Hierarchical organization and functional streams in the visual cortex

David C. Van Essen and John H. R. Maunsell

In the macaque monkey, a dozen distinct visual areas have been identified in the cerebral cortex. These areas can be arranged in a well-defined hierarchy on the basis of their pattern of interconnections. Physiological recordings suggest that there are at least two major functional streams in this hierarchy, one related to the analysis of motion and the other to the analysis of form and color.

In their pioneering studies of the cat's visual cortex, Hubel and Wiesel obtained evidence for many sequential stages of information processing along the visual pathway. They described cells in areas 17, 18 and 19 whose receptive-field properties differed greatly in their complexity and degree of selectivity. On the basis of these observations, they proposed that the properties of cells at any given stage could be derived through appropriate inputs from cells at the immediately preceding stage, in an order proceeding from cells of the lateral geniculate nucleus (LGN) to simple cells, complex cells, hypercomplex cells and, at the highest stage which they studied, 'higher-order hypercomplex cells'. Their scheme represented the simplest form of hierarchical organization, with information being processed in exclusively serial fashion.

As visual pathways were studied in greater detail during the ensuing two decades, a variety of evidence was obtained that did not support a strictly serial scheme of organization. One of the first pieces of evidence was Hubel and Wiesel's own finding that

Fig. 1. Cortical areas in the macaque monkey. Locations of areas are shown on a lateral view of the right hemisphere (inset) and on a two-dimensional unfolded map of the entire cerebral hemisphere. Visual areas are labelled and colored individually. A single shade is used for each of the other functional systems (auditory, somatosensory and motor), and individual areas are outlined but not labelled on the cortical map. Abbreviations for visual areas: MT (middle temporal)\textsuperscript{20}; MST (medial superior temporal)\textsuperscript{27}; VIP (ventral intraparietal)\textsuperscript{37}; VP (ventral posterior)\textsuperscript{39}; IT (inferotemporal)\textsuperscript{13}. Evidence for the location and extent of these areas is discussed in Refs 28 and 55. Area POa is tentatively split into two subdivisions on the basis of anatomical inhomogeneities\textsuperscript{39}. The prostriate area (PS), which is split by an artificial discontinuity, does not have known sensory functions in the macaque.

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area 17 projects to several cortical areas (18, 19 and lateral suprasylvian cortex), thus demonstrating parallel outputs from a single area. Other important observations, discussed in a number of recent reviews, include the demonstration of: (1) direct projections from the LGN to areas 18, 19 and lateral suprasylvian cortex as well as to area 17; (2) projections from areas 18 and 19 back to 17; (3) direct LGN inputs onto complex cells as well as simple cells; and (4) distinct retinal ganglion cell classes, the X, Y and W cells, whose outputs remain partially segregated at cortical as well as subcortical levels.

These various lines of evidence clearly suggest that information is to some degree processed in parallel fashion within the visual system. While a strictly sequential-processing scheme is thereby ruled out, it is equally clear that visual processing is not exclusively parallel, in so far as there does exist significant cross-talk between channels. Thus, it is unfortunate that the question of cortical organization has sometimes been treated as a debate over parallel versus serial processing, as though these were the only alternatives that needed to be considered. It makes sense first to address the question of whether the visual system is in fact organized in hierarchical fashion.

A hierarchy, by definition, is a system whose members can be unambiguously assigned to specific levels or ranks in relation to one another. For example, it is obvious from what is known about retinal organization that retinal ganglion cells are at a more advanced level of processing than bipolar cells, which in turn are at a more advanced level than photoreceptors. Within each cell class there are distinct subclasses, such as the X, Y and W ganglion cells, which provide parallel outputs from a single hierarchical level. Although a priori there is no guarantee that higher levels of the system follow the same organizational principle. In particular, visual cortex might be organized as a complex network in which distinct hierarchical levels of processing simply do not exist. Examples of well-studied neural networks which apparently lack hierarchical organization include oscillatory circuits involved in rhythmic motor activities in invertebrates.

The structural framework of a system (for example whether or not it is hierarchical) need not be the same at all levels of organization. For example, the aforementioned oscillatory circuits, even if not hierarchical in their internal organization, may nonetheless be members of a larger hierarchical system whose other members also consist of multicellular ensembles rather than individual cells or cell classes. Along similar lines, it is possible that in the visual system different cortical areas are related to one another in hierarchical fashion irrespective of whether the individual areas are internally organized as hierarchies. This article is concerned mainly with the relationships among visual areas, rather than with their internal circuitry.

