How do features of sensory representations develop?

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Summary
Sensory representations in the brainstem and cortex have a number of features that support the idea that neural activity patterns are important in their development. Many of these features vary across species in ways that could result from perturbances in the balance of the effects of activity patterns and position-dependent gene expression. (1) Most notably, disruptions or septa in sensory maps often reflect actual discontinuities in the receptor sheet, and the discontinuities may be reflected in a series of interconnected maps. Species with different disruption patterns in sensory sheets have different matching disruption patterns in the sensory maps and variant individuals and strains of the same species have matching variations in the receptor disruption patterns and their sensory maps. (2) In addition, mutations that misdirect some of the retinal afferents from one side of the brain to the other create new sensory maps that preserve continuities in the altered pattern of input, while creating new structural discontinuities. (3) Furthermore, functionally different classes of afferents that are mixed in the receptor sheet often segregate to activate separate populations of target cells. (4) Finally, early developing portions of receptor sheets may gain more than their share of territory in sensory maps. These and other variable features of sensory maps are most readily accommodated by theories that involve roles for instruction by evoked and spontaneous neural activity patterns. *BioEssays* 24:334–343, 2002.

Introduction

The brains of mammals are characterized by systems of interconnected subcortical and cortical representations of the sensory surfaces of the body, eye and ear. In all mammals, sensory representations occupy an important portion of the brain,(1) but larger brains contain more sensory representations than small brains. Sensory representations are typically isomorphs of the sensory surface in that neurons in different parts of the representation are activated by stimuli in a pattern that matches that of the sensory surface (see Fig. 1). The matching order of representation is created and maintained by matching patterns of connections of afferents from the receptor sheet to the brain, and from one brain structure to another. Such representations or maps of sensory surfaces have long been of interest to developmental neurobiologists because an understanding of how order emerges in the development of such maps and their connections may apply broadly to other parts of the brain and provide a general understanding of the development of topographic patterns in brains.

There have been two general types of explanations for the development of order in sensory maps. One, stemming from the chemospecificity theory of Sperry,(2) is that molecular gradients in two parts of the brain complement each other to form patterns of molecular cues that guide the formation and maintenance of orderly arrangements of connections. Presumably the molecular gradients would be the consequence of position-dependent gene expression. The other type of explanation is that patterns of neural activity are postulated to shape important aspects of sensory representations. This is founded on the findings of Hubel and Wiesel(3) that basic features of sensory maps can be altered by experience during development.

Most current investigators hold that the organizations of subcortical and cortical maps are shaped by a combination of both factors; that is, by some sort of patterning that is intrinsic to cortical areas and subcortical nuclei, and by some sort of self-organization(4) derived from patterns of induced or spontaneous neural activity.(5) Nevertheless, opinions vary on the relative roles of these two modes of inducing organization, and considerable uncertainty remains, especially in the face of important recent findings that challenge traditional assumptions about the role of experience and neural activity.(6,7) Because of this uncertainty, it may be useful to review some of the characteristics of sensory representations that appear to be molded by these two factors. We draw special attention to features of sensory maps that seem to require information from the receptor sheet.

Sensory maps vary in internal order

Each sensory system is characterized by topographic maps of the receptor array. Thus, visual maps are retinotopic, somatosensory maps are somatotopic, and auditory maps are tono-

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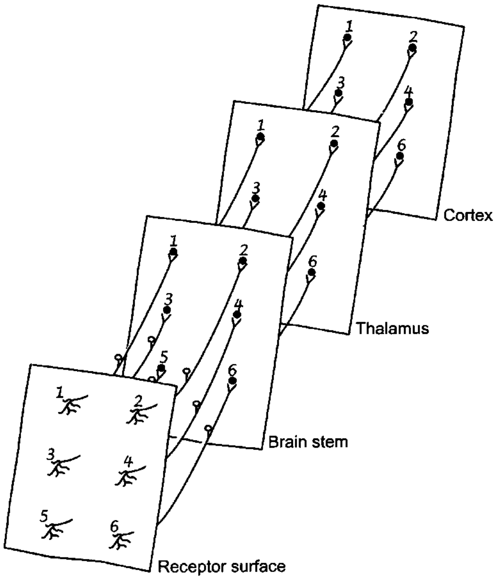

Figure 1. A simplified schematic of how axon projections from the receptor distribution on a sensory surface terminate in a topographic pattern in brainstem nuclei, and how this order is maintained over several steps of processing by similar topographic patterns of connections between subsequent nuclei and cortical areas. A longstanding question in neuroscience is how such order is created in development. Position-dependent molecular signals are undoubtedly important in forming the basic patterns, but here we argue that neural activity patterns shape important details of such patterns.

