Parallel processing strategies of the primate visual system

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Abstract | Incoming sensory information is sent to the brain along modality-specific channels corresponding to the five senses. Each of these channels further parses the incoming signals into parallel streams to provide a compact, efficient input to the brain. Ultimately, these parallel input signals must be elaborated on and integrated in the cortex to provide a unified and coherent percept. Recent studies in the primate visual cortex have greatly contributed to our understanding of how this goal is accomplished. Multiple strategies including retinal tiling, hierarchical and parallel processing and modularity, defined spatially and by cell type-specific connectivity, are used by the visual system to recover the intricate detail of our visual surroundings.

Percept
The perception that arises internally, in the mind, based on an external stimulus, such as a visual stimulus.

Parallel processing
Simultaneous processing of information through independent circuits.

Photoreceptor
A specialized cell in the retina that detects light and responds with a change in membrane potential and a change in neurotransmitter release.

Tiling
Relatively uniform and complete coverage of space.

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Our richest life experiences and longest-lasting memories are formed through our interactions with the sensory world around us and have a profound impact on our personality and sense of self. Each of these sensations is transmitted to our brains through distinct biological machinery such as that found in the nose or under the skin. Yet, rather than perceiving the world as a disjointed collection of attributes, we most often experience a single unified percept. Parallel processing of sensory information is a commonly used strategy in the mammalian brain, not only between sensory modalities but across features of a single sense as well. Gasser and Erlanger[1] first demonstrated that the sensations of pain and temperature are transmitted through axons of different calibre from those that transmit touch. This work was shortly followed up by Bishop[2], who proposed that the three different classes of axons he found in the optic nerve process different sensory qualities related to vision. These early discoveries laid the foundation for our current understanding of the nervous system's parallel processing strategies[3–8].

The need for parallel processing in the visual system is immediately appreciated when one considers the multitude of qualities that are present in the visual environment and the physical limitations of the way this information is initially encoded and signalled to the brain. Colour, depth, shape and motion are just a few of the many dimensions through which we interpret our visual environment and generate appropriate behaviour[9]. Remarkably, this complexity in our visual surroundings is first encoded as a pattern of light on a two-dimensional array of photoreceptors, with little direct resemblance to the original input or the ultimate percept. Within just a few hundred micrometres of retinal thickness, this initial signal encoded by our photoreceptors must be transformed into an adequate representation of the entire visual scene. This representation, however, must also be sufficiently condensed so that the axons carrying it can pass through the optic nerve, which forms an anatomical bottleneck along the route from the eye to the brain. Probably owing to these constraints, incoming visual signals are processed by at least 80 anatomically and physiologically distinct neural cell populations and 20 separate circuits in the retina. These circuits comprise at least a dozen parallel pathways that project to the brain for further processing[10]. The visual cortex has the job of extracting the relevant information from this reduced signal and of further elaborating and integrating the information into a unified and coherent perceptual experience.

Many years of research have uncovered important details concerning the anatomy and functional organization of the primate visual system. This Review focuses on recent advances in our understanding of how the primary visual cortex (V1) integrates parallel inputs and constructs new, parallel outputs. These findings have been particularly helpful in elucidating the complex relationship between early parallel pathways of the retina and the processing streams in the visual cortex. Instead of attempting to provide a comprehensive analysis at each level of the visual system, we highlight key principles, such as retinal tiling, hierarchical processing, parallel processing and modularity (defined spatially and by cell type-specific connectivity), with the aim of providing a unified and coherent understanding of the processing

Hierarchical processing
Processing that takes place in serial order, with more sophisticated properties emerging at higher levels through the build-up of simpler properties at lower levels.

Modularity
When repeating modules are used to conduct similar operations. Typically, in the visual cortex each module will perform an operation related to visual information from a portion of the visual space. Together the modules cover the space so that the operation is conducted over the entire visual scene.

Eccentricity
Distance from the centre. It is typically used to describe the distance of a visual receptive field from the centre of gaze and is expressed as an angle, in degrees.

Colour-opponent signal
The signal that results when a visual receptive field is excited in response to one colour and inhibited in response to another.

strategies in the visual system. We hope that this will inform the understanding not only of visual perception, but of sensory processing in general.

Parallel pathways from the retina to the cortex

The first steps in seeing begin in the retina, where a dense array of photoreceptors convert the incoming pattern of light into an electrochemical signal[11]. The photoreceptor mosaic encodes the intensity of light as a function of position (two dimensions), wavelength and time (BOX 1). Much information is lost from the outset, such as the exact spectral composition of the image. Nevertheless, computations carried out in our visual system are supplied with enough information to support highly precise hue discriminations and other perceptual abilities that inform our everyday behaviour. Remarkably, many of these computations are carried out in the retina, before the visual signals even leave the eye. Specialized circuits extract basic sensory cues, such as spatial contrast and temporal frequency, from the initial intensity distribution and encode these properties across approximately 1.5 million ganglion cells, which form the optic nerve that connects the eye to the brain.

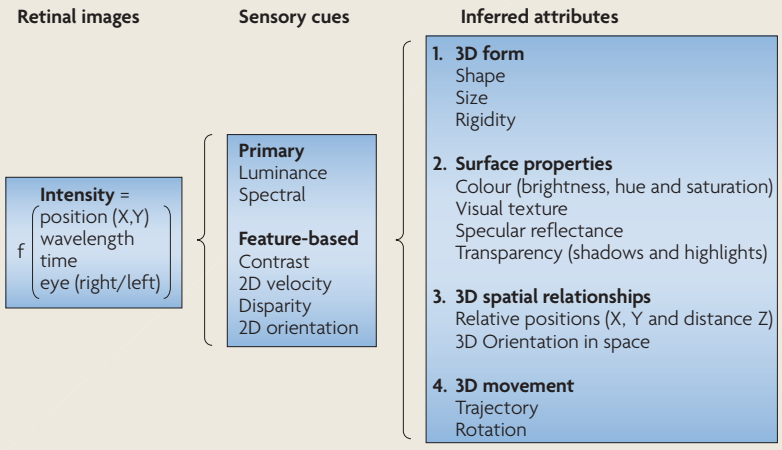
Owing to the anatomical bottleneck of the optic nerve, retinal output must be efficiently condensed. The strategy used by the mammalian visual system is to reduce the representation of the visual scene to a limited number of specialized, parallel output channels. Rather than send visual signals from the eye to the brain along a homogeneous population of ganglion cells, in the primate at least 17 distinct ganglion cell types exist in the retina and at least 13 of these project in parallel to the lateral geniculate nucleus (LGN) of the thalamus and on to the visual cortex[10] (FIG. 1). Each ganglion cell type is thought to tile the retina, providing a complete representation across the entire visual field of the primary sensory cues it conveys to the brain[12]. These cues include different spatial and temporal frequencies, luminance and colour contrasts in the image. At any given point in the visual field, multiple ganglion cell types convey different aspects of the visual input simultaneously and in parallel to the brain.

