

Cortical Columns

Intermediate article

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In many regions of the cortex, neuronal response properties remain relatively constant in a direction perpendicular to the surface of the cortex, while they vary in a direction parallel to the cortex. Such columnar organization is particularly evident in the visual system, in the form of ocular dominance and orientation columns.

INTRODUCTION

The most prominent feature of the architecture of the cortex is its horizontal organization into layers. Each layer contains different cell types, and forms different types of connections with other neurons. However, a strong vertical organization is often also apparent: neurons stacked on top of each other through the depth of the cortex tend to be connected and have similar response properties despite residing in different layers. This type of vertical structure is called a *cortical column*, and has been hypothesized to represent a basic functional unit for sensory processing or motor output. Columnar organization has been most extensively studied in the somatosensory and visual systems.

DISCOVERY OF COLUMNAR ORGANIZATION

Cortical columns were first discovered electrophysiologically by Mountcastle (1957). When he moved an electrode obliquely to the surface of somatosensory cortex, he encountered neurons that responded to different sensory submodalities (e.g. deep versus light touch). However, when the electrode was moved perpendicularly to the cortical surface, all neurons had similar response properties. He summarized his findings as follows:

These data ... support an hypothesis of the functional organization of this cortical area. This is that the neurons which lie in narrow vertical columns, or cylinders, extending from layer II through layer VI make up an elementary unit of organization, for they are activated by stimulation of the same single class of peripheral receptors, from almost identical peripheral receptive fields, at latencies which are not significantly different for the cells of the various layers.

Shortly following this, vertical uniformity was also found in the visual system by Hubel and Wiesel (1977). Here, response properties that vary across the cortical surface but not through the depth of the cortex include the location of the neuron's receptive field in visual space, and the degree to which neurons are dominated by one eye. Columnar organization has also since been found in the auditory cortices of cat and monkey, where alternating bands related to monaural or binaural responses occur. A number of techniques have been employed for the experimental determination of cortical columns since the original use of electrode penetrations. These include methods based on axonal transport of substances such as horseradish peroxidase; on the differential consumption of radioactive 2-deoxyglucose by neurons; on optical imaging techniques, where cortical activity is converted to a visual signal by changes in reflectance or by voltage-sensitive dyes; and most recently on functional magnetic resonance imaging (fMRI).

There are some difficulties with defining exactly what is meant by a column. In some cases it is relatively clear: for instance, 'barrels' in somatosensory cortex and ocular dominance columns in visual cortex have fairly discrete boundaries with neighboring columns. In other cases, for instance orientation columns, there is a smooth variation in response properties moving parallel to the cortical

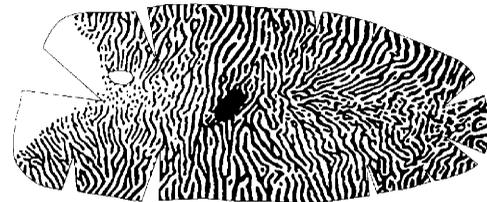
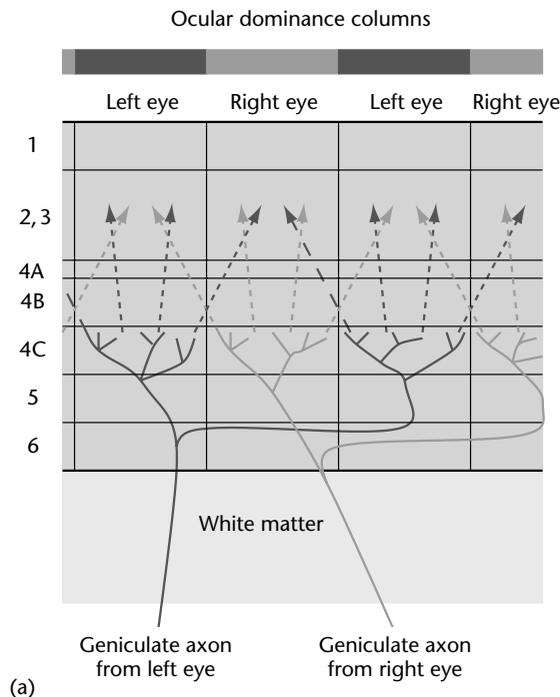
surface, rather than a series of discrete jumps. Another problem is that the term ‘column’ has been used to refer to structures at several different scales. At one extreme, from an anatomical point of view, are narrow vertical chains of neurons seen in Nissl-stained sections, barely more than one cell diameter wide, sometimes called *minicolumns*. At the other extreme, largely from a theoretical point of view, are complete functional units up to 1 mm in size, sometimes called *hypercolumns*. In between, Szentágothai (1978) specifies a generic column to be 200–300 μm wide. This article avoids such definitional issues by focusing on well-characterized examples of columnar organization. (See **Neuroimaging**)

