Cortical Columns

Geoffrey J. Goodhill   Miguel Á. Carreira-Perpiñán
Dept. of Neuroscience, Georgetown University Medical Center, Washington, DC
{miguel,geoff}@cns.georgetown.edu

April 8, 2002

Definition

In many regions of the cortex, neuronal response properties remain relatively constant as one moves 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 which responded to different sensory submodalities (e.g. deep vs light touch). However, when the electrode was moved perpendicular 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, reviewed in 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 versus the other eye (see later). Columnar organization has also since been found in the auditory cortex 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 fMRI.

There are some difficulties with defining exactly what is meant by a column. In some cases this 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 though, 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 1mm in size, sometimes called hypercolumns. In between, Szentágothai (1978) specifies a generic column to be 200–300μm wide. We will attempt to avoid such definitional issues by focussing just on some particularly well characterized examples of columnar organization.

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, one encounters a regular alternation between groups of neurons which respond best to input in the left eye and neurons which respond best to input in the right eye. The anatomical basis of this physiological pattern is the segregation of the thalamic input fibres (LGN afferents) representing the left and right eyes to the visual cortex (fig. 1(left)). Although these fibres 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 in 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 (fig. 1(right)). 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): in fact each ocular dominance pattern is apparently as unique as a fingerprint. It can be seen from fig. 1(right) 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 orientation columns. 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 fig. 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.

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 tumour 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. Colour-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 colour of a stimulus, but being mostly insensitive to orientation—unlike cells outside the blobs (the interblobs), which show marked orientation selectivity.
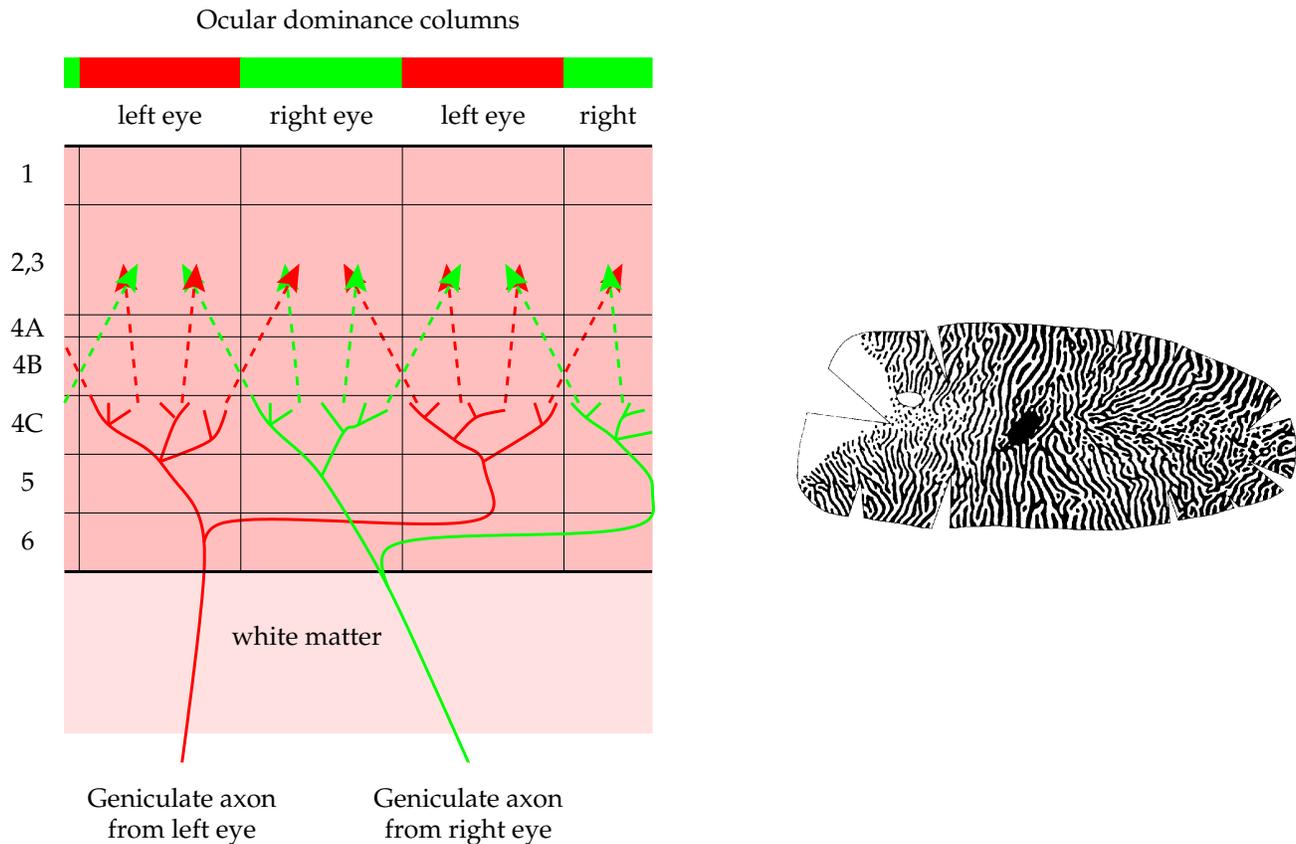
Figure 1: Ocular dominance columns in a monkey. *Left*: anatomical basis. Each afferent axon from LGN ascends through the deep layers of V1 (layers 5, 6) subdividing repeatedly and terminating in layer 4C in a couple of 0.5mm-wide clusters separated by 0.5mm-wide gaps (approximately). Axons from the 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 binocularity. (Adapted from: Hubel, 1995.) *Right*: 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 0.5mm–1mm. (Source: LeVay et al. 1985, *J. Neurosci.*, **5**, 486–501, © 1985 by the Society for Neuroscience.)

