52 Aschoff, J., Giedke, H., Poppel, E. and Wever, R. (1972) in *Aspects of Human Efficiency* (Colquhoun, W. P., ed.), pp. 135–150, The English Universities Press
53 Bennett, A. F. and Ruben, J. A. (1979) *Science* 206, 649–653
54 Czeiler, C. A., Weitzman, E. D., Moore-Ede, M. C. and Zimmerman, J. C. (1980) *Science* 210, 1264–1267
55 Shibolet, S., Lancaster, M. C. and Danon, Y. (1976) *Aviat. Space Environ. Med.* 47, 280–301
56 Carskadon, M. A. and Dement, W. (1981) *Psychophysiology* 18, 107–113
57 Kent, S., Price, M. and Satinoff, E. (1988) *Physiol. Behav.* 44, 709–715
58 Meijer, J. H. and Rietveld, W. J. (1989) *Physiol. Rev.* 69, 671–707

Is the cerebral cortex modular?

N. V. Swindale

N. V. Swindale is at the Department of Ophthalmology, 2550 Willow Street, University of British Columbia, Vancouver, BC, V5Z 3N9, Canada.

Two types of modular subunit, differing in size, have been hypothesized to exist in the cerebral cortex. The first, known as a mini-column, consists of a group of 110 ± 10 cells which form a fascicle about 30 μm in diameter oriented perpendicular to the cortical surface. Mini-columns are believed to be organized into larger modular groupings, referred to here as macro-columns, with a diameter of about a millimetre or less. Nicholas Swindale argues in this article that there is very little real evidence in favour of either type of module. As an alternative, he suggests that the diversity of types of columnar organization, both within and between different cortical areas, may reflect the diversity of types of information stored in the cortex. Consequently, columnar organization can be expected to vary within and between species, and even between different individuals of the same species. This new interpretation is in line with current neural network theories, which do not demand the existence of structural modularity, but show how complex forms of organization can result from the existence of simple processing rules between the elements of a structure given complex structured inputs.

The idea that the cerebral cortex is a mosaic of modular subunits, each similar in size and structure and containing a relatively small number of neurons, is obviously appealing. The process of trying to understand how the cortex works would be greatly simplified, because any finding made about the function of one module could be generalized to the whole cortex. Examples of repetitive structural groupings in other neural structures are not uncommon, and occur for example in the optic lobe of the fly and in the cerebellum. It seems natural to suspect that the mammalian cerebral cortex might have a similar repetitive, or modular, construction, and some eminent neuroscientists, notably Mountcastle[1], Szentágothai[2] and Eccles[3], have proposed that this is so.

In fact, not one but two kinds of modular subunit have been hypothesized to exist. The first, known as a mini-column, is defined by Mountcastle[1] as 'the basic modular unit of the neocortex... it is a vertically oriented cord of cells formed by the migration of neurons... it contains about 110 cells... (and)... occupies a gently curving, nearly vertical cylinder of cortical space with a diameter of about 30 μm'. The second kind of module consists of an aggregation of a few hundred mini-columns forming a larger processing unit, which it is useful to refer to as a macro-column. Thus, according to Szentágothai[2] 'the cerebral cortex has to be envisaged as a mosaic of columnar units of remarkably similar internal structure and surprisingly little variation of diameter (200–300 μm)'. Eccles[3] gives a similar definition, although according to Mountcastle[1] the larger unit (i.e. the macro-column) has a diameter of 500–1000 μm.

Mini-columns

Several observations have led to the idea that mini-columns are a basic structural and functional subunit of the cortex. Nissl stains of sections cut perpendicular to the surface of the cortex show that neuronal cell bodies are aggregated into chains or cords, separated by neuropile. These chains are about 30–50 μm apart, and give the appearance of running continuously from white matter to the pial surface. Counts of cell numbers in columns of cortical tissue about 30 μm in diameter and extending from white matter to pia[4] give remarkably constant values of 110 ± 10 cells in many different cortical areas and species, except in primate visual cortex where the number is about 270. Physiological studies[1,5] show that cells in the same column of tissue, and thus cells in the same mini-column, tend to have similar response properties, e.g. preferred orientation in the visual cortex or receptor modality in the somatosensory cortex.