Each ganglion cell type has its own distinct set of morphological features, such as soma size and dendritic field size and density[13]. Many of these features vary substantially as a function of retinal eccentricity, but at any given eccentricity they allow for nearly unambiguous cell type classification. Each ganglion cell type also has a distinct pattern of dendritic stratification in the inner plexiform layer (IPL), allowing for highly specific patterns of synaptic connectivity with functionally and/or anatomically defined bipolar and amacrine cell types[8] (FIG. 1a,b). These bipolar and amacrine cell types, in turn, have their own unique connections with photoreceptors and horizontal cells in the outer plexiform layer (OPL), forming distinct anatomical circuits from photoreceptors to ganglion cells (FIG. 1b). Finally, the somas of each ganglion cell type seem to be regularly spaced across the retina so that, collectively, their dendritic fields cover the retina uniformly and with constant overlap (FIG. 1c). This highly ordered mosaic architecture holds up only among ganglion cells of the same type: subsets of a type do not cover the entire visual field and different types display no systematic spatial relationship[12]. Together, these structural features suggest that each ganglion cell type is a fundamental unit of the retina and underlies a unique channel of visual information.

Three retinal ganglion cell types are particularly well characterized and have been linked to parallel pathways that remain anatomically segregated through the LGN and into the input layers and compartments of V1 (REFS 5,14) (FIG. 2). Midget, parasol and bistratified ganglion cells constitute approximately 90% of all ganglion cells found in the primate retina, and they functionally complement each other to extend the range of vision in the wavelength and spatiotemporal frequency domains[15]. Midget ganglion cells are considered to be the origin of the parvocellular pathway and constitute approximately 70% of the total population of cells that project to the LGN[14]. These cells convey a red–green colour-opponent signal to the parvocellular layers of the LGN, which in turn project to layers 4Cβ and 6 of V1 (REFS 14,16–19). Cells in this pathway typically have small receptive fields, low contrast sensitivity, slow axonal conduction velocities and sensitivity to high spatial and low temporal frequencies. Parasol ganglion cells are considered to be the origin of the magnocellular pathway and constitute approximately 10% of the total population of cells that project to the LGN[14]. These cells convey a broadband, achromatic signal to the magnocellular layers of the LGN and on to layers 4Cα and 6 of V1 (REFS 16–19). Cells in this pathway generally have large receptive fields, high contrast sensitivity, fast axonal conduction velocities and sensitivity to high temporal and low spatial frequencies. Finally, small and large bistratified ganglion cells make up at least part of the koniocellular pathway and together constitute

Box 1 | From retinal input to cortical processing and perception

Visual input is initially encoded in the retina as a two-dimensional (2D) distribution of light intensity, expressed as a function of position, wavelength and time in each of the two eyes. This retinal image is transferred to the visual cortex, where sensory cues and, later, inferred attributes are eventually computed (see the figure). Parallel processing strategies are used from the outset to overcome the constraints of individual ganglion cells' limited bandwidth and the anatomical bottleneck of the optic nerve. Figure is modified, with permission, from REF. 9 © (1988) Elsevier.



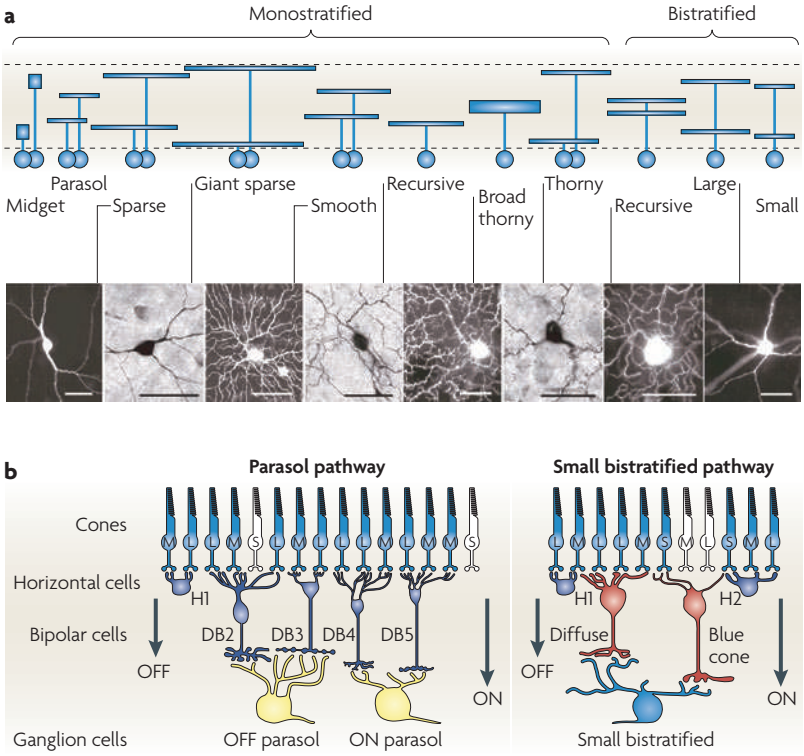


Figure 1 | **Parallel processing in the retina. a** | More than a dozen different ganglion cell types, each with their own distinct set of morphological features, exist in the retina. The top panel illustrates the monostratified or bistratified dendritic arborization of the distinct retinal ganglion cell types. The vertical position of each arbor indicates its characteristic stratification in the inner plexiform layer. The lower panel shows micrographs of the different cell types obtained using retrograde photostaining from rhodamine dextran injections into the lateral geniculate nucleus and the superior colliculus; the scale bars represent 50 μm. **b** | Each ganglion cell type, such as parasol (left) or small bistratified (right), has a unique set of inputs from photoreceptor cells (short (S), middle (M) and long (L)), horizontal cells (H1 and H2), diffuse bipolar cells (DB2, DB3, DB4 and DB5) and amacrine cells (not shown). These retinal subcircuits determine the physiological response properties of the ganglion cells[14]. **c** | The receptive field mosaic of a population of ON parasol ganglion cells (yellow; from REF. 12) is overlayed on an example visual scene (not drawn to scale). Each ganglion cell type tiles the retina so that, at any given point in the visual field, multiple ganglion cell types (represented by red, blue and yellow ellipses) signal complementary visual information simultaneously and in parallel to the brain. Part **a** is reproduced, with permission, from REF. 12 © (2007) Annual Reviews, inc. Data for part **b** are from REF. 14.

approximately 8% of the total population of cells that project to the LGN[14]. These cells convey a blue-on, yellow-off colour-opponent signal[20,21] to koniocellular layers 3 and 4 of the LGN, which in turn project to layer 1 and to the cytochrome oxidase blobs (CO blobs) of layer 2/3 in V1 (REFS 5,17,20,22,23). Koniocellular cells in the LGN are defined as cells that express α-calcium/calmodulin-dependent protein kinase and/or calbindin[22] and are found not only in the intercalated koniocellular layers but also scattered throughout the magnocellular and parvocellular layers. This has made it difficult to characterize the full range of physiological response properties that are carried by the koniocellular pathway. For example, layer 4A of V1 receives a blue-off, yellow-on colour-opponent input from the LGN[17], but neither the locations of these LGN cells nor the type of retinal ganglion cell providing their input has been determined with certainty.

