

The functional logic of cortical connections

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Patterns of anatomical connections in the visual cortex form the structural basis for segregating features of the visual image into separate cortical areas and for communication between these areas at all levels to produce a coherent percept. Such multi-stage integration may be a common strategy throughout the cortex for producing complex behaviour.

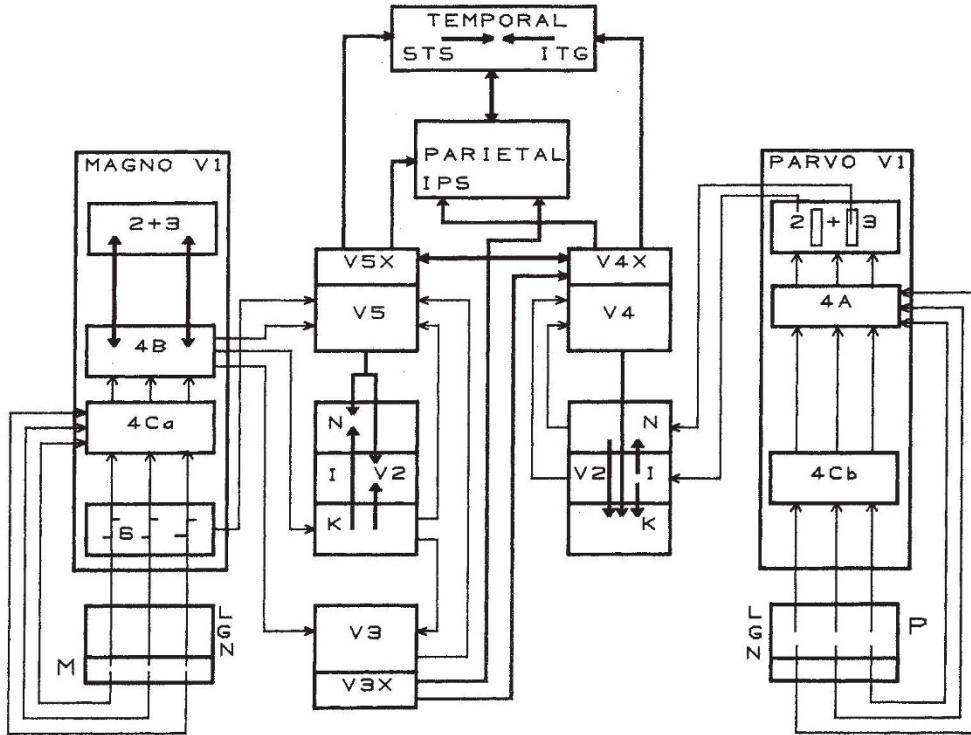
IT is an everyday experience that the visual world is perceived as a unified whole and that all the various properties of objects—their distances, shapes, sizes, colours, and directions of motion—are seen together in exact spatio-temporal registration. Yet this effortless coherence within the visual image bears little trace of the internal subdivisions of function in the visual cortex¹ that have become apparent from the past twenty years of research into the primate visual system. Anatomical, physiological and behavioural experiments in the monkey¹⁻⁴ and clinical studies of humans with cerebral lesions^{5,6} have established that different attributes of the visual scene, such as form, colour and motion, are processed in separate, anatomically distinct regions in the visual cortex, each executing its functions with considerable autonomy. Bilateral damage to a particular part of the human cerebral cortex, for instance, can result in a complete loss of the sensation of colour⁵ or of motion⁶, without any other notable deficit. In short, these findings support a theory of functional specialization in the visual cortex¹.

This separation of functions mirrors that found in the cerebral

cortex as a whole, where increasingly large numbers of specialized areas dealing with sensory and motor functions have been discovered. But with every addition a major problem, elegantly phrased by Karl Lashley⁷, has become increasingly apparent: "... how [it is that] the specialized areas of the cerebral cortex interact to produce the integration evident in thought and behavior". In effect the discovery of specialization renders this problem of integration more acute. In the older concept of cerebral organization, that of a single hierarchical chain of areas, integration was envisaged to occur progressively in the transition from one area to the next, each carrying out a higher level of analysis of all the same attributes than its predecessor^{8,9}. But it is now established that there are several serial pathways running in parallel, each of which is functionally specialized; these are actually physically segregated from each other and integration thus demands some form of communication between them.

We survey here the different strategies by which the visual cortex achieves both segregation and integration. They involve both forward and backward connections along a serial pathway,

Fig. 1 Diagrammatic representation of the projections of the P and M pathways to the specialized areas of the striate and prestriate visual cortex (black arrows) and the interconnections between them (coloured arrows). Forward connections are shown in green; like the connections shown in black, they are all reciprocated by a backward projection but only the forward direction is indicated. Connections in red are backward and those in blue are lateral or intrinsic. Interconnections between the specialized pathways and areas exist at many different levels but the early stages of the pathways are shown in greater detail because they have been more extensively studied than the later stages where the definition of cortical areas and their interconnections is not yet complete. The diagram shows the lateral geniculate nucleus (LGN) subdivided into magnocellular (M) and parvocellular (P) layers; V1, subdivided into layers 6, 4Cb, 4Ca, 4B, 4A, 3 & 2, with cytochrome oxidase blobs (small cylinders) in layers 2 & 3 in the P system on the right; V2, subdivided into cytochrome oxidase thick (K), thin (N), and inter (I)



stripes; areas V3, V4 and V5 as part of the third, fourth and fifth visual complexes denoted by V3X, V4X and V5X (connections shown to arise from V3X, V4X and V5X include the whole complex and do not exclude the areas V3, V4 and V5 proper); and the higher visual areas in the parietal and temporal lobes, the former including the intraparietal sulcus (IPS), among other subdivisions, and the latter the superior temporal sulcus (STS) and inferotemporal gyrus (ITG), all of which probably consist of several separate areas.