COLUMNS IN THE VISUAL SYSTEM

Ocular Dominance Columns

Moving parallel to the surface of the primary visual cortex (V1) of several mammalian species, notably

ferrets, cats, monkeys, and humans, there is a regular alternation between groups of neurons that respond best to input in the left eye and neurons that respond best to input in the right eye. The anatomical basis of this physiological pattern is the segregation of the thalamic input fibers – lateral geniculate nucleus (LGN) afferents – representing the left and right eyes to the visual cortex (Figure 1(a)). Although these fibers terminate primarily in layer 4 of the cortex, and this is where ocular preference is most sharply defined, a similar bias is also seen in higher and lower layers. This vertical structure of monocular preference is called an ‘ocular dominance column’ (reviewed by Hubel and Wiesel, 1977). When the entire pattern of eye preference is visualized in V1, for instance by injection of a radioactive tracer into one retina and its subsequent transport to the cortex, an alternating pattern of stripes is observed (Figure 1(b)). The periodicity of this pattern varies depending on the species and location in the cortex, and also varies substantially between individuals (Horton and Hocking, 1996):



(b)

Figure 1. Ocular dominance columns in a monkey. (a) Anatomical basis. Each afferent axon from the lateral geniculate nucleus ascends through the deep layers of V1 (layers 5, 6) subdividing repeatedly and terminating in layer 4C in a couple of 0.5 mm-wide clusters separated by 0.5 mm gaps (approximately). Axons from the two eyes alternate, giving ocular dominance columns in 4C. The presence of horizontal connections and the arborization between different layers brings about overlapping and blurring of ocular dominance columns beyond layer 4: the ocular dominance of a given cell varies then between pure monocularity and pure binocularly. Adapted from Hubel (1995). (b) The pattern of ocular dominance columns from the primary visual cortex of a macaque monkey. White represents regions of cortex dominated by input from one eye, black the other eye. The width of individual columns is 0.5–1 mm. Source: LeVay *et al.* (1985) *Journal of Neuroscience* 5: 486–501, © 1985 by the Society for Neuroscience.

in fact, each ocular dominance pattern is apparently as unique as a fingerprint. It can be seen from Figure 1 that these columns are in fact more like slabs, being long and relatively narrow rather than short and round.

Orientation Columns

Another type of columnar organization observed in the visual cortex is the orientation column. Many neurons in V1 respond best to an edge or bar of light at a specific orientation. This preferred orientation remains roughly constant through the depth of the cortex but varies mostly smoothly across the surface of the cortex. The overall pattern of orientation columns can be visualized by optical imaging methods. Cortical tissue changes its reflectance properties very slightly when neurons are active, and so by examining changes in reflected light from the cortical surface as visual stimuli of varying orientations are presented one can build up a picture of the complete map. An example is shown in Figure 2. A notable feature is the presence of pinwheels, point singularities around which all orientations are represented in a radial pattern. Superimposing the ocular dominance and orientation maps from the same animal, one observes regular geometric relationships between the two columnar systems. For instance, ocular dominance and orientation columns tend to meet at right angles, and orientation pinwheels tend to lie at the center rather than at the borders of ocular dominance columns.