Cortical visual areas
During the past decade considerable progress has been made in identifying a large number of specific, well-defined subdivisions of visually responsive cortex. Many of these visual areas differ greatly from the cytoarchitectonic subdivisions described by anatomists in the early 1900s. The currently recognized cortical areas have been identified on the basis of information relating to their connections, topographic organization, architecture and/or functional properties. The most reliable identifications are those in which a combination of these criteria have been successfully applied. Extensive studies along these lines have been made in the visual cortex of several species, including the cat, owl monkey and macaque monkey (see Refs 50 and 56). We will focus our discussion mainly on the macaque monkey, in which there are at least a dozen cortical areas that are largely or exclusively visual in function.

Many of the visual areas in the macaque are partly or entirely buried within deep cortical sulci. Their overall arrangement can best be appreciated by displaying all of the areas on a single two-dimensional map of the cortex, as shown in Fig. 1. This map represents the neocortex of the entire cerebral hemisphere after it has been unfolded. It allows one to visualize the large regions of cortex buried within sulci and at the same time provides a reasonably accurate indication of actual surface areas within the intact cortex. The various visual areas are shown in different shades of red, orange and yellow on the cortical map and also in the lateral view of the intact brain (inset). Visual cortex occupies the entire posterior half of the hemisphere, corresponding to the left half of the cortical map. Other sensory and motor areas are also indicated on the map, with auditory cortex shown in green, somatosensory cortex in blue, and motor cortex in grey, but without separate shades for the individual subdivisions.

It is obvious that V1 (area 17, or striate cortex) and V2 are by far the largest distinct areas in the macaque cortex. In the intact hemisphere they share a long, common border, but the map has been split along this border to reduce distortions in the representation of surface area. Areas which we consider to be reasonably well-defined entities by one or more criteria are shown in solid color. Not all of the areas shown in solid color have been identified or localized with absolute certainty, however. For example, there is some question as to whether VP is a distinct area rather than being a part of V3, as originally proposed. There are also significant uncertainties about the overall extent of V3A, V4 and MST. Other regions, such as area 7a in the parietal lobe and IT (infratemporal cortex) in the temporal lobe, are less well characterized.

A hierarchy of visual areas
Accompanying the increase in number of visual cortical areas that have been identified in various species has been an even more rapid increase in the number of identified pathways interconnected these areas. All visual areas which have been studied in any detail turn out to have multiple projections to other cortical areas. For example, V1 has major projections to three areas (V2, V3 and MT) as well as several minor projections, while MT projects to at least seven distinct areas (V1, V2, V3, V4, VP, MST and VIP). Altogether, there are at least thirty-three pathways that interlink the dozen identified visual areas in the macaque. The actual number is almost certainly much larger, as there are many areas whose connections have not been studied in detail.

The existence of so many areas and pathways raises the specter of a cortical network so hopelessly tangled as to be virtually indecipherable. Fortunately, though, these pathways adhere to several organizational principles which, taken together, provide the framework for constructing a remarkably orderly scheme of cortical organization. (1) Connections between cortical areas are, with few exceptions, organized in a reciprocal fashion. That is, if area A projects to area B, then B projects to A. (2) Within a reciprocal pair of connections, there generally are characteristic differences in the laminar distributions of axonal terminations and cells of origin. The basic pattern is illustrated in Fig. 2. In one direction, the projection arises mainly from cells in superficial layers, with a contribution of less than 10-15% from deep layers, and terminates most densely in layer IV, the granular layer. This is designated as the forward, or ascending, direction by virtue of the similarity to ascending thalamocortical pathways (for example the geniculostriate pathway), which also terminate preferentially in layer IV. In the other direction, the projection arises from cells in both superficial and deep layers and terminates preferentially outside layer IV, often most densely in layers I and/or VI. Accordingly,
this direction is designated as descending, or feedback. (3) From consideration of all pairwise-interconnected areas, it is possible to delineate an overall cortical hierarchy, in which each area has an unambiguous relationship to all other areas in the scheme (Fig. 3). The hierarchy was constructed by assigning each area to a level just above that of the highest area which provides an ascending input. This leads to six hierarchical levels for the dozen visual areas involved. Projections whose laminar organization is intermediate between forward and feedback patterns are considered to be lateral interconnections between areas at the same hierarchical level (see legend to Fig. 3). It is significant that a well-defined hierarchy can be inferred from these connections, as one can easily imagine connectivity patterns that would lead to major ambiguities in the overall relationships among different areas.