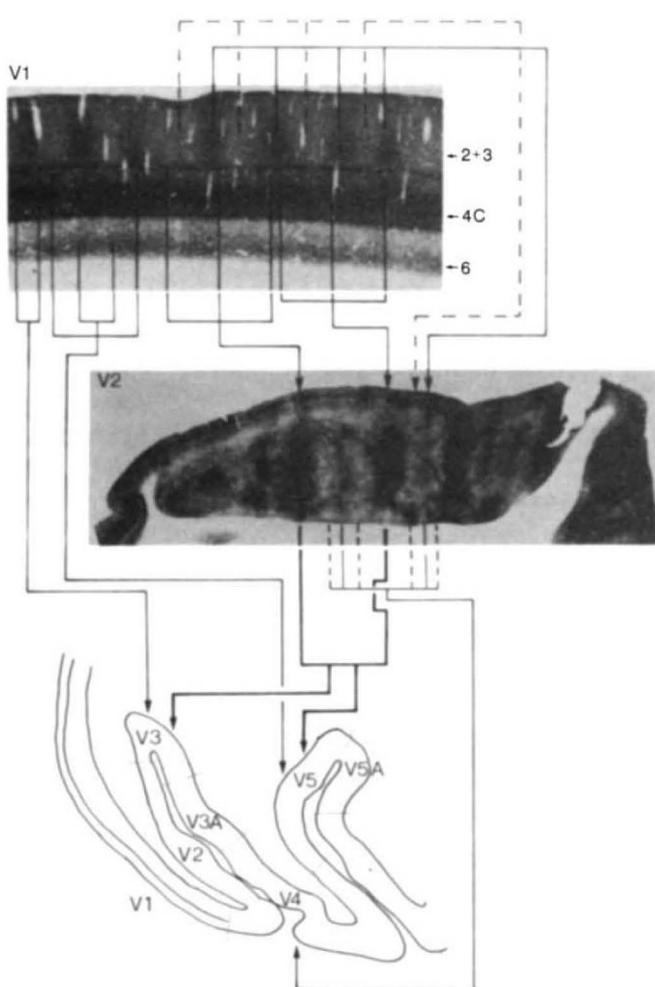


Fig. 2 The separate pathways leading from V1 through V2 to specialized areas V3, V4 and V5 in the prestriate cortex, shown by a stain for cytochrome oxidase activity. Sections through V1 and V2 taken at angles which most clearly reveal their cytochrome oxidase architecture are shown at the top and centre respectively. The M pathway includes the output from layers 4B and 6 directly to V5 and V3 and indirectly to the same areas through the thick dark stripes of V2 (heavy lines). The dark blobs and lighter interblobs of the upper layers of V1 are part of the P pathway. The blobs project through the thin dark stripes of V2 to area V4 (thin lines) and the interblobs project through the paler interstripes of V2 to V4 (dashed lines). A smaller direct projection from the upper layers of V1 to V4 is not shown.

as well as connections between pathways that are found to exist at all levels. Many of these strategies are used repetitively throughout the cortex, from which we derive some principles regarding the functional logic of cortical connections and make predictions about the general functional organization of uncharted cortical areas. Ultimately our hope is to provide an anatomical basis for tackling Lashley's question.

Segregation and specialization

The division of the visual system into specialized pathways begins at the very earliest stage, the retina, and continues through the subcortical visual relay, the lateral geniculate nucleus. In the retina, there are two major classes of ganglion cells, the $P\alpha$ and $P\beta$ cells^{10,11}. These have different properties and project separately to the cortex through the lateral geniculate nucleus— $P\alpha$ cells through its magnocellular (M) layers and $P\beta$ cells through its parvocellular (P) layers. Retinal ganglion cells and lateral geniculate cells have similar properties. Hence the two pathways are known as the P and M systems, terms that are