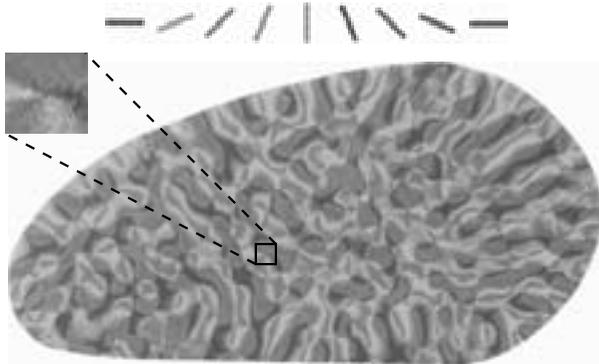


Figure 2. The orientation map in primary visual cortex of a tree shrew. The different degrees of shading represent patches that have different orientation preferences. The detail shows a pinwheel, where the orientation preference changes by 180° along a closed path around the center. Adapted from Bosking *et al.* (1997) *Journal of Neuroscience* 17: 2112–2127, © 1997 by the Society for Neuroscience.

Other Types of Columns

Besides ocular dominance and orientation columns, several other types of columns are also present in the visual cortex. The most fundamental of these are what might be called position columns. Neurons in V1 have small receptive fields localized at specific positions in visual space. Moving vertically through the cortex, neurons have receptive fields at similar positions, while moving horizontally there is a smooth progression of visual field position versus cortical position, forming a topographic map of visual space in the cortex. This locality of information processing in visual cortex can also be seen from the fact that a small injury (e.g. a tumor or stroke) in part of V1 can cause blindness in a localized area in the visual field (a scotoma) with normal vision elsewhere, rather than an overall worsening of vision. Other receptive field properties that are organized into columns include preference for the spatial frequency of a stimulus across the receptive field, preference for the direction of movement of a stimulus, and disparity of inputs from the two eyes. All these columnar systems occupy the same cortical territory as the ocular dominance and orientation columns, and show complex geometric relationships that have yet to be fully characterized. Color-sensitive cells in layers 2–3 of monkey visual cortex (although not in other layers) are grouped in blobs, in which neurons respond to the color of a stimulus, but are mostly insensitive to orientation – unlike cells outside the blobs (the interblobs) which show marked orientation selectivity. (See **Color Vision, Neural Basis of; Depth Perception**)

Factors Driving the Formation of Columns

A number of different experiments on visual deprivation, where the visual experience that an animal receives is distorted, have shown that it is possible to produce physiological and structural changes in the columnar organization of visual cortex. For example, if one eye is sutured closed or strabismus is induced then most cells become monocular; if animals are presented with only bands at a specific orientation angle, then the proportion of cells that respond to that angle increases; if movement in a particular direction is excluded, the cells that would have responded to that movement direction no longer do so. Recovery to normal structure is also possible. However, both deprivation and recovery are effective only in an early period of the life when the connections are

developing. These experiments suggest that the development of ocular dominance columns is the result of two competing processes: segregation is promoted when neural activity is equal in each eye but not correlated between both eyes; and binocular innervation of neurons and merging of the two sets of columns is promoted by the correlation in activity between corresponding retinal areas of the two eyes that results from normal binocular vision.

However, the relative importance of intrinsic, or genetically programmed, factors versus extrinsic, or activity-driven, factors is still not clear. On the one hand, Crowley and Katz (1999) found that total removal of retinal influence early in visual development did not prevent segregation of geniculocortical axons into ocular dominance columns of normal periodicity. They thus propose that ocular dominance column formation relies on molecular cues present on thalamic axons, cortical cells, or both. On the other hand, Sur and colleagues (e.g. Sharma *et al.*, 2000) have surgically rewired the optic nerve of newborn ferrets to feed into auditory thalamus (itself deprived of auditory inputs), which in turn projects to primary auditory cortex (A1) – rather than the normal pathway, optic nerve to LGN to V1. Such rewired ferrets develop in A1 a pattern of orientation columns with some similarities to that normally present in V1, though with a less regular periodicity. Such new cortical structure perceptually acts as visual; that is, the animals use the rewired A1 to see, rather than hear – although the resulting visual acuity is lower than normal. This suggests that retinal inputs can drive the formation of columns.