It is likely that there are many more parallel pathways between the retina and V1. The remaining retinal ganglion cells in this pathway are less numerous (12% of the total), but they consist of more types that are likely to provide diverse information about the visual scene. In fact, assuming that each ganglion cell type uniformly tiles the retina, most of the variation in the numbers of ganglion cells for each cell type might be explained simply by dendritic field size: the larger the cell type's dendritic field size, the fewer of those cells will be required to cover the entire retina[12]. Whether these additional cell types maintain strict segregation in their connections through the LGN and into V1 remains unclear. Nevertheless, many studies have indicated functional and anatomical heterogeneity in the LGN that might be explained by additional, unidentified parallel pathways. Two prevalent types of visual response properties have been reported in the magnocellular layers of the LGN and three have been reported in the parvocellular layers[24,25]. Furthermore, there is some indication that the two dorsal, central and ventral koniocellular layers of the LGN each have their own characteristic response properties and projection targets in V1 (REF. 5.) Finally, the rod- and cone-mediated responses of intrinsically photosensitive, melanopsin-expressing retinal ganglion cells have recently been characterized and suggest that this cell population may constitute a separate projection pathway to the visual cortex that conveys luminance and colour-opponent information[26].

The sensory cues that are carried by the parallel pathways bear little resemblance to our perceptual experience, and the functional role of each pathway is still poorly understood. Visual attributes such as motion, shape and colour must be computed from these sensory cues and integrated in the cortex to create a unified and coherent percept. Lesion studies have shown that computing these attributes does not rely on one pathway alone. Magnocellular lesions, for example, result in a large decrease in luminance contrast sensitivity for stimuli of high temporal and low spatial frequencies[27], and have little effect on colour contrast sensitivity[27,28] or the speed and direction of motion discriminations. By contrast, parvocellular (and possibly koniocellular) lesions

Receptive field
The location in visual space where a change in light can cause a change in neuronal activity.

Broadband
Typically used to describe visual receptive fields that are not colour-opponent. Whether a broadband cell is excited or inhibited by a stimulus at a particular part of its receptive field is relatively independent of the wavelength of the light.

Cytochrome oxidase blobs
Patches in the upper layers of the primate primary visual cortex with high concentrations of the metabolic enzyme cytochrome oxidase.

cause an almost complete loss of colour vision[28–30], reduce luminance contrast sensitivity for stimuli of high spatial and low temporal frequencies[27,28,31], and have little effect on shape discriminations[30,32]. These findings are consistent with the visual response properties of the cells in each pathway and highlight the fact that no single pathway seems to have a monopoly over any particular set of computations, such as those related to motion or shape perception. Ultimately, the key to uncovering the role of the early parallel pathways may be a better understanding of the relationship between these pathways and processing streams in the visual cortex.

V1 and parallel processing strategies

Once the condensed and parallel signals from the retina and LGN arrive in the visual cortex, the original components of the visual scene must be extracted, elaborated on and integrated into a unified percept. The visual cortex uses both hierarchical and modular processing to accomplish these goals[33]. Although the basic tuning properties of cells do not differ substantially between the retina and the LGN, in the first cortical synapses of V1 new and more complex information is extracted, such as orientation, direction and colour selectivity[6]. These sensory cues (BOX 1) are organized into overlapping functional maps, with a columnar organization for orientation tuning, ocular dominance and visual space[34,35]. As visual information passes through V1 and on to the extrastriate cortex, the response properties in each subsequent area tend to increase in complexity and selectivity. New computations are carried out along the way, eventually resulting in highly specialized areas concerned with object recognition and sensorimotor integration[36]. Information flow in this hierarchical network is not unidirectional, and dense feedback connections provide a substrate for recurrent processing[37]. However, the functional details of this feedback system remain largely unknown and are beyond the scope of this Review.

Most visual information from the LGN passes through V1 before being processed further in the extrastriate visual cortex. Different strategies might be used in V1 to transfer parallel input signals into multiple output streams (FIG. 3a). One possibility is that the parallel inputs stay separate in the cortex and continue on past V1. A second possibility is that the parallel inputs converge indiscriminately in V1 and lack any organization or relationship with processing streams in the extrastriate cortex. A third possibility, which current evidence favours, is that the parallel inputs converge in V1 but do so in an organized and specific way so that new parallel streams of information are systematically conveyed to the rest of the visual cortex.

Originally, it was thought that the early parallel pathways might maintain strict segregation in V1 and underlie separate processing streams in the extrastriate cortex[6,38] (FIG. 3b). The distinctive laminar organization of V1 and the alternating light and dark staining for the mitochondrial enzyme CO in the superficial layers[39], which reflects the level of metabolic activity in those regions (with the darker-stained areas correlating to areas of direct thalamic input), suggested a high degree of processing modularity and the possibility that parallel inputs to V1 remain well segregated. Furthermore, the functional parcellation of the extrastriate cortex into separate processing streams (discussed further below), which suggested magnocellular- and parvocellular-like segregation of function well beyond V1, led Livingstone and Hubel[6] to propose that the parvocellular pathway forms the basis for colour and form processing in the CO blobs (dark staining) and interblobs (light staining) in layer 2/3, and that the magnocellular pathway forms the basis for motion- and depth-related processing in layer 4B. This scheme was attractive in its simplicity and was supported by early studies that suggested there is a clean anatomical segregation of magnocellular and parvocellular inputs to layers 4B and 2/3, respectively[40], as well as a functional segregation of fast, achromatic responses in layer 4B and colour-opponent or orientation-selective responses in blobs and interblobs, respectively[41–43]. More recent studies, however, have called into question such a strict segregation[44].

Although the concept of modular function in V1 has stood the test of time, it is now clear that, rather than maintain strict segregation, the early parallel pathways converge significantly in the first few synapses in V1 (FIG. 3c). This is most evident in the connections from layer 4C to the CO blobs and interblobs of layer 2/3,

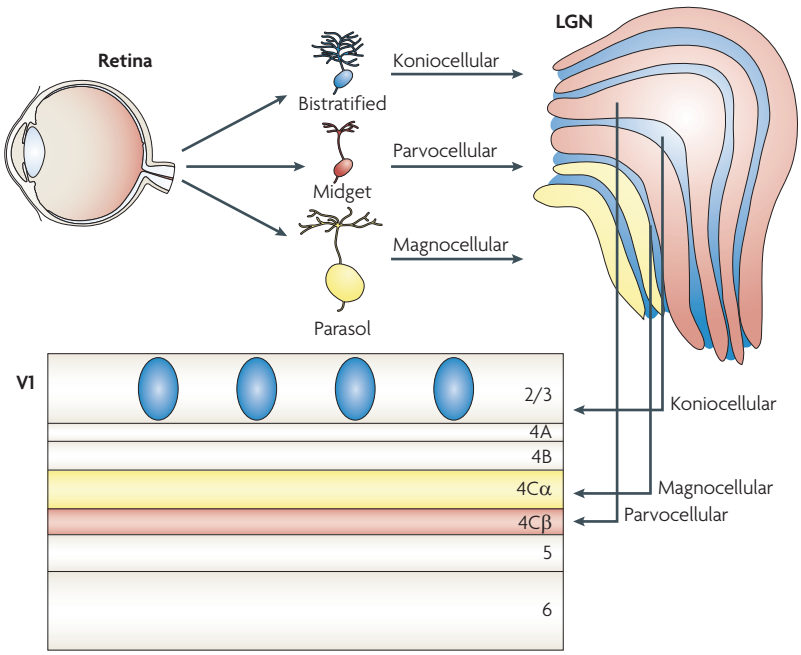


Figure 2 | **Parallel pathways from the retina to the cortex.** Midget, parasol and bistratified ganglion cells are well characterized and have been linked to parallel pathways that remain anatomically separate through the lateral geniculate nucleus (LGN) and into the primary visual cortex (V1). Midget ganglion cells project to parvocellular layers of the LGN and on to layer 4Cβ of V1 (red). Parasol ganglion cells project to magnocellular layers of the LGN and on to layer 4Cα of V1 (yellow). Small and large bistratified ganglion cells project to koniocellular layers of the LGN and on to the cytochrome oxidase-expressing patches (or blobs) of layer 2/3 (blue). Although these ganglion cell types are numerically dominant in the retina, many more types are known to exist and are likely to subserve important parallel pathways that are yet to be identified.