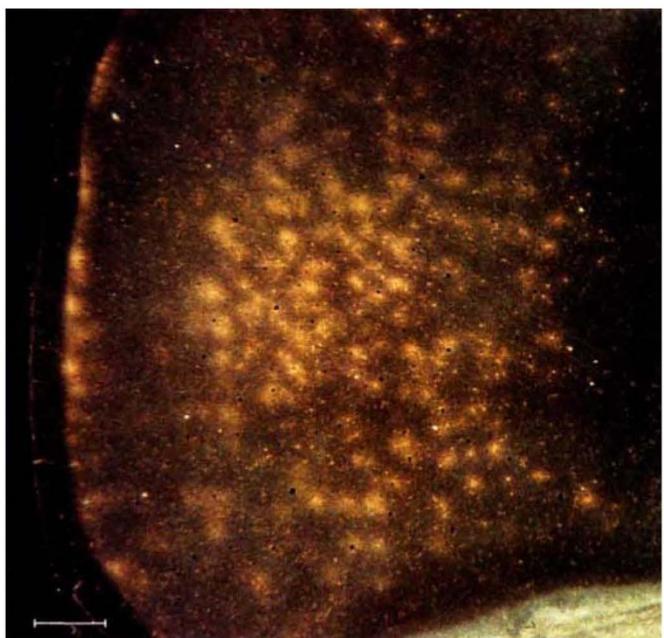
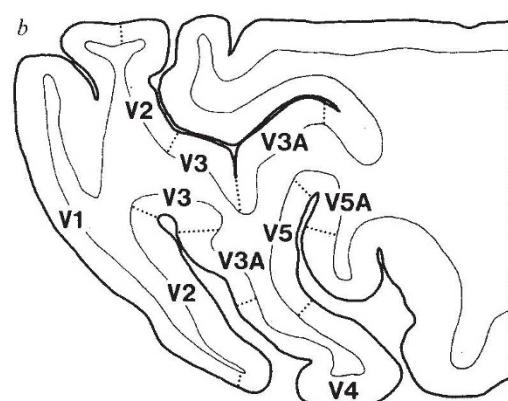
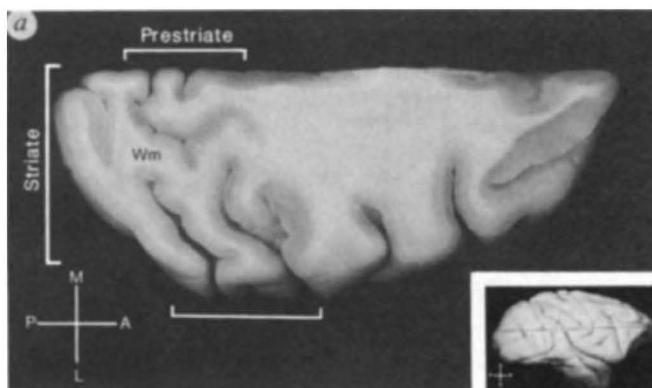


Fig. 3 The patchy connections of the primary visual cortex (area V1) with one of the specialized areas of the prestriate cortex, area V5, revealed by injecting V5 with the enzyme horseradish peroxidase. The enzyme is taken up by the terminals in the area and transported back to the cell bodies in V1; these appear golden. The section was cut parallel to the cortical surface, through the layer of V1 that contains the cells projecting to V5. The patchiness is evidence that not all cells in V1 have direct connections with V5, indicative of further functional subdivision in V1. Scale bar, 100 μ m.

applied throughout the visual system because they remain segregated in and beyond the primary visual cortex. Throughout, the two systems are involved in processing different attributes of the visual scene, building on the basic characteristics already evident in the retina and lateral geniculate nucleus. $P\beta$ and P cells are selective for wavelength and have slow tonic responses, whereas $P\alpha$ and M cells are not wavelength selective, have faster, transient responses, larger receptive fields and greater sensitivity to contrasts. They also have faster conduction velocities¹²⁻¹⁴.

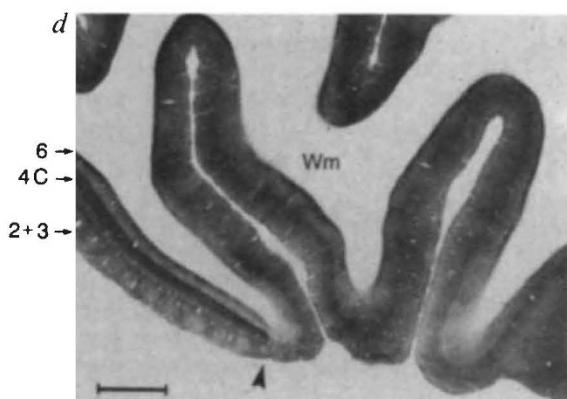
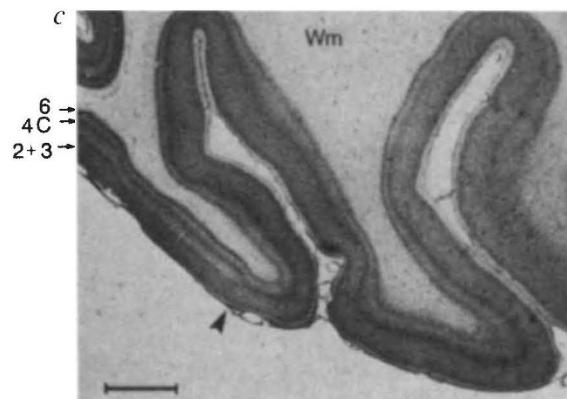
The P and M systems have different destinations in the visual cortex (Box and Fig. 1). They project to different parts of V1^{15,16}, the primary visual area, and of the second visual area (V2)^{17,18}, which surrounds it. V1 and V2 have a distinctive modular organization which is fortuitously revealed by staining for the metabolic enzyme, cytochrome oxidase. V1 contains darkly staining columns perpendicular to the cortical surface and intersecting the layers. The columns are especially prominent in layers 2 and 3 where they form 'blobs', separated from each other by the more lightly staining regions termed interblobs^{19,20}. In V2, there are alternate thick and thin dark stripes, separated from each other by more lightly staining interstripes^{21,22} (Fig. 2). Both V1 and V2 project to more specialized visual areas, including V3, V4 and V5 (also termed MT)^{17,18,23}.

