Cortical organization: **Modules, polymaps and mosaics**
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Recent studies of functional maps in the mammalian visual cortex fail to support the widespread belief that the cortex contains millimetre-sized modules; instead, they reveal a more fluid arrangement in which several separate maps are superimposed, with relatively weak geometric linkages and no common modular subunit.

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Modules

The human cerebral cortex has a total surface area of about 1800 cm^2, a thickness of 2–3 mm, and a relatively uniform structure. It contains a large proportion of the brain's neurons and is probably the repository of most of our remembered knowledge of the world, as well as being the source of planned behaviour, perception and consciousness itself. Understanding how all this might be done, by one piece of neural tissue whose most obvious qualification is perhaps its size, seems formidably difficult. One simplification comes from the discovery in the 19th century that the cortex can be subdivided into different areas (perhaps 100 or more in each hemisphere) each specialized for some particular task, such as representing visual or auditory information, or planning the movements involved in speech.

Further simplification would occur if it could be shown that cortical neurons within each area were organized into modular assemblies, each performing a similar transformation on its inputs. This seems intuitively plausible, and early studies by Mountcastle [1] and Hubel and Wiesel [2] showed that neurons with similar response properties tended to be grouped in vertical columns, about 0.5–1 mm in diameter, with each column oriented perpendicular to the surface of the cortex and spanning its full thickness. Correspondingly, anatomical studies showed that connections between one cortical region and another were often distributed in periodically spaced patches about 1 mm apart. A more recent indication of modular organization in the primate visual cortex came from the results of histological staining for the enzyme cytochrome oxidase [3]: this shows that the enzyme is concentrated in punctate regions which have a strikingly regular spacing of about 350 μm (Figure 1a).

These and related observations have been interpreted by many as demonstrating that the cortex is fundamentally modular in its organization, and references to such modularity abound in the literature. Yet precisely what is meant by a cortical module has never really been made clear. Given that modules are, by definition, discrete entities, there should be some unambiguous way of defining the centre and boundaries of each module so that they can be counted. It ought also to be shown that connectivity within a module is different in some way from connectivity between different modules. As a result, a module

Figure 1

Patterns in macaque monkey visual cortex that are suggestive of modular organization. **(a)** Patches of cytochrome oxidase enzyme (dark regions have relatively higher levels of the enzyme) in the upper layers of the cortex (reproduced with permission from [14]). **(b)** Layout of orientation preference in the upper layers of the cortex, colour-coded for orientation preference, with the cycle red→orange→yellow→green→blue→purple representing a single 180° cycle of orientation preferences. Note the pinwheel regions, where single complete sets of colours (iso-orientation domains) meet at point singularities (reproduced with permission from [15]) **(c)** Pattern of ocular dominance stripes in layer IV (reproduced with permission from [16]). The panels are not to the same scale: the bars represent approximately 1 mm, 0.5 mm and 2 mm, in (a), (b), and (c), respectivly.

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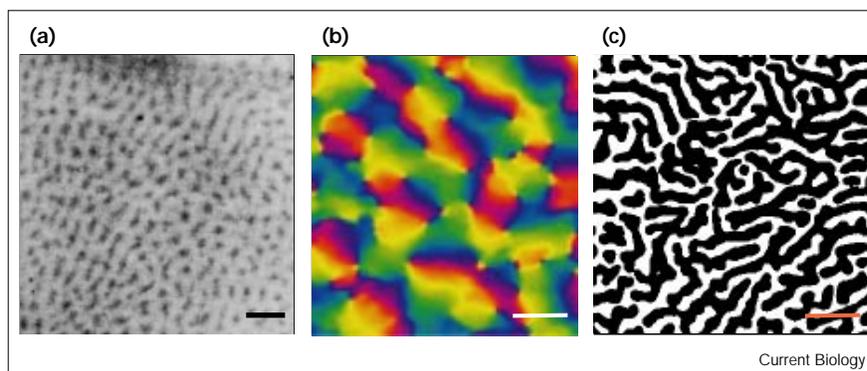
defined by one set of criteria — for example, anatomical — should have centres and boundaries that agree with those obtained using a different set of criteria, such as physiological ones. But as I [4] and others [5,6] have argued, defining modules unambiguously is problematic, especially in the visual cortex, which is perhaps the most intensively studied region of the cortex. To understand why, consider first some of the ways in which the visual cortex is known to be organized anatomically and physiologically.