However, the evidence for mini-columns is not easy to interpret. The origin of the vertical striations seen in Nissl-stained tissue is unclear, and it is difficult to determine whether they define single groups of cells extending from white matter to pia. The phenomenon of dendritic bundling (see Feldman[6], for review) in which groups of apical dendrites run in close proximity from cell body to layer I of the cortex might be related to this . Tissue sections cut parallel to the cortical surface show that the bundles have a spacing of about 30–50 μm, which is similar to mini-column spacing, and since the bundles exclude cell bodies it may be this that causes cell bodies to be grouped in apparently vertical configurations. The bundles themselves might contain dendrites from cells in different mini-columns, and it might legitimately be supposed that this method of grouping cells would be as valid as the groupings revealed by cell body staining.

Evidence based on the constancy of cell number within mini-columns is similarly difficult to interpret. Although the variation in cell numbers measured by Rockel *et al.*[4] was strikingly small, a subsequent study[7] found a much greater range of cell numbers per unit (30 μm diameter) column in area 17 of the monkey. Beaulieu and Colonnier[8] also report a considerable variation in the density of cells per unit area in different cortical areas of the cat (e.g. 44 300 per mm^2 in area 4, 59 100 per mm^2 in area 18 and 78 400 per mm^2 in area 17).

Even if the evidence for constancy of areal cell density is correct, however, it is no more than evidence that modules of a constant areal size will contain constant cell numbers. It is not evidence that modules have any particular size. Rockel *et al.*'s findings are equally good evidence for the existence of mini-columns that are 15 μm in diameter and contain 55 cells, or for columns that are 60 μm in diameter and contain 220 cells.

If mini-columns are functional, as well as anatomical, units of organization, it is to be expected that cells in the same mini-column would have more in common with each other than with cells in adjacent mini-columns. Because the principle of columnar organization implies that cells in the same mini-column will have similar response properties and because response properties tend to change gradually with distance across the surface of the cortex (receptive field position for example), cells within mini-columns will tend, on average, to be more similar in their properties than those within adjacent columns. These differences are likely to be small, however, and would not imply that mini-columns are functionally discrete. Hubel and Wiesel[9] suggested that there might be discrete differences between cells in columns about 25–50 μm in diameter: their physiological recordings from electrode penetrations made approximately perpendicular to the surface of monkey visual cortex suggested that cells in such columns had identical orientation preferences (i.e. to within ± 5°). As the recording electrode moved laterally, orientation preference sometimes appeared to change discontinuously by about 10°. The relationship between these shifts and the vertical striations was not clearly established, however, and they were unable to rule out the possibility of a continuous variation in orientation preference with horizontal cortical distance. In similar experiments in the cat visual cortex, Lee *et al.*[10] found considerable scatter (± 8° to ± 23°) of orientation preference in recordings made perpendicular to the cortical surface. So far, the work of Hubel and Wiesel[9] is the only evidence for a physiologically discrete representation of any stimulus property on a scale comparable in size to that of mini-columns.

The evidence that cells in the same mini-column form a functional unit would be strengthened if it could be shown that they had a common embryological origin and were clonally related. Rakic[11] has proposed that the cortex consists of narrow units, defined ontogenetically by the migration of neurons along a single radial glial cell. (Although he remarks that these ontogenetic units should not be confused with mini-columns, it is difficult to see how they differ.) Recent evidence, however, suggests that the neural descendants of single precursor cells are typically found in several differently located radial units[12]. A similar study using retroviruses[13] found a strong tendency for migrating, clonally related cells to remain in the same radial unit, but the authors emphasize that some lateral dispersion always occurs. This is greater in the cerebral cortex than in other laminated structures such as the tectum[14] and the retina[15]. Therefore, if there are functionally modular groupings of cells in the cortex defined by common clonal origins these are unlikely to be identical with mini-columns. This of course does not mean that clonal relationships are unimportant in defining functional relationships between groups of cortical neurons.