P-cell outputs are relayed to the blobs and interblobs of layers 2 and 3 of V1²⁴. Wavelength selectivity is concentrated in the blobs, in cells which lack orientation selectivity; many have double-opponent concentric receptive fields different from those found in lateral geniculate cells²⁵ and are especially suited to extracting information about colour. By contrast, interblob cells are usually orientation selective²⁵ and are capable of responding to contours generated by differences in wavelength or luminance^{26,27}. Mathematical considerations suggest that P cells signal a combination of colour and luminant variations in the visual field, the balance depending on the sizes, or spatial frequencies,



The visual cortex

Both in man and macaque monkey, shown here, the cerebral cortex is a highly convoluted sheet, much of it buried inside the folds or sulci, seen in (a), a section through the brain at the level indicated in the inset in (a). Visual cortex occupies the posterior third of the cortex and can be divided into many distinct visual areas, shown in (b) on a drawing of a section at the same level as in (a). One of the oldest methods used to identify areas anatomically is the study of cytoarchitecture, the grouping of cells into different layers. A section through the posterior third of the macaque brain treated to stain the cell bodies (c) shows two distinctive regions, the primary visual striate cortex, area V1 (left) and the prestriate cortex lying in front of it. The border is indicated by an arrowhead. The striate cortex, so named because of its richly laminated appearance, receives all the fibres from the retina through the lateral geniculate nucleus, a relay nucleus below the cortex. The prestriate cortex has a less elaborate cytoarchitecture. Staining for the activity of the metabolic enzyme cytochrome oxidase reveals complex subdivisions in the striate and prestriate areas (d), shown in more detail in Fig. 2. Techniques for tracing anatomical connections between the striate and prestriate areas and functional studies reveal several distinct areas in the prestriate cortex (V2–V5) (b), each specialized to process different attributes of the visual scene. Wm, white matter.



of the patterns to which they respond²⁸. The signal thus contains primarily wavelength information at low spatial frequencies, to which blob cells are more sensitive²², and luminance information at high spatial frequencies, to which interblob cells are more sensitive²².

Thus the P system seems to split in the upper layers of V1 into one pathway concerned primarily with colour and another primarily with form. But both lead through V2 to the same area, V4, the blobs by way of the thin stripes, and the interblobs by way of the interstripes^{25,29,30}, subdivisions of V2 which maintain these functional distinctions^{29–31}. As a whole, V4 is specialized for colour^{1,32}. Whether form signals are processed independently of colour in V4 and whether the two subdivisions of the P system retain independent identities within it is not known^{33–35}.

The M system input terminates quite separately, in layer 4B of V1²⁴ where, again, at least two new categories, orientation and direction selectivity, are generated^{36,37}. The M pathway then projects to areas V3 and V5, both directly^{38,39} and through the thick stripes of V2^{29,30}. Like layer 4B of V1, the thick stripes of

V2 are characterized by a concentration of directionally selective cells and an absence of wavelength selectivity^{29–31}. Most cells in V5 are also directionally selective—to such an extent that V5 was called the motion area when first described⁴⁰. By contrast, the chief feature of V3 is orientation selectivity⁴¹.

Separation of motion, form and colour

The temporal properties of cells in the M system give it a much greater ability to follow events changing with time, consistent with its involvement in the analysis of motion, as seen especially in V5^{40,42,43}. Orientation selectivity is generated in both the P and the M systems so it seems that both are involved in form perception, the P system through its inputs to V4 and the M system through V3. But most V4 cells, unlike V3 cells, are also wavelength selective, and the nature of the relationship between colour and form processing in V4 remains to be determined. It seems that the M system is relatively more concerned with the form of moving objects and with generating structure from motion, whereas the smaller fields and larger number of cells,

at least within the lateral geniculate nucleus and V1, enables the P system to undertake a finer grain construction of a static visual image that incorporates both wavelength and luminance information. The restriction of motion and colour to separate cortical areas explains clinical observations of cerebral lesions leading to pure losses of these attributes^{5,6}, whereas form vision, which involves both the M and P systems, is normally less impaired.

The anatomy of segregation

We can now examine some of the general principles governing cortical connections. The cortex is a highly convoluted, thin and layered sheet of tissue whose surface area greatly exceeds its thickness (see Box). Variations in its structure, which correspond to the segregation of function, are expressed along all three dimensions and no single anatomical method can reveal them all. Conventional techniques for examining the architecture of the cortex—the manner in which cells and myelinated fibres are grouped together—have defined the layering in depth of the sheet. They have generally been less successful at revealing structural variations across its length and breadth, that is, within a single area or between areas. Consequently this aspect of cortical organization was overlooked in the past, even when some functional evidence was available, until new anatomical techniques revealed the subdivisions. The two examples we mention below illustrate the inferences about functional segregation that can be drawn from anatomical observations. First, however, we describe the segregation of function across the more prominent layering of the cortex. This can be related systematically to the hierarchical organization of pathways.

