Visual processing: **Parallel-er and Parallel-er**

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The mammalian visual system processes many different aspects of the visual scene in separate, parallel channels. Recent experiments suggest that the visual cortex, like the retina, forms parallel circuits even at very fine spatial scales.

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One of the remarkable features of the mammalian nervous system is the rich variety of cell types it contains. What are we to make of this diversity? If we adhere to the Aristotelian notion that 'form follows function', we must consider the possibility that each member of the menagerie is performing some unique role. This has been most eloquently argued by students of the retina, who have provided evidence that each of a large variety of cell types (about 55) appears to have a distinct function [1]. For example, each of the 28 different types of amacrine cell completely 'tiles' the retina, as one would expect if they were performing unique functions in parallel [2]. The same is also true for the 11 distinct classes of retinal ganglion cell [3]. And most significantly, according to a recent review of this topic [4], "every morphologically distinct cell for which the function is known or can be strongly inferred indeed constitutes a functional 'type', just as understood by Cajal".

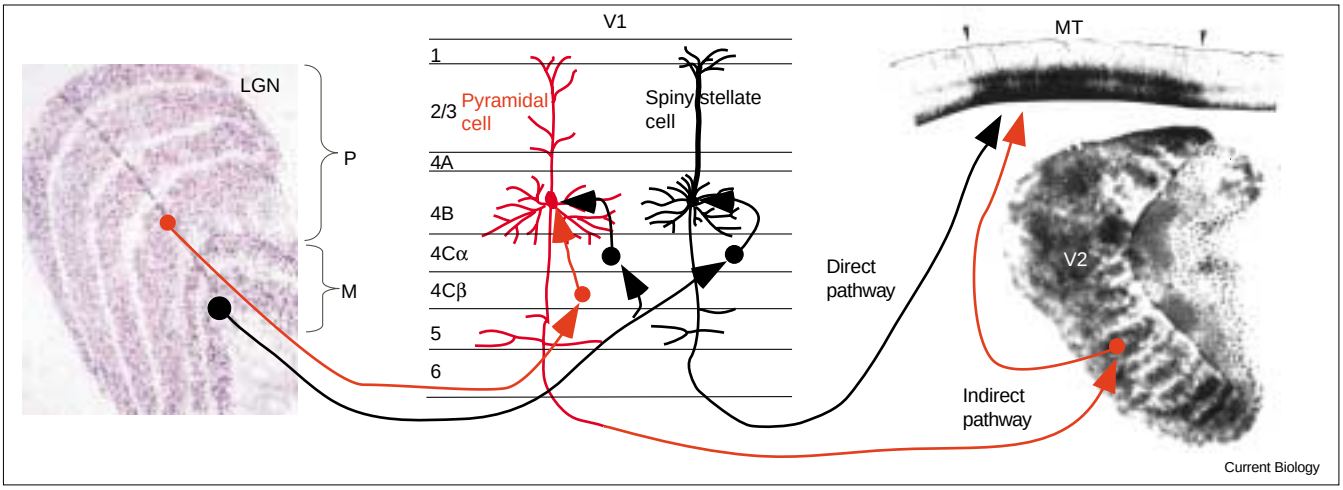
The primary visual cortex of primates is as morphologically diverse as the retina. A ballpark guess for the number of unique neuronal types, based on a number of earlier studies, is that there are about two dozen types of excitatory neuron and one dozen types of inhibitory neuron (E.M. Callaway, personal communication). And an earlier study [5] suggests that the situation may be even more complex than is indicated by morphology. In a sample of 31 neurons, all from a single layer (3B) of macaque striate cortex, these investigators found that "no two cells of the same morphological type received significant input from the same combination of layers". That is, the 'connectional' diversity created by the local circuits of the cortex could greatly increase the number of unique functional types. This finding makes it likely that a *minimum* of 156 unique types — based on a combination of morphology and differential input from different cortical layers — exist in layer 3B alone. But is there good reason, apart from the exhortations of our retinal colleagues, to think that all of these possibilities really constitute parallel channels of information processing? While we lack a definitive answer to this question, the latest findings from Callaway and colleagues [6] indicate that there is indeed tremendous potential for parallelism in the visual cortex.