COLUMNS IN THE SOMATOSENSORY SYSTEM

The first physiological indication of cortical columns came from experiments by Mountcastle (1957) in the somatosensory cortex of cats. He found three types of neurons: those activated by light pressure on the skin, those activated by movement of hairs, and those activated by deformation of deep tissues (as occurs during for instance joint movement). As summarized by Mountcastle:

Cells belonging to each subgroup were found in all the cellular layers. In 84 per cent of penetrations across the cellular layers which were directed perpendicularly, all the neurons encountered belonged to either cutaneous or deep subgroups. These modality-specific vertical columns of cells are intermingled for any given topographical region.

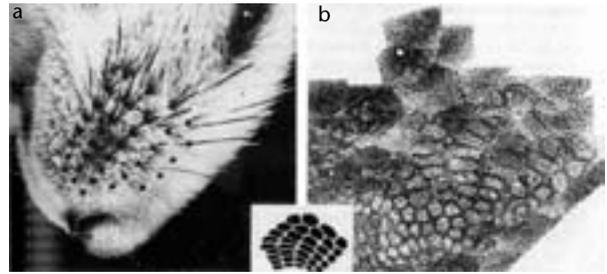


Figure 3. Posteromedial barrel subfield from a mouse's muzzle. Reprinted from Woolsey TA and van der Loos H (1970) The structural organization of layer IV in the somatosensory region (SI) of mouse cerebral cortex. *Brain Research* 17: 205–242, © 1970, with permission from Elsevier Science.

More recent results have amplified this. For instance, Favorov and Diamond (1990) found discrete jumps in receptive field location between neighboring columns in cat primary somatosensory cortex, with no significant receptive field shifts within a column. However, the most striking example of columns in somatosensory cortex are the 'barrels' discovered by Woolsey and van der Loos (1970). In animals such as mice and rats, the long whiskers of the face are present in a stereotyped spatial pattern of rows. This is reflected in the posterior-medial barrel subfield of primary somatosensory cortex by a similar spatial pattern of columns, one column for each whisker (Figure 3). These are best defined in layer 4 where the thalamic afferents terminate. However, specialization to a single whisker is also apparent in higher and lower layers, and owing to their three-dimensional shape these columns were dubbed 'barrels'. The number and layout of these barrels can be altered by manipulations of the sensory periphery, such as removing a whisker.

COLUMNS IN OTHER SYSTEMS

The primary auditory cortex (A1) of animals such as cats and bats shows a systematic, spatially distributed representation of several independent auditory stimuli (reviewed in Schreiner, 1995). However, these auditory maps appear somewhat disordered because the local scatter of receptive field properties can vary over a wide range. The most regular map is that of preferred frequency, organized along a tonotopic axis without gradient reversals that mimics the tonotopic organization of the cochlea. Orthogonal to this axis, no systematic change of the preferred frequency is observed, with neurons being arranged along isofrequency contours. Other response parameters vary along the

isofrequency contours in a systematic way, such as the bandwidth and shape of tuning curves. Further maps also appear to be represented in a columnar fashion, such as the coding of intensity and sound localization, but the details of their organization are still unclear. (See **Audition, Neural Basis of**)

Inferotemporal (IT) cortex is a visual area essential for object perception and recognition. Using intrinsic signal imaging and extracellular recording in macaque monkeys, Tsunoda *et al.* (2001) showed that the neural activity evoked in IT by complex objects is laid out spatially as distributed patches. This result suggests that an object is represented by a combination of cortical columns, each of which represents a visual feature. However, not all the columns related to a particular feature were necessarily activated by the original objects. Thus, objects would be represented by using a variety of combinations of active and inactive columns for individual features, rather than simply by the addition of feature columns. It is unclear, though, whether an object is represented by a combination of modules, each specific to a visual feature or a part of the object (feature-based or part-based representation), or whether modules are specific to the object (object-based representation). (See **Temporal Cortex; Object Perception, Neural Basis of; Vision: Object Recognition**)

Columnar maps also exist outside the cortical areas, such as in the brainstem (maps of interaural delay, of interaural intensity difference, and of auditory space) and the superior colliculus (map of motor space, or gaze direction). (See **Motor Areas of the Cerebral Cortex**)

INTRACOLUMNAR AND INTERCOLUMNAR CIRCUITRY

Cortical columns are also distinguished from each other by their patterns of circuitry. The majority of intracortical circuits are local, connecting neurons within the same columns, with only a minority of connections being between columns. Again, this organization has been most extensively studied in the visual system.