Laminar segregation of function. By convention the cortex is divided into six layers, with layer 1 at its surface and layer 6 at the junction with white matter (see Box). V1 is unusual in having a more complex pattern of layering with cells related to different visual attributes segregated between its layers. But more generally throughout the cortex cells in different layers vary in their functions by playing different roles in the input-output relationships of an area (Fig. 4a-d). Forward projections, for instance the projection from V2 to V5, originate predominantly from the upper cortical layers and terminate in layer 4. They are invariably reciprocated by an asymmetrically organized backward projection, for example from V5 back to V2, that arises from both the upper and lower layers, but its termination avoids layer 4 to concentrate in layers 1 and 6⁴⁴⁻⁴⁷. Thus the terms 'forward' and 'backward', in addition to describing the direction of a connection within a hierarchical sequence, also correspond to a particular pattern of laminar organization, although such a pattern has not yet been shown to be universal for the visual cortex.

Because the forward and backward outputs of an area arise from segregated populations of cells, it seems likely that they transmit non-identical signals. This, in a sense, is a form of specialization different from that which we have so far considered. But it is one about which there is little physiological knowledge. There are also reciprocal connections between a pair of areas that arise and terminate equally in all layers, giving a symmetrical organization intermediate between the forward and backward patterns. These connections are referred to as 'sideways' or 'lateral'.

Divergent connections as an indication of functional segregation. It has been axiomatic in cortical studies that functional differences are reflected in anatomical ones and, conversely, that an area of uniform structure should also be one of uniform function⁴⁸. Because the early studies of cortical architecture resulted in a rather uniform picture, the existing clinical evidence which suggested that a part of the human prestriate cortex is specifically involved in colour vision⁴⁹ was actually dismissed, largely because the area involved could not be distinguished from the rest of the prestriate cortex⁵⁰.

The first evidence for the separation of form, motion and colour in the visual system¹ came from the identification of

distinct areas, V2, V3, V4 and V5, in the architecturally uniform prestriate cortex because each receives separate inputs from V1 and from the opposite hemisphere^{17,18,51}. The discovery of independent outputs from each mm² of V1 to separate prestriate areas provided a powerful hint for the functional specialization of these areas³³, later confirmed by physiological studies¹. Because each mm² of V1, which represents a particular region of visual space, was known to contain a functionally heterogeneous population of cells³⁷, it seemed likely that V1 would send different rather than identical categories of signals to each prestriate area. In other words, it must act as a segregator of different types of signal³³, a role also played by V2 for similar reasons.

Modular architecture and stripy connectivity as an indication of functional segregation in an area. From this evidence it was reasoned³³ that V1 and V2 might themselves conceal a separation of form, motion and colour. Such a prediction was inconsistent with the then accepted picture of V1, which was heavily influenced by the work of Hubel and Wiesel, who had reported all cells outside layer 4C to be orientation selective^{36,52}. And that work in turn was influenced, to some degree at least, by the apparent architectural uniformity of V1: for "with no anatomical indication of nonhomogeneity in the upper cortical layers, it would have been easy to dismiss occasional, apparently sporadic groups of unoriented cells"²⁵. Hubel and Wiesel's picture of V1, then, contained no hint of the separation of form, motion and colour—a concept which has now come to dominate our thinking about the visual system—even though such a separation had already been demonstrated in the prestriate visual cortex¹.

In a repeat of history, the evidence for a separation of function in V1, as well as V2, was pursued only after non-uniformity had been shown anatomically—this time the modular or patchy architecture revealed by cytochrome oxidase histochemistry. This led to two correlations: that the specialized groupings of cells in V1 and V2 either avoid or coincide with the blobs and stripes, and that the pattern of outputs from either area to the specialized areas of the prestriate cortex, and to each other, are also patchy, the output patches again either avoiding or coinciding with the cytochrome oxidase patches. The latter finding was particularly significant because patchy patterns of connection are now known to be a widespread feature of cortical connectivity.

