to inputs relayed from the parts of the hand innervated by the remaining radial and ulnar nerves. If the damaged nerve is allowed to regenerate, the nerve can recapture much or all of its former cortical territory. After a nerve crush, the regeneration is usually complete and orderly, and normal organization in cortex returns. However, a cut nerve fails to regenerate all of the axons into the skin, and the reinnervation pattern is disorderly. As a result, cortex never recovers normal organization. Instead, parts of the median nerve field remain responsive to ulnar and radial nerve inputs, and only islands of cortex within the median nerve field recover responsiveness to the regenerated median nerve. Furthermore, the somatotopic pattern of the recovered islands is disordered, and many neurons have disjunctive, multiple receptive fields.

Recent experiments (Wall et al. 1986; unpublished observations) demonstrate that the cortical reorganization occurring after nerve cut and regeneration in newborn monkeys is basically similar to the reorganization that occurs in adult monkeys. Thus, median nerve cut and ligation in newborn monkeys was followed by an expansion of the radial and ulnar nerve activation fields into the median nerve cortical field, and nerve repair and regeneration were followed by a partial and disorderly reorganization of the deprived cortex by regenerated median nerve inputs. We conclude from these experiments that alterations in the significance of sensory inputs, even when they occur at a very early postnatal age, may induce reorganizational changes not notably different from those that occur in adult mammals.

9. Higher order maps develop later and are more susceptible to the influences of the postnatal environment than primary maps. Anatomically, there is rather extensive evidence that the primary sensory fields develop before the adjoining "association" cortex which contains the higher order fields in cortical processing hierarchies (e.g., Rakic 1976). The physiological evidence for the sequential development of cortical maps in a hierarchy is more limited, but it is consistent with the anatomical observations. For example, recently Krubitzer and Kaas (unpublished observations) discovered that S-I proper (area 3b) was responsive to somatosensory stimuli in newborn marmosets and squirrel monkeys, while area 1 (the next processing station in the sequence) was not. Similarly, in a one-day-old macaque monkey, area 3b was weakly responsive while area 1 was not. Thus, primary maps may be well in place and fully organized near the time of birth, while higher order maps are not. Therefore, higher order maps are likely to be much more susceptible to modifications induced by factors in the postnatal environment.

10. Mammals vary from altricial to precocial in development at the time of birth, and therefore postnatal environmental influences on cortical maps are probably species–dependent. The issue of species differences in the organization of maps at the time of birth has not been well addressed in experimental studies, but it is obvious that the visual system of sheep is more mature at birth than that of cats, and that of cats more mature than that of ferrets. In our own studies (Krubitzer and Kaas, unpublished observations), we find that responsiveness of area 3b to somatosensory stimulation matures later in Old World macaque monkeys than in New World monkeys. The fact that birth occurs at a different developmental point for different species could be a major factor in determining species differences in sensory systems. As a speculative example, the segregation of cells responsive to light onset from those responsive to light offset ("ON" and "OFF" cells) in separate layers of the lateral geniculate nucleus of adult ferrets (Stryker and Zahs 1983), and the mixture of these cells in the same layers in adult cats, might well relate to differences in the maturity of the system at birth rather than genetic factors subject to selection for function. The unusual separation of "ON" and "OFF" cells into sublayers in primary visual cortex of tree shrews (Kretz et al. 1986) may also relate to the altricial state of the visual system at birth. Species differences in the rate of postnatal development could also be a significant factor in altering how the postnatal environment affects cortical maps.

AN EMERGING THEORY FOR THE DEVELOPMENT OF CORTICAL MAPS

The reviewed observations and conclusions are consistent with a general theory for the development of sensory maps that involves only a few factors and does not depend on genetic instructions that are prohibitively information–rich. Elements of the theory can be found in the papers and reviews of many researchers, but note especially Gaze and Keating 1972; Hubel et al. 1977; Purves and Lichtman 1980; Stryker 1982; Constantine-Paton 1982; Easter et al. 1985; and Casagrande and Condo 1987.

Briefly, the formation of map topology, cortical layers, modular organization, and neuron response properties can all be related to the roles of a few major factors. First, axons of neurons appear to know roughly where to go. They may have a hierarchy of choices, as suggested by the observations that connections can be experimentally induced in abnormal targets, but they seem guided to certain structures and the guidance seems specific enough to form at least rough topographic patterns. The variables governing this guidance and crude order are uncertain, but consistencies in maps, such as orientation, support the conclusion that something like chemoattraction and limited chemospecificity operate. In addition, other genetically specified factors such as spatiotemporal gradients in cell maturation and substrate cues are likely to be important in map formation.

