

Cortical maps

James A. Bednar & Stuart P. Wilson

Abstract

In this paper we review functional organization in sensory cortical regions – how the cortex represents the world. We consider four interrelated aspects of this organization: (1) the set of receptive fields of individual cortical sensory neurons, (2) how lateral interaction between these neurons reflects similarity of their receptive fields, (3) the spatial distribution of receptive-field properties across the horizontal extent of the cortical tissue, and (4) how the spatial distributions of different receptive field properties interact with one another. We show how this data is generally well explained by the theory of input-driven self-organization, with a family of computational models of cortical maps offering a parsimonious account for a wide range of map-related phenomena. We then discuss important challenges to this explanation, with respect to the maps present at birth, maps present under activity blockade, the limits of adult plasticity, and the lack of some maps in rodents. Because there is not at present another credible general theory for cortical map development, we conclude by proposing key experiments to help uncover other mechanisms that might also be operating during map development.

Keywords: cortical map, topological map, topographic map, receptive field, visual cortex, self-organization, primate, rodent.

Introduction

Understanding how external stimuli are represented in the brain is one of the central questions of neuroscience. Researchers have attacked this issue on many fronts, but perhaps most directly by studying cortical maps: the response properties and organization of the entire set of neurons comprising a cortical area. Cortical maps provide important clues about how brains form and maintain representations of the external world. We first present a summary of a wide variety of experiments showing the properties of cortical maps. We then discuss models

that demonstrate how maps of the world can emerge from self-organizing principles, that is, how maps emerge from individually simple interactions between neurons, without plan or instruction. The success of these models in accounting for a wealth of experimental data on cortical maps motivates self-organization as an important theory of cortical maps, with no other type of model currently able to account for this range of observations. However, there remain significant unsolved issues that challenge this theory, which we discuss with an eye towards possible future experiments to resolve the outstanding issues. We begin by defining the key terms used to describe the functional properties and organization of cortical maps.

What are cortical maps?

A map is a representation. A *neural map* is a representation in a network of neurons that respond systematically to events outside the network. A neural map in one network may be defined with respect to another network, such as when an experimenter activates cells of one brain area and observes correlated responses in cells of another. Neural maps may also be defined for events that occur external to the brain, such as when we measure neural responses to external stimuli activating sensors in the skin, cochlea, or retina. By a *cortical map* we refer specifically to a correspondence between responses in an anatomically defined network of cortical neurons and some events external to the brain (i.e., the *functional properties* of these neurons, and their *functional organization*). Commonly studied examples of cortical maps are found in the primary somatosensory, auditory, and visual cortices, as well as areas of the motor cortex. Here we will focus primarily on sensory maps, where the functional organization has been established most clearly. Figure 1 shows examples of the anatomical pathway from the sensory surfaces to the primary somatosensory and visual cortex regions of a rat, including both subcortical and cortical maps. Figure 2 shows the details of the retinotopic mapping between the eye, the thalamus, and the primate primary visual cortex.

Neural maps are made up of neurons, and the *receptive field* of a neuron is an important concept in sensory maps. Often the term is used in a narrow sense to describe a physical location on a two or three dimensional sensory surface, i.e., the region on that sensory surface in which activation elicits a selective response from a given neuron. But because multiple components of a sensory stimulus

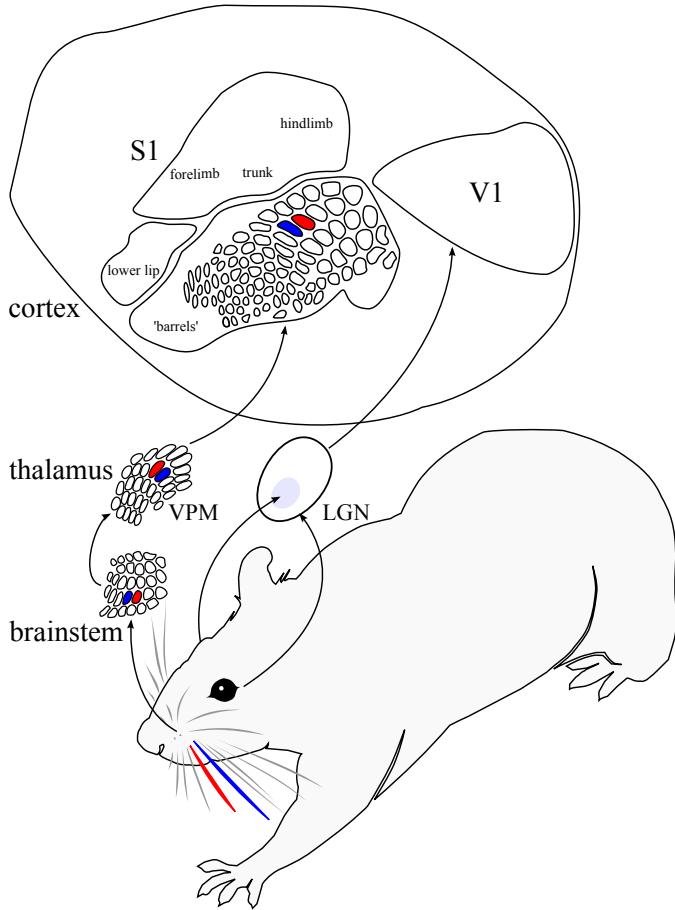


Figure 1: Neural maps and cortical maps. For a mammal, the surface of the cortex (shown enlarged and schematically flattened above) can be parcellated into a number of different cortical maps, such as the rat primary visual cortex (V1) and primary somatosensory cortex (S1). V1 is organized as a topographic map of the lateral geniculate nucleus (LGN) of the thalamus, which itself is a topographic map of the surface of the retina; each of these regions is retinotopically organized such that nearby locations on the retina are nearby in their LGN and V1 representations (see figure 2). S1 similarly has a topographic map of its thalamic input (VPM), which has a topographic map of its input from the brainstem, which in turn has a topographic map of the body surface. The whisker pad of a rodent has a clearly distinguishable pattern of representation at each of these levels, with nearby whiskers mapping to nearby locations in each of the subsequent subcortical and cortical regions. In S1, the areas responding to each whisker are termed “barrels”, and within each barrel neurons appear to be organized according to functional preferences such as for whisker deflection direction (see figure 8). Similarly, local areas in V1 are organized according to various visual features, such as orientation preference, within this overall retinotopic topographic map.