Callaway (1998) proposed a generic model of vertical connectivity linking layers within a column in primary visual cortex of cats and monkeys (Figure 4). The model is based on three simplifying assumptions: only excitatory synapses are considered; each cortical layer provides its primary output to only one layer; and only two types of connections are considered (feedforward and feedback). A direct path from inputs (coming from the LGN) to outputs (going mainly to other areas in the

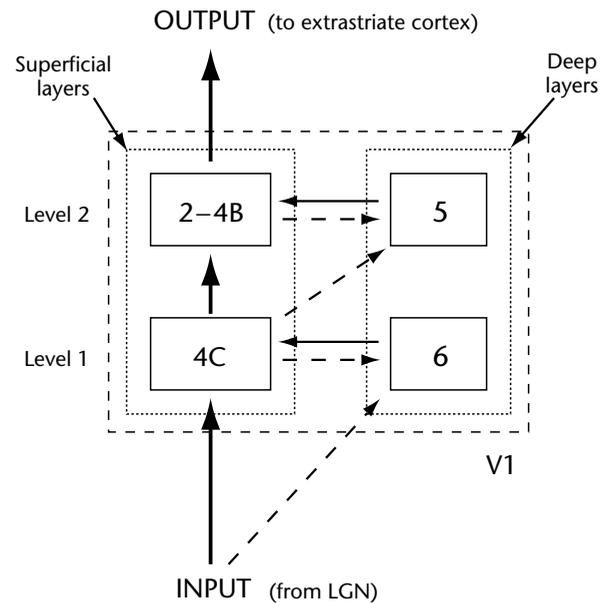


Figure 4. Two-level model of local cortical circuitry in V1. A direct path from input (from the lateral geniculate nucleus, LGN) to output (to extrastriate cortex) is provided by the two feedforward superficial layers 2–4B and 4C; feedback deep layers 5 and 6 modulate the activity of each level. Adapted from Callaway (1998).

cortex) passes through cortical layers 4C and 2–4B, with layers 6 and 5 providing feedback (modulatory) connections, respectively. Since these dense connections are mostly confined within a column, this provides a great deal of purely intracolumnar – and therefore local – information processing. Long-range connections (generally up to a few millimeters long) between columns mostly project within layer 2/3. They are generally sparse and patchy, and tend to connect spatially separated columns with the same feature preference, such as the same orientation or ocular dominance preference (although some recent experiments do not fully agree with this cluster-like connection pattern). It is easy to imagine how such specific patterns could arise as a result of Hebbian learning, since columns with similar feature preferences would be expected to have highly correlated activity. Likewise, it has been suggested that color blobs are preferentially linked to color blobs of the same ocular dominance, and interblobs to interblobs.

COLUMNAR DEVELOPMENT AND COMPUTATIONAL MODELS

The high degree of order displayed by columnar structures and the large amount of data acquired,

especially regarding the development of ocular dominance columns in primary visual cortex, has inspired several computational models of columnar development. Such models are useful to explain the processes at work as well as to produce predictions that can guide future experiments. They should also be able to account for interspecies variations and be generalizable to models for other areas of the cortex, assuming that the underlying mechanisms of cortical development are reasonably universal. An excellent review of such developmental models can be found in Swindale (1996). (See **Neural Development; Neural Development, Models of**)