Second, neural activity patterns are important in maintaining connections. The central premise of this hypothesis is that synapses on a neuron that are active while that neuron discharges will be strengthened while others are weakened (the "Hebbian" synapse). Synapses from differing inputs that are active at the same time on the same neuron are likely to be reinforced and selected over others, especially when correlated with the activity of highly effective synapses. Correlated activity, starting from the receptor sheets, is based on proximity and receptor transducing factors. Of course, considerable correlated activity, based on neural interconnections, may be independent of sensory stimuli and a functional receptor sheet. Potentially, selection based on correlated activity can not only fine-tune topographic order, but can fully create topographic order. Yet, the consistent orientations of maps and other observations indicate that some guided polarization of inputs occurs. Selection based on correlated activity can also account for laminar and modular segregations of neuron types when receptor transductions and centrally encoded (synthesized) selectivity discorrelates inputs on neurons normally (or previously) correlated by proximity. Because the "environment" is changing during growth (with a major change at birth, but also with other changes related to the maturation of body tissues and neuron circuits), the correlations have the potential of greatly changing during the course of development, with proximity generally being more important early and transducing properties being more important later.

Third, neurons may be programmed to acquire a certain number of synapses. If this is the case, axon arbors may grow until they achieve a satisfactory number. In the experimentally induced absence of the correlating influences of proximity in the receptor sheet, central axon arbors will spread out, having larger territories with less concentrated synapses. Correlation based on proximity has the potential to spatially concentrate synapses. More active neurons are more successful in competing for synapses. Axon branches with inadequate synapses are retracted, and neurons with inadequate synapses die or fail to grow.

Fourth, the magnitudes and types of changes possible in axon arbors change over time. Early, considerable growth and extension of axon branches are possible. Later, growth and retraction occur over moderate distances. Finally, only local changes at the synaptic level are possible, and this stage appears to extend into adult ages. It also seems likely that later developing neurons and subsystems are altered in development by the differing neural environment. For example, high levels of established competition for synaptic space may both restrict and enhance arbor growth of late developing neurons.

As a consequence of these factors, input axons initially form crude topographic patterns. At early stages of development, low levels of correlated activity may induce widespread growth and extension of axon branches as neurons almost randomly and nearly equally compete for synaptic space. Growth stops and is even reversed when maturation factors introduce high local levels of neural correlation, since discorrelated synapses are eliminated, thereby creating new local opportunities for the synapses of correlated inputs. Thus, correlated activity concentrates synapses, first to fine-tune topology, then to form modules and functionally distinct layers, and finally to determine neuron response properties. The scale of changes in connections potentially proceeds from retracting branches across and within structures, to restriction to the proper modules and layers, to restriction to the proper cells.

Of course, the full scale of developmental changes may not occur when competition is artificially reduced so that synaptic potential can be reached without full growth. Thus, reducing the role of one or two partially competing inputs to somatic cortex in rats (Wall and Cusick 1986) appears to free synaptic space locally so that full axon arbors never develop. Removing a principal source of correlation by cutting the nerve to a large skin area (Jenson and Killackey 1987) maintains local competition and forces widespread arbor growth so that individual axons achieve a full complement of synapses.

The overall theory has several implications and extensions:

1) Slight variations in the timing and possibly the magnitude of the various factors can produce major differences in the same map in different

species. Thus, ocular dominance columns or sublayers may or may not form; cells selective for stimulus onset or stimulus offset may or may not segregate into layers; and perhaps even orientation columns may be missing.

2) Major features of maps may not have functional significance, but may be necessary outcomes when natural selection favors other features. For example, selection for high levels of correlation in striate cortex might inseparably lead to small receptive fields, concentric receptive fields, and ocular bands in layer IV, with possibly only the small receptive fields having biological significance (increased visual acuity).
3) Higher order maps, by developing later, are in principle more subject to modifications based on postnatal experiences. In addition, the response properties of input neurons may largely depend on central computations. Because of the new correlations, new map features will emerge.
4) Certain features are unlikely to be represented in cortical maps because it is difficult to create high levels of correlations. For example, afferents from receptors that signal a steady state by a maintained discharge are unlikely to be reflected in higher-order maps, except by analogue codes, because precise correlations may be difficult to maintain over long chains of neurons. Multimodal areas are rare because correlation is difficult to achieve.
5) Parallel thalamocortical inputs to otherwise higher-order maps may be important in imposing basic features of map organization in those fields. If such connections only have importance in map construction, they may be transitory. Thus, some connections which are eliminated during maturation may have a role in the construction of the nervous system.

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