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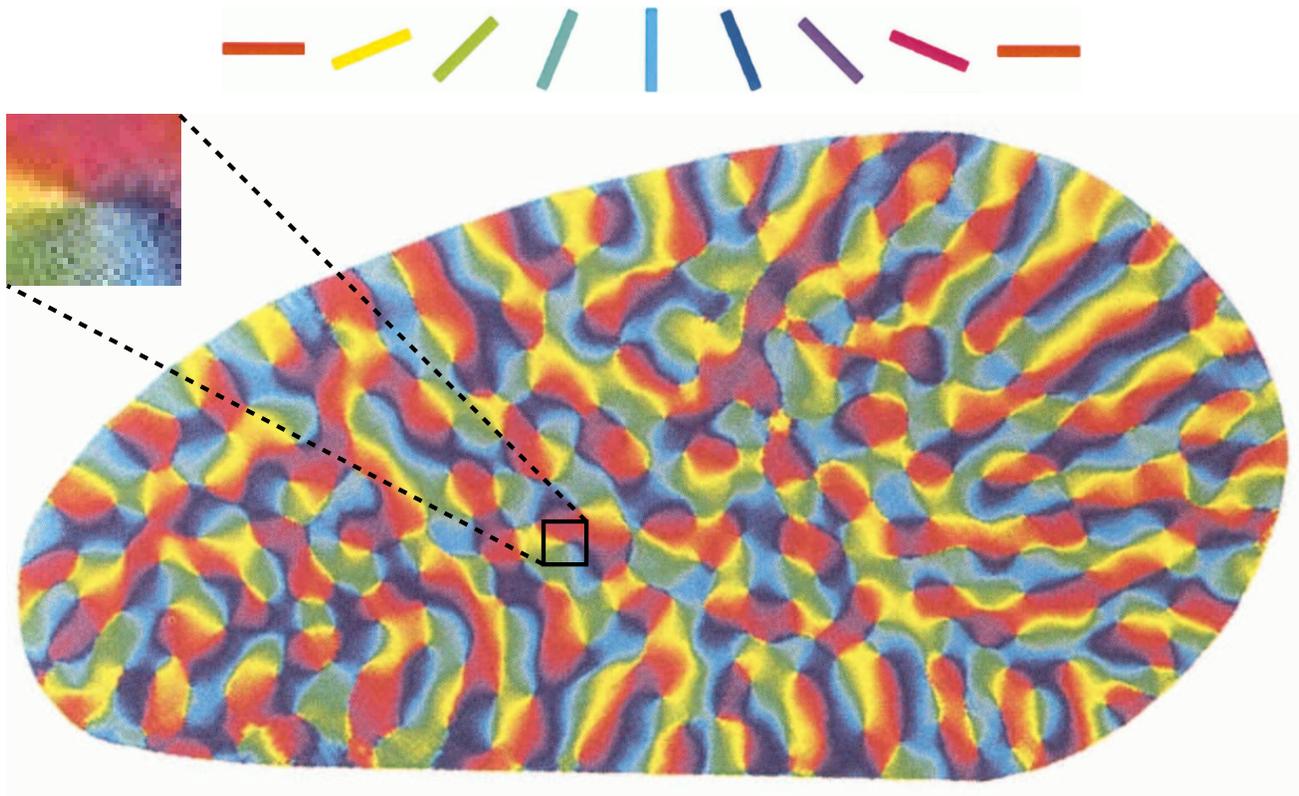
Figure 2: The orientation map in primary visual cortex of a tree shrew. The different colours represent patches that have different orientation preferences. The detail shows a pinwheel, where the orientation preference changes by 180° along a closed path around the center. (Adapted from: Bosking et al.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