The argument can also be made, although it is a weaker one, that not all mini-columns can be the same because some cell types have a sparser distribution than that of mini-columns. Thus Meynert cells (large pyramidal neurons with cell bodies in lower layer V) have an average spacing of a few hundred micrometres[16]. Different mini-columns therefore cannot be anatomically identical, although the fact that there is a variety of types of mini-column would not in itself invalidate the concept of modularity.

Macro-columns

The basis of the argument against cortical modularity on a millimetre scale is the difficulty of arriving at a consistent estimate for the size of a module. If the concept of modularity is to be useful, i.e. if it is to simplify a description of cortical organization, then different methods of revealing modules ought to yield similar estimates of their size and shape. In fact, almost no two methods agree, and indeed the originators of the idea give quite different definitions of their size. Thus Eccles and Szentágothai state that the modules are about 200–300 μm across, whereas according to Mountcastle they are 500–1000 μm in diameter. In areal terms this latter estimate is 3–25 times larger than that of Eccles and Szentágothai. Quantitative studies of columnar structures in the visual cortex and other areas, discussed below, show that this difficulty is real and not the result of poor initial estimates of module size or inter-areal or inter-species variability.

Primate visual cortex

Many of the anatomical, physiological and biochemical properties of the primate visual cortex vary periodically across its surface. These periodicities have been generally regarded as indicative of modularity. Their substrates include such things as the distribution of afferents from subcortical structures, receptive field properties such as eye or orientation preference and the concentrations of enzymes such as cytochrome oxidase or glutamic acid decarboxylase. The degree of local disorder in the retinotopic map on the cortex (i.e. the cortical blur of the retinal image, or equivalently the scatter in receptive field positions at any one cortical location) has also been taken to suggest the existence of a spatial scale in cortical processing that is a fundamental unit of cortical design[17]. If a single unifying principle of modular organization is at work, the sizes or periodicities of these structures ought to be the same, or perhaps low integer multiples of each other, with a constant phase relationship. Although many properties in primate visual cortex do correlate spatially, such as the distributions of cytochrome oxidase and glutamic acid decarboxylase[18], many others do not. In the monkey for example, eye preference changes with a period of about 800 μm whereas preferred orientation has a period of about 570 μm (Refs 9, 19). Cytochrome oxidase concentration (which correlates with the distribution of certain colour selective cells, and of cells lacking orientation selectivity)[20] changes with a period of 250–350 μm. The size of the processing unit suggested by the degree of receptive field scatter is larger than any of these values and is estimated by Hubel and Wiesel[21] to be about 1–2 mm in diameter. This processing unit could contain between eight and as many as 64 modules defined by cytochrome oxidase distribution.

Arguments based on differences in periodicity are not watertight, since it is possible to find ways of overlaying differently periodic structures so that a common subunit emerges. For example, sets of parallel stripes with different periods can be overlaid at 90° or other angles to produce a common rectangular or rhombohedral subunit. Although proposed by Hubel and Wiesel, this arrangement does not seem to exist in monkey visual cortex because, although eye dominance columns are arranged for the most part in parallel stripes, regions of constant orientation (iso-orientation domains) are locally elongated blobs that intersect ocular dominance stripes at a variety of angles[19,22].

Cytochrome oxidase patches

Because of their regular spacing and the fact that many other properties correlate with them, the cytochrome patches are perhaps the most compelling indication of the existence of cortical modularity, yet there is evidence for modules in monkey striate cortex that are of similar size but structurally unrelated to the cytochrome ones. The modules defined by Blasdel and Salama[22] on the basis of the orientation gradient map are not aligned with those defined by cytochrome oxidase staining and are likely to be independent of them. A histochemical stain for butyryl-cholinesterase reveals a pattern similar, but structurally unrelated, to that for cytochrome oxidase[23].