Polymaps

Perhaps the most salient feature of visual cortex organization is the presence of an orderly topographic map of visual space. Neighbouring neurons tend to have receptive fields in similar positions in visual space, and these positions change predictably as a function of position on the cortex. The receptive fields are large enough that the fields of adjacent neurons overlap and, on average, the receptive fields of cells about 1–2 mm apart will be near each other, but will not overlap. Superimposed on this 'retinotopic' map (representing spatial position on the retina) are maps of other response properties. For example, most cells respond selectively to edges within a narrow range of orientations; nearby cells tend to respond best to similar edge orientations, and the preferred orientation rotates systematically with distance over the surface of the cortex.

A distinctive feature of the orientation map is the presence of regions known as pinwheels, in which a single complete set of iso-orientation domains comes together to meet at a point discontinuity known as a singularity (Figure 1b). In addition to orientation, visual neurons vary in their preference for the direction of motion of an oriented bar or edge; in their preference for stimuli delivered to one eye or the other, a property known as ocular dominance (Figure 1c); and in their preference for low versus high spatial frequencies in the visual image [7]. All of these properties have been found to vary in an orderly way with position on the cortical surface, so that, typically, a complete set of values occurs at least once every millimetre or so. The complete arrangement of multiple, superimposed maps of different stimulus attributes has been termed a 'polymap' by Eric Schwartz and his coworkers (see [8]).

Mosaics

If modules were a ubiquitous feature of cortical organization, one might expect polymap organization to reveal unambiguously the centres and boundaries of each module. This seems to be difficult in the case of orientation and ocular-dominance columns, because in both cat and monkey visual cortex the repeat periods of the columns differ and are in a non-integer ratio. It is possible nevertheless, that two structures with different periodici-

ties might be superimposed in such a way as to reveal a common subunit. Recent optical imaging data from area 17 of the cat visual cortex, obtained by Hübener *et al.* [9], fail to support this idea, however. They compared maps for three different properties — preferred orientation, ocular dominance and spatial frequency — obtained simultaneously from the same region of the cortex. Superposition of the different maps reveals, at first sight, no obvious structural relationships between any of the pairs (Figure 2). For example, the boundaries of ocular-dominance regions intersect the boundaries of the low-spatial-frequency regions in an apparently haphazard fashion, while orientation singularities can be found close to the edges as well as in the middle of left- or right-eye ocular-dominance patches. Similarly, low-spatial-frequency patches may or may not contain a singularity.

Closer examination, however, shows that the different maps, though lacking any type of common subunit, are not structurally independent. Perhaps the most obvious relationship is a tendency for singularities to be located in the centres of ocular-dominance patches, a relationship which had earlier been noted in studies of the macaque monkey visual cortex [10,11]. As in the macaque, there is a tendency for the borders of ocular-dominance patches (denoted by the upper set of black lines in Figure 2) and the borders of iso-orientation domains (the coloured lines in Figure 2) to intersect at right angles. It is hard to be sure of this by visual inspection, but statistical analysis shows that the tendency is significant. Similar, albeit weaker, relationships are found between the orientation and spatial-frequency columns. Although this might seem to imply that the layouts of spatial-frequency and ocular-dominance columns should be similar, these two maps are also relatively independent, although a weak tendency for the

Figure 2
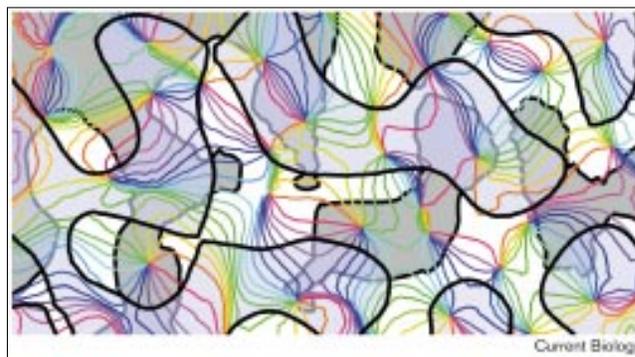
Polymap of orientation, ocular dominance and spatial frequency in the cat visual cortex. Thick black lines mark the boundaries of ocular-dominance patches (light blue shaded regions are those preferring input from the contralateral eye); lighter lines mark the boundaries of spatial-frequency patches (grey shaded regions are those preferring low spatial frequencies) and coloured lines mark the borders of iso-orientation domains [9]. Figure kindly supplied by Mark Hübener.

centres of the low-spatial-frequency patches to be close to the centres of the ocular-dominance patches was noted.