topic. This means that the central representations reflect the spatial arrangement of receptors across the retina, the contralateral body surface, or along the length of the cochlea, the auditory receptor organ. Yet, within this general framework, considerable variability exists both for sensory representations across species and for different representations in a system within a species. This is most obvious in the somatosensory system where a number of different ways of representing the contralateral body surface have been described. The trunk of the body, for instance, is generally represented in a continuous manner in a part of the primary somatosensory cortex (S1 or area 3b) that is between the representations of the forelimb and hindlimb.(8) However, in tree shrews (a small mammal related to primates), only the ventral trunk is represented in the expected location lateral to the hindlimb and the dorsal trunk is represented in cortex medial to the hindlimb.(9) Within primates, the continuous representation of the trunk from dorsal to ventral appears to have opposite orientations in S1 of different species of monkeys.(10) In many monkeys, the arm is represented in cortex medial to cortex for the hand. However, in prosimian galagos the anterior arm is represented lateral to the hand while the posterior arm is medial to the hand.(11) Subcortically in the cuneate nucleus of the brainstem, which receives direct cutaneous afferents from the forelimb, digits are represented dorsally in squirrel monkeys and most studied mammals, but ventrally in macaque monkeys.(12) In S1 of bats, the representation of the digits of the forelimb is reversed in orientation from that in S1 of other studied mammals.(13) While somatosensory areas share many broad topographic features in common, such as a medial cortical representation of the tail and hindlimb and a lateral representations of the face, the details of the internal order vary widely across even closely related species.

Visual representations also vary in retinotopic organization. We commonly think of retinotopic maps as having a continuous representation of the contralateral half of the visual field via a superimposition of the inputs from the two matching hemiretinas. Yet, clear variations of this prevalent pattern exist. Most notably, the superior colliculus of the visual midbrain represents the complete retina of the contralateral eye in most mammals, while the superior colliculus of all studied primates represents only the contralateral hemiretina.(14–16) Even in visual cortex where representation of the contralateral visual hemifield seems to be the rule, some partial representation of the ipsilateral visual hemifield near the zero vertical meridian does occur, and the extent of this representation appears to be variable across various species.(17–19) In extrastriate visual cortex, representations include both continuous maps of the contralateral hemifield and maps in which the representation is partially split in various ways. The split in the map is commonly along the representation of the zero horizontal meridian so that the representation of the upper and lower visual quadrants are largely separate from each other,(20) but the split may instead be along a line well into the lower visual quadrant in some maps.(21,22) A split in a representation allows one visual area to wrap around another to form a retinotopically matched border, and shorter interconnections between the fields may result, but it is not clear why the location of the split is so variable.

These examples demonstrate the extensive variation in the internal organization of sensory representations and it is not obvious that any of these rearrangements have important functional consequences. Yet, their existence does suggest that small alterations in the balance of developmental mechanisms can have major consequences. While the basic patterns of internal organization in at least primary sensory maps appears to be generated by gradients of signaling proteins,(23) activity patterns related to species differences in the number and arrangement of sensory afferents could be a significant source of the alterations in these patterns.

The modular and laminar subdivisions of representations are variable

Nuclei and cortical areas are commonly subdivided into layers and modular patchworks of two or more functionally distinct classes of neurons. The ways nuclei and areas of different mammals vary in laminar and modular patterns has not been extensively studied, but there is clear evidence for much variability.(24,25) For instance, the mammalian retina has two basic classes of ganglion cells, one that responds to an increase in illumination in the receptive field center (ON-center) and one that responds to a decrease (OFF-center). The projections of these two classes of ganglion cells usually have mixed terminations in the same layers of the lateral geniculate nucleus of the thalamus and in the subsequent relay to layers of visual cortex, but not in all mammals. In tree shrews, for example, ON and OFF ganglion cells project to different geniculate layers,(26) and these geniculate layers relay to different sublayers in visual cortex.(27) Even closely related species may differ in how they segregate and merge ON and OFF inputs. Cats have overlapping gradients of ON and OFF cell inputs in the same geniculate layers,(28) while ferrets and mink have separate geniculate layers for ON and OFF inputs.(29,30) Species differences in the laminar segregation of other types of retinal ganglion cell projections (“X” and “Y” cells in cats and primates) also exist.(31) These two types (X and Y) are mixed in the same layers in cats and segregated in the “P” and “M” layers in primates. In some species of monkeys, inputs to layer 4 of primary visual cortex are highly segregated within eye-specific ocular dominance columns (groups of neurons activated exclusively or mainly by the right or left eye), but this is not true for other species of monkeys where only a weak or transient segregation occurs, and no segregation is apparent in most other mammals.(32,33) Yet, such segregations are apparent in cats(34) and several other species. Variable modular arrangements are also common in the second visual area (V2) of tree shrews, monkeys and squirrels.(35)

