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Topographic Maps are Fundamental to Sensory Processing

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ABSTRACT: In all mammals, much of the neocortex consists of orderly representations or maps of receptor surfaces that are typically topographic at a global level, while being modular at the local level. These representations appear to emerge in development as a result of a few interacting factors, and different aspects of brain maps may be developmentally linked. As a result, evolutionary selection for some map features may require other features that may not be adaptive. Yet, an overall adaptiveness of brain maps seems likely. Most notably, topographic representations permit interconnections between appropriate sets of neurons to be made in a highly efficient manner. Topographic maps provide an especially suitable substrate for the common spatiotemporal computations for neural circuits. Finally, aspects of perception suggest the functional importance of topographic maps.   © 1997 Elsevier Science Inc.

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INTRODUCTION

We have long known that orderly representations of the sensory surfaces exist in cortex and other parts of the brain. Early evidence for these maps came from electrical stimulation of the cortex (e.g., [54]), sequences of sensation, or movement in focal epilepsy (e.g., [38]), and impairments after restricted cortical lesions [35], but the details and more compelling evidence came only after surface electrode, and then microelectrode stimulation and recording techniques came into common use. Adrian [2] and Woolsey (e.g., [55]) were in the forefront of those recording from the cortex and demonstrating somatotopic maps. These approaches have been applied to the auditory and visual systems, and numerous cortical and subcortical representations of the cochlea, retina, and body surface have been described (see [5,26,29,45,57,58,67]). Subcortical and cortical representations reflect the order of the receptor sheet with the greatest fidelity in structures early in the hierarchy of processing stations (see [26]). At higher levels, neurons acquire larger receptive

fields, and somatotopic, cochleotopic, and retinotopic organizations become less apparent or possibly lost.

Opinions about the meaning of topographic order have varied. Some investigators, especially those involved in disclosing the order of cortical maps, regarded the topographic patterns as essential for sensory discrimination. The arguments were made, for example, that the spatial separation of foci of neural activity in the cortical maps was the basis for localizing and distinguishing stimuli as separate on the body (see [72]). Others seemed to have held that whatever order exists in sensory maps is of little significance, and that such order should disappear as soon as possible in sensory hierarchies. Hebb [34], for example, reflected a common view when he stated that after area 18 "all topological organization in the visual system seems to have disappeared." Doty [20] once concluded that "the topographical arrangement of the retinocortical projection is in itself of minor or no importance in the visual analysis of geometric patterns." Likewise, the tonotopic organization in auditory cortex once was viewed as weak, at best, and unimportant for cortical functions (e.g. [24]). A widespread early view was that topographic organization is detrimental or incompatible with the presumed associative functions of cortex (for review, see [57]). In contrast, the now widely held opinion is that the topographic features of cortical and subcortical maps are not incidental, but essential to much brain function.

THE NATURE OF BRAIN MAPS

Until recently, we had little experimental evidence on the organization of most of the neocortex. The cortical sensory fields were thought to be few in number, and most of the cortex was thought to be associational and multimodal, and thus unlikely to have any topographic organization (see [57]). We now know that even mammals with little neocortex and few subdivisions devote much of this cortex to maps of sensory surfaces (see [46]). For example, marsupial opossums, with very little neocortex, appear to have at least five somatotopic representations of the body in the cortex [9]. Mammals with much more

neocortex have many more topographic representations (see [26,42,45,67]). At the cortical level, none of the representations appears to be topographically simple. Rather, they contain local, modular repeats of small segments of receptor locations within a global topography (see [43,51,61]) that may also include splits, disproportionate magnifications, and other transformations [4,58,67]. As examples, primary somatosensory cortex (area 3b) of monkeys appears to contain two locally interdigitated maps, one for slowly adapting and one for rapidly adapting afferents [71], while middle layers of primary visual cortex have separate local representations of inputs from each eye [36]. Local repetition is especially notable in cortical motor maps of body movements (e.g., [29]). Such motor maps seem to consist of mosaics of cortical patches, each devoted to a particular movement with several patches for each movement within an overall global somatotopy. Finally, there are also highly derived or "computational" maps [49] that reflect important aspects of the sensory environment rather than a sensory surface. Most notably, auditory space is derived from differences in the stimulation of the two ears and then is topographically represented in the optic tectum of owls.

While brain maps may not be simple, and in some cases they may reflect a derived stimulus dimension rather than a receptor sheet, it is no longer possible to deny their existence or conclude that they disappear after only one or two stages of cortical processing. Thus, the question becomes "why are they so prevalent?" This question can be addressed in several different ways. We start by considering how orderly maps develop, because cortical maps are subject to developmental constraints and probably the linking of map features.