These relationships seem to have one thing in common, namely a tendency for gradients in the different maps to be locally orthogonal. Because of the lack of strong structural relationships, Hübener *et al.* [9] conclude that "the visual cortex cannot be considered a 'crystalline' structure built from identical modules, but rather it is composed of 'mosaics' of functional domains for the different properties."

The design of the visual cortex

What do these relatively subtle relationships tell us about cortical organization? It is an intuitively obvious idea that the cortex may be trying to squeeze in as many combinations of functionally relevant stimulus parameters as possible within a given area. This requirement for uniform 'coverage' can be made more precise by imagining the cortex as a two-dimensional sheet embedded in a multi dimensional stimulus space whose axes represent the stimulus parameters in question, such as preferred orientation and ocular dominance. The position in this space of a point in the cortical sheet thus represents the set of stimulus parameters assigned to it. Given that cortical maps are effectively two-dimensional, not every point in a stimulus space of more than two dimensions can coincide with a cortical location. So, getting all the dimensions in is, in

principle, not possible for stimulus spaces of more than two dimensions. But the cortex may be folded in such a way that it at least comes within some minimum distance of every point in the space, and this will optimize the uniformity of coverage.

It is fairly easy to see, as Hubel and Wiesel [2] realized, that orthogonal gradient relationships between orientation and ocular dominance columns will lead to good coverage of these two parameters, while parallel gradient relationships will do the opposite and lead to the absence of certain combinations (Figure 3). But this is just for two dimensions: for more complex stimulus spaces, the answer is less clear — for example, for three sets of columns, would intersections at 60° rather than 90° be the best solution?

One way of testing whether or not the visual cortex is designed to optimize coverage would be to calculate measures of coverage uniformity from real maps, and then see whether the values were degraded by changing the structural relationships in the maps, for example by sliding them relative to each other. Other insights may come from modelling results (reviewed in an earlier dispatch [12]) which can achieve projections from multi-dimensional stimulus spaces onto two-dimensional surfaces, subject to constraints of completeness (good coverage) and smoothness (local continuity). These models reproduce the

Figure 3

How orthogonal gradient relationships between maps lead to better coverage. The left panels show two different cortical map arrangements for two hypothetical stimulus parameters, A and B, while the right panels show the projection of the cortex into the stimulus space whose axes represent the values of A and B. In the upper half of the figure the map gradients for A and B are orthogonal, and all combinations of A and B are represented in the stimulus space on the right. In the bottom half of the figure the gradients are parallel, and only a small subset of points in the stimulus space is represented in the cortex.

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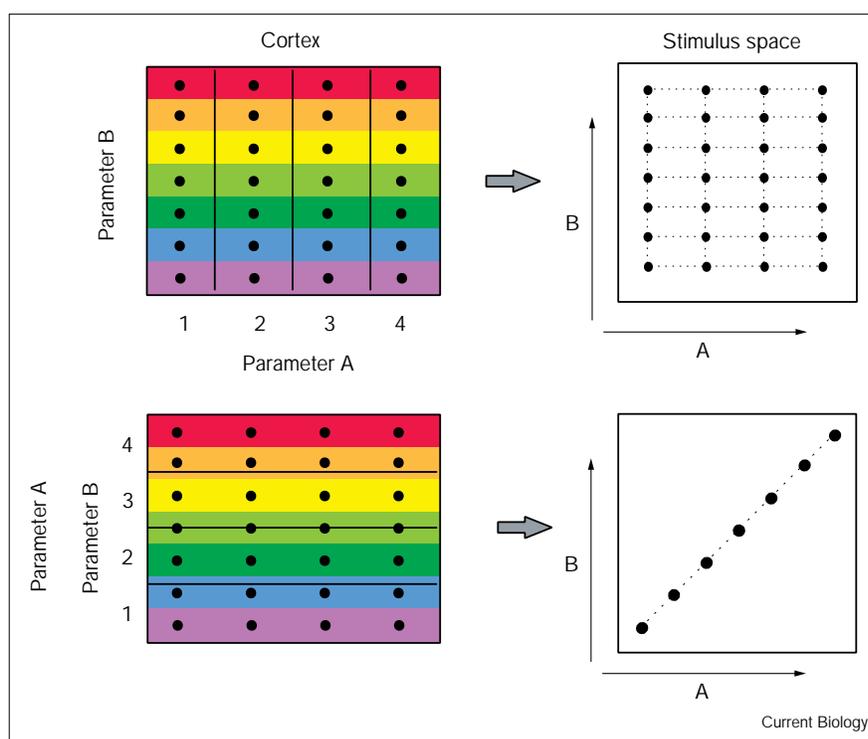
known structural properties of the orientation and ocular-dominance maps [13], as well as the orthogonal gradient relationships between the two sets of columns. They have yet to be applied to the more complete set of stimulus properties studied by Hübener *et al.* [9], and it will be intriguing to see whether these results can also be replicated by the models. If they are, it will lend further credence to the idea that the organization of visual cortex maps is determined by functional requirements, including uniform coverage and local continuity, rather than by an underlying principle of modularity.