Similar variations in the segregation of the inputs from different receptor classes are found in the somatosensory system. For example the duck-billed platypus has both mechanoreceptors and electroreceptors in its bill and the cortical representation of the bill is subdivided into sets of alternating tactile or electroreceptive modules.(36) In monkeys(37) and cats,(38) slowly adapting (SA) and rapidly adapting (RA) cutaneous afferents are represented in different modules or columns in primary somatosensory cortex, but in rats and most other mammals no such segregation is apparent. How is this variability generated during development? A variable role for activity-based segregation is certainly suggested by the common isolation of inputs by response type.

Disruptions in the sensory sheet are reflected by septa in sensory representations

Sensory representations commonly have visible septa between groups of cells that are activated by separated arrays of peripheral receptors. Perhaps the “barrel field” of somatosensory cortex of rats and mice is most well known.(39) In these rodents, a distinct barrel-like structure in primary somatosensory cortex (S1) can be identified for each whisker of the face (Fig. 2). More recently, it has become apparent that every distinct part of the rat’s body, for instance the digits and pads of the hands and feet, can be seen as a highly metabolically active island of densely packed cells separated by metabolically weak, cell-poor septa.(40) When the pattern of projections from the somatosensory thalamus to cortex is considered, these islands receive inputs from matching subdivisions of the ventroposterior nucleus, while the septa are devoid of such inputs.(41) An additional matching pattern of modules exists in the brainstem where afferents from the face and other parts of the body are segregated by body part.(42) Thus, sensory inputs related to each whisker, digit, or pad of the foot or forepaw are isolated from each other in anatomically distinct modules in the brainstem, thalamus, and cortex. Such architectonically identifiable groups of cells, “barrels” or “barreloids”, have been variably identified in several other rodents, some marsupials, and rabbits. Woolsey et al.(38) concluded from such observations that the organization of the barrel field of cortex in these mammals is “dictated by the organization of the sensory periphery.”

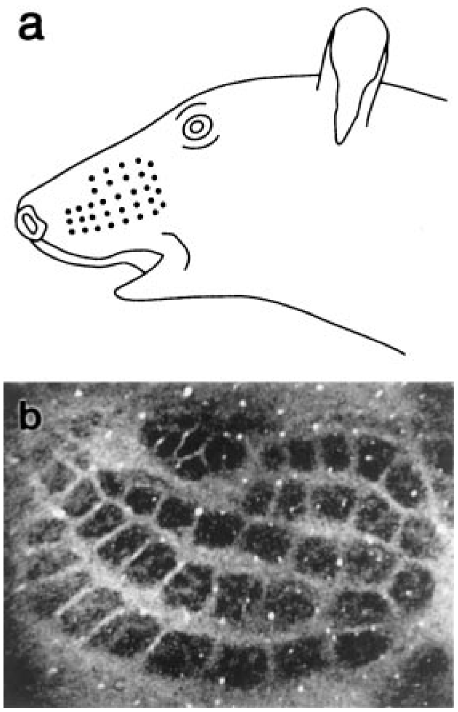

Figure 2. The barrel field of primary somatosensory cortex of rats. Each whisker on the side of the face (a) activates a specific cluster of cells or “barrel” in cortex (b). A portion of a brain section through primary somatosensory cortex has been cut parallel to the surface to reveal the barrels as ovals of tissue densely expressing the metabolic enzyme, cytochrome oxidase (CO). The ovals are separated by CO light septa. See Woolsey et al.(39) for further details.