Over the past several years, Callaway and his team have exploited a powerful combination of techniques to study the sources of local cortical input into individually identified and labeled neurons in the monkey striate cortex (the primary visual area, V1). They record intracellularly from single neurons in cortical slices while using a laser beam to release a puff of glutamate that will cause neurons in the immediate vicinity to fire action potentials. By systematically puffing the neurotransmitter in a fine array of sites and determining which elicit monosynaptic excitatory currents from the recorded neuron, they are able to generate a map of that neuron's inputs from different cortical layers.

In their latest work, Yabuta *et al.* [6] found that two distinct morphological types within layer 4B, spiny stellate cells and pyramidal cells, receive distinct patterns of local inputs. Apart from being a satisfying functional correlate of different neuronal forms, their result reveals a remarkable specificity in the way that information from two different processing streams, the so-called M and P pathways, is parceled out in the cortex. As hinted at by a previous study from the same group [7], the spiny stellate neurons receive a 'pure' M input from layer 4Cα. In turn, the spiny stellate neurons project to the middle temporal visual area (MT) [8], which is well known for its important role in motion perception [9]. The pyramidal neurons receive mixed M and P signals via inputs from both layers 4Cα and 4Cβ, and their axons travel to other areas, such as V3 [10] and the thick stripes of V2 [11]. Both of these other regions also project to MT [12,13], so MT gets both a *direct*, M-dominated input from the spiny stellate cells and an *indirect*, mixed input via the pyramidal cell pathway (Figure 1).

Why is this interesting? To understand this, it is essential to know something about the information carried by the two pathways (Figure 1). The pathways originate in the retina, but receive their names from the major divisions of the lateral geniculate nucleus (LGN): 'M' for the ventral magnocellular layers and 'P' for the dorsal parvocellular layers. It is generally agreed that the two groups of cells have different properties along several important dimensions: M cells give fast and transient responses, are very sensitive to low contrasts, and are color blind; P cells give slower, more sustained responses, are relatively contrast insensitive, and are color opponent (meaning they can convey information about color).

Figure 1



Two parallel routes to visual area MT. Information from two different processing streams converges in striate cortex (V1). The streams take their initials from the ventral 'magnocellular' (M) and dorsal 'parvocellular' (P) layers of the lateral geniculate nucleus (LGN), shown here in a Nissl stain of a coronal section [20]. Two routes by which the information in these two streams might arrive at MT are shown in red (indirect route) or black (direct route). The M cells project to layer 4Cα of V1, which projects to both pyramidal (red) and spiny stellate (black) cells of layer 4B. The P cells project to layer 4Cβ and then to the pyramidal cells (but not the spiny stellate cells) of layer 4B. The spiny stellate cells send their M-dominated signals directly to MT, which is distinguished from surrounding areas by its heavy myelination [21]. The pyramidal cells relay their presumably mixed M and P signals to MT indirectly via either the thick stripes of V2, revealed by staining for cytochrome oxidase [22], or V3 (not shown). The diagrams of the pyramidal and spiny stellate cells are modified from images available at: http://retina.umh.es/Webvision/imagesvv/BasicCells.jpg; WEBVISION: The organization of the vertebrate retina; Helga Kolb, Eduardo Fernandez, and Ralph Nelson.