Most models of visual cortical development are based on the following assumptions (which are partially supported by experimental data): patterned retinal activity in the afferents to cortical neurons; Hebb synapses; radially symmetric, short-range excitatory and long-range inhibitory lateral cortical connections; and normalization of synapse strength. Thus, most of these models largely disregard genetic factors and assume that the columns in the primary visual cortex appear during development from an apparently uniform cortical sheet by a process of activity-dependent self-organization that modifies synaptic strengths in response to patterns of visual stimulation. These patterns can be produced both externally by the world, and generated internally by spontaneous activity in the retina (Meister *et al.*, 1991). The rule by which synaptic strengths appear to change is roughly the one proposed by Hebb (1949): 'neurons that fire together wire together'. The models often represent the cortex as a two-dimensional array of neural units (each representing a collection of real neurons) and thus directly embody the definition of column. The visual stimulus is represented either in an abstract, low-dimensional way, as a vector of independent components representing ocular dominance, orientation preference, retinotopic position or direction preference; or in a concrete, high-dimensional way, as a vector containing the connection strengths between a cortical cell and a set of receptor cells in the retina. (See **Hebb Synapses: Modeling of Neuronal Selectivity; Hebb, Donald Olding**)

A common characteristic of these models is that they try to maximize coverage as well as continuity, as originally suggested by Hubel and Wiesel. Coverage refers to the fact that all combinations of eye and orientation preference occur at least once within any region (of a certain, small size) in stimulus space – otherwise, the animal might be blind to the unrepresented stimulus (although it has

been suggested that higher cortical areas could interpolate between incomplete representations in lower cortical areas). Continuity refers to the fact that the preferences of neighboring neurons in cortex tend to be similar. Representing a high-dimensional stimulus space in a two-dimensional cortex results in coverage and continuity competing at the expense of each other, with the striped organization observed being perhaps a locally optimal solution to their trade-off. (See **Vision: Occlusion, Illusory Contours and 'Filling-in'**)

Two particularly important types of models are correlational (e.g. Miller *et al.*, 1989) and competitive (e.g. Goodhill, 1993). In correlational models the input–output function of neurons is linear, and receptive field development is driven by the eigenvectors of an operator dependent on the correlation of the input patterns, the intracortical connections, and the LGN arborization. In competitive models the input–output function of neurons is highly non-linear, and such models implement something more akin to cluster analysis. Generally speaking, these models account for much of the observed phenomenology of cortical maps, including the striped structure of ocular dominance and orientation columns with the appropriate periodicity and interrelations, and the location of pinwheels and fractures. However, no model so far can account for all observed features for both ocular dominance and orientation maps at the same time, or for some of the more elusive data. (See **Pattern Recognition, Statistical; Receptive Fields**)

WHY A COLUMNAR ORGANIZATION?

The presence of a columnar organization in various regions of the cortex of many mammalian species has suggested that columns form the basic information processing elements of the cortex, with each column being responsible for analyzing a small range of stimuli, and the same modular unit being repeated multiple times to span the entire range of stimuli (e.g. Szentágothai, 1978). As such, columns have been considered to be a fundamental functional feature important for perception, cognition, memory, and even consciousness (Szentágothai, 1978; Eccles, 1981). However, there is no general agreement about the reason for the existence of such groupings. Such columnar structure has not been found in some mammalian species closely related to other species that do have columns (Purves *et al.*, 1992). Thus, it has been argued that the columnar organization of the cortex may not imply a functionally modular organization (Swindale, 1990; Purves *et al.*, 1992). In particular,

Purves *et al.* suggested that the production of iterated patterns of circuitry might be an incidental consequence of the activity-dependent elaboration of synaptic connections and be of little significance to cortical function. In other words, a given cortical system might work just as well if columns did not form. Purves *et al.* suggest several factors that could drive such origin. (See **Modularity in Neural Systems and Localization of Function; Synaptic Plasticity, Mechanisms of**)

CONCLUSION

Many areas of the cortex, particularly in the visual and somatosensory system, can be divided into repeating modules characterized by discrete patterns in both function and anatomy. The best-studied examples are 'barrels' and touch-modality columns in primary somatosensory cortex, and orientation and ocular dominance columns in primary visual cortex. There are many vertical connections linking neurons within a column, and a few horizontal connections linking different columns. Columnar development may be driven by activity-dependent self-organization, and can often be modeled using Hebbian learning rules – although the relative importance of genetic factors and patterned activity is not clear. As yet no compelling justification has emerged for why columnar structure exists. (See **Vision, Early; Pattern Vision, Neural Basis of; Cortical Map Formation**)

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