References

1. Mountcastle VB: **Modality and topographic properties of single neurons of cat's somatic sensory cortex.** *J Neurophysiol* 1957, **20**:408-434.
2. Hubel DH, Wiesel TN: **Functional architecture of macaque monkey visual cortex.** *Proc R Soc Lond B* 1977, **198**:1-59.
3. Horton JC: **Cytochrome oxidase patches: a new cytoarchitectonic feature of monkey visual cortex.** *Phil Trans R Soc Lond [Biol]* 1984, **304**:199-253.
4. Swindale NV: **Is the cerebral cortex modular?** *Trends Neurosci* 1990, **13**:487-492.
5. Crick FHC, Asanuma C: **Certain aspects of the anatomy and physiology of the cerebral cortex.** In: *Parallel Distributed Processing: Explorations in the Microstructure of Cognition*, vol. 2. Edited by McClelland JL, Rumelhart DE. New York: Wiley; 1986:333-371.
6. LeVay S, Nelson SB: **Columnar organization of the visual cortex.** In *The Neural Basis of Visual Function*. Edited by JR Cronly-Dillon. London: Macmillan;1991.
7. Swindale NV: **Visual cortex: A cat's eye view of the visual system.** *Curr Biol* 1997, **7**:R387-R389
8. Landau P, Schwartz EL: **Computer simulation of cortical polymaps: a proto-column algorithm.** *Neural Networks* 1991, **5**:187-206
9. Hübener M, Shoham D, Grinvald A, Bonhoeffer T: **Spatial relationships among three columnar systems in cat area 17.** *J Neurosci* 1997, **17**:9270-9284.
10. Bartfeld E, Grinvald A: **Relationships between orientation-preference pinwheels, cytochrome oxidase blobs, and ocular dominance columns in primate striate cortex.** *Proc Natl Acad Sci USA* 1992, **89**:11905-11909.
11. Obermayer K, Blasdel GG: **Geometry of orientation and ocular dominance columns in monkey striate cortex.** *J Neurosci* 1993, **13**:4114-4129.
12. Swindale NV: **Elastic nets, travelling salesmen and cortical maps.** *Curr Biol* 1992, **2**:429-431.
13. Obermayer K, Blasdel GG, Schulten K: **Statistical-mechanical analysis of self-organization and pattern formation during the development of visual maps.** *Phys Rev* 1992, **A45**:7568-7589.
14. Tootell RBH, Hamilton SL, Silverman MS, Switkes E: **Functional anatomy of macaque striate cortex: I. Ocular dominance, binocular interactions and baseline conditions.** *J Neurosci* 1988, **8**:1500-1530.
15. Florence SL, Kaas JH: **Ocular dominance columns in area 17 of Old World macaque and talapoin monkeys: complete reconstructions and quantitative analyses.** *Visual Neurosci* 1992, **8**:449-462.
16. Blasdel G: **Orientation selectivity, preference, and continuity in monkey striate cortex.** *J Neurosci* 1992, **12**:3193-3161.