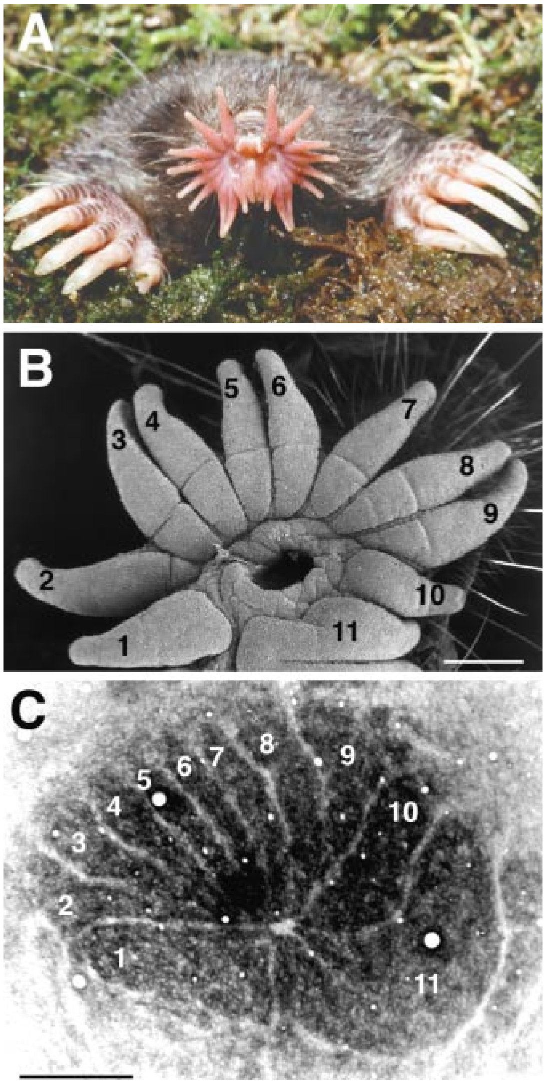

Figure 3. The brain of the star-nosed mole ismorphically represents the unique fleshy appendages of the tactile nose. **A:** A face-on view of the mole with 11 rays on each side of the nose. They detect and locate food by repeatedly contacting the ground with their nose. **B:** A rotated view of the left half of the nose. Ray 11 is just over the mouth. Scale bar = 1 mm. **C:** The cytochrome oxidase (CO) dense bands that represent each ray of the nose in S1. Light, CO-poor septa separate the representations of the rays. A similar array of bands for each ray is apparent in the second somatosensory area, S2, and a third less distinct pattern is found in a third somatosensory area. Scale bar = 500 μm. See Catania and Kaas(44) for review.

Comparable subdivisions in the brain exist for each of the 11 fleshly appendages on each side of the face of the star-nosed mole (Fig. 3).(43–45) Cell-dense bands of neurons for each appendage (or ray) of the nose are separated from each other by narrow septa in each of three different cortical representations of the face, as well as in subcortical representations in the thalamus and brainstem. The representations of the digits of the forepaw in these moles are also separated by septa (Fig. 4). In monkeys, narrow septa separate the representations of digits of the hand, and a wider septum separates the representation of the hand from that of the face; other septa separate areas of cortex devoted to the upper lip, lower lip and chin, teeth, and tongue.(46,47)

The common finding in rats, moles, monkeys and other mammals is that disruptions in the receptor sheet resulting from protuberances like digits, folds between pads of the palm, and separations in the skin between the lips and between the hand and the face (when the hand is represented next to the face) are reflected in representations by narrow septa between homogenous regions of neural tissue that are activated by continuous parts of the receptor sheet. These separating septa are variably visible in somatosensory nuclei and cortical areas, according to the species, the level in the somatosensory system and the body features.

Such subdivisions are unknown in the auditory system where the receptor surface for each ear comprises a single continuous row of hair cells. The visual system, however, has a small disruption of the retina, the optic disc or nerve head, where axons exit from the center of the retina. This receptor-free portion of the retina is commonly reflected as a rod-like septum through the layers of the lateral geniculate nucleus with inputs from the contralateral hemiretina, which is the hemiretina that contains the optic disc.(48) In ground squirrels, the optic disc is horizontally elongated across much of the retina. Presumably, this reduces the impact of having a blind spot, as predators are less likely to be masked by a strip than an oval. This elongated horizontal optic disc is represented by a narrow septum across much of the primary visual cortex.(49)

The varying patterns of lamination in the lateral geniculate nucleus are more well known. Septa commonly separate layers devoted to inputs from each eye, but they also often separate classes of ganglion cells.(48) Why do such septa occur, and why are they variably apparent? When they occur, they always separate groups of neurons with discorrelated activities as a result of receiving inputs from separated locations on the receptor sheet or from receptors with different transduction properties.

