The prominence of repeating patterns of circuitry in the mammalian brain has led to the general view that iterated modular units reflect a fundamental principle of cortical function. Here we argue that these intriguing patterns arise not because the functional organization of the brain demands them, but as an incidental consequence of the rules of synapse formation.

Many regions of the mammalian cerebral cortex comprise repeating elements arrayed with surprising regularity (Fig. 1). These elements are most often called columns or modules, although a variety of other terms have also been used, resulting in a sometimes confusing nomenclature (see Box 1 for definitions). Whatever terminology is chosen, these structures are generally thought to represent a basic unit of cortical function. Not all investigators, of course, have been enthusiastic about the status accorded cortical columns, and some have disputed their importance and even their existence. Our purpose here is not to question the reality of this impressive structural arrangement, but to suggest that such patterns arise as an incidental consequence of the developmental rules that govern the formation of synaptic connections.

The discovery of cortical columns

The hypothesis that the cortex comprises elementary units was first suggested by Lorente de Nô's based on anatomical studies of the rat brain. This idea and its significance remained mostly unexplored until the 1950s when electrophysiological experiments carried out by Mountcastle demonstrated a pattern of repeating units in the cat cortex. Vertical microelectrode penetrations in the primary somatosensory cortex encountered neurons with similar receptive fields that responded to the same types of cutaneous stimuli. 'These data', wrote Mountcastle, 'support an hypothesis of the fundamental organization of this cortical area. That 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 ...'

Soon after Mountcastle's pioneering work, Hubel and Wiesel discovered a similar arrangement in the primary visual cortex of the cat. Vertical microelectrode penetrations encountered neurons that responded best to visual stimuli having the same orientation; in contrast, tangential penetrations encountered cells whose orientation preference shifted systematically. The pattern of these modular units (called orientation columns) has since been demonstrated anatomically, most recently by video imaging in vivo. This arrangement of the somatosensory and visual cortices led Mountcastle to the more general conclusion that 'the elementary pattern of organization in the cerebral cortex is a vertically oriented column or cylinder of cells'.

Prevalence of iterated patterns of cortical circuitry

Since these initial discoveries, the view that modular circuits represent a fundamental unit of the mammalian brain has gained wide acceptance. This consensus derives from apparently similar patterns in a variety of cortical (and other) regions in many mammalian species (Fig. 1 and Table I). Iterated circuits are especially prominent — and well characterized — in the primate visual cortex. In addition to orientation columns, layer IV of the primary visual cortex (V1) of the rhesus monkey is divided into parallel stripes that are usually called ocular dominance columns. Each of these columns comprises neurons driven by thalamic inputs related to one eye or the other. Other iterated units in the monkey visual cortex are the 'blobs' in layers II and III of V1 (Ref. 18), in which many neurons respond...
to the color of a stimulus without much regard to its
orientation and several varieties of 'stripes' in the
secondary visual cortex (V2) (Refs 20, 33, 34).

The consensus that iterated patterns are a general
feature of the mammalian cortex was broadened
further when patchy arrangements of terminal fields
were discovered in other cortical regions. Alternating
bands of cortico-cortical connections related
to monaural or binaural responses occur in the audi-
tory system of cats and monkeys, and callosal
projections that interdigitate with ipsilateral cortico-
cortical projections are apparent in various cortical
areas. A further addition to this canon is the pattern of 'barrels' in the somatic sensory
cortex; these units process information from the
facial whiskers and other somatic sensory specializ-
ations in rodents and many other mammals.

Summing up, iterated modular units are present
in a variety of brain regions and species (Fig. 1 and
Table I). This wealth of evidence has led to the con-
clusion that modular units are a fundamental feature
of the mammalian cortex, important for perception,
cognition, memory and perhaps even conscious-
ness. Several observations, however, raise
questions about the wider significance of these
striking arrays, and the purposes they serve.

Some countervailing observations

At least three facts undermine the conventional
view that iterated modular patterns are essential for
cortical function. First, although modular circuits of
a given class are readily apparent in the brains of
some species, they have not been found in other,
sometimes closely related, animals. Second, these
iterated patterns have been difficult to discern
outside the primary sensory systems of the mam-
malian cortex. And third, no compelling rationale
for a modular arrangement of brain circuitry has
been forthcoming, much effort and speculation not-
withstanding.

Inconstancy of modules among related species.