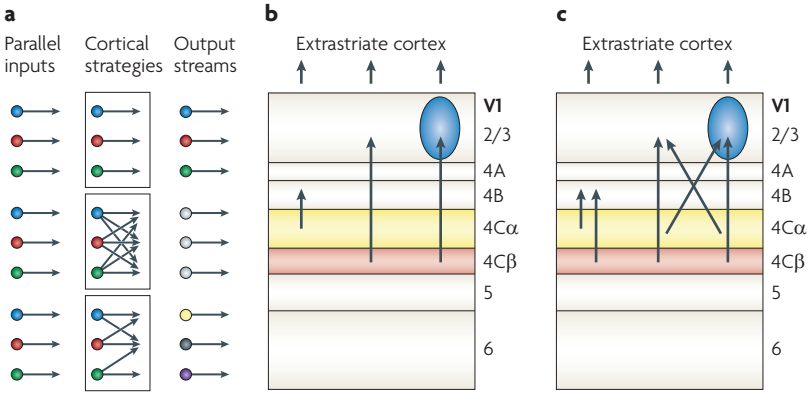


Figure 3 | **Cortical processing strategies. a** | A visual cortical area might use multiple strategies to transform parallel inputs into multiple outputs. One possibility (top) is that the segregation of the inputs is maintained and passed directly on to the outputs. A second possibility (middle) is that these inputs mix indiscriminately and bear no systematic relationship to the outputs. A third possibility (bottom) is that the parallel inputs converge in an organized and specific way so as to form the basis for specialized outputs. **b** | Early models of the primary visual cortex (V1) proposed that magnocellular (yellow) and parvocellular (red) pathway inputs remained segregated in V1 as they passed through layers 4B and 2/3, respectively, and on to the extrastriate cortex. **c** | Recent studies have provided evidence for extensive mixing and convergence of magnocellular, parvocellular and koniocellular (blue) pathway inputs, suggesting that V1 outputs bear little or no systematic relationship to its parallel inputs. Cytochrome oxidase-expressing blobs are shown as ellipses in layer 2/3.

which provide ample opportunity for mixing of early parallel pathways. The blobs and interblobs of layer 2/3 receive convergent input from magnocellular and parvocellular pathways, with the blobs receiving additional direct input from the koniocellular layers of the LGN[22,45–48]. Importantly, the koniocellular pathway was discovered after Livingstone and Hubel's theory was first proposed, leaving its contributions to colour, form, motion and depth processing largely unaccounted for. Functionally, the intermixing of magnocellular, parvocellular and koniocellular pathways in V1 has been confirmed by showing that lesions of either magnocellular or parvocellular layers of the LGN can strongly affect the response properties of cells in both CO blobs and interblobs of V1 (REFS 49,50). It is therefore unsurprising that recent studies have often failed to find a clear relationship between the CO-stained compartments and form or colour processing[51–53], with several indicating that orientation and colour tuning are commonly found in the same V1 cells and across almost all layers[52,54,55]. It is tempting to conclude from these data that early parallel pathways converge indiscriminately in V1 and lack any systematic influence on the computations that form outputs to the rest of the brain. Nevertheless, a closer inspection of V1 modularity at the level of specific cell types and their connections tells a different story.

Recent evidence suggests that functional modules in the visual cortex are defined not only by their laminar and spatial compartmentalization, but also by their specialized connectivity (FIG. 4). For example, in layer 4B of V1 (FIG. 4a), cells from the magnocellular-recipient layer 4Cα form dense axonal branches, whereas cells from the parvocellular-recipient layer 4Cβ pass through layer 4B without branching. Likewise, pyramidal cells in the koniocellular-recipient layer 2/3 blobs have only sparse axonal branches in layer 4B[45,56], suggesting that layer 4B is a segregated conduit of information from the magnocellular pathway, with little or no intermixing from the parvocellular or koniocellular pathways. However, layer 4B contains two types of morphologically distinct projection neurons: spiny stellates and pyramids. Whereas the dendrites of spiny stellates are almost entirely confined to layers 4B and 4Cα, pyramids have an apical dendrite that extends through layer 2/3 and into layer 1. This places the apical dendrites of pyramids in a position to receive input from both parvocellular and koniocellular pathways in the superficial layers. Photostimulation studies in monkey V1 slices have confirmed that although spiny stellates receive input from only the magnocellular-recipient layer 4Cα, pyramids receive substantial, although less dominant, input from the parvocellular-recipient layer 4Cβ as well[57] (FIG. 4a). Analysis at the laminar level proved to be misleading, as the most common cell type in layer 4B (pyramids) receives mixed magnocellular and parvocellular inputs and possibly koniocellular inputs as well.

Modularity based on cell types and connectivity has been supported by subsequent studies. Photostimulation data have shown that local neurons in layer 3 receive convergent input from both magnocellular-recipient layer 4Cα and parvocellular-recipient layer 4Cβ, but projection neurons in that layer receive direct input only from layer 4Cα (FIG. 4b). These layer 3 projection neurons have densely tufted apical dendrites that distinguish them morphologically from neighbouring local neurons[58]. Many different cell types exist in layer 6 of V1 and each receives a unique combination of inputs from the other layers of V1 (REF. 59). It seems that cell type-specific connectivity allows for systematic combinations of early parallel pathway inputs despite the misleading appearance of indiscriminate intermixing at the laminar or compartmental level (FIGS 3,4). It remains unclear how these different connection patterns might underlie different visual response properties. Eventually, highly specialized functional properties found in V1, including the modularity of function proposed by Livingstone and Hubel, might be mapped onto the different cell types discussed above.