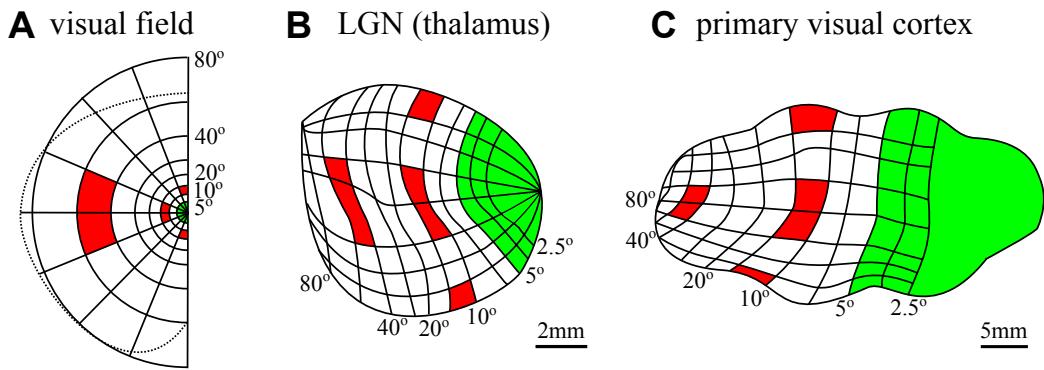


Figure 2: Visuotopic maps. Visually responsive neurons typically respond to specific areas of the visual field and are excited by specific neurons in the regions from which they receive connections. The mappings from the visual field to the retinal surface, the visual field to the layers of the thalamus, from the thalamus to the layers of the primary visual cortex, from the visual field to the layers of the primary visual cortex, and so on are all examples of *neural maps*, with those whose targets are in the cortex called *cortical maps*. These maps are all *topographic maps*, where nearby locations in the source region are mapped to nearby locations in the target, though the mappings are highly nonlinear because of the disproportionate representation of the very center of the visual field. These distortions can be seen schematically for a macaque monkey visual system here, with the given pattern **A** in the visual field transformed in **B** and **C** according to the spatial location of the neurons responding to that pattern. Adapted from Connolly and Van Essen (1984).

can modulate neuronal activity, such as the location, contrast, color, orientation, or spatial frequency of an edge in an image, the receptive field may be defined functionally in terms of feature dimensions. The receptive field of a neuron thus more generally refers to a localized region in a multidimensional *feature space* (see Obermayer and others, 1992). For instance, a V1 neuron might have a preference for a certain range of retinal locations (x, y), orientations, motion directions, colors, spatial frequencies, and contrasts, responding selectively to some region of this seven-dimensional space (cf. Adelson and Bergen, 1991). The receptive field thus defines a relation such that the activity of this neuron represents (corresponds to with some probability) an occurrence of an external event in the corresponding portion of the feature space. Along a given dimension, the preferred region of space might be very local (e.g. for a neuron highly selective for orientation), or extended (for a neuron responding to a wide range of contrasts). The shape of this region of space characterizes the patterns to which a neuron will respond, at least for stimuli presented in isolation. Figure 3 shows an example of mapping a receptive field as a region of a three-dimensional space (x, y , orientation).

It is often convenient to summarize a receptive field in terms of the *preference* and the *selectivity* of the neuron, with respect to a particular dimension of the feature space. Given a parametric stimulus characterized by some feature dimensions, the preference of a neuron is the value of the parameter that elicits the maximum response in the neuron. For example, a visual cortex neuron might have a preference for edges at a particular location on the retina, of a particular orientation. The selectivity is then usually defined as the ratio between the response to the preferred stimulus, and the mean response to other stimuli that vary with respect to that dimension of the feature space. An orientation-selective neuron will have a high response to its preferred orientation and low responses to others (see e.g. figure 3D).

When considering the functional organization of neural maps, it is useful to make a distinction between the connectivity and the interaction between neurons. Connections are a direct physical relationship between cells, as may be reflected by the number and efficacy of synaptic processes that allow chemical or electrical communication between two neurons. An interaction instead refers to the *functional* consequence of communication between neurons, with the distinction that an interaction may occur indirectly via intermediate connections or even by volumetric processes like extracellular diffusion. For instance, the interaction between two neurons A and B may be net inhibitory even if A and B are both excitatory, if A directly excites inhibitory interneuron X, and X then directly inhibits B. In-

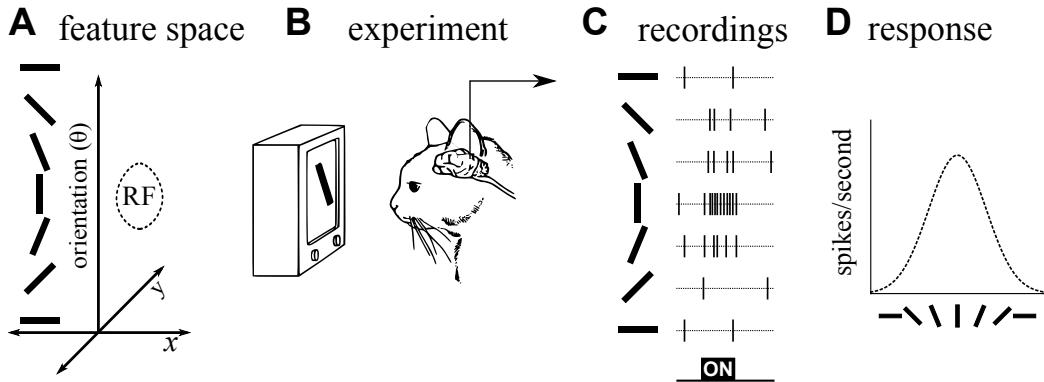


Figure 3: Mapping a receptive field (RF) in feature space. To map the RF as a region of some feature space, stimuli first are constructed that cover that space. **A.** An example three-dimensional feature space of location (x,y) and orientation θ , with each point in the space corresponding to an oriented bar presented at a specific location on a monitor. **B.** The response of a cortical neuron is recorded for each such combination of parameters. **C.** The firing rate during the period in which the stimulus was ON varies according to the stimulus parameters. By pooling across responses to all orientations, a preferred region in (x,y) space can be mapped out. For this optimal location, how the responses vary with orientation can then be determined. **D.** Converting the spike trains to firing rates allows an orientation *tuning curve* to be constructed, showing how the response varies along the orientation dimension. This neuron has a preference for vertical orientations, since it spiked most frequently for such patterns. The combined orientation and (x,y) preference is the receptive field in (x,y,θ) space, indicated with an oval at the far left, characterizing the region of the three-dimensional feature space to which this neuron responds.

teractions may be described in terms of spatial relationships between neurons, as one might graph the excitation of one neuron by another against the distance that separates them in the tissue. Or an interaction may be described in terms of the functional relationships between neurons, as one might graph the correspondence between neurons as a function of the similarity of their receptive fields.