Not surprisingly, V1, which receives the major input from the LGN, is at the lowest level of the hierarchy, and the areas in the temporal, parietal and frontal lobes are at the highest levels. In this scheme, areas which are well defined by a combination of anatomical and physiological criteria are enclosed by rectangles, whereas those regions which are less distinct and may comprise multiple areas have been enclosed by ellipses. Not all of these areas are exclusively visual in function; for example, at least some of those in parietal and frontal cortex have visuomotor function or receive other sensory inputs. Although each of the visual areas in the first four levels of the hierarchy is topographically organized, it is significant that several of them lack a complete representation of the contralateral visual hemifield. In particular, the representation in VP is restricted to the upper part of the visual field, while that in V3 and V4 (as delineated in Fig. 1) is restricted to the lower part of the visual field. V4 is the primary source of lower-field input to inferotemporal cortex. Upper-field input to inferotemporal cortex is mainly from an unnamed region directly anterior to VP. Although many important details remain to be worked out, it seems apparent that there are substantial differences in the way information is processed from upper versus lower halves of the visual field.

**Functional specializations**

The hierarchy shown in Fig. 3 is a heuristic scheme that is based solely on anatomical considerations, but its ultimate usefulness depends largely on how well it relates to cortical function. With respect to one physiological parameter, receptive-field size, there is an excellent correlation to be noted. Receptive fields are smallest in V1, and they increase in size at successive stages of the hierarchy. This indicates that the relative ordering of areas is a reasonable one. A more critical issue concerns the transformations in information content represented by neural activity at different levels. In general, one would expect successively higher levels of the hierarchy to be associated with correspondingly more advanced levels of visual analysis. It would also be reasonable to anticipate that different visual areas at the same hierarchical level would be involved in qualitatively different kinds of processing. In keeping with this expectation, a number of recent studies have provided evidence for two distinct streams of visual processing which are segregated at the level of V1, if not earlier, and which can be traced through multiple stages of the hierarchy. One pathway includes the middle temporal area (MT) and the medial superior temporal area (MST), and it appears to be involved primarily in the analysis of visual motion. The other pathway includes areas V4, VP and inferotemporal cortex (IT) and is mainly involved in the analysis of form and color.

**Motion analysis**

The first indication of a visual area specialized for motion analysis came from studies a decade ago showing a high incidence of direction-selective cells in a region of the superior temporal sulcus now recognized to be part of MT. More recently, it has been found that the majority of MT neurons are selective not only for the direction of stimulus motion, but also for speed and binocular disparity. These cells typically show little or no selectivity for stimulus shape or color, however. A very small percentage of cells in MT have opposite direction preferences for the two eyes and respond optimally to motion towards or away from the animal. The remaining disparity-tuned cells respond best to fronto-parallel motions but, since there are cells representing a range of preferred depths, the population as a whole can...
signal information about various motions in depth\textsuperscript{26}. Thus, MT seems eminently well suited for analysing the three-dimensional trajectories of objects moving in visual space, irrespective of their particular form.

MT is the lowest area in the cortical hierarchy in which a selective emphasis on motion analysis is apparent. However, the basic properties of selectivity for direction, speed and disparity are present in a substantial percentage of cells in V1 and V2\textsuperscript{4, 8, 18, 30, 61}. Moreover, direction-selective cells in V1 are especially concentrated in layer IV\textsuperscript{b}, which is the major source of the projection from V1 to MT\textsuperscript{23, 27}. It thus becomes important to ask what distinguishes the cells in MT from those at lower levels, aside from the higher overall incidence of direction selectivity. The most obvious difference is that receptive fields are approximately two orders of magnitude larger in MT than in V1\textsuperscript{a}, reflecting a high degree of convergence in this pathway. These larger receptive fields are presumably related to functional capacities not found in V1. For example, the range of preferred speeds for the overall population of cells is nearly an order of magnitude greater in MT than in V1\textsuperscript{a}. This increased range may be important in providing for the analysis of rapid motion in the visual field. Another important feature, demonstrated in MT of the owl monkey\textsuperscript{26}, is the presence of pronounced surround interactions, in which responses to stimulation within the excitatory receptive field can be inhibited by motion in other parts of the visual field. Cells with this property are capable of signalling information about relative motion. Additional interesting features of cells in MT are likely to be found as selectivity for more complex aspects of stimulus motion are tested.