The same spatial and cell type-specific modules that allow for specialized intermixing of early parallel pathway input also form the substrates for multiple output streams to the extrastriate cortex (FIG. 4c,d). Outputs from V1 to the second visual area (V2) have been particularly well studied. In V2, there is a repeating pattern of CO-stained compartments known as thick, pale and thin stripes, each with their own characteristic functional properties and afferent and efferent connection patterns[60–63]. It was originally thought that layer 4B of V1 projected to the thick stripes of V2, and that the CO blobs and interblobs projected to the thin and pale stripes, respectively[64,65] (FIG. 4c). However, recent studies using intrinsic optical imaging and/or improved anatomical tracers have shown that such a clean correspondence between compartments in V1

and V2 is unlikely. One of these studies has suggested that all projection layers underneath interblobs, including layer 4B, project to both thick and pale stripes in V2 (REF. 66), whereas another study has proposed that layer 2/3 blobs and interblobs provide substantial input to thin stripes[67]. Despite this apparent breakdown in the spatial segregation of outputs from V1 to V2, it is likely that, at a submodular level, segregated outputs do indeed exist. There are increasingly convincing indications that each of the V2 stripe compartments can be further broken down into functionally specialized submodules, such as hue-selective maps in the thin stripes or

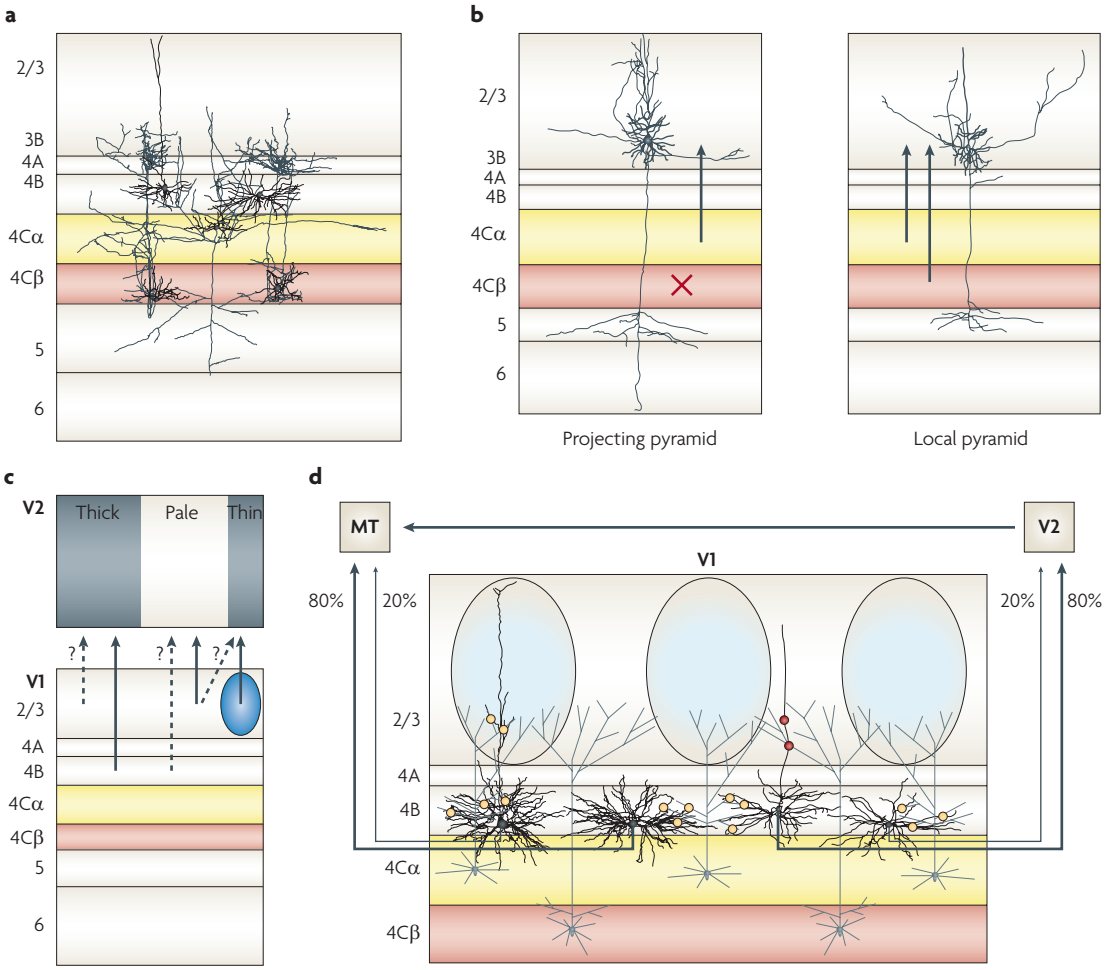


Figure 4 | **Spatial and cell type-specific connectivity in V1. a** | Layer 4B of the primary visual cortex (V1) contains two excitatory cell types known as pyramidal (black, left) and stellate (black, right) cells. Both of these cell types receive direct input from cells in magnocellular-dominated layer 4Cα (yellow), but only pyramids have apical dendrites that pass above layer 4B and into layer 2/3. The apical dendrites of these pyramids are in a position to receive inputs from parvocellular-dominated layer 4Cβ (red) projections into layer 2/3. Mixed magnocellular and parvocellular inputs onto pyramids and magnocellular-only inputs onto stellates have been confirmed in photostimulation studies on macaque monkey V1 slices[57]. **b** | Layer 3B contains pyramidal cells that project out of V1 (projecting pyramids) and ones that remain in V1 (local pyramids). Projecting pyramids (left) receive input only from magnocellular-dominated layer 4Cα, whereas local pyramids receive mixed input from both magnocellular-dominated layer 4Cα and parvocellular-dominated layer 4Cβ. The red X denotes lack of input from layer 4Cβ. **c** | Outputs from V1 to V2 were originally thought to maintain strict segregation, with layer 4B of V1 projecting to the cytochrome oxidase (CO)-stained thick stripes of V2, and the CO blobs and interblobs of layer 2/3 respectively projecting to the thin and pale stripes of V2 (arrows). This spatial modularity of outputs has recently been called into question with evidence that layer 2/3 blobs and interblobs in V1 provide substantial input to the thin stripes in V2, and with evidence that all projection layers underneath interblobs, including layer 4B, project to thick and/or pale stripes (dashed arrows with question marks). **d** | Specialized and distinct populations of cells (black) project from layer 4B of V1 to the middle temporal area (MT; also known as visual area V5) or V2. MT receives input from a population of cells with large cell bodies and dense dendritic trees. Most of these cells (80%) are stellates, but a smaller number of pyramids (20% of the cells) also project to MT and are positioned preferentially underneath CO blobs, where their apical dendrites can receive magnocellular inputs from layer 4Cα (yellow circles). V2 receives input from a population of cells with smaller cell bodies and sparse dendritic trees, most of which (80%) are pyramids located preferentially underneath CO interblobs, where their apical dendrites can receive parvocellular inputs from layer 4Cβ (red circles). Together, these anatomical specializations are consistent with layer 4B of V1 relaying a quick, magnocellular-dominated signal to MT and a more mixed magnocellular and parvocellular signal to V2 (REF. 73).