inance 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

As already noted, the first physiological indication of cortical columns came from experiments by Mountcastle (1957) in the somatosensory cortex of cat. 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." 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 so-called 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
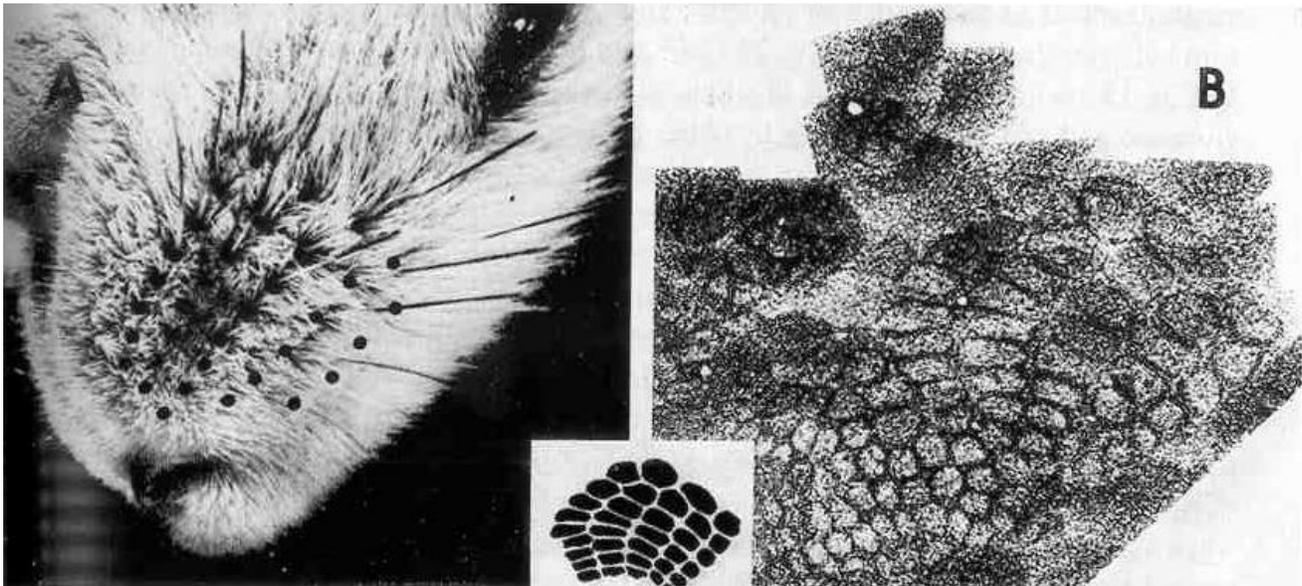
Figure 3: Posteromedial barrel subfield from a mouse's muzzle. (Reprinted from *Brain Research*, **17**, Woolsey and van der Loos, "The structural organization of layer IV in the somatosensory region (SI) of mouse cerebral cortex", pp. 205–242, © (1970), with permission from Elsevier Science.)

subfield of primary somatosensory cortex by a similar spatial pattern of columns, one column for each whisker (fig. 3). These are best defined in layer IV where the thalamic afferents terminate. However specialization to a single whisker is also apparent in higher and lower layers, and due to their three-dimensional shape these columns were christened 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.