Although some types of modules (e.g. orientation
columns in primary visual cortex) have been found
in all species so far examined, most are quite
variable in their occurrence. An example is the
presence of ocular dominance columns in Old World
monkeys and their absence in most New World
monkeys. In spite of this structural difference,
the visual abilities of these animals are similar;
evidently, ocular dominance columns are not essential
for stereoscopic vision in the
tree shrew. Like ocular dominance columns, blobs
in various species have not yet been associated with
any obvious difference in cortical function or be-
havior (although see Ref. 50 for an interesting
hypothesis in this regard).

A third case in point is the variable presence
of barrels in the primary somatosensory cortex in
mammals. Barrels are well developed in mice, rats,
squirrels, muskrats, porcupines and walruses, but
are absent in other species that have prominent
facial whiskers such as dogs, cats, raccoons, beavers,
tree shrews and monkeys. Barrels are present in the
brains of the Australian brush-tailed opossum,
but not in American opossums and other
marsupials. Moreover, barrels occur in the
guinea pig, which hardly uses its whiskers, and in
the chinchilla, another cavimorph that has no
whisking behavior at all. A third animal of this order
(the capybara, a South American mammal related to
the guinea pig) does not have barrels. As in the
case of ocular dominance columns and blobs, there

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**Fig. 1.** Examples of modular circuitry in the
mammalian brain. 
(A) Ocular dominance columns in layer IV in
primary visual cortex (V1) of a rhesus monkey
(autoradiograph after injection of
radioactive proline into one eye). 
(B) Blobs in layers II-III in V1 of a
squirrel monkey (cytochrome oxidase
histochemistry). 
(C) Stripes in layers II-III in V2 of a
squirrel monkey (cytochrome oxidase
histochemistry). 
(D) Barrels in layer IV in primary sensory
cortex (S1) of a rat (succinic
dehydrogenase histochemistry). 
(E) Barreloid in the
ventrobasal nucleus of the thalamus in a
rat (succinic dehydrogenase
histochemistry). 
(F) Glomeruli in the
olfactory bulb of a
mouse (Sudan Black
staining). (A) was
provided courtesy of
S. LeVay; other
panels are from the
authors' work.
The terminology that has grown up over the years to describe iterated patterns of circuitry in the brain can be confusing. The following definitions reflect both history and current usage.

**Columns**

Columns are groups of vertically linked cortical cells that have common response properties. Initially detected by electrophysiological recordings, most classes of columns have now been revealed by anatomical techniques. Columns are quite variable in shape; for example, some varieties of columns are actually stripes that can be many millimeters long (see Fig. 1). Columns often extend vertically through several cortical layers, and are most prominent in primary sensory cortices, particularly in the laminae that receive input from the thalamic relay nuclei.

**Minicolumns**

S. Ramón y Cajal, and others since⁵⁷, have emphasized that, from a strictly anatomical perspective, the cortex comprises small radial columns one or a few cells in thickness, stacked from the white matter to the pial surface. This arrangement has been studied in detail by Powell and colleagues⁵⁸, who have suggested that these 'minicolumns' are the fundamental structural subunit of the cortical columns⁵⁸. In instances where the functional column (see above) is small, as in the case of Mountcastle's somatosensory columns, a column could, in principle, be equivalent to a minicolumn. There is, however, no evidence to support (or refute) a link between these anatomical minicolumns and the columnar organization of the cortex detected by other techniques.

**Hypercolumns**

The hypercolumn, a largely theoretical construct, is defined as a region of cortex that includes all of the columnar circuitry necessary for the analysis of a class of information derived from a single point in sensory space. In the case of the visual system, for which the idea was conceived,⁶ a hypercolumn for orientation would therefore include the cortical circuitry for analysing all stimulus orientations pertinent to a given point in visual space. Whether hypercolumns exist in any specific sense is as yet unclear; there must, of course, be some set of neurons that performs the full set of analyses for a given stimulus parameter.

**Modules**

The term 'modules' is used by most neurobiologists as a synonym for cortical columns. It has come to have a somewhat broader connotation, however, and is often used to include iterated circuits outside the cortex, such as olfactory glomeruli and striasomes. Theoreticians, particularly those working in artificial intelligence, have sometimes used the term more loosely to mean any functional grouping in the brain (or 'mind' in some instances).

**References**

a Ramón y Cajal, S. (1900) Rev. Trim. Micrograf. 5, 185–198

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seems little rhyme or reason for the presence of barrels in various species.