Errors and alterations in the receptor sheet are transmitted through the system to cortex

Typically, the pattern of sensory input from a receptor sheet is very consistent across individuals within a species. However, gene mutations may alter this pattern so that strains of species differ, and individuals may also occasionally vary from the population in this regard for unknown reasons. In an innovative study, Van der Loos and Dörfl(50) took advantage of the rare occasion of finding mice with an atypical number of vibrissae on their muzzle. As noted above, normal mice have

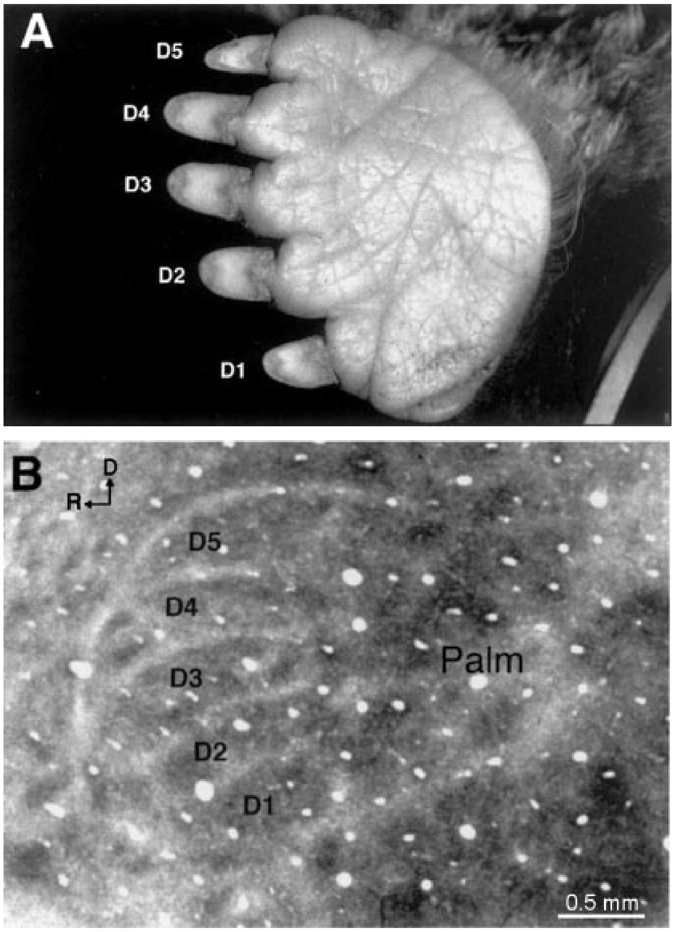

Figure 4. The modular representation of the digits of the forepaw of the star-nosed mole in the second somatosensory area of cortex (S2). A. The ventral glabrous surface of the forepaw with the digits from the "thumb" numbered D1–D5. B. In cortex, bands of cytochrome oxidase (CO) dense tissue that are separated by narrow CO light septa are activated by touching each digit, as numbered D1–D5. The palm activates a more caudal portion of the hand representation without septa. Rostral (R) and dorsal (D) on the brain are indicated. Based on Catania and Kaas.(43)

a morphologically distinct structure, the "barrel," in cortex for each whisker on the side of the face (Fig. 2), as well as equivalent "barreloids" for each whisker in the thalamus and brainstem. When they examined those individuals with one or two extra or less whiskers, they found the same changes in the number of barrels in cortex and barreloids at each subcortical level.(51) Similarly, when star-nosed moles have an extra appendage, or one less, on their tactile nose, a series of separate bands in cortex always matches the number of appendages (Fig. 5) .(52) Van der Loos and Dörfle(50) concluded from their observations on mice that the cortical array of barrels is "slaved" to the peripheral array of whiskers "as a result of a cascaded induction over three synaptic stations" (brain stem, thalamus, and primary somatosensory cortex). In star-nosed moles, an altered pattern of bands is also obvious in the second somatosensory area, S2, so the cascade of induction occurs over at least four levels of processing.

To us, the most parsimonious interpretation of the matching changes in the number of whiskers or rays on the nose and the number of related neural structure at three or four levels of processing in the somatosensory systems is that a genetic change or environmental event during development altered the number of whiskers or rays on the face. Information about this change, most likely in the form of a neural activity pattern, traveled from the face to the brainstem, then the thalamus, and then to one or two levels of cortex, altering the development at each level to produce a matching pattern.