Other visual cortical areas

Comparison of monkey area 17 with area 17 of non-primate species reveals many differences in the kinds of organization present, although there is a similar variability in the relative sizes of different columns within the area. For example, cytochrome oxidase patches are absent from the visual cortex of all non-primate species so far examined. In cat area 17, periodicities of eye preference and orientation selectivity determined by spectral analysis are, as in the monkey, in a non-integer ratio (850 μm for eye preference and 1100 μm for orientation[24,25]). In area 18 of the same species, the periodicity values are also different, and the ratio is reversed (1800 μm for eye preference, and 1300 μm for orientation[26]). Comparisons of the layout of these two properties[26,27] have failed to reveal any relationship that would suggest the existence of a common subunit.

In area 18 of Old World monkeys, cytochrome oxidase staining reveals a pattern[20,28] of alternating thick and thin stripes (Fig. 1A). This pattern is indicative both of the anatomical and functional organization of area 18 as thick and thin stripes differ in terms of afferent and efferent connections and physiological properties of colour and movement selectivity[29]. Nevertheless, the pattern and its scale (the overall repeat period is about 2.2 mm) is entirely different from that found in area 17, or in any other cortical area so far examined. Outside of areas 17 and 18, cytochrome oxidase concentration varies in an irregular fashion, with no obvious periodicity (Fig. 1A).

Non-visual cortex

Evidence that a modular organization prevails in the cortex as a whole has often been obtained by studying the distribution of afferent terminals within an area using tracer techniques such as autoradiography or horseradish peroxidase transport. The afferents concerned may arise in the thalamus, other cortical areas or via the corpus callosum from the homologous cortical area in the contralateral hemisphere. Afferents are typically found to be segregated in patches approximately 200–500 μm across[30]. The classic example of such a projection pattern is the pattern of ocular dominance bands found in monkey visual cortex following injection of one eye with a radioactive tracer (Fig. 1B). This is highly regular and periodic but, more than 15 years after the pattern was first discovered, there is no evidence that any other projection pattern to or from any other cortical area approaches this degree of regularity. In cat auditory cortex the projection patterns that have been demonstrated[31] are irregular (Fig. 1C), with little evidence of any predominant spatial frequency and no evidence for the existence of a uniformly sized modular subunit.

Another example, and one that might be proposed as a paradigm of cortical modularity, is the barrelfield area of rodent somatosensory cortex. Barrels, however, seem to be absent from nearly all other cortical areas. Study of genetic mutations affecting the number of whiskers suggests that cortical barrelfield structure reflects the structure of the sensory periphery (the rodent's large and individually mobile whiskers) rather than a general tendency of cortical tissue to form barrel-like structures[32].

Lack of uniformity

Although limited to only a small number of cortical areas in a few species, the existing evidence gives little support, if any, to the idea that the cerebral cortex is composed of modules of uniform