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).

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).

OUTPUT   (to extrastriate cortex)

Superficial
layers

Deep
layers

Level 2

| 2 - 4B | | 5 |

Level 1

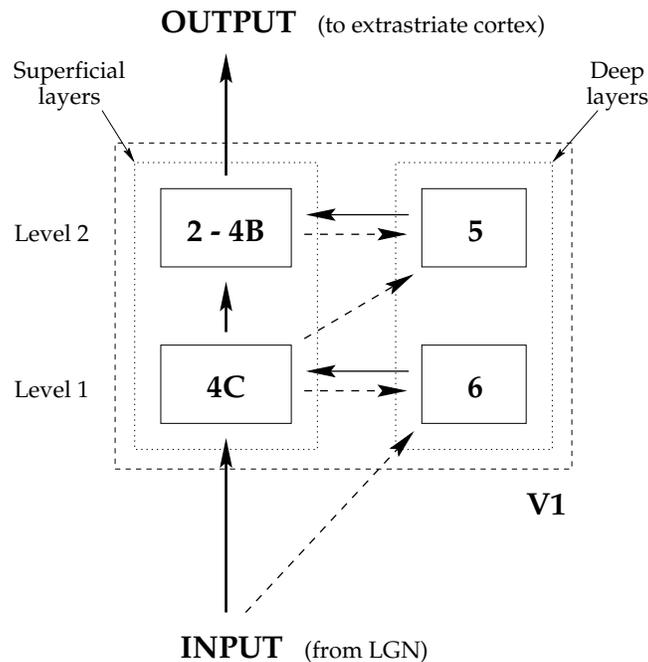| 4C | | 6 |

V1

INPUT   (from LGN)

Figure 4: Schematic of a two-level model of local cortical circuitry in V1 (adapted from Callaway, 1998). A direct path from input (from 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.

Intra- and inter-columnar 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) has proposed a generic model of vertical connectivity connecting layers within a column in primary visual cortex of cats and monkeys (see fig. 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 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 millimetres 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 colour blobs are preferentially linked to colour 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 that have been 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).

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.

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 neighbouring 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 tradeoff.

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 coonections 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.

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 a fundamental functional feature important for perception, cognition, memory and even consciousness (Szentágothai, 1978; Eccles, 1981). However, at present there is no general agreement in the reason for the existence of such groupings. Such columnar structure has not been found in some mammalian species sometimes 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. suggest 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.

Summary

Many areas of the cortex, particularly in the visual and somatosensory system, can be divided up 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 modelled 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.

References

Callaway, E. M. (1998). Local circuits in primary visual cortex of the macaque monkey. *Annual Review of Neuroscience*, 21:47–74.

Crowley, J. C. and Katz, L. C. (1999). Development of ocular dominance columns in the absence of retinal input. *Nature Neuroscience*, 2(12):1125–1130.

Eccles, J. C. (1981). The modular operation of the cerebral neocortex considered as the material basis of mental events. *Neuroscience*, 6(10):1839–1856.

Favorov, O. V. and Diamond, M. E. (1990). Demonstration of discrete place-defined columns–segregates–in the cat SI. *Journal of Comparative Neurology*, 298(1):97–112.

Goodhill, G. J. (1993). Topography and ocular dominance: A model exploring positive correlations. *Biological Cybernetics*, 69(2):109–118.

Hebb, D. O. (1949). *The Organization of Behaviour*. John Wiley & Sons, New York.