Much remains to be learned about how the properties characteristic of MT neurons are generated and about how this information is processed at higher stages of the motion pathway. There are two major ascending outputs of MT: an adjoining area, MST, and an area in the fundus of the intraparietal sulcus, the ventral intraparietal area (VIP)\textsuperscript{9}. Nothing is known about the properties of cells in VIP, but for MST the available evidence is consistent with a role in motion analysis more advanced than found in MT. Cells in MST are direction selective and have very large receptive fields\textsuperscript{52}. A more interesting property, not found in MT, is that some cells in MST respond differently to a moving object when the eyes are stationary than to the equivalent retinal stimulation produced by a stationary object when the animal moves its eyes\textsuperscript{38}. MST is reciprocally connected with area 7a in the parietal lobe\textsuperscript{28, 33}, from the limited evidence available on laminar distribution, the two areas appear to be at the same hierarchical level. In any event, parietal cortex contains direction-selective cells with very large receptive fields and with preferred directions that vary with location within the receptive field (for example towards the fovea or away from the fovea)\textsuperscript{59}. In addition, visual attention, direction of gaze, tracking movements and other manifestations of behavioral states affect the responses of parietal neurons\textsuperscript{24, 30, 37}.

**Form and color analysis**

The pathway associated with analysis of form and color leads from V1 to IT in the temporal lobe. The most detailed studies have been on V1, where there are substantial numbers of cells selective for stimulus orientation, length, width (i.e. spatial frequency) and color, as well as for direction and speed, the parameters more specifically relevant to the motion pathway, and for binocular disparity, a parameter relevant to both motion and form analysis\textsuperscript{18, 30, 46}. Much of the current interest in V1 lies in relating these diverse kinds of selectivities to the modular features revealed by cytochrome oxidase staining and other anatomical techniques\textsuperscript{16, 19}.

With regard to the processing that occurs in extrastriate cortex, one of the central questions is the degree to which individual areas are specialized for particular functions. The evidence linking MT and MST to the analysis of motion has already been discussed. A more controversial claim about functional specialization has been the suggestion that V4 is specifically and selectively involved in color analysis. Zeki\textsuperscript{59, 63} reported a high incidence of color-selective cells in V4 and a much lower incidence in other extrastriate areas, including V2, V3, V3A and MT. There appears to be general agreement that very little color selectivity is present in V3 and MT\textsuperscript{22, 25}. For V4, however, various estimates of the incidence of color selectivity range from 100% to only a small minority\textsuperscript{1, 29, 34, 45}. Much of the variability in these estimates may be attributable to differences in experimental conditions or in the qualitative criteria that have been used for judging color selectivity. In order to provide a firmer basis for analysing color properties, it is desirable to have quantitative measurements and numerical indices of color-tuning properties. Prelim-

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**Fig. 3.** A hierarchy of visual areas in the macaque. Each area is assigned to a specific hierarchical level on the basis of criteria discussed in the text. The majority of pathways indicated on the diagram have been shown to be reciprocal, while the remainder have not been adequately tested (see Ref. 27). Not shown on the diagram are major inputs to IT from an unnamed region anterior to VP which in turn receives ascending inputs from VP (A. B. Burkhalter and D. C. Van Essen, unpublished observations). (Modified from Ref. 27, with permission.)
inary reports based on such an approach have now been presented for V4 (Ref. 1; S. J. Schein, R. Desimone and F. M. de Monasterio, unpublished observations) and for the ventral posterior area (VP) and adjoining V2\(^+\). The results suggest that in all three areas a clear majority of cells have pronounced color selectivity. There appears to be a fairly continuous distribution, from highly selective cells to non-selective cells, so that the incidence of color selectivity depends heavily on the specific criteria used in designating this category. Nonetheless, it seems clear that there are at least three extrastriate visual areas (V2, V4 and VP) that play a major role in color analysis. Many cells in these areas are also orientation selective, and many are disparity selective as well, at least in V2 and VP. Thus, none of these areas is specialized for color in the sense that MT is specialized for motion, and it would be inappropriate to regard any of them as a ‘color area’.

This conclusion is in keeping with what is known about the anatomical pathways leading to IT. V4 receives its major ascending inputs from V3 and dorsal V2, with only inconsistent and relatively minor inputs from V1\(^2,5,7\). Thus, the cells providing inputs to color cells in V4 presumably reside largely in V2 and/or V3, and one might therefore expect to find reasonable numbers of color cells in at least one of these areas. One would also expect to find many cells in V4 conveying information about stimulus form in addition to whatever color selectivity they may have, given that V4 provides the major inputs from lower visual fields to IT\(^6\) and that IT is known from lesion studies to play a major role in pattern vision and form recognition\(^5,6\).