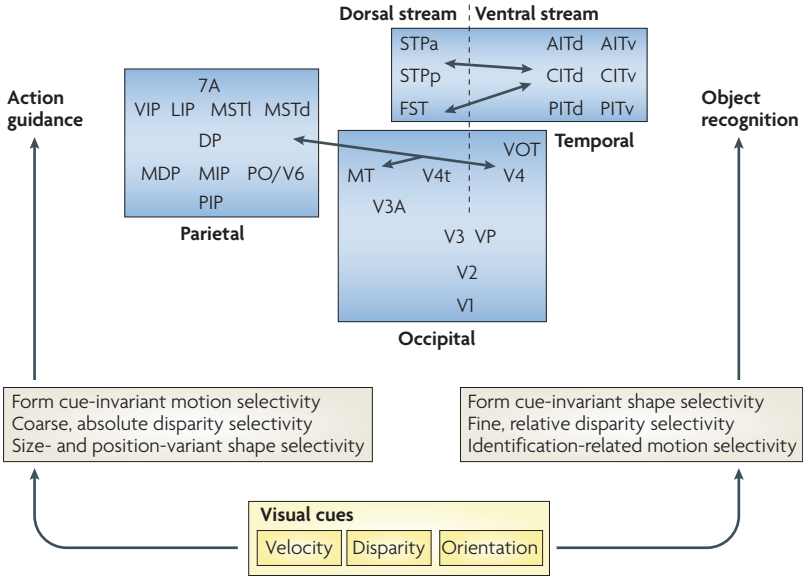


Figure 5 | **Parallel processing streams of the extrastriate cortex.** Dorsal (left of vertical dotted line) and ventral (right of vertical dotted line) streams constitute separate but interconnected pathways that are processed through the occipital, the parietal and the temporal extrastriate visual cortex. Vertical position indicates the hierarchical relationship between the areas. Interconnections between streams can be found at essentially every level of the hierarchy. For simplicity, not all areas have been included and only those cross-stream connections mentioned in the text have been drawn. Dorsal and ventral processing streams subserve different behavioural goals, with the dorsal stream aimed at the visual control of skilled actions and the ventral stream aimed at object recognition. The same visual cues, such as velocity, disparity and orientation, are processed along both streams, but in each stream distinct computations are performed on these features in order to support different behavioural goals. 7A, visual area 7A; AITd, anterior inferotemporal (dorsal); AITv, anterior inferotemporal (ventral); CITd, central inferotemporal (dorsal); CITv, central inferotemporal (ventral); DP, dorsal prelunate; FST, fundus of superior temporal; LIP, lateral intraparietal; MDP, medial dorsal parietal; MIP, medial intraparietal; MSTd, medial superior temporal (dorsal); MSTl, medial superior temporal (lateral); MT, middle temporal; PIP, posterior intraparietal; PITd, posterior inferotemporal (dorsal); PITv, posterior inferotemporal (ventral); PO, parieto-occipital; STPa, superior temporal polysensory (anterior); STPp, superior temporal polysensory (posterior); V1, visual area 1; V2, visual area 2; V3, visual area 3; V3A, visual area 3A; V4, visual area 4; V4t, visual area 4 transitional; V6, visual area 6; VIP, ventral intraparietal; VOT, ventral occipitotemporal; VP, ventral posterior.

disparity-selective clustering in the thick stripes[68,69]. Although the cell type-specific connection patterns in V2 remain unknown, it is likely that these smaller functional compartments, or even the specific cell types in them, receive segregated input patterns from V1. Inspection of V1 at the level of specific cell types and their connection patterns may also help us to understand the degree of segregation in the outputs from V1 to V2 and the rest of the visual cortex.

Output modularity based on cell type-specific connectivity has been demonstrated in the connections between layer 4B of V1 and the extrastriate cortex (FIG. 4d). Cells that project to V2, to the third visual area (V3) or to the middle temporal visual area (MT; also known as visual area V5) are intermixed in layer 4B[70–72]. It was unclear whether these different output streams were anatomically and/or functionally distinct at a sublaminar level. Early studies suggested that most of the layer 4B cells that project to MT are large spiny stellates and, as such, anatomically distinct from other output cells in this layer of V1 (REFS 71,72). A recent study using a modified rabies virus that expresses green fluorescent protein confirmed these earlier findings and uncovered other important anatomical differences[73]. Layer 4B cells that project to MT are large cells with dense dendritic trees that lie close to the bottom of the layer. Most of these cells are spiny stellates, but a substantial minority are pyramidal cells located preferentially underneath CO blobs. By contrast, layer 4B cells that project to V2 are smaller, with sparse dendritic trees situated throughout the layer, and are mostly pyramidal cells located preferentially underneath CO interblobs. These anatomical specializations are consistent with these two cell populations conveying quick[74,75], magnocellular-dominated signals to MT and more mixed magnocellular and parvocellular signals to V2. Therefore, it seems that early parallel pathways of the retina and the LGN are recombined in V1 into both spatial and cell type-specific modules to form multiple output channels that project to specific areas of the extrastriate cortex.

Processing strategies in the extrastriate cortex

The outputs from V1 and V2 to MT and visual area 4 (V4) represent the beginning of a more pronounced anatomical and functional segregation of signals into what are known as the dorsal and ventral streams[76] (FIG. 5). MT is specialized for processing motion and depth, whereas V4 is specialized for processing form and possibly colour[36,77–79]. These two areas reflect earlier segregation in the output modules of V1 and V2, as cells in layer 4B of V1 and the thick stripes of V2 project to MT, whereas the pale and thin stripes of V2 project to V4 (REFS 60,62,70,71,80). Functional evidence provides additional support for such segregation, as layer 4B of V1 and the thick stripes of V2 have a high proportion of direction- and disparity-selective neurons, whereas layer 2/3 of V1 and the pale and thin stripes of V2 consist mainly of neurons that are selective for orientation and colour. It would seem, therefore, that one of the goals of the systematic integration of parallel inputs that occurs in V1 and V2 is to construct new output channels that can support at least two new parallel streams of information flow.

Anatomical studies have established that the extrastriate cortex is indeed composed of at least two segregated but interacting parallel processing streams (FIG. 5). The dorsal pathway consists of a large number of interconnected extrastriate cortical areas in the parietal cortex downstream of MT, including the medial superior temporal area (MST), the fundus of the superior temporal area (FST), the superior temporal polysensory area (STP), the ventral intraparietal area (VIP), the lateral intraparietal area (LIP) and visual area 7A, to name just a few[81–85]. The apparent absence of substantial crosstalk between a dorsal–dorsal pathway through visual area 6 (V6) and the superior parietal lobule (SPL) and a ventral–dorsal pathway through MT and the inferior parietal lobule (IPL) indicates that the dorsal stream may actually consist of two relatively segregated subcircuits[86]. The ventral pathway also consists of a large number of

interconnected extrastriate cortical areas in the temporal cortex downstream of V4, including the various subdivisions of the inferotemporal (IT) cortex[87–89]. It has been suggested that these parallel dorsal and ventral pathways maintain segregation all the way into motor-related frontal cortical areas, such as the frontal eye field (FEF)[90]. Likewise, in the dorsal stream segregated inputs from the SPL to the dorsal premotor area (PMd) and from the IPL to the ventral premotor area (PMv) have been shown to exist[91]. Although the dorsal and ventral streams clearly make up two relatively separate circuits, the anatomical segregation between the two streams is by no means absolute. There is clear evidence of crosstalk between the streams, such as the reported connections between V4 and areas MT and LIP[81,82,85], as well as between the anterior inferotemporal (AIT) cortex and areas FST, VIP and STP[83,84,92]. New subdivisions of the parietal and the temporal cortex continue to be established[93–95], and the specific connection patterns of these areas have, for the most part, reinforced the notion of segregated but interacting dorsal and ventral processing streams[96,97].