THE DEVELOPMENT OF BRAIN MAPS

Somatotopic and other isomorphic maps of receptor surfaces are thought to emerge in development through a process of matching of inputs with targets based on molecular recognition (see [73]) followed by an activity-dependent local sorting of terminals (see [48]). The molecular matching creates the topographic representations within structures throughout processing hierarchies, while the local selection of synapses and connections, based on the strengthening effects of temporal correlations and weakening effects of discorrelations in neural discharges, modifies and refines the maps (e.g. [77]). Maps at lower levels in processing sequences are likely to reflect the order of receptor arrays more closely because they emerge early in development during periods when adjacent inputs are more likely to have highly correlated activity patterns that are relatively undisturbed by transformations of central circuitry. Thus, these patterns reinforce and refine the topography created by molecular matching. However, activity patterns do not always refine the topographic maps. In structures receiving inputs from the two eyes (see [14]), the retinal inputs are identically matched chemically for the same targets, but have different patterns of correlated activity (due to local connections in each retina). Thus, a global retinotopy emerges, while local populations of neurons are dominated by one eye or the other. As a result, ocular dominance bands emerge. Later in development, processing transformations in the retina become important, so that the afferents activated by light onset become discorrelated from those activated by light offset, and some mammals have separate layers in primary visual cortex for "on" retinal ganglion cell inputs and "off" ganglion cell inputs, as well as separate layers for each eye [50]. Such findings suggest that the development of modular subdivisions of topographic areas may be largely dependent on activity patterns.

Afferents appear to have narrowing windows of susceptibility to the effects of activity so that initially activity can preserve or eliminate connections over a larger territory, but this territory becomes restricted with the loss of connections over the course of maturation. Module size is highly related to the relative roles of activity patterns and chemical matching, with chemical matching favoring more uniform topography and activity patterns typically promoting modularity within a global topography [14]. The timing of the maturation process in relation to the sensory environment is critical, and small differences in timing can promote considerable species (and individual) variability [41]. Higher stations in the hierarchy mature later, and are more subject to alterations based on computations that transform sensory inputs. In addition, correlations based on local coactivations of receptors become less precise in higher levels of sensory systems, reducing the congruence between selection based on activity and chemoselectivity. Thus, small adjustments in relative roles of chemospecificity, neural activity, and the time of maturation have the potential of producing quite different yet globally topographic maps at different levels within a processing system. Variation in such adjustments can also produce different maps for different species. Of course, other factors are undoubtedly important, but the point here is to indicate that the regulation of three major variables may account for much of the variation seen in map organization.

Why is this brief discussion of development relevant to understanding the functional significance of map topography? If map organization is indeed the result of the interaction of just a few variables, then possible outcomes are limited. If all features of brain maps are not independently developed, some may not be optimal if these features are unavoidable outcomes of the selection for other features. To explain this conclusion further, it is useful to consider brain maps over a longer time scale, that of the evolutionary history that led to specific maps.

THE EVOLUTION OF MAP STRUCTURE

Existing structures and behaviors have been subjected to selection over alternative structures and behaviors in evolution. While selection would seem to push structures toward optimal design, this can occur only within the constraints of the system. As a sometimes stated example, wheels may be the best structure for locomotion on hard, flat surfaces, but biologically, wheels are difficult to create. Thus, the optimal design often may not be possible. As suggested above, another consideration is that design features may be linked. The attractive pattern of coat pigmentation of the Siamese cat is the consequence of a gene that also results in an abnormal visual system (e.g., [32]). Breeders that select for the coat and eye pigmentation also selected for undesirable attributes of impaired vision and the possibility of misaligned eyes. As a somewhat different example, the sexual selection that produces the long, attractive tail feathers of the male peacock also produces a bird that is conspicuous to predators and slow to escape. Thus, when we consider functional significance of cortical maps, we should allow that the outcome is a compromise imposed by selection in evolution of some organizations over other alternatives. As a result, some features may not be optimal, or may not even contribute to the functions of the area. As a plausible example, adjusting developmental factors to create a fine-grain topographic map of the retina with neurons with small receptive fields may provide a substrate for high visual acuity, and thus be subject to positive selection. However, if the fine-grain map is achieved by requiring a high degree of coactivation to limit

converging cortical inputs, then ocular dominance territories (columns) might also result, although such territories may have no adaptive significance ([41,61] for a related discussion). As discussed by Gould and Lewontin [30], it is not necessary to assume that all features of biological structures have adaptive significance. If map features are linked, they cannot be independently optimized by selection. Possibly even the global topography, so common in sensory areas, is not selected for, but is inadvertently linked to some other useful feature. To address this possibility, we need to consider why topographic maps might be the outcome of selection.