Many cortical maps reveal themselves as a strong relationship between these two types of interactions, such that the proximity of neurons in physical space is correlated with the proximity of what they represent in feature space. For example, as Hubel and Wiesel (1974) moved a recording electrode from position A to points B at increasing distance along the V1 cortical surface, the difference in preferred edge orientation between A and B increased. Hubel and Wiesel (1974) had measured a *topological map*, as the topology of the feature space was conserved in the projection of the map onto the cortical surface. Since adjacent regions in the feature space project to adjacent regions in the tissue of such a map, topological maps are described as having good *continuity* (Obermayer and others, 1990).

When neurons are labeled by their preferences, and the labels are arranged on an image to reflect the position of each neuron in the tissue, topological maps can be visualized as continuously varying spatial patterns. Separate map images for each dimension of the feature space can be derived from a single set of neurons. For example, if we establish the preferred orientations of V1 neurons, we can construct an orientation preference map (see figure 4). Orientation and other feature maps are functional phenomena, reflecting how the neurons in the maps behave for visual stimuli, but the patterns have been shown to have anatomical correlates too (figure 5). Specifically, injecting a tracer into a local patch of iso-oriented neurons has been found to label neurons with similar preferences at distant locations in the map (Bosking and others, 1997). This map-specific connectivity is thought to underlie a wide variety of surprising phenomena, such as visual surround modulation (reviewed in Angelucci and Bressloff, 2006).

It is not known whether there is any functional significance to the specific smoothly varying map patterns that are observed in non-rodent species, but characteristic features of these patterns are preserved across a wide range of evolutionarily distant species. Specifically, primate and cat V1 orientation maps are largely continuous, but they are punctuated by discontinuous points, known as *pinwheels*, about which preferred orientations vary smoothly in a circular pattern (Bonhoeffer and Grinvald, 1991; Blasdel, 1992). Pinwheels may be an inevitable compromise when attempting to continuously and uniformly project a dimension with

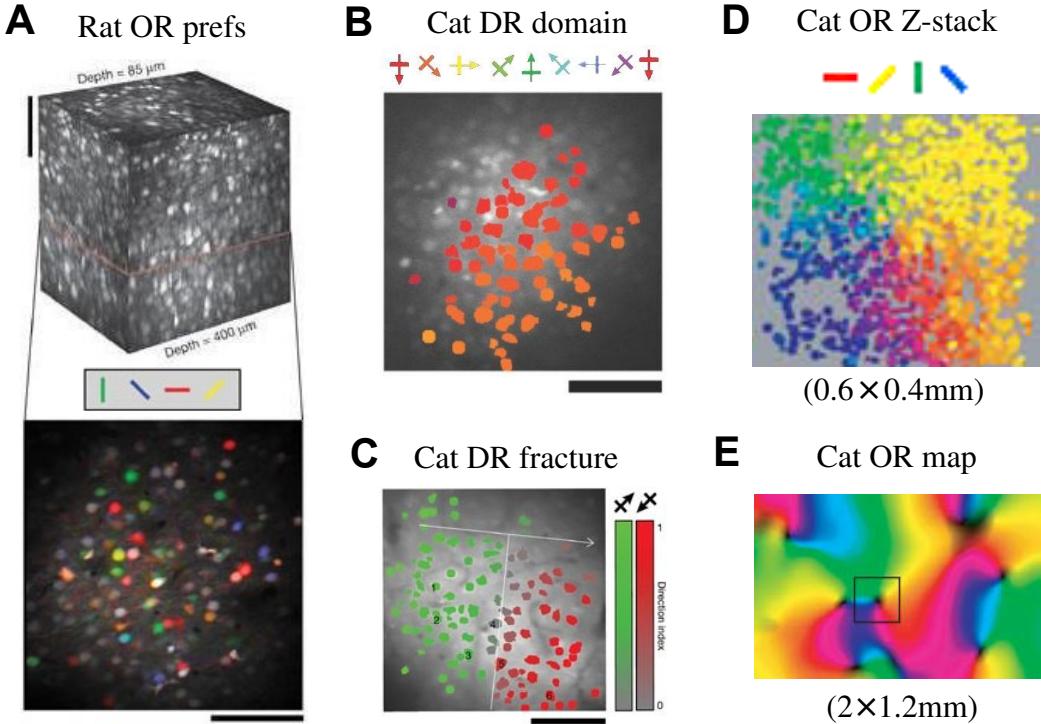


Figure 4: Orientation and direction maps in rodents and cats. Two-photon imaging techniques allow every neuron in a small volume to be labeled with its feature preference, similarly to how preferences of single neurons were measured in figure 3. **A.** The rodent V1 map for orientation preference has no evident spatial structure—even though individual neurons are orientation selective, and despite an overall retinotopic map, orientation preferences are locally highly disordered. **B,C.** Similar methods in non-rodent mammals show highly ordered maps, e.g. for motion direction preference in cat V1 as shown here. **D.** Preferences in non-rodent species are highly ordered vertically as well, with similar orientation preference in each layer of the visual cortex that can be imaged using this technique. **E.** In non-rodents, the maps measured in this way validate the coarse but large-area maps found using optical imaging techniques (compare the inset box from **E** to the per-neuron data in **D**). The overall organization for orientation preference has interesting and systematic properties, such as pinwheels (point discontinuities, such as the one shown in the box here) and linear zones (rainbow-like regions covering all orientations in spatial patch). Reprinted by permission from Macmillan Publishers, Ltd: Nature, Ohki and others (2005a, 2006a), copyright (2005,2006); scale bars are 0.1mm.