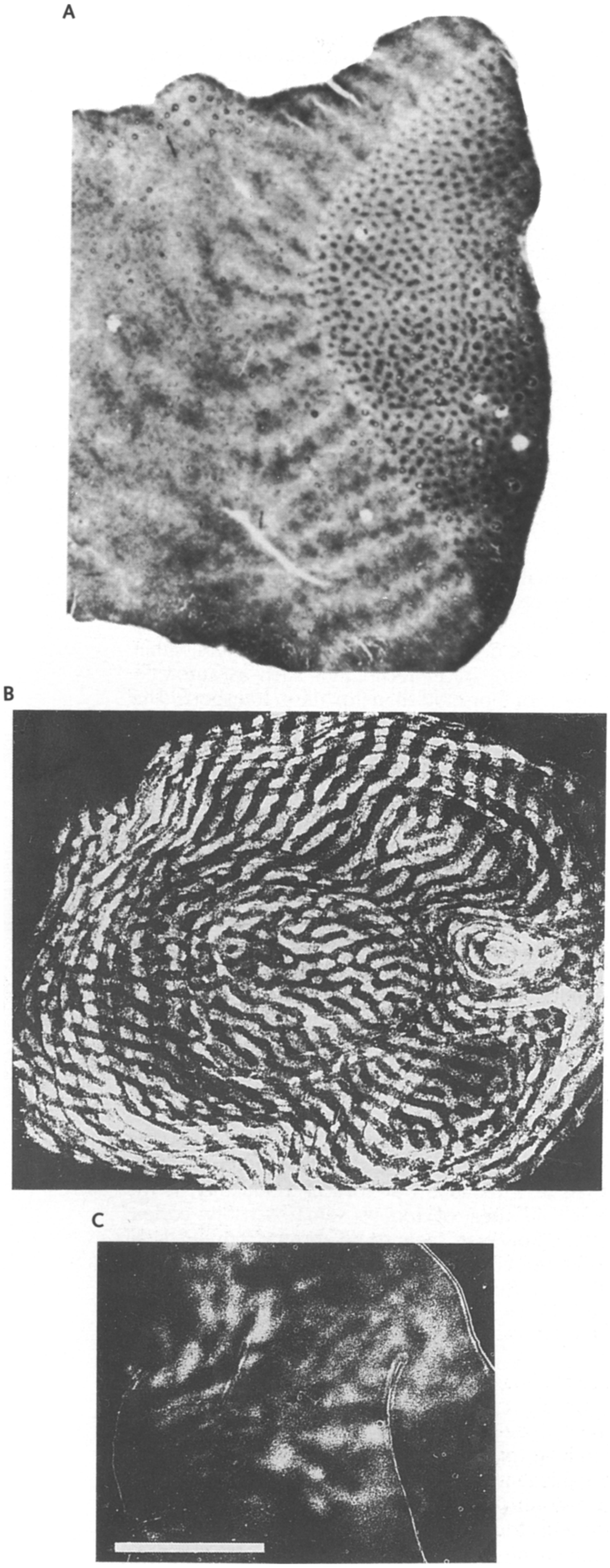

Fig. 1. (A) *Pattern of cytochrome oxidase staining in a flat mount that includes portions of area 17 and 18 in a squirrel monkey. Area 17 is to the right of the crescent-shaped border between the two areas and area 18 is immediately to the left of it. Note the differences in periodicity and pattern of staining in areas 17 and 18, and also the irregular variations in the density of staining to the left of area 18.* (Taken, with permission, from Ref. 28.) *Although the regularity of the staining pattern in area 17 is strongly suggestive of modularity, other subunits, similar in size to the cytochrome spots but not aligned with them, have also been proposed*[22]. **(B)** *Pattern of ocular dominance bands in sections cut tangential to the surface of macaque monkey visual cortex, as shown by transneuronal autoradiography. This figure is reproduced at the same scale as A and C.* (Taken, with permission, from Ref. 40.) **(C)** *Distribution of callosal afferents in auditory cortex (A1) of the cat, as shown by autoradiography. Note the irregularity and apparent lack of periodicity in the pattern.* (Taken, with permission, from Ref. 31.) *Scale bar is 5 mm for A, B and C.*

size. Although various forms of clustering and continuity are present in many cases, the particular kinds of organization found in different cortical areas and in different species seem to have rather little in common and depend instead on the modality that is represented, the particular cortical areas under study and the species concerned. This seems to be true whether cortical organization is studied anatomically, physiologically or biochemically. Why might this be so?