THE ARGUMENT OF GOOD DESIGN

Why are the maps topographical and why so many? A major answer for both questions is that it is good biological design (see [62]) to have both topography within areas, and have multiple areas. We presume that a fundamental operation of local circuits within sensory systems is to make context-dependent comparisons. Biologically important information often results from an assessment of how input coming in from one focus of receptors is different from that coming in from adjoining sets of receptors. As Hartline [33] and Kuffler [52] first demonstrated, the center-surround organization of receptive fields occurs for neurons early in the processing of visual information. Center-surround organization comparisons provide context (e.g., is the center brighter, greener, further, or moving differently than the surround?) and context is crucially important in the interpretation of sensory information. The center-surround organization of receptive fields exists not only for neurons in the retina, but more generally for neurons within cortical and subcortical sensory structures [6]. When receptive fields are small, the comparison is between very limited parts of a receptor surface, but neurons with large receptive fields make more global comparisons.

It is easy to see how topographic maps allow center-surround receptive fields to be the outcome of rather simple, local connections among neurons. Barlow [7] has pointed out that topographic maps also permit local neural circuits that effectively average or interpolate over space and time. For example, Barlow indicated how neurons in a retinotopic V1 might smooth sample points to yield different signals if three closely spaced dots are aligned or not, a task that can be done perceptually with great accuracy. In the time domain, Barlow indicated how a topographic map permits local neural circuits that detect direction of motion. Other types of brain organization would require longer and more complex arrays of connections. In many computer simulations of neuronal processing, any "neuron" can be connected with any other, and thus, inputs from a sensory surface may distribute randomly to the next level and still be useful if one adjusts synaptic (connectional) strengths to create the desired outcome. But neurons are very different from the components of electronic processors (see [25]). For neurons, it is metabolically costly to make long connections, and the trade off of connection distance is time, a very serious constraint [65,66]. Thus, it is good design to group neurons together that are to be highly interconnected (see [8,17,18,39,42]) for most types of neuronal computations. In contrast, a massively parallel and massively interconnected neural network would "require a brain the size of a bathtub" [13], and a fully interconnected brain would be much larger [39]. Computational models that require such hardware have been called "impossibility engines" [13].

A related question is why are there multiple maps? Part of the answer is so that maps can be of different sizes. For any map, there is a connectional problem. Within the map, each neuron has connections with other neurons, and if this number is relatively constant, then the proportion of the map sampled

by any neuron depends on the size of the map (number of contained neurons). If fine-grain discriminations are desirable, receptor densities can be increased and cortical representations or parts of cortical representations can be enlarged. But there is a scaling problem [68] in enlarging cortical maps. Neurons do not get proportionately larger, but instead, the maps have more neurons. Thus, each neuron must have more and longer connections, or each neuron is interconnected with proportionately fewer of the neurons in the map.

The general solution to this problem is to have maps of different sizes, so that local comparisons can be made in large maps or in enlarged parts of maps, while global comparisons are made in small maps (also see [22]). In the small primary visual area of rats or opossums, neurons in any part access neurons over much of the rest of the representation (see [10]), while neurons in any part of the large VI of macaque monkeys have connections over only a small fraction of the map (see [11]). Thus, VI in rats is suited for more global comparisons and V1 in monkeys for more local comparisons. Animals with small brains, little neocortex, and few areas generally emphasize the global comparisons favored by small areas, while animals with large brains generally have both large and small areas, and thus both types of processing. The middle temporal visual area (MT) in monkeys is 1/10 the size of V1 [3], and neurons in MT make more global comparisons [6].

Regardless of size, the fundamental advantage of having multiple maps is that maps can be specialized for preferentially addressing different stimulus attributes, such as motion in MT (e.g., [8]). To some extent, this advantage can be realized in a large map by having specialized sets of modules. The principle advantage of multiple small maps over a single large map is that neurons that frequently interact are close to each other in the small maps, where they can interact over short, efficient connections. Of course, the separate maps must interconnect over longer connections, but relatively few such connections are needed. In addition, long interconnections are generally between adjacent fields [78], and the general congruence of topographic maps along common borders [5] further shortens these connections. Furthermore, connections between areas may be shortened by folding the brain [74]. Interconnections between maps are especially short when the maps are stacked upon each other, as for the neural maps of visual, auditory, and tactile space in the superior colliculus [70]. Thus, topographic maps and multiple maps provide a processing substrate with greatly reduced requirements for long, slow, and metabolically expensive connections (see [15] on the metabolic adaptiveness of reducing brain pathways).