Similar alterations occur in the visual system. Siamese cats result from a mutation that changes coat color and eye color by reducing pigmentation in parts of the body with normal body temperatures. The reduced pigment in the retina has the unexplained developmental consequence of misdirecting most of the axons from the temporal half of the retina that normally project to the ipsilateral lateral geniculate nucleus to the contralateral lateral geniculate nucleus (Fig. 6).(53) This causes the end of the A1 layer, now abnormally innervated from the contralateral eye, to fuse with the end of the A layer with normal inputs from the contralateral eye. This results in a continuous representation that has been enlarged by including an extra 20° of contralateral retina.(54) The enlarged representation is preserved in a single enlarged pattern in the projection to

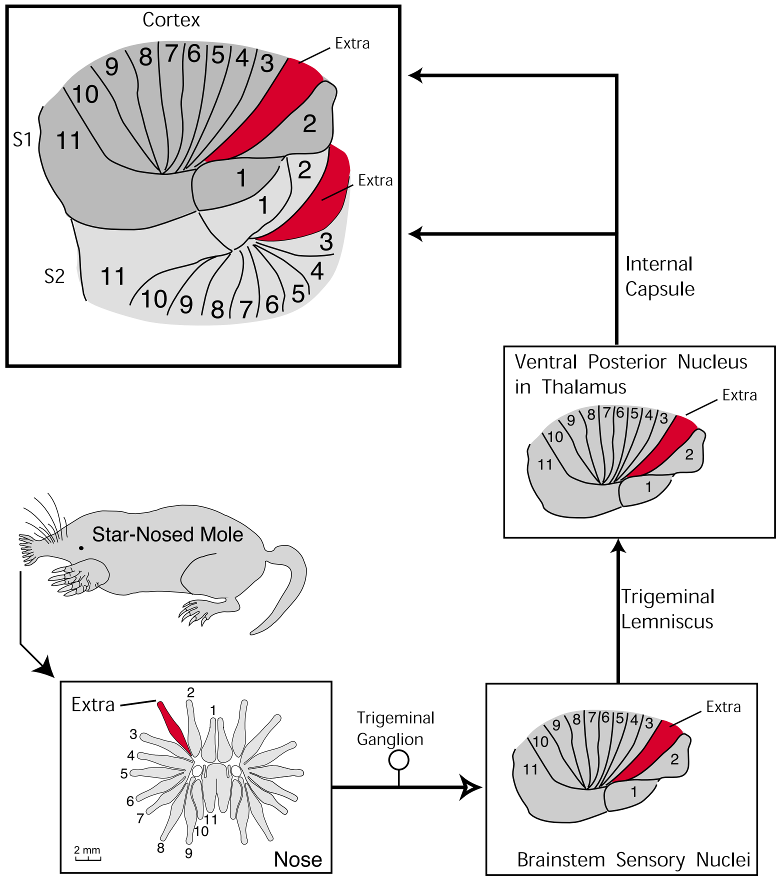

Figure 5. Star-nosed moles with extra or fewer rays on the nose have matching alterations in the numbers of isomorphic structures in brain stem, thalamus and cortex. Based on Catania and Kaas(52) and subsequent, unpublished research.

cortex in some Siamese cats,(55) but in others the A1 layer inputs to cortex are suppressed.(56)

Related alterations in the extent of geniculate and cortical maps of the retina have been reported for two different mutant phenotypes of Belgian sheepdogs. In one type, most of the retinal ganglion cells of both eyes project to the lateral geniculate nucleus of one hemisphere and not the other.(57) In the other phenotype, retinal axons of each eye project only to the ipsilateral hemisphere.(58) Nevertheless, topological maps of the altered inputs were found in visual cortex. Thus, when the pattern of inputs from the retina is abnormal, the organizations of the relay nuclei in the thalamus and their sensory areas in the cortex adjust to accommodate the abnormal pattern. Such adjustments strongly suggest a role for activity patterns that are altered with the misdirected inputs.

Some types of modular organization have evolved more than once

Primary visual cortex in cats and monkeys is characterized by a pattern of alternating ocular dominance bands (OD) or columns, and a distribution of dot-like modules that are marked by high concentrations of the metabolic enzyme, cytochrome oxidase (the CO-blobs). However, ocular dominance (OD) bands and CO-blobs are not found in most mammals.(32,33,59,60) Such distributions lead to the conclusion that the common ancestors of cats and primates had neither CO-blobs or OD bands in cortex.(16,25) Thus, these highly similar patterns of modular organization evolved independently. In addition, alternating OD bands have even been created in the optic tectum of frogs, normally with input from only the contralateral eye, by artificially providing an extra eye to equally innervate the structure.(5) Other examples include the independent evolution of the SA and RA modules in S1 of cats and monkeys. The independent evolution of similar types of modules in sensory nuclei and areas likely reflects similar expressions of basic self-organizing factors that have the potential to be revealed in all sensory representations. Computer models indicate that alternating bands can result from activity-based competition that is balanced, while an imbalance creates a dot (blob) and surround pattern.(61) The variability that exists across species in the expression of activity-based modules may relate to factors that alter the period of susceptibility.(62)