Consequences of information storage

Underlying the notion of modularity is the idea that the cortex is a machine that performs a certain kind of calculation over and over again across its surface. However, the cortex is also believed to be a device that stores and represents information about the world that is useful or of interest to its possessor. The contents of any kind of memory are unlikely to show regularity unless there is redundancy in storage. For example, the pattern of bits in the memory of a computer that is running an efficiently written program will show few kinds of simple regularity and no kinds that are common to the whole program. Similarly, the pattern of base pairs in those parts of the DNA molecule that code for proteins is irregular (although of course far from random); those parts of DNA that, to the eyes of a cortical neuroanatomist, would appear to be highly organized because they contain regularly repeating sequences, are believed to be either useless[33] or to serve a subsidiary regulatory function.

Information-storing devices are usually modular in terms of structure, and are perhaps necessarily so, even though the contents are not. For example, the chips on a computer memory board are identical in structure and the organization of the board is therefore highly modular. The information stored is present in the pattern of charge distribution within the chip, and is hardly apparent at a structural level. In the same way, it could be argued, the cortex might be structurally modular at some multicellular scale, and information storage only apparent at a much lower level, for example in terms of the connection strengths of individual synapses. But the fact that the cortex does not appear to be modular on any scale suggests that this is not the case and that cortex does not achieve the same separation between hardware and software that is present in digital computers. Thus the reason why columnar structures in the cortex are so variable in their organization could be that they are 'firmware': consequently the fact that the cortex is not modular may be a crucial clue to understanding the significance of columnar organization.

Superposition of feature maps

If these arguments are correct, the kinds of organization found in visual cortex must represent information about the visual world in some sense. Can visual cortex structure be interpreted in this way? Among other things, the visual cortex contains representations or maps of stimulus features such as receptive field position, edge orientation, direction of motion and eye preference. Although cells in the visual cortex vary their rate of firing in response to changes in each of these (and other) parameters, each cell typically responds best to some unique combination of them. In many cases the 'best value' of each parameter is independent of the values of the others (for example the preferred orientation, or preferred direction of motion is independent of the eye being tested, and of other parameters such as stimulus length or contrast). This independence is important because it makes it possible to define, within a single cortical area, separate but overlaid maps for different stimulus parameters (such as orientation, ocular dominance and preferred direction of movement). As mentioned above, many of these representations are periodic but perhaps their most interesting property is that the way in which they are overlaid ensures that varied combinations of features are represented[26].

These associations may be the same as the 'suspicious coincidences' of Barlow[34] (or at least those long enough established to have become permanently established in memory). However, not just visual cortex but, as suggested by Barlow, the whole cerebral cortex could consist of organized maps of features or attributes. These may be overlaid in such a way as to represent permutations of simpler features that have been experienced by the possessor of that particular cortex. It is usually possible to reduce familiar concepts to combinations of simpler features: for example, the existence of the concept of a grandmother might involve the intersection of maps for the dimensions of sex, age and relatedness, at the point where these dimensions have the values 'female', 'aged' and 'strongly related'.

The way in which maps in visual cortex are overlaid may therefore be said to represent a kind of knowledge, namely that edges of all orientations and directions of movement occur in the visual image, and in both eyes. In this context it is interesting that experiments have shown that when certain specific combinations of stimulus features are absent from the environment of cats early in life (such as vertically oriented bars in the left eye), columnar structures change in such a way that this combination of stimulus features is not represented[35,36].

Why is the visual cortex so regular?

Although even primate striate cortex does not appear to be modular, different parts of the visual cortex are nevertheless very similar in structure. This implies that the properties of the visual world that are represented in area 17 do not change with position on the retina and are invariant with respect to the spatial scale at which they are analysed by the visual cortex, as this varies with retinal location. It could be argued that there are properties of the visual world experienced by most animals that might change with retinal position, e.g. above and below the horizon, but because primates change their direction of gaze frequently, such differences are unlikely to correlate much with retinal location. Scale invariance (i.e. invariance with respect to the overall magnification of the retinal image on the cortex) may be a consequence of the observation that the intensity distribution in many naturally occurring visual scenes is fractal in character[37]. This means that the statistical properties of the cortical visual image will be independent of variations in cortical magnification of the retinal image and of magnification differences caused by variations in the distance of the field of view from the eye.