Horton, J. C. and Hocking, D. R. (1996). Intrinsic variability of ocular dominance column periodicity in normal macaque monkeys. *Journal of Neuroscience*, 16(22):7228–7339.

Hubel, D. H. and Wiesel, T. N. (1977). Functional architecture of the macaque monkey visual cortex. *Proceedings of the Royal Society of London B*, 198(1130):1–59.

Meister, M., Wong, R. O. L., Baylor, D. A., and Shatz, C. J. (1991). Synchronous bursts of action potentials in ganglion cells of the developing mammalian retina. *Science*, 252(5008):939–943.

Miller, K. D., Keller, J. B., and Stryker, M. P. (1989). Ocular dominance column development: Analysis and simulation. *Science*, 245(4918):605–615.

Mountcastle, V. (1957). Modality and topographic properties of single neurons of cat's somatic sensory cortex. *Journal of Neurophysiology*, 20:408–434.

Purves, D., Riddle, D. R., and LaMantia, A. S. (1992). Iterated patterns of brain circuitry (or how the brain gets its spots). *Trends in Neurosciences*, 15(10):362–368.

Schreiner, C. E. (1995). Order and disorder in auditory cortical maps. *Current Opinion in Neurobiology*, 5(4):489–496.

Sharma, J., Angelucci, A., and Sur, M. (2000). Induction of visual orientation modules in auditory cortex. *Nature*, 404(6780):841–847.

Swindale, N. V. (1990). Is the cerebral cortex modular? *Trends in Neurosciences*, 13(12):487–92.

Swindale, N. V. (1996). The development of topography in the visual cortex: A review of models. *Network: Computation in Neural Systems*, 7(2):161–247.

Szentágothai, J. (1978). The neuron network of the cerebral cortex: A functional interpretation. *Proceedings of the Royal Society of London B*, 201(1144):219–248.

Tsunoda, K., Yamane, Y., Nishizaki, M., and Tanifuji, M. (2001). Complex objects are represented in macaque inferotemporal cortex by the combination of feature columns. *Nature Neuroscience*, 4(8):832–838.

Woolsey, T. A. and van der Loos, H. (1970). The structural organization of layer IV in the somatosensory region (SI) of mouse cerebral cortex. *Brain Research*, 17(2):205–242.

Bibliography

Erwin, E., Obermayer, K., and Schulten, K. (1995). Models of orientation and ocular dominance columns in the visual cortex: A critical comparison. *Neural Computation*, 7(3):425–468.

Hubel, D. H. (1995). *Eye, Brain, and Vision*. Number 22 in Scientific American Library. W. H. Freeman, San Francisco, New York.

Jones, E. G. and Diamond, I. T., editors (1995). *The Barrel Cortex of Rodents*, volume 11 of *Cerebral Cortex*. Plenum Press, New York and London.

Nicholls, J. G., Martin, A. R., and Wallace, B. G. (2000). *From Neuron to Brain: A Cellular and Molecular Approach to the Function of the Nervous System*. Sinauer Associates, Inc., Sunderland, MA, fourth edition.

Peters, A. and Rockland, K. S., editors (1994). *Primary Visual Cortex in Primates*, volume 10 of *Cerebral Cortex*. Plenum Press, New York and London.

Glossary

Barrel columns in primary somatosensory cortex of rodents, each of which is associated to a single whisker.

Cortical column vertical arrangement (not necessarily of circular shape) of neurons that have similar response properties.

Disparity lack of correspondence between the retinal projection of two points in visual space.

Hypercolumn column larger than a minicolumn that includes circuitry necessary to process a certain kind of information from a single point in sensory space, e.g. an orientation hypercolumn deals with all stimulus orientations at a given point in visual space.

LGN lateral geniculate nucleus.

Minicolumn anatomical column one or a few cells thick.

Pinwheel singularity point in an orientation preference map, where different orientations converge.

Receptive field (of a cell in V1) the area of receptors in the retina to which the cell responds, in a specific way, when a light stimulus is presented.

V1 primary visual cortex (or striate cortex, or area 17).