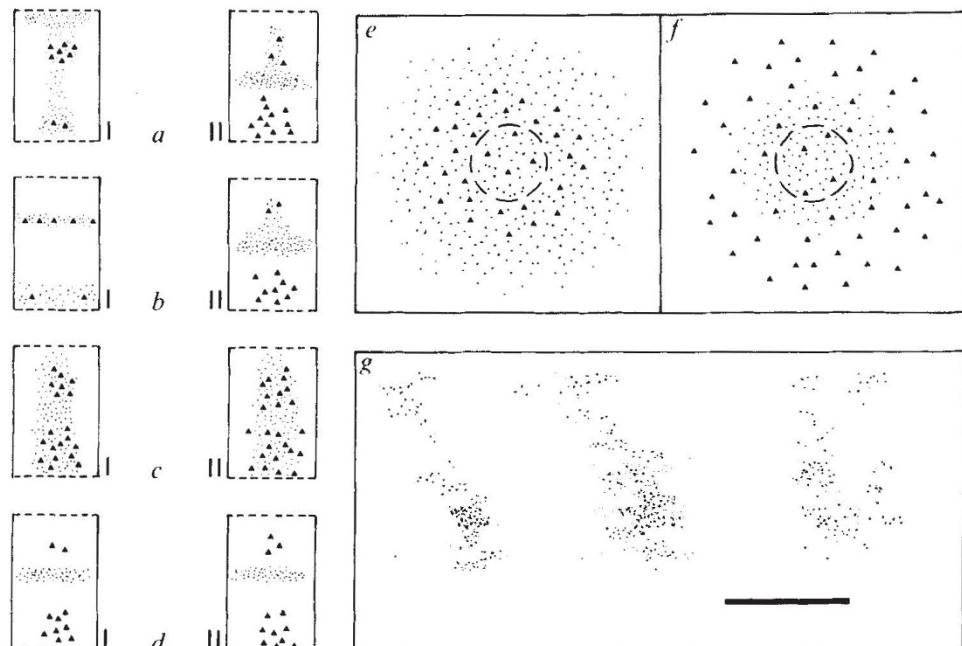
The inferences of anatomy. The lesson to be learned is that if an area has divergent projections, a modular architecture, or stripy connections with one or more areas, it is also likely to contain functionally distinct, and segregated, groups of cells. If any one of these features is observed it may be inferred that the others are also present. Layer 4B of V1 is a good example. It is known to project to both V3 and V5^{38,39} and we have recently found that its connections with V5 arise from a fairly regular array of patches (Fig. 3), similar in appearance to the blobs though not systematically related to them. This leads us to suppose that there is a further system of segregation in V1 and that cells in these patches differ from those outside, perhaps in the finer details of the analysis of motion.

Table 1 Examples of the two types of convergence

	Topical	Confluent
Forward	Blobs → thin stripes → V4 V1 → V5	V2 (thin stripes) + V3 → V4 V4 + V5 → IPS + STS
Intrinsic	in V4	in V1, V2 and IPS
Lateral		$V4 \leftrightarrow V5$
Backward	V5 → V1	V3 + V5 → V1 (layer 4B) V4 + V5 → V2 (K + I + N stripes)

For abbreviations see Fig. 1.

Fig. 4 Schematic representations of asymmetries in the connections between cortical areas, where projecting cells from an area are shown as pyramids and the fibres terminating in an area are shown in stippling. *a-d* show asymmetries in laminar patterns of connection. *a*, The standard pattern in which area I sends a forward projection to area II and II a backward projection to I. *b*, A variant, the connections between V1 (I) and V5 (II). It is atypical because in V1 both the cells of origin of the forward projection and the terminals of the backward projection are in the same layers. *c*, Symmetrical organization of most other connections that are not readily identifiable as either forward or backward. Many other symmetrical patterns, such as *d*, could be envisaged but have never been observed. *e, f*, Topical convergence in the asymmetrical connections between two areas: cells and terminals in *e* are the source of output to and the target of input from a circumscribed unit in *f* indicated by a dashed outline, and vice versa. The forward projection to a small part of *f* from a larger zone in *e* is characteristic of topical convergence. The asymmetry demonstrated by the different extents of the cells and terminals in *e* and *f*—some parts of *e* receive input from parts of *f* to which they do not project and some parts of *f* send output to parts of *e* from which they do not receive input—provides further topical convergence in the back projection from *f* to *e*. *g*, An experimental reconstruction of asymmetry similar to that in *e*, showing a small section of V2 and its connections with V5. Whereas the cells in V2 (heavy dots) projecting to V5 are grouped together in stripes, the return input to V2 from V5 (stipple) is more widely distributed and includes the territory between the stripes giving a pattern of confluent convergence.



Correlations between these features may prove to be a ubiquitous phenomenon in the organization of the cerebral cortex. All areas so far investigated make connections with many others and most of these are patchy in both origin and termination. The prediction is that they will also be found to possess a modular architecture and functional segregation. Perhaps the most studied visual area other than V1 and V2 is V5, which we also predict has an internal subdivision of function. The input to V5 from V1 and V2 terminates patchily^{53,54}, as does the input from V5 in the opposite hemisphere⁵⁵. In addition V5 is itself the source of widespread divergent projections^{47,56,57} and, at least in some species, it has a lattice-patterned cytochrome oxidase architecture^{58,59}. The functional logic of cortical connections therefore predicts that V5 is also a segregator, with functionally distinct groups of cells occupying anatomically distinct subdivisions.

Functional integration

We use the term integration broadly, to cover a number of distinct operations performed by the visual system. Perhaps the simplest is that envisaged by hierarchical theories of brain function, the progressive elaboration of increasingly more complex response properties in a specialized pathway by a pattern of spatially convergent connections repeated at each stage. A classic example is the simple-complex-hypercomplex model^{9,52} for the progressive elaboration of the orientation, position and length of a contour.