There is less reason to expect such forms of invariance to be present in higher level representations of the visual image (i.e. in higher cortical areas) and thus less reason to expect redundancy in the structures that are the substrate of such representations. Even if such invariances are present they may be expected to constrain columnar structures in different ways than in the primary representation in striate cortex. An equivalent regularity also may not be present in the inputs to other primary sensory cortical areas, such as auditory cortex, and this may explain why the equivalent cortical maps are much less regular. In audition for example, the cortical analogue of position on the retina is the pitch of a sound, but for many species the information present in auditory stimuli is frequency specific. The kinds of stimulus features represented in the auditory cortex may vary depending on the particular frequencies concerned, and this in turn would be expected to be accompanied by a corresponding variation in physiological and anatomical correlates of such representations, as is apparently found in cat auditory cortex (Fig. 1C).

Concluding remarks

Despite the importance and attraction of the idea, there seems to be little evidence for a general modular organizing principle of cerebral cortical organization on a submillimetre scale as proposed by Mountcastle, Szentágothai, Eccles and others. Instead, the kinds of organization found, whether studied physiologically, anatomically or biochemically, vary within single cortical areas, from one cortical area to another, and in related cortical areas in different species. Within a single cortical area, different submodalities can have similar or different periodicities, can be aperiodic, and can be structurally related in a complex way, or be apparently unrelated to each other. Consequently, it seems misleading to refer to the various columns, hypercolumns, slabs, stripes, strips, bands, barrels, beads, blobs, patches, puffs and lattices that have been discovered in cortex as modules in any but a limited and strictly local sense. Not only does it seem wrong to describe the cortex as modular, use of the term obscures the real complexity of cortical organization and fails to do justice to the diversity of forms of columnar order that are actually present.

Crick and Asanuma[38] have also pointed out that the cortex does not seem to be modular although they did not give reasons why this might be so. Towe[39] also questioned the notion of the existence of 'elementary functional units' in the cortex. In this paper, it has been argued that there might be an essential reason why the cortex is not modular: the structural diversity of the cortex may simply reflect the diversity of information that is stored there. It is suggested also that the cortex stores associations between different sets of features by superimposing separate columnar maps for the different features. There is no reason for supposing that this will lead to representations that are of uniform periodicity and this is consistent with the lack of evidence for cortical modularity. Although it may be difficult to discard the concepts of modularity and repetitive structural organization[5] that have existed since 1957, the alternative insight, that the cortex is essentially non-modular in construction, may be a more powerful and helpful clue in the search for unifying principles of cortical organization.

Acknowledgements

I thank H. B. Barlow, M. S. Cynader and A. J. Cohen for their comments on an earlier version of the manuscript. This work was supported by grants from the MRC of Canada and the British Columbia Health Care Research Foundation.