Functional evidence indicates that the dorsal and ventral processing streams operate relatively independently as well. Neuronal processing along the dorsal stream is best characterized by direction of motion and binocular disparity selectivity in MT[98,99], by more complex motion analysis related to locomotion and pursuit or tracking in areas downstream from MT in the STS (MST, FST and STP)[100,101], and by computations that inform target selection for arm and eye movements, object manipulation and visuospatial attention in areas of the IPL (LIP, VIP and V6). By contrast, neuronal processing along the ventral stream is best characterized by colour and contour selectivity in V4 (REFS 77,78,102), by more complex combinations of colours, patterns and/or shapes in the posterior inferotemporal (PIT) cortex[103,104], and by invariant representations of two-dimensional and three-dimensional shapes and objects in AIT. Lesion studies have further corroborated the observed physiological differences along the two processing streams, with dorsal stream lesions affecting smooth pursuit eye movements, speed discriminations, complex-motion perception and the accurate encoding of visual space[105–109], and with ventral stream lesions affecting orientation and complex-shape discriminations, perceptual invariance and attention[110–112].

Although the existence of relatively separate and independent dorsal and ventral streams is now firmly established, our understanding of these two processing streams has undergone important revision in recent years. Ungerleider and Mishkin[7] first proposed that the dorsal and ventral streams mediate spatial and object-related visual capacities, suggesting that each stream might process different visual attributes. In more recent years, however, a slightly different perspective has emphasized distinctions in the processing goals of each stream. In this view, the dorsal stream's goal is to mediate navigation and the visual control of skilled actions directed at objects, whereas the ventral stream's goal is to transform visual inputs into representations that embody the enduring characteristics of objects and their spatial relationships[113]. Building on this conceptualization, Rizzolatti *et al.*[86] proposed that the two anatomically segregated subcircuits of the dorsal stream might mediate different behavioural goals as well, with the dorsal–dorsal pathway concerned with the control of action 'online' (while the action is ongoing) and the ventral–dorsal pathway concerned with space perception and 'action understanding' (the recognition of actions made by others). This framework implies that the visual attributes that are processed along parallel streams in the extrastriate cortex might actually be similar, and that important differences between the streams can be found in the manner by which these attributes are used to inform their respective goals. This would be consistent with the systematic mixing of parallel inputs that occurs in V1, as the resulting outputs formed there, which subserve the dorsal and ventral streams, do not maintain exclusive rights over the visual cues conveyed along any single input channel. Instead, these cues are integrated in varying combinations and to differing degrees along each output channel, the details of which might be particularly relevant to the computations and behavioural goals of the dorsal and ventral streams.

Indeed, it has become clear that the dorsal and ventral streams are likely to process the same set of visual attributes, but for different behavioural goals (FIG. 5). Possibly the best example of a visual feature that is processed along both dorsal and ventral streams is binocular disparity. Binocular disparity information is found dorsally, in MT and MST[114,115], as well as ventrally, in V4 and IT[116–118]. In recent years, however, it has been shown that there are crucial differences in the way that the two streams encode disparity and in the types of behaviour that such encoding schemes might inform. Sensitivity along the dorsal stream to coarse and absolute disparities and to anti-correlated random-dot stereograms (RDSs) suggests that such processing might be used to spatially orient and guide actions[119,120]. By contrast, sensitivity along the ventral stream to fine and relative disparities, and reduced or absent responses to anti-correlated random-dot stereograms suggest that such processing might be closely linked to three-dimensional shape perception[121,122]. Disparity is not the only visual attribute that is processed in both dorsal and ventral streams: shape- and motion-related computations can be found throughout the extrastriate cortex as well[123–127]. Again, recent studies have shown important differences in the way that these attributes are encoded and in the behaviour or perception that they are likely to inform[128–130]. Finally, recent studies have also shown that many extrastriate areas can become selective to stimulus properties that are not typically encoded by neurons in that area, such as the shape selectivity that is found in MT following associative learning between directions of motion and static shapes[131]. These findings demonstrate that the visual signals that can activate cortical neurons can be modified under conditions in which a novel visual cue is associated with the core function that is normally inherent to those cells. Such changes suggest that even those visual cues that are not normally associated with a given

Random-dot stereogram
A pair of random-dot images that generate the sensation of depth when the eyes are positioned so that they focus at a location in front of or behind the images.

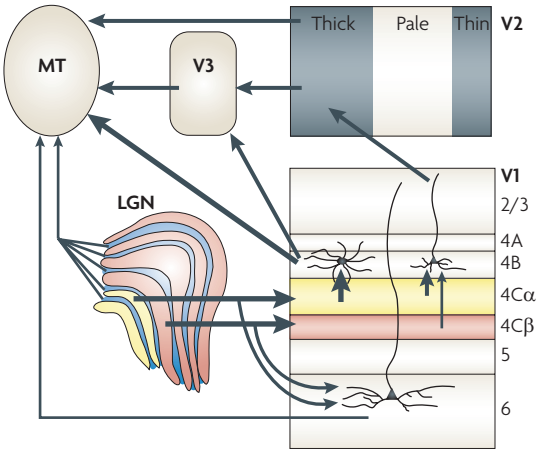


Figure 6 | **Multiple input streams to MT.** There are multiple input streams from the lateral geniculate nucleus (LGN) to the middle temporal (MT) area. The major ascending input to MT passes through magnocellular layers of the LGN (yellow) and through layers 4Cα and 4B of the primary visual cortex (V1). V2 and V3 provide indirect inputs from layers 4Cα and 4B of V1, with V2 probably providing inputs from parvocellular layers of the LGN (red) and layer 4Cβ after a small number of additional synapses[134]. Bypassing layer 4C altogether, a sparse monosynaptic projection from koniocellular layers of the LGN (blue) to MT and a disynaptic projection from magnocellular and parvocellular layers of the LGN through layer 6 Meynert cells in V1 to MT have both been identified[132,133]. MT is likely to use similar strategies to those found in V1 to process these parallel inputs and transform their signals into multiple output streams. The thickness of each arrow represents the approximate strength of the connection.

processing stream can become influential when they are behaviourally relevant.

As with V1, each extrastriate cortical area receives inputs from multiple areas upstream and sends outputs to multiple areas downstream. MT provides a good example of such an extrastriate cortical area, as it receives inputs from many sources in parallel (FIG. 6). Although the bulk of visual information to MT passes through layer 4C of V1, it has recently been discovered that MT receives at least two separate input streams that bypass this main route altogether. Sparsely scattered koniocellular cells in the LGN provide a direct, monosynaptic input to MT[132], and a denser population of magnocellular and parvocellular cells provides a disynaptic input to MT through layer 6 Meynert cells in V1 (REF. 133). The main ascending input through layer 4B of V1, both directly to MT and indirectly through V3, is dominated by layer 4Cα and the magnocellular pathway. Nevertheless, MT eventually receives parvocellular input through layer 4Cβ — probably an indirect input through V2 (REF. 134). These data, along with numerous lesion studies[27], suggest that MT and the dorsal stream rely heavily, but not exclusively, on visual information provided by the magnocellular pathway. Each of the input pathways to MT allows varying degrees of magnocellular-, parvocellular- and koniocellular-pathway convergence, probably providing visual information that is uniquely suited for specific computations and visual tasks.