The absence of modules in some cortical regions. A second problem in assigning modular patterns a general role in cortical function is their lack of prominence outside of the brain's primary sensory systems. The motor areas of the cerebral cortex, like the primary sensory cortices, are organized into maps that reflect the periphery⁵⁷. Despite this basic similarity, modular units analogous to ocular dominance columns, orientation columns, blobs and barrels have not been demonstrated unequivocally in this region of the brain. Microelectrode recordings along vertical tracks in motor cortex do encounter neurons related to particular muscles⁵⁸–⁶⁰. This organization, however, differs in several respects from the modular arrangement observed in the primary sensory cortices. Functionally related groups of motor neurons are larger and more variable in size than sensory modules, being up to several millimeters in diameter, compared to a standard 200–500 µm for sensory modules. Moreover, the neuronal groupings described in motor cortex are often overlapping, whereas sensory modules, by both anatomical and electrophysiological assessment, are usually discrete. Thus, the iterated patterns of circuitry demonstrated in various sensory cortices have not been observed in motor cortex.

In the other major constituent of the cortical mantle – the association cortex – modular arrays are also less well developed, or do not exist as an organizing principle. Other than a tendency for patchy cortico-cortical connections⁴⁴–⁴⁶, a modular arrangement comparable to that in the sensory cortices has so far eluded detection. It is possible, of course, that modular organizations do exist in such areas, but are not readily observed using present techniques. Since the association cortices process particularly complex stimuli, such as the image of a face or the sound of a spoken word, some caution is certainly in order. Nevertheless, over the past two decades, the response properties of neurons in these higher order areas have been characterized in the occipital cortex⁶¹–⁶³, the parietal cortex⁶⁴, the frontal cortex⁶⁵–⁶⁶, and the temporal cortex⁶⁷–⁶⁹. Despite a now extensive catalog of specialized neuronal types, little evidence has emerged for a modular organization in these regions (although see Refs 70 and 71).

In short, the crystalline organization apparent in many primary sensory systems has not been clearly demonstrated in the two other major functional subdivisions of the cerebral cortex, namely, the motor and association cortices.

The absence of a functional rationale for cortical modules. A third problem that arises in attaching special significance to modular arrangements in the cortex is the failure, over several decades now, to establish any clear purpose served by this arrangement. A number of possibilities have been suggested, but none has gained general acceptance or is supported by much evidence. Some of these suggestions are:

1. that modules provide a means of augmenting cortical surface area during speciation⁵⁵,⁷⁷,⁷³;
2. that modules segregate inputs that must be kept apart for appropriate cortical function¹,⁷,⁷¹;
3. that modules facilitate computation by dividing complex brain structures into simpler, repeating elements that enhance information processing²⁷,²⁸,³⁰,⁷⁴,⁷⁵.

Attractive though these ideas may be, each is weakened by the inconstancy of modular organization among species, and by the absence (or at least the degeneracy) of a modular arrangement in many
cortical regions. It is hard to argue, for example, that cortical modularity facilitates evolutionary changes in cortical surface area if this arrangement is so capricious among related animals. The idea that segregation by modules is essential to cortical processing is belied by the behavioral abilities of the animals that do not possess modules of a particular class. Finally, it is hard to maintain that a modular organization is important for enhanced computation when this arrangement is less apparent in higher order association areas, where the most complex computations carried out presumably occur.

An alternative interpretation

A clue to the derivation of cortical modules is the presence of similar patterns of iterated circuitry in a variety of extra-cortical brain regions (see Fig. 1 and Table I). Thus, in the thalamus and the brainstem, iterated units called ‘barreloids’ and ‘barrelettes’, respectively, have been found that mirror the arrangement of cortical barrels27,28,76. In the olfactory bulb (a laminated telencephalic structure), modules called glomeruli have been known for more than a century75; and in the caudate and putamen iterated circuits called striosomes have been studied intensively in recent years78.

Might there be a common basis for this kind of arrangement that has little or nothing to do with any functional imperative of the cerebral cortex? Here we argue that modular patterns in the cortex – or elsewhere – arise coincidentally during maturation as a consequence of three developmental requirements: that synaptic partners be identified according to their function; that the growth of functionally appropriate synaptic partnerships be promoted by positive feedback; and that rich sets of local connections be established between central neurons for complex processing functions.

Functional identification of potential synaptic partners. The formation of appropriate synaptic connections depends first and foremost on molecular recognition79–81. This mechanism alone, however, cannot produce a fully functional nervous system because the restrictions imposed by ‘chemoaffinity’ are not exclusive81. Thus, when unusual partners are brought into contact with one another by experimental manipulation, synapses often form between the mismatched elements81–83. Accordingly, neurons must have a means of distinguishing between the range of synaptic partnerships permitted by molecular recognition and the connections that make precise functional sense.