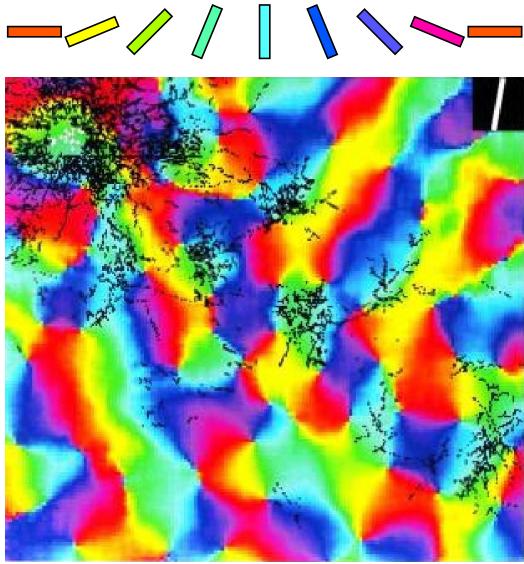


Figure 5: **Patchy connectivity.** If a tracer is injected into a local region (marked with white dots in the upper left above) of this 2.5×2.5 mm tree shrew orientation map, it labels neurons with a wide range of orientation preferences locally, but distant neurons are labeled only if they have orientation preferences similar to that of the neurons in the injection site. Similar properties have been reported for other visual features, such as motion direction preference. Reproduced from Bosking and others (1997), with permission of Society for Neuroscience.

a periodic topology onto a two-dimensional surface (see Durbin and Mitchison, 1990).

When spatial map patterns for different features are compared, map contours tend to intersect at right angles, as is the case when contours delineating spatial frequency or eye preferences are superimposed on iso-orientation contours (Issa and others, 2008; Blasdel, 1992). Such mappings are said to be *orthogonal*, meaning that within an area of preference for one specific parameter value the mapping of a second feature has good *coverage* with respect to the first, e.g., for each orientation, all spatial frequencies will tend to be represented (Nauhaus and others, 2012). Topological map patterns have been described as reflecting an optimal trade-off between continuity and coverage constraints (Swindale, 1991; Swindale and others, 2000), although the details of how to test this claim have been controversial.

Topographic maps are a subset of topological maps where nearby locations in the target region correspond to nearby locations in the source region, at least at some spatial scale. The prototypical example of a topographic map is the retinotopic map, which is the largest-scale functional organization of responses found in V1, i.e. the organization by the preferred location of stimuli on the retina (figure 2). Topographic maps typically reflect the spatial organization of receptor cells on a sensory surface, such as the overall pattern of tactile receptive fields that define the homunculi in illustrations of the map of the body surface in primary somatosensory cortex (S1; Penfield and Boldrey, 1937; see also Wilson and Moore, 2015).

Cortical maps, whether or not they reveal themselves as spatial patterns across the tissue, are perhaps most fundamentally collections of receptive fields, and maps have been found for a huge range of different ways in which receptive fields vary, across the sensory cortices. We do not yet know whether the intriguing spatial patterns they make on the cortical surface are important for neural computation (Purves and others, 1992; Wilson and Bednar, 2015), but the following section shows that these patterns do help reveal the underlying processes that generate receptive fields as the building blocks of neural representation.

A theory of cortical map formation

Given the observations about how cortical maps represent the external world, an obvious and longstanding question is how this relationship comes about. Is such a mapping established according to a pre-set program, which supports adaptive behavior to the extent that the hardwiring happens to be a good fit to the actual environment? Or is the functional organization (and thus representation) an emergent property of an interaction between the organism and its environment during development?

Theories about the process of map formation have been formalized as a series of numerous computational models over the past forty years, to allow our intuitions to be expressed precisely and tested for consistency. Here we first describe in some detail a model of map self-organization developed by von der Malsburg (1973), which captures several of the fundamental building blocks for a theory of cortical maps, and upon which an appreciation of more recent refinements to this theory may be built.

The model of von der Malsburg (1973) comprises three populations of cells: a set of 19 photoreceptor cells, a population of 169 excitatory cortical neurons, and a population of 169 inhibitory cortical neurons (see figure 6). Photoreceptors are arranged on a two-dimensional sheet corresponding to a small patch of the retina, and cortical neurons are arranged on a two-dimensional sheet corresponding to a small patch of V1. When the photoreceptors are activated by a pattern of light on the retina they increase the activity of the excitatory neurons; these in turn increase the activity of neurons nearby in V1; when inhibitory neurons are excited they reduce the activity of nearby excitatory neurons. Crucially, the influence of excitatory neurons is limited to other neurons falling within a small radius centered on their position in V1, whereas the influence of inhibitory neurons extends over a somewhat larger range. (This model predicated the discovery of the long-range patchy excitatory connections like those in figure 5, but most such models even today also omit those connections because they are not required for the self-organization process.)

Connections from the photoreceptors to the excitatory neurons are via initially random synaptic weights, each represented by a single number, modification of which constitutes learning. A pattern of light on the retina is defined by switching the activity of a subset of the photoreceptors from 0 to 1. The response of each excitatory neuron is then computed by multiplying each weight value by each