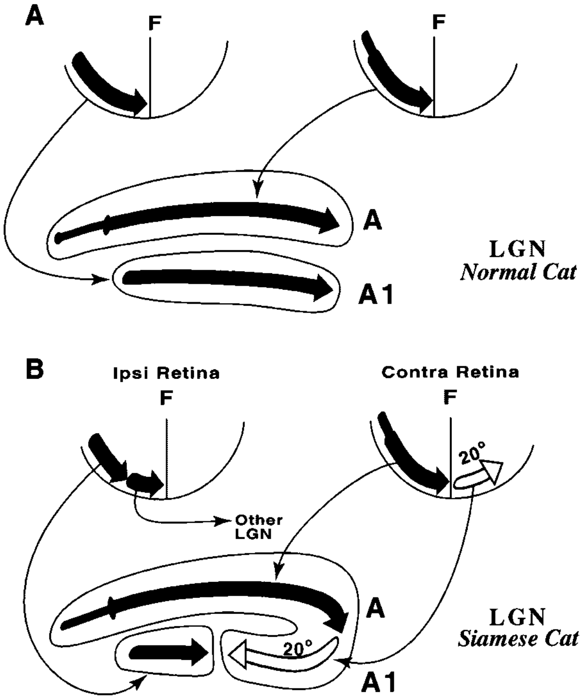

Figure 6. Retinal projections and lateral geniculate organization in normal and Siamese cats. **A:** In normal cats, inputs from the nasal hemiretina of the contralateral eye (above right) terminate in a retinotopic sequence in the dorsal "A" layer of the lateral geniculate nucleus (LGN), while the inputs form the temporal hemiretina of the ipsilateral eye (above left) terminate in the "A1" layer. The thin part of the arrows in the right eye and the A layer corresponds to the monocular visual field. The A and A1 layers are isolated from each other by a narrow cell-poor septum. **B:** In Siamese cats, about 20° of the temporal hemiretina projects abnormally to the contralateral LGN instead of the ipsilateral LGN. These misdirected inputs still terminate in the correct layer for the temporal retina (the A1 layer), but the end of the A layer now fuses with the end of the A1 layer, as these ends are now activated by adjoining portions of the contralateral retina. However, the A1 layer also develops an abnormal septum separating a medial segment of the layer with input from the contralateral eye from a lateral segment of the layer with input from the ipsilateral eye. This altered pattern indicates that the septa are not based on factors intrinsic to the LGN but depend instead on the nature of the input. However, misdirected inputs go to the correct layer, and this likely depends on intrinsic guidance factors. Based on Guillery and Kaas.(54)

Early maturing parts of receptor sheets capture more representational space

In general, the proportions of sensory representations that are devoted to different parts of receptor arrays seem to reflect the varying densities of receptors in the arrays.(63,64) Thus, finger tips with high numbers of receptors activate more cortical space than equal sectors of the backs of the digits with far fewer receptors. Such proportional activation could result from afferents competing for equal space as they grow into brainstem nuclei, and similar competitions by afferents in each relay to cortex. The time of development might be an additional factor. The central or foveal region of the retina is the first to develop, and the ganglion cells of the fovea activate a greater proportion of primary visual cortex than would be predicted by their number.(65) In a similar manner, the tactile appendage or ray of the nose of star-nosed moles that is just over the mouth (ray 11 of each side of the face) develops sooner than the other rays and captures more of somatosensory cortex than predicted by the number of afferents from the ray.(66) Early maturing receptors and afferents could have an advantage in activity-based competition for representational territory,(67) or this activity could even promote local brain growth.(68)

Adjoining sensory representations have matching borders

Typically, cortical representations are precisely matched along their common borders so that receptive fields overlap for adjoining neurons on each side of the border. Such congruent borders(20) are clearly apparent for S1 and S2 of somatosensory cortex of the star-nosed mole, as the two cortical isomorphs of the rays of the nose are precisely aligned (Fig. 5). Other examples include the borders between the four somatosensory representations (areas 3a, 3b, 1 and 2) of anterior parietal cortex of primates, the border between visual areas 1 and 2 , and the borders between core auditory areas in primates. Such precise alignments suggest that some organizing factor (possibly activity) is communicated across the border during development.