The precise functional identity of a neuron is evidently conferred by its pattern of electrical activity, thus resolving the degree of ambiguity inherent in molecular recognition alone. The seminal experiment on this point was performed by Wiesel84 about 30 years ago, when they demonstrated that closing one eye of a cat during the development of the visual system causes a marked change in the innervation of target neurons; cortical connections related to the deprived eye are lost or suppressed, whereas those related to the intact eye are maintained and promoted. Whether a cortical target cell is, in the end, innervated by a particular set of axons depends on the functional activity of the synaptic partners.

| Table I. Some examples of iterated circuitry in the mammalian brain |
|-----------------|-----------------|-----------------|-----------------|-----------------|
| Module type     | Location        | Physiologically identified | Anatomically identified | Orders in which found |
| Cortical        | S1              | Yes             | No              | C, R, P           | 7               |
| Somatic-sensory | columns         |                 |                 |                  |
| Barrels         | S1              | Yes             | Yes             | C, R              | 16              |
| Orientation     | columns         |                 |                 |                  |
| columns         | V1              | Yes             | Yes             | C, R, P           | 17              |
| Ocular          | dominance       |                 |                 |                  |
| columns         | V1              | Yes             | Yes             | C, P              | 17              |
| Blobs           | V1              | Yes             | Yes             | P (and maybe 18–20 | some C)         |
| Monstrals       | V2              | Yes             | Yes             | P                 | 18, 19          |
| and binaural    | columns         |                 |                 |                  |
| columns         | A1              | Yes             | Yes             | C, R              | 21–23           |
| Callosal        | Frontal and     | Yes             | Yes             | P                 | 24–26           |
| and          | parietal        |                 |                 |                  |
| columns/patches |                 |                 |                 |                  |
| Striomes        | Caudate/putamen | Yes             | Yes             | All mammals      | 27              |
| Glomeruli       | Olfactory bulb  | Yes             | Yes             | All mammals      | 28, 29          |
| Barreloids      | Thalamus        | Yes             | Yes             | R (probably C)   | 30              |
| Barrelettes     | Brainstem       | Yes             | Yes             | R (probably C)   | 30              |

Abbreviations: S1, primary somatosensory sensory cortex; V1, primary visual cortex; V2, secondary visual cortex; A1, primary auditory cortex; C, carnivores; R, rodents; P, primates.

TINS, Vol. 15, No. 10, 1992
neurons, each becomes heavily innervated by the axon that supplies it. Since all the target neurons are initially innervated by several axons that make only a few synapses, this final arrangement indicates that each innervating axon makes more and more synapses on fewer and fewer target neurons as development proceeds. As in the visual system, individual target cells acquire their full complement of synapses through a positive feedback mechanism that depends on neural activity. Confirmation of this interpretation has come from experiments in both the central and peripheral nervous systems that show that blocking activity prevents this normal focusing of innervation on appropriate sets of target cells.

Local connections extend the regional coherence of activity. The topographic mapping of afferent innervation to most sensory cortices means that neighboring neurons will often have similar patterns of electrical activity. This bias towards local coherence of activity is abetted by the tendency of cortical neurons to make synaptic connections with nearby cells. Unlike neurons in peripheral ganglia, which have few local connections and show no evidence of modular organization, nerve cells in the brain are characterized by extremely rich local circuits. These florid local connections presumably reflect the complex processing of information that is characteristic of the brain. The prevalence of local connections in the brain may also be a necessary (but not sufficient) condition for the emergence of patterns involving the hundreds or thousands of neurons that comprise cortical (and subcortical) brain modules.

Regardless of the exact function of local connections, they allow a population of nearby target cells to behave as a set during synapse formation, much as a single axon and its target neurons behave in simple systems like autonomic ganglia.

In summary, we suggest that three aspects of synaptogenesis lead, incidentally, to the formation of iterated brain circuitry. First, appropriate synaptic partnerships are precisely identified by patterns of electrical activity, thus resolving the ambiguity arising from molecular recognition alone. Second, identification of appropriate partnerships leads to the elaboration of very large numbers of additional synapses through activity-dependent reinforcement and growth. And third, the formation of rich local connections among central neurons extends the arena of these interactions from individual pre- and postsynaptic neurons to the sets of nerve cells that ultimately participate in each modular circuit. The purpose of these synaptogenic rules, however, is not to construct modules, but to establish appropriate connections between individual target cells. Since these rules (particularly the third) will not be realized equally in every brain region and species, a continuum in the anatomical and electrophysiological definition of modules should be evident, as is, in fact, the case.