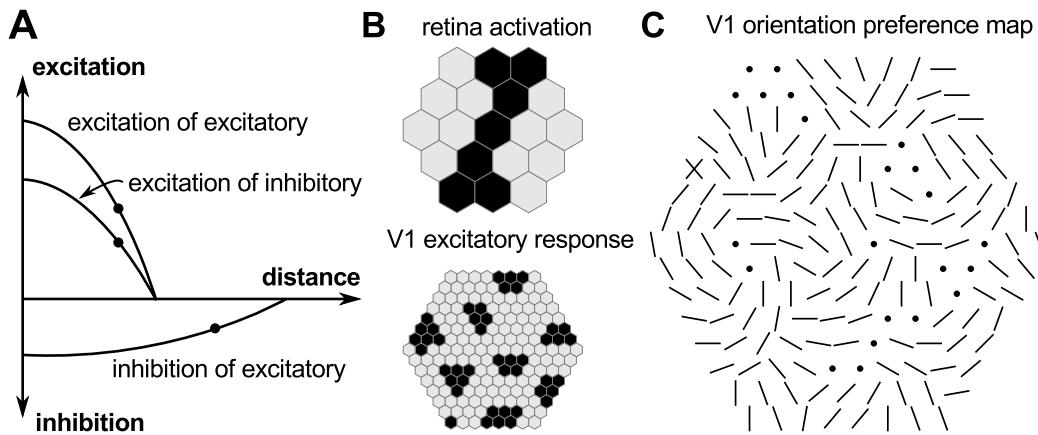


Figure 6: The model of V1 orientation-preference map self-organization by von der Malsburg (1973). **A.** The strength and spatial profile of connections used to wire up a network of 169 excitatory and 169 inhibitory cells in a sheet corresponding to a region of primary visual cortex (V1). Crucially, the effect of the excitatory cells is short-ranging compared to the long-ranging effects of inhibitory cells (dots mark the cutoff distance for the influence of each cell type), although the longest-range connections in V1 are known to be excitatory. **B.** Cells are arranged in three separate populations as hexagonal arrays corresponding to the retina, and V1 excitatory and inhibitory neurons (inhibitory units not shown). A pattern of retinal activation revealing an oriented bar is shown above the response to that pattern from the V1 excitatory neurons, after the network has been trained on 100 similar patterns of various orientation. V1 responses are clustered into local patches. **C.** The orientation of the bar(s) in the retinal pattern eliciting the maximal response is shown for each cortical neuron, after training on 100 patterns. Neurons responding equally to all patterns (or not at all) are indicated by dots. The arrangement of orientation preferences reveals a smooth topological map. Adapted from von der Malsburg (1973).

corresponding photoreceptor activity, and then summing over the connections for each neuron. Because the initial weights are random, the very first pattern of activation across the cortex is random too. But as the neurons interact, the influence of the short-range excitation is to cause any random initial groupings of activity in V1 to be strengthened, while the longer-range inhibition causes nearby groupings to compete with one another, with the combined inhibition from the strongest initial groupings effectively silencing the initially weaker groupings nearby. The net effect as these dynamics settle is to collect the initially random distribution of activity across V1 into discrete bubbles. The dynamics are consolidated by modifying the weights in proportion to the combined presynaptic and postsynaptic activity, which increases weights between active photoreceptors and neurons that fall within the emergent activity bubbles. Hence if a similar pattern of light is next presented on the retina, these particular neurons are more likely to win the competition again. The learning mechanism is similar to that proposed by Hebb (1949), with an additional constraint that the weights are scaled after each step so that the total remains constant for each neuron. Consequently, as the weights to the active photoreceptors increase slightly, the weights to the inactive photoreceptors decrease to compensate, hence the winners of the first competition are less likely to respond to a second pattern of light that is dissimilar to the first.

von der Malsburg (1973) trained his network on patterns corresponding to bars of light across the center of the retina, with each bar oriented randomly in the full range from 0 to π radians. He found that over time the patterns of weight values came to match the range of oriented patterns used to train the network, and as the alignment between the retinal patterns and the weight patterns defines the magnitude of the each neuron's response a preferred orientation could be assigned to each, and thus an orientation map could be measured in the model V1. Remarkably, the emergent orientation maps revealed smooth topological patterns punctuated by pinwheels (figure 6C).

The model of von der Malsburg (1973) makes explicit several of the concepts introduced in the previous section. Here the feature space comprises a single dimension with a periodic topology, with one parameter value uniquely determining each retinal input pattern. As the V1 neurons are directly connected to the representation of the retina (and hence no intermediate thalamic circuitry is modeled) the pattern of afferent weights is a good estimate of the receptive fields of the neurons. Lateral interactions lead to self-sustaining activity bubbles from the lateral connections between cortical neurons. Crucially, the receptive fields and their spatial distribution across V1 emerge from a process of learning that is driven

by homogeneous and local communication between neurons. The emergent organization is the result of self-organization, because once the architecture of the network has been configured, no mechanism with access to the state of all cortical neurons is required to give rise to a pattern of organization defined across the population.

The von der Malsburg (1973) networks were trained by presenting all oriented patterns at a single location on the small patch of simulated retina, and thus learnt to represent only orientation and not other feature dimensions like retinotopic position. Willshaw and von der Malsburg (1976) showed how a very similar model could explain aspects of retinotopic mapping instead, if retinal patterns vary in their position rather than orientation. The Laterally Interconnected Synergetically Self-Organizing Map model (LISSOM) of Sirosh and Miikkulainen (1994) further extended this model to include both retinotopy and orientation or another feature preference simultaneously, and to allow plasticity of lateral connections to explain the type of patchy connectivity shown in figure 5. LISSOM also abstracted over some of the features of the original 1973 model, such as describing cortical units as mini-columns and thus collapsing V1 to a single population of units that can both excite and inhibit neighbors. Related self-organizing-map (SOM) models further abstracted the lateral interactions into a process of picking single winning neurons, but could generate similar results (Obermayer and others, 1990; Ritter and others, 1992). Later versions of the LISSOM model instead added biological details not in the 1973 model, such as a representation of thalamic processing between the sensory and cortical sheets that allows them to accept natural images as input, as well as modeling numerous feature dimensions simultaneously (e.g. orientation, ocular dominance, and motion direction; Miikkulainen and others, 2005; Bednar and Miikkulainen, 2006). The LISSOM model otherwise retains the essential normalized Hebbian learning rule and recurrent architecture of short-range excitation and long-range inhibition as in the original 1973 model (see also Carreira-Perpin and Goodhill, 2004). More recent versions of the LISSOM model, called GCAL (Gain Control, Adaptation, Laterally connected; Stevens and others, 2013), replace many of the hand-tuned parameters of earlier models with automatic homeostatic mechanisms, which make the model robustly and stably generate map patterns and representations that reflect the feature dimensions of the environment, as observed in animals (Chapman and others, 1996; Tanaka and others, 2006).