Experimental changes in sensory activation and innervation patterns alter the course of development

A great deal of evidence has accumulated about how sensory loss or deprivation alters the course of the development of sensory systems, and many of these changes have been used as evidence that neural activity patterns play an important role in shaping the detailed organization of sensory representations.(69) For example, the two sets of ocular dominance bands in primary visual cortex of monkeys and cats develop unequally if one eye is deprived of normal vision. As a result, the bands are narrower for the deprived eye. Impressive recent evidence for an instructive role of neural activity in brain development also comes from experiments where selectively blocking the activity of retinal ganglion cells prevents the development of orientation selective cells in visual cortex.(70,71)

Sensory loss of one type may even result in the deprived brain regions being activated by other types of sensory inputs. In the anterior ectosylvian region of cortex in cats, visual deprivation early in development leads to an expansion of neighboring auditory and somatosensory areas into the deprived visual region.(72)

Quite dramatic alterations in activity patterns have been produced by allowing retinal axons to grow into the auditory thalamus after removing auditory inputs in developing mammals so that auditory cortex becomes activated by visual stimuli.(73) This manipulation changes the course of development of auditory cortex to create neurons with orientated visual receptive fields that resemble those normally found in visual cortex. Thus, auditory cortex has the potential to create some of the basic features of a visual representation when it is induced to receive visual information. These and related results seem to indicate that alterations in the nature of activity patterns in the sensory inputs from the thalamus have an organizing influence on cortex.

Related experiments also show that visual maps can be induced to form in non-visual cortex. When the portion of posterior neocortex that normally develops into visual cortex is largely or completely removed before innervation by the visual thalamus, the visual inputs from the thalamus grow instead to remaining portions of cortex to form visual maps.(74)

Implications of normal and induced features of sensory maps for theories of map formation

Many of the features of sensory maps that we have outlined here are most easily explained by the assumption that information is transported from the receptor sheet to sequentially inform and guide the development of each subsequent station in the processing sequence. This is possible since representations do develop according to position in the processing sequence. While it seems possible that factors intrinsic to an area of cortex could code for all the major organizational features of a sensory representation, it seems more likely that major aspects of internal organization are determined by the nature of the sensory input. For example, in mice with an extra whisker on the face or moles with an extra ray on the nose, this change in the parcellation of afferents results in matching changes in at least three or four sensory maps in the brain. It seems extremely unlikely that a number of genes have mutated in consort so that independent intrinsic guidance factors in the face and at each of several levels of the nervous system have all been changed to precisely match modular components in a single or a few generations. Instead, it seems more reasonable to propose that information from the sensory sheet instructs the formation of central sensory representations in a cascading fashion. The nature of this instruction could be chemical, as neurons do effectively transport substances, but neurons are specialized to send information in discharge patterns. Neural activity patterns have the potential to alter gene expression and other cellular processes that mediate neural growth and synapse formation, as well as axon retractions and synaptic loss.(75)

We have argued here and elsewhere(49) that neural activity patterns likely create the detailed order within representations, the general proportions devoted to sensory surfaces, the variations in representational order, the septa between adjoining representations of separate regions in the receptor sheet, various types of modules within areas, and possibly congruent borders between representations. The commonly expressed view is that “neurons that fire together wire together”.(76,77) According to this model of development, neurons that are activated at the same time maintain and enlarge shared connections, while neurons that are activated at slightly different times reduce or lose shared connections, apparently to the extent that isolating septa sometimes form between differently activated populations of neurons. Co-activations can depend not only on sensory stimuli and on the spatial arrangement of receptors, but also on the transduction and response properties of receptors and neurons. The spontaneous activity within brain structures can also have an important role as adjacent neurons respond together.

Conclusions

Position-dependent differences in gene expression and the resulting gradients of signaling molecules appear to have a critical role in the positioning of cortical and subcortical representations of sensory surfaces. They likely guide the formation of overall patterns of connections between such representations, and shape at least a crude pattern of internal organization. We have reviewed some of the evidence that seems to indicate that information from the receptor sheet is passed on from level to level in sensory systems to modify the crude patterns of organization into detailed and often modular representations. Part of the evidence comes from experimental manipulations of the sensory environment during development that alter developmental outcomes. These experiments have been more extensively reviewed elsewhere. Here we concentrated on describing variations in the internal organizations of sensory maps within and across species that seem most parsimoniously explained by assuming that information from the sensory sheet guides the construction of sensory maps. This information would most likely transfer from level to level via patterns of action potentials, but the transfer of chemical signals by axon transport or the release of chemical signals in axon arbors as a result of non-spiking neural activity are other possibilities. While further comparative studies of variations in map structure may usefully suggest classes of mechanisms, the roles of such proposed mechanisms in the course of development need to be evaluated with experimental manipulations.

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