A second type of integration concerns the combination or interaction of attributes between pathways. Previous discussions have emphasized the divergence between the M and P pathways, or 'streams', and their continuation beyond the prestriate cortex—the M pathway, concerned chiefly with motion/spatial awareness, leading into the parietal lobe and the P pathway, concerned with object recognition, leading into the temporal lobe⁶⁰⁻⁶². The question as to how categories within these broad subdivisions are associated has been ignored or deferred to a further structure such as frontal cortex or the limbic system⁶¹. But the notion of two isolated, hierarchically organized and

functionally specialized pathways fails to explain one of the single most impressive facts about cortical connections—that no area of the cerebral cortex connects with only one or two other areas. Instead, from the multiple divergent projections of all areas we can deduce that the visual system employs an intricate combination of both hierarchical and parallel strategies, endowing it with a richness of connectivity that must facilitate all manner of interactions between different specializations. This is in accord with the subtle interplay between attributes known to occur perceptually. For instance velocity gradients can give information about relative depths, but erroneous depth perception can also give rise to an illusory percept of motion (the Mach illusion)⁶³.

This is an instance of one attribute being used in the computation of another but some attributes, of which motion and colour are the best examples, are probably computationally entirely independent of each other. But the percepts of motion and of colour must both be referred to the correct object in the field of view which is their source. This, third, kind of integration might use a different mechanism but, to indicate that the activity arising separately in each area is due to the same object, it too must involve intercommunication between the specialized pathways.

Integration through convergence

The anatomical means of assembling information is convergence. We define two categories, topical and confluent convergence. The first operates within a specialized pathway and involves integration across space; the second operates between pathways and involves integration between different attributes. Both are found in all types of cortical projections, forward, backward and lateral or intrinsic (Table 1), providing a substrate for convergent associations between the specialized pathways at many levels, including those at which functional segregation is first established. This leads us to a theory of multi-stage integration in the visual system.

Forward and lateral connections. Forward topical convergence occurs wherever a small part of a higher area receives input

from a larger part of a lower area (Fig. 4e, f). This generates a set of cells at each stage that have larger receptive fields and more complex properties than those at the previous stage. In the colour pathway, for instance, many blobs in V1 project to one thin stripe in V2²⁵ and several thin stripes to a small ($\sim 4 \text{ mm}^2$) part of V4^{29,30}, such that cells in V4 have larger receptive fields and more complex properties than their counterparts in V1.

The strategy of generating larger receptive fields—that is, gathering information from a wider part of the field of view—is probably essential to the computational process. In colour vision, for example, the property of colour constancy—colours of surfaces are largely unaffected by the spectral composition of the prevailing illumination—depends on a comparison of the spectral composition of the light reflected from many different surfaces in the field of view⁶⁴. Some V4 cells have the property of colour constancy, which is absent from V1 cells⁶⁵. This increase in complexity results from the comparison of information from larger parts of the field of view, to which the widespread intrinsic connections of V4 may also contribute⁶⁵.

Confluent convergence includes any pattern of connectivity where one area receives input from several others. It is commonly considered to be the means of uniting signals from different sources, first within a single modality such as vision, and then between modalities, for example, vision and audition⁶⁶. In the visual system (Fig. 1), confluent convergence occurs both within a pathway (for instance, in the M pathway the convergence of the output of areas V1, V2 and V3 to V5) and also between the different functional pathways (shown by heavier arrows in Fig. 1). The latter involves not only the direct connections that V3, V5 and V4 make with each other but also the connections that each makes with higher areas in temporal and parietal cortex.

V4, like V5, receives a forward projection from V3, but the interconnections between V4 and V5 are of the lateral variety^{47,56}. The direct projections of V4 and V5 to the temporal lobe are largely to separate zones^{47,56,67}, but these zones are known to be interconnected⁶⁸ and physiological evidence for convergence has been obtained in a region where neurons selective for faces are found in juxtaposition with neurons which respond to characteristic locomotor or other body movements⁶⁹. The former is likely to represent the culmination of a pathway derived from the P system through V4, but possibly also involving V3, and the latter the culmination of a pathway derived from the M system through V5. In the parietal lobe the inputs from V4 and V5 converge directly at the same region^{47,55,56,70}, whereas that from V3 (through V3A, a neighbouring area with similar properties) is predominantly to a separate zone (S.Z. and S.S., unpublished results). But, the two zones are probably also interconnected (S.Z. and S.S., unpublished results) and both project into the temporal cortex^{68,71}.

The fact that both V4 and V5 have projections to the parietal as well as the temporal cortex is good evidence that the proposed division into two isolated and serially organized ‘streams’^{60–62} is an oversimplification. Without denying the evident specialization of the temporal and parietal lobes, the convergent anatomy emphasizes the scope that exists for interactions between them. It seems that an area performing a specialized higher function will tap any source of information that is useful. V3 provides a forward output to both of these areas but, because of its independent output to parietal cortex, it should not be thought of simply as a step in these pathways. Instead, like V4 and V5, we regard it as a pivotal area for marshalling and redistributing the output of V1 and V2 to higher areas.

Intrinsic connections. The projections from two areas may both lead to a third area, but terminate in different parts or layers within it. Intrinsic connections between their termination zones provides another type of convergence. The projections to the temporal and parietal lobes from the specialized prestriate areas are stripy (S.Z. and S.S., unpublished results) though it is not known how the inputs from different areas relate to each other.