Complementary to the mechanistic approach taken by von der Malsburg (1973), Willshaw and von der Malsburg (1976), Miikkulainen and others (2005), and

Stevens and others (2013), a different approach is to simply assume that stable maps of the feature space will emerge, and to ask under what regime of the network particular types of overall map pattern are most stable. A model developed by Wolf (2005) describes the lateral interactions between neurons by a mathematical kernel applied across a continuous two-dimensional cortical surface, and describes learning not in explicitly cortical terms but implicitly as a function of the distance between neuronal receptive fields in feature space. When described in this way, the functional organization can be shown to yield realistic topological map patterns only when certain constraints are imposed. Wolf (2005) proved mathematically, and demonstrated computationally, that the key constraint that guarantees that orientation maps will emerge as the tiling of pinwheels seen in primate V1 is inhibitory interactions that are strongest between neurons representing similar orientations and long-ranging across the cortex compared to excitation. When this constraint is enforced via the kernel a clear prediction of the model can be derived from its equations; pinwheels should on average be spaced π hypercolumns apart (Kaschube and others, 2008). The same property was also found in the GCAL model (Stevens and others, 2013; see figure 7). Quite remarkably, when the pinwheel density of maps in tree shrews, bush babies, and ferrets were later measured, they were found to converge to π (Kaschube and others, 2010; see also Keil and others, 2012). These mammalian lineages diverged over 65 million years ago, hence orientation-specific long-range inhibitory interactions seem to have been either an evolutionarily well conserved constraint on the mechanisms of map formation, or an example of convergent evolution.

Complications

Models implementing the self-organization theory of cortical map formation have been able to replicate many of the properties of cortical maps, including topographic map formation, a wide range of specific feature maps, interactions between overlaid maps, feature coverage, receptive field formation, patterns of lateral connectivity, emergence of selectivity over time, changes to the maps due to altered environments, and plasticity in response to lesions of the receptors or cortical surface (reviewed in Miikkulainen and others, 2005; Bednar, 2012; Swindale, 1996). Models not based on neural activity and plasticity have not been able to account for even a fraction of these phenomena, and there is not currently a credible alternative to the self-organizing models in most cases.

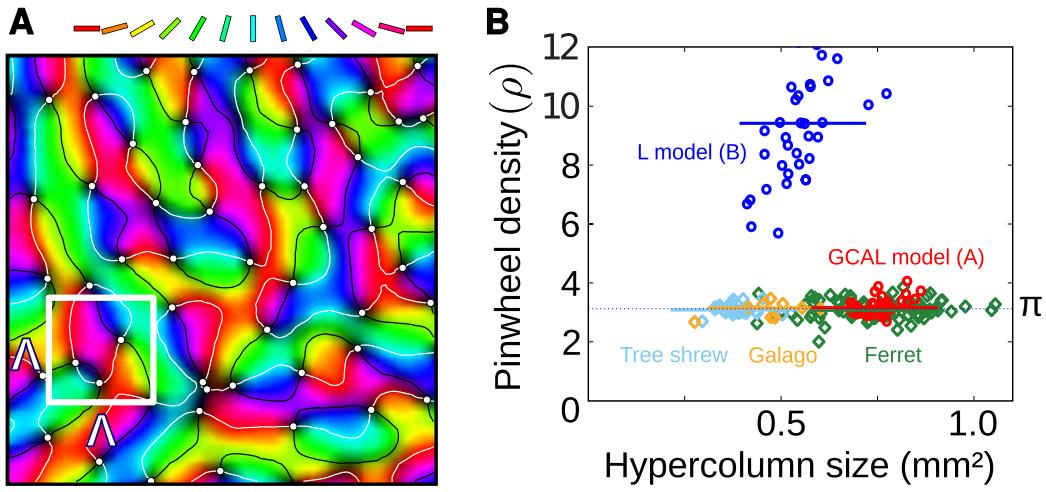


Figure 7: Universal properties of maps across species. **A.** Pinwheels (point singularities) in the orientation map can be labeled automatically, as shown with white dots here for a GCAL model orientation map from Stevens and others (2013). **B.** If an area is drawn corresponding to the average distance Λ at which orientations repeat across the map, the average number of pinwheels in this area is π (Kaschube and others, 2008) across a large number of non-rodent species tested. Data for animals from three species is shown here, where each dot is a cortical hemisphere analyzed as in **A**. This property was predicted from a model (Kaschube and others, 2008) and is true of the GCAL model, but has not been found for other mechanistic models tested so far, such as the simpler L model also from Stevens and others (2013). Reproduced from Stevens and others (2013), with permission of Society for Neuroscience.

However, there remain numerous important phenomena not explained by self-organizing models, or which appear to be in direct conflict with these models. The subsections provide a guide to these issues, suggesting alternative models or extensions to the models in each case.

Activity-independent development of topography

Even though self-organizing models *can* develop realistic maps based on cues from neural activity, experimental evidence strongly suggests that at least the initial topographic maps between regions are actually independent of neural activity, and thus require other mechanisms. For instance, neurons from the eye still locate their targets in downstream regions reliably and in the same rough topographic order even if neural activity is disrupted using tetrodotoxin (reviewed in Huberman and others, 2008).

This initial development has been well described by a series of models based on chemoaffinity, using gradients of chemical markers expressed in the source and target regions that axons can use to provide a rough relative coordinate system sufficient to establish the mapping (Flanagan, 2006; Hjorth and others, 2015). Activity has only apparently minor influence on this process (Kita and others, 2015). Thus in practice, current self-organizing models simply assume an initial rough topography to have been set up by such mechanisms, and focus on subsequent activity-dependent processes (Stevens and others, 2013).

Feature maps present at birth

An even more serious issue is that most of the properties of primary sensory maps reviewed above are found even in animals deprived of the relevant sensory input, and possibly before the relevant sensors are even capable of relaying information from the environment (Huberman and others, 2008). At first these findings would seem to contradict theories based on incoming neural activity, but it turns out that for primary sensory regions, the requisite neural activity is apparently present even without external environmental stimulation. Such spontaneous activity has been found throughout the sensory regions, and in the retina has been shown to share important properties with subsequent visual experience (such as spatiotemporal

locality; Feller and others, 1996; Huberman and others, 2006; Cang and others, 2005).

Self-organizing models have been shown to develop realistic maps when given approximations to spontaneous activity patterns as input (Stevens and others, 2013). However, because the detailed properties of the spontaneous activity patterns are not well established, it is not yet clear if the activity does have all the features necessary to develop realistic patterns of the maps seen prior to visual experience, or whether the models will account for the detailed interaction between the environment and previously established map structure. For instance, orientation maps in V1 match between the two eyes even without visual experience, which would not be expected if the eyes generate spontaneous activity independently (Jegelka and others, 2006), but recent evidence shows correlations between activity in the two eyes that could be sufficient for such matching (Ackman and others, 2012). Making comprehensive measurements of spontaneous activity across early sensory systems will be crucial for testing hypotheses about the source of the initial organization.