Selected references

1 Mountcastle, V. (1978) in *The Mindful Brain* (Schmitt, F. O., ed.), pp. 7–50, MIT Press
2 Szentágothai, J. (1977) *Proc. R. Soc. London Ser. B* 201, 219–248
3 Eccles, J. C. (1981) *Neuroscience* 6, 1839–1855
4 Rockel, A. J., Hiorns, R. W. and Powell, T. P. S. (1980) *Brain* 103, 221–244
5 Mountcastle, V. (1957) *J. Neurophysiol.* 20, 408–434
6 Feldman, M. L. (1984) in *Cerebral Cortex* (Vol. 1) (Peters, A. and Jones, E. G., eds), pp. 123–200, Plenum Press
7 Williams, R. W., Ryder, K. and Rakic, P. (1987) *Soc. Neurosci. Abstr.* 13, 1044
8 Beaulieu, C. and Colonnier, M. (1989) *J. Comp. Neurol.* 279, 228–234
9 Hubel, D. H. and Wiesel, T. N. (1974) *J. Comp. Neurol.* 158, 267–294
10 Lee, B. B., Albus, K., Heggelund, P., Hulme, M. J. and Creutzfeld, O. D. (1977) *Exp. Brain Res.* 27, 301–314
11 Rakic, P. (1988) *Science* 241, 170–176
12 Walsh, C. and Cepko, C. L. (1988) *Science* 241, 1342–1345
13 Luskin, M. B., Pearlman, A. L. and Sanes, J. R. (1988) *Neuron* 1, 635–647
14 Gray, G. E., Glover, J. C., Majors, J. and Sanes, J. R. (1988) *Proc. Natl Acad. Sci. USA* 85, 7356–7360
15 Holt, C. E., Bertsch, T. W., Ellis, H. M. and Harris, W. A. (1988) *Neuron* 1, 15–26
16 Winfield, D. A., Rivera-Dominuez, M. and Powell, T. P. S. (1981) *Proc. R. Soc. London Ser. B* 213, 27–40
17 Hubel, D. H. and Wiesel, T. N. (1974) *J. Comp. Neurol.* 158, 295–306
18 Hendrickson, A. E., Hunt, S. P. and Wu, J-Y. (1981) *Nature* 292, 605–607
19 Hubel, D. H., Wiesel, T. N. and Stryker, M. P. (1978) *J. Comp. Neurol.* 177, 361–380
20 Horton, J. C. (1984) *Phil. Trans. R. Soc. London Ser. B* 304, 199–253
21 Hubel, D. H. and Wiesel, T. N. (1977) *Proc. R. Soc. London Ser. B* 198, 1–59
22 Blasdel, G. G. and Salama, G. (1986) *Nature* 231, 579–585
23 Graybiel, A. M. and Ragsdale, C. W. Jr (1982) *Nature* 299, 439–442
24 Löwel, S. and Singer, W. (1987) *Exp. Brain Res.* 68, 661–666
25 Löwel, S., Freeman, B. and Singer, W. (1987) *J. Comp. Neurol.* 255, 401–415
26 Cynader, M. S., Swindale, N. V. and Matsubara, J. A. (1987) *J. Neurosci.* 7, 1401–1413
27 Löwel, S. and Singer, W. (1987) *Soc. Neurosci. Abstr.* 13, 4
28 Tootell, R. B. H., Silverman, M. S., De Valois, R. L. and Jacobs, G. H. (1983) *Science* 220, 737–739
29 DeYoe, E. A. and Van Essen, D. C. (1985) *Nature* 317, 58–61
30 Goldman-Rakic, P. S. and Schwartz, M. L. (1982) *Science* 216, 755–757
31 Imig, T. J. and Brugge, J. F. (1978) *J. Comp. Neurol.* 182, 637–660
32 Van der Loos, H. and Dörfl, J. (1978) *Neurosci. Lett.* 7, 23–30
33 Orgel, L. E. and Crick, F. H. C. (1980) *Nature* 284, 604–607
34 Barlow, H. B. (1985) *Models of the Visual Cortex* (Rose, D. and Dobson, V., eds), pp. 37–46, J. Wiley
35 Rauschecker, J. P. and Singer, W. (1981) *J. Physiol.* 310, 215–239
36 Cynader, M. S. and Mitchell, D. E. (1977) *Nature* 270, 177–178
37 Pentland, A. P. (1984) IEEE Transactions on Pattern Analysis and Machine Intelligence 6, 661–674
38 Crick, F. H. C. and Asanuma, C. (1986) in *Parallel Distributed Processing: Explorations in the Microstructure of Cognition* (Vol. 2) (McClelland, J. L. and Rumelhart, D. E., eds), pp. 333–371, J. Wiley
39 Towe, A. L. (1975) *Brain, Behav. Evol.* 11, 16–47
40 LeVay, S., Connolly, M., Houde, J. and Van Essen, D. C. (1985) *J. Neurosci.* 5, 486–501