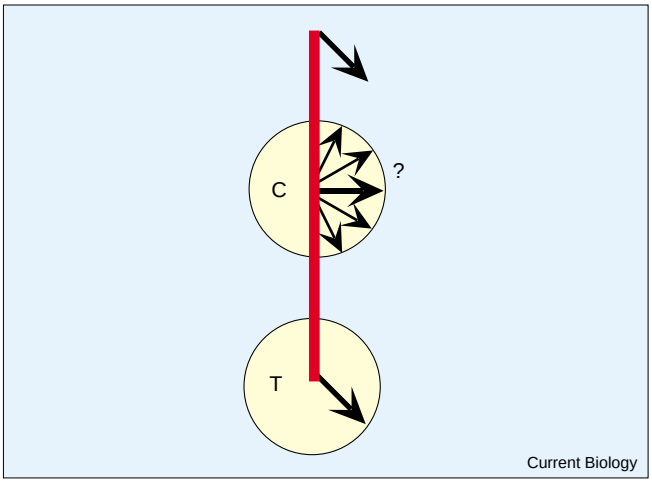
There is considerable debate on how cleanly segregated these two streams remain at higher levels of the visual pathways (see [14,15] for overviews). One point frequently lost in the heat of this debate is that mixing of the two functional streams does *not* mean that parallel processing is *not* occurring at later stages — it may simply be organized along different dimensions than 'pure M' versus 'pure P'. It would seem that one good reason for segregating certain functional types is so that the information they convey can be recombined in precise ways according to the demands of a particular task. Consider a culinary analogy: the chef desires orderly segregation of the various spices in his kitchen, not so that he may make an entire meal of one or another spice, but rather so that different spices can be mixed in precise ways in order to yield new and interesting flavors. He will have multiple levels of segregation: pure spices, such as cardamom, along with specific combinations of spices, such as for a curry, which may in turn be components of complete recipes.

Indeed, the tremendous specificity in the mixing of M and P streams discovered by Yabuta *et al.* [6] suggests that something interesting is cooking. But what? What might be the function of this particular instance of micro-parallelism? The authors speculate that the pure M pathway to MT might provide inputs to a specific set of 'columns' — vertically organized sets of neurons with related response specificities — the functions of which might be degraded by P input. This is certainly possible and quite testable, as pointed out by the authors, using combinations of anatomical tracers and functional labeling of cortical columns.

Another possibility, however, is that the parallel sources of input to MT provide different types of information to the same MT neurons. To see how and why this might play out, consider a problem whose solution requires the *integration* of motion information, such as the 'aperture problem' (Figure 2). If a vertically oriented bar moves downward and rightward at a constant velocity, a tiny V1 receptive field positioned along the length of the contour can 'see' only the rightward component of motion. Only a receptive field positioned over one of the endpoints of the bar, or 'terminators', can measure the motion direction accurately. Thus solving the aperture problem ultimately involves selecting terminator motion and ignoring, or at least reinterpreting, the ambiguous measurements made along the contour.

We have recently found that MT neurons do indeed 'solve' the aperture problem [16], but the solution takes time. It appears that these neurons initially derive a rough estimate of direction by averaging all of the local motion signals, and subsequently refine this estimate over the ensuing 100 milliseconds. Interestingly, this process is reflected both in the perception of such stimuli [17] and in

Figure 2



The aperture problem. For a vertical bar (red) moving downwards and to the right, a V1 neuron with a small receptive field positioned along the contour (C) can measure only the rightward component of motion. This measurement is consistent with many possible directions of actual bar motion (?), and is therefore ambiguous. Only neurons whose receptive fields are positioned over the bar's terminators (T) can measure the direction of motion accurately.

eye movements used to track them [16,18]. These observations might be explained by a fast, but 'dumb' channel (perhaps the M-dominated pathway from V1 to MT?) which quickly gets things moving in the right general direction (for example, the eyes during visual tracking), followed by the more time-consuming integration of additional, highly selective information (such as the directional signals from terminators, perhaps via V2 or V3?) to converge on the correct direction of motion. If this is the case, selective inactivation of one or both of the indirect pathways might be expected to eliminate the iterative solution found in MT neurons.

This is obviously speculative, as we do not yet know the exact nature of the visual signals carried by the direct versus indirect pathways to MT. It is clear that the spiny stellate cells — the population characterized by Movshon and Newsome [19], who identified them by antidromic (that is, backwards) activation from MT — comprise a very homogeneous class of direction-selective 'special complex' cells. It would be especially interesting, though heroic, to similarly characterize the pyramidal neurons in layer 4B by using antidromic stimulation from V3, or the thick stripes of V2, or both. Only heroic efforts of this kind will ultimately tell us whether the beautiful piece of anatomy described by Yabuta *et al.* [6] has important functional consequences. Almost certainly, it does. It would seem uncharacteristically profligate of nature to squander such precision.

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