Postnatal plasticity

Of course, feature-map models have been proposed that use mechanisms fully independent of activity, such as relying on geometric patterns formed by overlapping arbors of sensory cells (Paik and Ringach, 2011), although these models have so far failed key tests of plausibility (Hore and others, 2012; Schottdorf and others, 2014). There are also models based on spontaneous intracortical activity rather than sensory activity (Grabska-Barwinska and von der Malsburg, 2008; Ernst and others, 2001). In any case, it is difficult to reconcile any of these types of models with the postnatal effects of visual experience. For instance, kittens reared using goggles that blur all but vertical orientations develop orientation maps dominated by vertical-preferring neurons (Tanaka and others, 2006),

In principle, input-driven self-organizing models should be able to explain the various effects of the rearing environment on the resulting functional properties and organization, such as the goggle-rearing experiments (Stevens and others, 2013). However, these models have the opposite problem, i.e., explaining the limited plasticity actually observed in primary sensory areas in animal systems. Many studies have failed to find significant effects of the environment on measurable properties of sensory cortical areas, and when they have been established

it has typically only been during specific critical periods after birth (Huberman and others, 2008). A detailed explanation for why there should be such limits to plasticity, including what mechanisms achieve this, remains to be formulated, and will require substantial further experimentation.

The rodent problem

Finally, a major problem with theories based on self-organization is explaining cases where maps are *not* well organized, yet individual neurons are selective. In particular, although primates, carnivorans, and many other species exhibit the smooth, continuous map organization predicted by these models, rodent primary visual cortex maps with orientation-selective cells appear randomly organized (Ohki and others, 2005b, 2006b; Ohki and Reid, 2007; see figure 4A). There is as yet no consensus on what causes these qualitative differences between species, but some speculative theories have been advanced, as described next. For instance, given that the smoothly varying preferences are established by lateral connectivity, larger variations in this connectivity in rodents could be sufficient to explain the lack of orientation maps (Law, 2009).

Another possibility is based on the observation that the ‘salt-and-pepper’ random maps were measured by Ohki and others (2005b) in 27-31 day old mice. Interestingly, there is evidence from rodent S1 that smooth maps can emerge as late as three months postnatally, suggesting an intriguing though highly speculative possibility that rodent maps simply generally emerge later in development. Andermann and Moore (2006) measured a topographic pinwheel map within a whisker-related barrel column of three-month old rats, such that deflection of whisker A towards whisker B selectively activates barrel A neurons closest to barrel B (see also Bruno and others, 2003; Tsytsarev and others, 2010). A subsequent two-photon imaging study reported only weak tuning for whisker direction and a random whisker direction map in younger animals (25-35 days; Kerr and others, 2007, see also Clancy and others, 2015 for recent evidence of ‘salt-and-pepper’ maps for whisker identity). A self-organizing model driven by multi-whisker input generates topographic pinwheels (Wilson and others, 2010), and the prediction of the model that whisker maps emerge late was confirmed by Kremer and others (2011) who found both weak map patterns in juveniles (32-39 days) and pinwheels in adults (81-112 days, see figure 8). An interesting parallel may also be drawn with the study of tonotopic maps in mouse primary auditory

cortex (A1). The existence of smooth tonotopic maps in mouse A1 appeared first to be accepted (Stiebler and others, 1997; Zhang and others, 2005), before being disputed by two-photon calcium imaging data showing a tonotopic arrangement on a macroscale but not at the resolution of individual neurons (Rothschild and others, 2010, and Bandyopadhyay and others, 2010, in 13-35 day old mice), and later accepted again (Hackett and others, 2011), most recently using two-photon imaging in slightly older animals (24-43 days; Winkowski and Kanold, 2013).

It is therefore possible that topological orientation preference maps may yet be found in V1 of older rodents. Interestingly, a study of spiking synchrony between pairs of V1 neurons in older mice (56-168 days) found stronger synchrony between neurons with similar orientation preferences and between neurons that are closer together (Denman and Contreras, 2014). The authors assumed that topological maps are absent in mouse V1 and thus concluded that the functional organization was independent of an underlying map pattern, but in light of the evidence that rodent S1 maps emerge late it would be interesting to establish whether these correlations together in fact define a topological map. In a study of 2-5 month old mice, Bonin and others (2011) similarly found that (weak) correlations in calcium signals reduce as a function of the distance between cortical neurons, but also as differences in the preferred orientation and retinotopic location of neurons increases, although they attribute most of the organization to an overall retinotopic mapping.

Making the conservative assumption that rodents never do develop smooth V1 orientation maps, then one may instead try to explain this with reference to the size of rodent V1 (see Meng and others, 2012, and Keil and others, 2012, for discussion). As cortical neurons cannot be scaled down too far without losing the ability to generate spikes (Kaas, 2000), connections across the relatively small mouse V1 will span a large portion of the visual field. Hence the effects of local interactions shown by self-organizing models to be so important for the emergence of topological maps may be masked by an effectively global interaction range for each neuron across V1 (see Harris and Mrsic-Flogel, 2013). Orientation-specific interactions could thus be established by the same self-organizing learning process, but operating in a non-local regime where spatially smooth maps would not form. Evidence in support comes from recent data showing that the firing patterns of supragranular neurons in mouse V1 are strongly correlated between neurons representing similar orientations (Ko and others, 2013; Denman and Contreras, 2014, see also Kaschube, 2014). Ko and others (2013) also report that orientation-specific interactions in mouse V1 are stronger in mice tested after the