THE ARGUMENT THAT PERCEPTION IS BASED ON TOPOGRAPHIC MAPS

One type of argument for the functional importance of topographic maps is based on parallel relationships between map structure and perception. Adrian [1] illustrated this type of relationship long ago when he pointed out that the decay in the discharge of a cutaneous afferent to a maintained stimulus reflected the decay in the magnitude of sensation, and thus the sensation must be based on the discharge rate. A similar type of reasoning followed when Adrian [2] showed that the parts of somatotopic maps for sensitive skin surfaces are magnified. About this time, Marshall and Talbot [55,72] proposed that stimuli are perceived as spatially separate when they activate separate populations of neurons in cortical maps.

Many of the perceptual features and illusions discussed by Gestalt Psychologists have been attributed to local neuronal inter-

actions within topographic maps. More recently, the distance effects in many studies of perception can be viewed as an outcome of the effectiveness of local processing in cortical maps. Thus, visual distractors near a target interfere more with detection, and the benefits of directed attention diminish with lateral distance from locus of attention (e.g., [2,3,12]). In addition, greater deficits in target detection have sometimes been noted when targets are in an unattended hemifield or visual quadrant (e.g., [37]). Such results reflect the separate representations of visual hemifields and sometimes quadrants in visual cortex. Finally, at least some behavioral effects vary with "cortical distance" rather than visual angle [21].

Most theories of visual perception involve at least one topographic map, although feature modules (maps) may be nonretinotopic. However, some investigators (e.g., [28]) conclude that the bulk of the evidence favors a network model where feature maps are topographic and interconnected. In a more specific manner, Schwartz [69] has discussed the possible relevance of the geometric properties of cortical maps to perception (also see Rosa [67]). For example, map structure in visual cortex may provide a substrate for "scale invariance," so that changes in viewing distance do not alter resolution during maintained fixation [76].

The significance of some cortical maps in perception is also suggested by the localized perceptual effects produced by direct electrical stimulation of cortical neurons (e.g., [60]), and the localized perceptions produced by the advance of deactivating migraines [31,64]. Finally, sensation in phantom limbs, the persistence of a mental image of a limb that has been amputated, can be evoked by stimuli on the stump of the arm or the side of the face (e.g., [63]). These evoked sensations can reflect aspects of the actual stimuli, such as movement, as well as specific locations on the phantom with specific stimulation sites. These aberrant sensations seem best explained by the assumption that topographic maps of the missing limb are being accessed over new pathways from the trigger zones [27].

Topographic maps may also provide a substrate for local modifications in circuits that occur as a result of experience or training that improves perceptual and motor skills (see [47]), and such modifications possibly mediate recovery after local brain damage [59]. Thus, sensory representations seem to provide an organization that can be locally modified to provide behavioral flexibility throughout life [44].

A COUNTER ARGUMENT

A major argument against the view that topographic maps are functionally significant is that lesions often do not produce the expected consequences. When Doty [20] argued that the topographic organization of visual cortex was of "minor or no importance," he did so because it seemed that lesions that disrupted the topography had so little effect on visual performance. Lashley's [53] well-known conclusions based on the effects of lesions on visual performance in rats were similar. Investigators noted that lesions of tonotopically organized cortex in cats did not abolish the ability of cats to discriminate tones in the simple manner expected [19], and many spatiotactile abilities remain after deactivations of primary somatotopic maps in the cortex of monkeys [75]. However, the evidence derived from such studies of remaining abilities does not seem as compelling as it once did, in part because we are more aware of what can be done with surviving remnants of systems. Mechanisms mediating brain plasticity may amplify the effectiveness of remaining parts of systems (e.g., [40]). Furthermore, major impairments often may be revealed by more rigorous testing. In addition, many behaviors may be mediated by subcor-

tical topographic maps, possibly with access to cortex over less direct paths. Blindsight, where monkeys or humans can localize visual objects without visual awareness after lesions of primary visual cortex, is one example. Remaining visual abilities apparently depend on the topographic map in the superior colliculus, and the projections of the superior colliculus to the pulvinar complex and cortex (see [18]).

CONCLUSIONS

1. Topographic maps of receptor surfaces occupy much of neocortex of all mammalian species. This suggests that they are important.
2. To the extent that such maps emerge in development as a result of an interaction between relatively few factors, map features may be linked. Thus, all features of maps may not be adaptive or have useful functional consequences.
3. Topographical maps effectively group neurons that most commonly interact, thus decreasing requirements for long, slow, and metabolically costly connections. Such connections are also reduced by the topographic congruences of adjoining maps, and the grouping of maps that interact the most.
4. Topographic maps are important components of many current theories of how visual information is processed. The maps seem especially well-suited for the construction of local neural circuits that make center-surround comparisons.
5. An isomorphism seems to exist between many aspects of perception and imagery and the topographic features of maps.
6. While lesions of topographic maps do not always disrupt perception in ways expected from the presumed functional roles of such maps, preserved functions may depend on other representations, or on the repair and recovery of damaged representations.

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