Several important stages of form analysis must take place between V1, where selectivity for a variety of relatively simple stimulus parameters is established, and IT and other temporal lobe regions, where some cells appear to be selective for highly complex features contained with stimuli such as a hand or a face\(^14,20\). However, the nature of the processing that occurs at each of the stages beyond V1 remains a major enigma. The finding of orientation-selective cells in V2, V4 and VP and of cells selective for length and width is evidence that these areas convey information about form and pattern, but it seems likely that they should also be involved in higher levels of analysis, involving transformations of information that are qualitatively different from those occurring in striate cortex. The description of ‘higher-order hypercomplex’ cells in area 19 of the cat, which require simultaneous stimulation with two orientations, illustrates one such transformation\(^7\). No cells of this type have been described in primates, but this may simply reflect an inadequate search in the appropriate regions. Additional clues as to how to approach these issues may come from psychophysical studies of early stages of visual perception\(^21-40\).

Conclusions and overview
The number of identified visual areas in the macaque has increased rapidly in recent years, and the list will undoubtedly grow in the future. Based on the extent of cortex which has not yet been thoroughly characterized, the total number of visual areas can plausibly be estimated as somewhere between 15 and 20. There are a number of general questions about hierarchial organization that will be of interest to explore as additional data are obtained on the connections and functional properties of existing and newly found areas. First, do all of the relevant new data support the existing hierarchical scheme for macaque visual cortex? If not, there are several options to be considered. It might be necessary, of course, to abandon the hierarchy altogether or to restrict its applicability to only a portion of the visual pathway. Alternatively, it may be sufficient simply to revise the criteria for distinguishing forward, feedback and lateral connections. Another possibility is that the discrepancies may have arisen from inadequacies in the identification of the areas under consideration. This is of particular importance in evaluating results concerning the various areas in temporal, parietal and frontal cortex which have not been extensively characterized. A second question is whether the hierarchical scheme is extended to other functional systems (for example somatosensory and motor areas) and to other species. The limited evidence available suggests that hierarchies of areas may exist in somatosensory cortex of the macaque\(^8\) and in visual cortex of the squirrel monkey\(^9\) and cat\(^11\). Third, can the numerous connections with subcortical areas, particularly the pulvinar, be incorporated into an expanded hierarchical scheme in a coherent and sensible fashion? Fourth, can the hierarchy in visual cortex be extended to a finer level of resolution, namely, cell layers and/or individual cell types? As already mentioned, the question of hierarchical processing within V1 is still a controversial issue after two decades of intensive study and debate. For the various extrastriate areas, there has simply not been sufficient information to generate extensive discussion of possible cellular hierarchies.

The cortical hierarchy has provided a framework for hypothesizing at least two major streams of processing. This suggestion is similar in several respects to the hypothesis of Ungerleider and Mishkin\(^10\) that there are separate functional systems for spatial localization, carried out in posterior parietal cortex, and for object perception, carried out in inferior temporal cortex. However, we are using a different set of criteria for identifying functional streams, which are related mainly to the physiology and anatomical connections of individual extrastriate areas. Also, we are suggesting that one stream is involved specifically in motion analysis, rather than spatial localization in the broader sense. Although there is substantial evidence suggesting that these streams are functionally distinct in many respects, it is obvious that they are not totally independent. At an anatomical level, many potential pathways for cross-talk are provided by lateral and feedback connections, as well as extensive linkages with many subcortical centers. There is also cross-talk at a physiological level, in so far as there exist direction-selective cells in what we have suggested to be the form/color pathway, and orientation-selective cells within the motion pathway. At a perceptual level, we are able to use form cues in the analysis of motion as well as motion cues in the analysis of form\(^44\). There may also be additional functional streams besides the two already delineated in the hierarchy. Lesion studies of the parietal lobe point to a broader role in spatial perception than just the analysis of motion\(^44,49\). Lesions of temporal lobe regions suggest the possibility of separate areas for higher-level analysis of color, depth and form\(^13-34\). However, it remains to be determined whether these functions involve pathways distinct enough to be regarded as separate streams. Resolution of such issues should be possible with the combined application of increasingly powerful anatomical, physiological and perceptual approaches to the study of cortical function.

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David Van Essen is at the Division of Biology, California Institute of Technology, Pasadena, CA 91125, USA.
John Maunsell is at the Department of Psychology, Massachusetts Institute of Technology, Cambridge, MA 02139, USA.