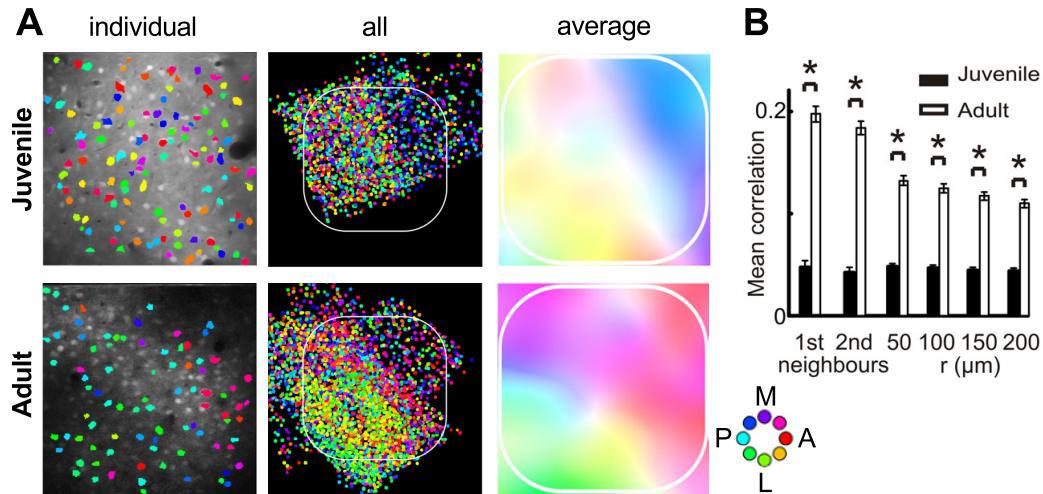


Figure 8: Postnatal development of whisker direction preference maps in rodent barrel cortex. **A.** The organization of direction preferences in juvenile (32–39 days postnatal) versus adult (81–112 days) rats. The preferences are shown for a $300 \times 300 \mu\text{m}$ region from a representative individual from each group in the left column, as a superposition of 29 juvenile barrel fields and 41 adult barrel fields in the center column, and as a smoothed plot on the right, where saturated colors represent locally homogeneous preference values. Colors indicate preferences for whisker deflections medial, lateral, posterior, anterior, or intermediate, using the key shown at right. The smoothed plots reveal a pinwheel organization in adults that is oriented somatotopically with the alignment of the barrel compared to other barrels in S1. **B.** Mean correlations between neighboring neurons across all barrel fields are significantly higher in adults, and fall off with the cortical distance between them r . Reproduced from Kremer and others (2011), with permission of Society for Neuroscience.

eyes open than before. Specifically, orientation tuning was higher in mice aged 28-35 days compared to mice aged 14-15 days. The data were well described by a self-organizing model driven by visual experience, suggesting that recurrent cortical circuitry is refined by activity-dependent processes, although a subsequent study from the same group found that orientation-specific connectivity emerged surprisingly robustly in dark-reared animals, thus suggesting an important role for intrinsic factors too (Ko and others, 2014).

Squirrels, however, are an interesting challenge to most such explanations for the lack of rodent feature maps. Squirrels are highly visual, high-acuity rodents with a V1 comparable in size to ferrets, and with an ecological niche comparable to that of tree shrews, yet they do not appear to have smooth orientation maps (van Hooser and others, 2005). It is of course possible that despite these similarities, squirrels share common evolutionary pressures with other rodents that they do not share with animals with topological maps. Theoretically, primate-like topological maps have been found to optimize intracortical wiring lengths under the constraint that similarly tuned features should be preferentially connected, while random maps optimize wiring lengths under the constraint that neurons should form connections to others covering the full range of features (Koulakov and Chklovskii, 2001). Perhaps, for reasons as yet unknown, such patterns of connectivity are more suited to the problems being solved by squirrel visual systems, though if so they are difficult to reconcile with the orientation-specific connections observed in mouse (Ko and others, 2013).

According to most self-organizing models, orientation preferences are constructed in V1 by a spatially specific combination of outputs from orientation-unselective LGN neurons, as proposed originally by Hubel and Wiesel (1962; see also Linsker, 1988). However, recent data suggest that LGN neurons may already have a degree of orientation selectivity in many species. Orientation preferences have recently been reported in the LGN of marmoset monkeys (Cheong and others, 2013), ferrets (Van Hooser and others, 2013, albeit with rather weak selectivity), and cats (Scholl and others, 2013). Compared to cats, rodents have up to four times as many orientation (and direction) tuned LGN neurons (Scholl and others, 2013), and detailed evidence for orientation (and direction) preferences in rodent LGN has been accumulating recently (see Niell, 2013, and Dhane and Huberman, 2014, for reviews). It is possible that an orientation preference map may be revealed across rodent LGN, as whisker movement directions have found to be mapped topologically across the vertical extent of somatosensory thalamic ‘bar-reloids’ (Timofeeva and others, 2003; Li and Ebner, 2007), and as tonotopic maps

have been established in auditory thalamic nuclei (Hackett and others, 2011).

Interestingly, Piscopo and others (2013) found that many orientation and direction selective neurons in mouse LGN had non-linear receptive fields, i.e., they were orientation and/or direction selective and fired at similar rates for all spatial phases of a drifting sinusoidal image. In contrast to other cells with linear phase response properties, these neurons had linearity indices of $F = 1.0 \pm 0.18$, placing them on the border between simple ($F = 0$) and complex ($F = 2$) cells (Skottun and others, 1991). In primates, cells with nonlinear phase responses are first found in V1 (Hubel and Wiesel, 1962), and self-organizing models have explained this emergent property as a process of local pooling in V1 from cells that are selective for similar orientations (because of primate V1's topological map of orientation) but different phases (due to local variability in receptive field structure; Antolik and Bednar, 2011; Hyvärinen and others, 2009; Weber, 2001). This finding raises the intriguing possibility that orientation preference maps may not emerge at the cortical level in rodents, simply because such nonlinear cells are already present at the LGN level (in line with the hypotheses of Nauhaus and Nielsen, 2014, and Wilson and Bednar, 2015).

Conclusions

A wide range of properties of cortical maps have now been established based on studies of sensory cortical areas. Self-organization provides a strong theory of how map patterns form, through local activity-based interactions between neurons with plastic connections. Despite the lack of serious alternative theories for the bulk of cortical map phenomena, there are numerous outstanding issues with this explanation, and extensive further experimentation will be required so that the limits can be determined and other such mechanisms revealed. It is also not yet clear whether cortical map patterns are themselves useful, with some authors arguing that they are simply epiphenomena of important evolutionary or developmental processes, rather than being specifically adaptive (Purves and others, 1992; Wilson and Bednar, 2015). In any case, developing coordinated sets of neurons with response properties that together represent the external world is clearly important, establishing a fundamental role for cortical maps in brain function.

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