What type of information might each of these parallel input pathways provide to MT? Few studies have been able to directly assess the function of an identified cell population or pathway in the primate visual cortex. Movshon and Newsome[135] used antidromic stimulation to identify and functionally characterize neurons in V1 that project directly to MT. In a technically challenging set of experiments, the authors were able to identify and functionally characterize only 9 MT-projecting cells out of the 745 total cells recorded. Nevertheless, they reported a highly specialized and homogeneous population of direction-selective cells that are distinct from the general population in V1. Whether this direct input from V1 provides information to MT that is different from that provided by indirect inputs through V2 or V3 was investigated in awake, fixating monkeys in which the indirect pathway to MT through V2 and/or V3 was reversibly inactivated by cooling the lunate sulcus[136]. MT disparity selectivity was severely disrupted even though direction and speed selectivity remained largely intact. These results suggest that the direct pathway from V1 to MT provides speed and direction of motion information, whereas the indirect pathway provides disparity information. Although we know much less about other input pathways to MT and pathways that provide input to other extrastriate cortical areas, segregation of function along parallel inputs is likely to be similar in the case of V4 and the rest of the extrastriate cortex.

Disynaptic
Traversing two synaptic contacts. If a trans-synaptic anatomical tracer were to spread from one neuron across synaptic contacts to a second neuron, the spread would be monosynaptic. If the tracer continued to spread from the second neuron across more synaptic contacts to a third neuron, the spread would be disynaptic.

Meynert cell
A large projection neuron in the deep layers of the visual cortex.

Antidromic stimulation
Stimulation that is used to determine whether a neuron recorded in one location projects to another, distant location. Antidromic stimulation at the distant location generates action potentials that propagate back to, and are detected at, the recorded neuron.

Fixating
Maintaining the eye position at a particular location.

Box 2 | **Parallel processing in other sensory systems**

Parallel processing is not only a ubiquitous property of the visual system, it is found across the brain in all other sensory modalities as well. The multiple touch receptors underneath our skin and the different olfactory receptors in our nose carry out the beginnings of a similar process by which incoming sensory information is parsed into separate channels of information and eventually recombined to form a unified and coherent percept. Some of the properties discussed in this Review may be unique to the visual system, but many are likely to be shared with other sensory systems. For instance, the mosaic tiling that is found along the body wall in the periphery of the somatosensory system is structured similarly to the tiling that occurs in the retina[153–155]. There is also evidence for mosaic organization in the olfactory epithelium[156], but these mosaics do not show the same degree of spatial order as that found in the retina, probably owing to the fact that the olfactory system processes an essentially non-spatial modality. The modularity that exists in the visual cortex seems to be typical of sensory cortical areas in general[157–159], and in the few cases for which it has been studied, cell type-specific connectivity seems to be common as well[160–163]. Finally, there is substantial support for the existence of hierarchically organized, parallel processing streams in each of the other sensory cortices[164–168].

Ultimately, we must understand how each of these inputs is processed and integrated to form outputs to areas downstream. As the problem faced in the extrastriate cortex is so similar to that faced in V1 (parallel inputs and multiple outputs), we might expect to find similar strategies, such as modularity that is defined spatially and by cell type-specific connections. Indeed, in many extrastriate cortical areas there are clear examples of spatial modularity that are similar to those seen in V1 and V2. MT contains direction and disparity columns and clustered speed-tuning modules[137–139], and V3 contains modules for disparity and orientation[140,141]. There is also evidence that V4 contains separate modules[142–144], possibly related to segregated processing of colour[77]. Few studies have directly investigated the vertical organization of extrastriate cortical areas, but those that have find evidence for distinct computations performed in different cortical layers[145,146]. There is also evidence that these functional modules serve as a substrate for the formation of a new set of segregated outputs to be sent downstream[147]. We have few details on these modules of the extrastriate cortex, but there is strong evidence that they are ubiquitous and that they have submodular organization and specialized connectivity similar to that seen in the compartments of V1 and V2.

Summary and future directions

Over the past 50 years, we have gained great insight into the ways in which the brain processes incoming visual inputs and recovers the information that is necessary to adequately inform our perception and everyday behaviour. It is clear that parallel processing is a ubiquitous feature of the visual system. Several key principles of parallel processing strategies have been elucidated that will help us in understanding visual perception and sensory processing in general (BOX 2). In the retina, over a dozen distinct ganglion cell types parse the incoming visual signals into functionally and anatomically specialized channels that project in parallel to the LGN and on to V1. Each of these ganglion cell types tiles the retina and provides a complete representation across the entire visual field of the attributes it conveys to the brain. Once in V1, these parallel input channels are recombined in modules that are defined spatially and by local connectivity, and thus new parallel channels of information are formed that can be sent on to the rest of the brain. The outputs that are formed in V1 and V2 lead to segregated but interacting dorsal and ventral processing streams in the extrastriate cortex. The two streams make use of a similar set of visual attributes but perform different computations in order to mediate non-overlapping behavioural goals. Within each stream, however, each extrastriate cortical area probably uses the same strategies that are found in V1 to recombine and integrate multiple inputs and form new outputs to send downstream.

Although much has been uncovered regarding parallel processing strategies in the visual system, many questions remain. How many more parallel pathways are there between the retina and V1, and what are their anatomical and functional properties? How many different output pathways are formed in V1 and what is the functional contribution of each pathway to processing in the dorsal and ventral streams of the extrastriate cortex? In order to answer some of these questions, methods that can directly relate detailed cell morphology and connection patterns to visual response properties and perception will be needed. Some recently developed methods are already helping us in this endeavour[73,148–152] (BOX 3). Two-photon microscopy, viral tracing and reversible inactivation or activation methods can all be useful in taking the next step in understanding parallel processing strategies in the visual system. Further research is necessary to fully understand how parallel processing strategies are used in, and between, each sensory modality so that we can enjoy our seamless perception of the world around us.

Box 3 | **Techniques for investigating parallel processing in the visual system**

Numerous techniques have recently been developed that will enable us to directly relate detailed cell morphology and connection patterns to visual response properties and perception[73,133,134,148–152]. These new methods promise to advance our understanding of the mechanisms that underlie parallel processing in the primate visual system.

Two-photon Ca^{2+} imaging

Using femtosecond-pulsed laser light in combination with genetically encoded or bulk-loaded fluorescent Ca^{2+} indicators, it is possible to image the visual response properties of neurons deep in the intact brain. This technique offers the possibility of studying modularity of visual cortical areas at single-cell resolution, as well as the possibility of correlating function with specific cell types and circuits[148].

Viral tracing

Genetically modified viruses have become increasingly useful for tracing mono- and multisynaptic connections and for introducing foreign genes into neurons of the primate brain. Rabies virus, in particular, has proved to be a powerful tool for uncovering multisynaptic connections of the primate visual system with the hope of elucidating the complex circuitry in and between different visual areas[73,133,134,150].

Reversible activation and inactivation

Only recently has the possibility of activating and inactivating specific cell types and circuits become a reality. By introducing non-mammalian receptors into specific neuron populations of the primate visual system and activating them, these neurons can be hyperpolarized or depolarized. For example, activation of the allatostatin receptor by application of its ligand opens inwardly rectifying K^+ channels and hyperpolarizes the neurons so that they are no longer visually responsive[149]. Alternatively, the receptors channelrhodopsin and halorhodopsin can be activated by light and depolarize and hyperpolarize the neurons, respectively [151,152].

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