Explanation of the inconstancy of modular arrays among species and cortical regions

This general account can explain the capricious appearance of modules of a given class among species, as well as the elusiveness of modules in motor and association cortices. Modules often develop in the primary sensory cortices because it is at this initial level of sensory processing that interconnected neurons and their inputs have the greatest likelihood of generating highly coherent activity among groups of target cells. In cortical association areas, the relative coherence of neuronal activity at lower levels is progressively diluted by increasingly complex integration of different pathways, making module formation less likely. By the same token, modules do not form in the primary motor cortex because the diverse inputs to cortical motor neurons generate less regional coherence of activity than does the thalamic innervation of the primary sensory cortices. Even in a primary sensory cortex, however, whether or not modules actually develop to a point that allows anatomical or electrophysiological detection depends on the degree of coherent activity among the participating neurons.

The degree of coherent neural activity in a given region of the brain will vary from species to species for a variety of circumstantial reasons (e.g. the synchrony of thalamic inputs, the nature and extent of local connections, the quality of topographic mapping in the region, the specific mechanisms of positive feedback found there, and so on – see for example Ref. 96). This interpretation is supported by the fact that a modular organization can be induced in the brain by changing the afferent innervation to a target region. Thus, when the olfactory placode in a developing frog is implanted in an unusual location, olfactory ‘glomeruli’ are induced in a part of the brain that normally lacks these structures. Similarly, when the occipital cortex of a rat is transplanted to a location in which the transplant receives innervation from the somatic sensory system, barrel-like structures are induced in what presumably would have been visual cortex. Perhaps the most impressive manipulation of this sort is the implantation of an extra eye in the developing frog. In this circumstance, the axons of the supernumerary eye grow into the optic tectum and form stripes that are similar to mammalian ocular dominance columns. In each of these cases, modular circuitry is generated by experimental manipulations that elicit distinct patterns of coherent activity in a region of the brain that normally lacks them. These experimental observations accord well with the view that such patterns arise as a by-product of the basic rules that govern the growth and elaboration of synaptic connections throughout the nervous system.

Some implications

If this argument is roughly correct, modularity per se may be of less general significance to cortical function than is now supposed. By this we simply mean that a given cortical system would work quite as well if modules of a particular class did not form, as is demonstrably the case among related species that differ in this respect. We do not mean to imply that the specific connections that develop in any given class of module are not important. Quite the
contrary, the operational identification of individual neurons by patterns of activity, and the subsequent growth and maintenance of functionally precise connections is essential. Moreover, wherever modules do appear, their presence will provide, as has been true over the past several decades, powerful clues about cortical connectivity in that region. The production of iterated patterns of circuitry, however, may be an incidental consequence of the activity-dependent elaboration of synaptic connections.

Although our surmise that these impressive arrays of repeating circuitry are a by-product of synaptic development may seem heretical, it is well to remember that not all biological patterns represent an important function. The spots, stripes, whorls which an iterated arrangement is universal among mammals, as in the case of orientation columns in the visual cortex and glomeruli in the olfactory lobe. Just as often, however, iterated patterns in the brain may represent a structural record of the rules that govern synaptic growth and development, rather than any imperative related to higher brain function.

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The idea that microenvironmental cues act alone late in development to determine a cell's phenotype has dominated recent research into retinal development, and has successfully replaced the notion of any role for cell lineage in the process of cell determination. We argue that there is, in fact, evidence favoring a degree of lineage restriction during the development of the vertebrate retina. We propose that environmental factors modulate a process of progressive lineage restriction. In this model, progenitor cells are viewed as having unequal potential, and their progeny are viewed as being committed to one of the major retinal cell classes before the stage at which they become postmitotic.

Much progress has been made in the past ten years in developing methods to mark and analyse descendants of single progenitor cells — cellular clones — in the vertebrate CNS. A compelling reason to study these families of cells is that a careful analysis of their size, placement and cell composition gives us insight into the genetic and developmental mechanisms that generate fully differentiated cell and tissue types from initially undifferentiated progenitors1-5. In this article we focus on the retina, an accessible part of the CNS with a comparatively simple layout that makes it a particularly favorable tissue in which to explore the relationships between a cell's lineage, its environment and its phenotype.

In a set of recent studies, progenitor cells in the retina have been marked at different stages of development, using a variety of methods (Refs 6–10; Huang, S. and Moody, S. A., unpublished observations). Without exception, these studies have shown that the resulting clones of retinal cells are tightly interknit clusters of cells that are aligned radially across the retinal layers (Fig. 1). Whether by design or happenstance, cells in a clone work together in adult retina, processing information from the same region of visual space.

A menagerie of clone types — dependence on time of labeling

When progenitor cells are marked early in development by combining genetically distinguishable four- to eight-cell mouse blastocysts into a single embryo17, the resulting clones contain a balanced...