But even if they occupy non-overlapping zones, they would still fall within the range of lateral intrinsic connections that would permit interactions between them. An obvious analogy is in V1, where the inputs from the two eyes maintain separate territories in layer 4C, but converge to yield binocularly driven cells thereafter⁵². A similar process could integrate the information from V4 and V5 in the intraparietal sulcus (see Fig. 1), if the patchy inputs from these two areas do not coincide directly.

Intrinsic connections can also provide communication between the specialized pathways at earlier levels. The horizontally coursing fibre plexus in layer 3B of V2 contains collateral axons which are sufficiently long (up to 4 mm⁷²) to allow interactions between all three types of stripe. And in V1 there are modest connections between layers 2 and 3 and layer 4B⁷³. No sign of interaction has been detected physiologically, so it seems that these connections are not strong enough to undermine the essentially segregatory processes in these areas; hence their particular influence remains to be understood.

Backward connections. Most connections between areas in the cortex appear to be reciprocal but within an area the distributions of the forward and backward components do not precisely coincide (Fig. 4). This asymmetry gives rise to confluent and topical patterns of convergence in the backward direction. Good examples are the projections of V5 and V4 back to V2⁵⁹ (Fig. 4g). V5 projects back most heavily to the thick stripes from which it receives its input but the projection also encompasses the territory of the intervening thin stripes and interstripes. Similarly, the back projection from V4 is most concentrated in the thin stripes and interstripes but also stretches across the thick stripes. Thus areas V4 and V5 have confluent projections back to each type of stripe in V2, so that they may influence each other at an earlier stage in their respective pathways than through the direct link between them. A similarly asymmetrical backward system is found in layer 4B of V1, which contains cells projecting to both V3 and V5. The diffuse back projection from V5 to V1 thus has the potential of influencing the cells with output to V3—and hence of informing one subdivision of the M system of the activity in another. It is interesting that the back projection from V5 to V1 is atypical in that it avoids the upper layers of V1, where the P system is situated; the backwardly-mediated interaction between the M and P systems is thus deferred until V2.

The back projections from V5 to V1 and V2 also provide a system of topical convergence, because the output from a prescribed part of V5 is sufficiently diffuse to influence regions of V1 and V2 which do not themselves provide an input to that part of V5 (Fig. 4e, f). But whereas forward topical convergence produces larger excitatory receptive fields, this is not so for backward convergence: backward connections seem not to excite cells in lower areas, but instead influence the way they respond to stimuli within their smaller receptive fields. A direction-selective cell in V1, for instance, might be less excited by its preferred stimulus when many objects outside its classical receptive field are also moving in the same direction⁷⁴.

Multi-stage integration in the visual cortex

The functional logic of the cortical connections described above is twofold—to achieve segregation and to allow for integration. The first two visual areas, V1 and V2, are segregators, containing separate groupings of orientation, wavelength, and direction selective cells. Divergent and convergent outputs from V1 and V2 assemble signals related to these basic attributes of vision in three pivotal areas: areas V3 and V3A (the V3 complex) involved in dynamic form analysis; area V4 (the V4 complex) involved with colour in association with static form analysis; and the V5 complex (areas V5 and V5A) involved with motion. None of these functions is necessarily unique to these areas, as implied by the term specialization, because each is part of a pathway that involves several areas. Furthermore, cells selective for certain basic attributes, such as disparity, may be found in

each⁷⁵. The pivotal areas may communicate with each other at three distinct levels: directly; through confluent backward connections with V1 and V2; and through confluent forward connections with areas in the parietal and temporal lobes. We suppose that these higher areas also communicate with each other using the same three strategies, further emphasizing the multi-stage integrative process used to produce the visual image in the brain.

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ARTICLES

Controls of the structure of subducted slabs

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Numerical simulations of subducting slabs are formulated in which the shape and dip of the slab are determined by the dynamics of the flow, rather than imposed a priori. The dip of slabs is a function of the time since the initiation of subduction. Slabs fold, develop a kink in dip, and thicken on entry into a high-viscosity lower mantle. Comparison of the simulations with seismic observations suggest that the lower mantle is at least 10–30 times more viscous than the upper mantle.

THE shapes and dips of seismic Benioff zones are the strongest constraint on the pattern of flow in the mantle. Benioff zones always have positive dips and generally lack any major change in dip just above the 670-km discontinuity, which suggests that slabs penetrate into the lower mantle^{1–3}. This is consistent with interpretations by residual sphere analysis⁴ that there are tongues of seismically fast mantle directly under Benioff zones in the Western Pacific. These observations at first seem to be at odds with the down-dip compression of slabs that penetrate through the transition region⁵, with the contortions apparent in the Tonga

slab from seismicity⁶, and with a detailed tomographic study of Western Pacific slabs⁷ which shows that slabs are apparently deflected away from the 670-km discontinuity in a few places. Two hybrid models of mantle dynamics have been advanced⁸ in an attempt to reconcile these observations: mantle-wide flow with depth-dependent viscosity, and penetrative convection. Both models allow slab penetration into the lower mantle, at the same time having increased resistance to flow through the seismic transition zone (400 to 670 km depth); one model has a viscosity jump and the other a compositional jump at 670 km depth.

Here we explore the first hybrid model, mantle-wide flow with depth-dependent viscosity, using a new class of finite element

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