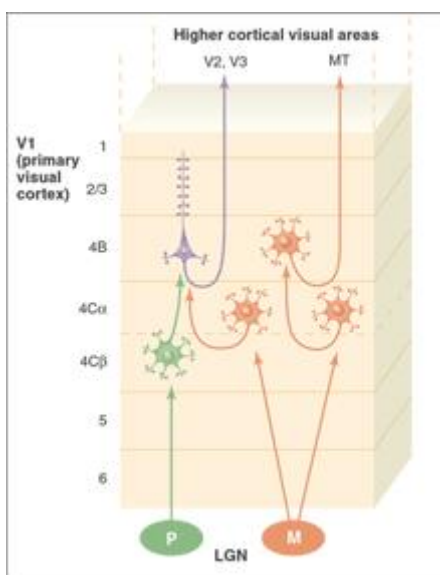


Perspectives NEUROBIOLOGY: Function Following Form

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Does the morphology of a neuron and its many processes (axons and dendrites) tell us what it does for a living? If so, anatomical information could serve to classify neurons into distinct functional classes. This issue has been of interest to neurobiologists ever since Cajal used a silver stain to demonstrate the dazzling complexity and diversity of neuronal forms throughout the central nervous system. In certain neurons, such as retinal ganglion cells, there is a strong correlation between the structure of their dendrites (slender extensions emanating from the neuronal cell body), the pattern of incoming electrical signals (inputs) they receive from other neurons, and their function. But elsewhere in the brain, for example in the cerebral cortex, we have only hints as to these relationships (1, 2). On page 297 of this issue, Yabuta *et al.* (3) report a striking correlation in the primary visual cortex (area V1) of the monkey. They show that two different morphological classes of V1 neurons, spiny stellate cells and pyramidal cells, receive different signals from two major streams of visual information from the retina and then direct this information to higher cortical visual areas.

The visual system relays different types of visual information in parallel through the magnocellular (M) and parvocellular (P) pathways of the retina. The M and P pathways transmit this information to separate divisions of the visual thalamus and themselves terminate in separate layers of V1 (layers 4Ca and 4Cb, respectively). Layer 4C neurons project to other layers of the visual cortex, which provide outputs to higher cortical areas (V2, V3, MT) that are thought to mediate distinct visual abilities, such as seeing color or motion (see the figure). The different activities of these areas might reflect differential contributions from the P and M pathways. Layer 4B, one of the targets of relays from layer 4C, contains many direction-selective neurons that respond better to stimulus motion in one direction than in the opposite direction. Layer 4B neurons receive a prominent M input, and provide a substantial output to visual cortical areas such as area MT (V5) known to be important in motion perception. Convergence of M and P signals onto single cells in layer 4B has previously been demonstrated (4), but Yabuta *et al.* now show that this convergence occurs only on certain cells in this layer. Using an elegant combination of anatomical and electrophysiological techniques in monkey brain slices from cortical area V1, Yabuta *et al.* determined the locations of neurons providing excitatory inputs to neurons in layer 4B. They then labeled the cells whose activity they had recorded. Their results show that different morphological classes of cells within layer 4B receive distinct patterns of input from layer 4C. Spiny stellate neurons receive strong input from layer 4Ca but none from 4Cb, whereas pyramidal neurons receive strong input from both layers 4Ca and 4Cb (see the figure).



Information relays in the visual cortex. Distinct types of visual signals (M and P) are relayed from the retina through separate divisions of the lateral geniculate nucleus of the thalamus (LGN) to different portions of primary input layer 4C of the primary visual cortex (V1). A further relay conveys these signals to layer 4B, which provides a major output from V1 to higher visual areas (V2, V3, MT). Spiny stellate cells in layer 4B (orange), which project to area MT (V5), receive a strong M input but no P input. Pyramidal cells (purple), which project to areas V2 and V3, receive both M and P inputs.

These results are important beyond simply classifying cells on the basis of morphology. Because stellate and pyramidal cells of layer 4B appear to project to separate higher visual areas (5, 6), knowing which visual signals they carry may help to distinguish the different streams of information transmitted through visual areas of mammalian cerebral cortex (particularly those areas that mediate motion perception) (7, 8). For example, the pathway emanating from layer 4B is thought to be dominated by the M system and therefore is essentially insensitive to color information. Can P signals be detected emanating from layer 4B in experiments *in vivo*? If so, what perceptual relevance might they have? Also, not all cells in layer 4B are directionally selective; are these cells primarily stellate or

pyramidal in morphology? What are the visual response properties of these cells? Do they too project to visual motion areas such as MT? Yabuta *et al.*'s data make an important contribution to our understanding of how differences among the various parallel pathways emanating from V1 might acquire their unique functional characteristics.

Why might the cerebral cortex segregate relays of visual information in this way? Perhaps there is a need to isolate particular projection pathways leaving V1 from the influence of feedback inputs (from higher cortical areas back to V1). Pyramidal cells can be distinguished from stellate cells because they have access through their apical dendrites to feedback projections from higher cortical areas, which terminate in the upper cortical layers. It may be that some visual computations use feedback from downstream cortical areas, whereas others do not. Cells in layer 4B retain some of the characteristics of their inputs, but they are more selective for the spatial frequency, direction of motion, and orientation of the stimulus. This clearly indicates that they perform further computations on incoming information. The Yabuta *et al.* findings suggest that some aspects of visual motion are analyzed solely in a feedforward ("bottom-up") manner, whereas others make use of feedback ("top-down") signals. Different motion perception pathways could consist of a color-blind motion channel versus one multiplexed with chromatic information, or of channels concerned with motion at different spatial scales or speeds. The suggestion of selective access to feedback is complicated by the fact that certain feedback pathways to V1 (from areas V3 and MT) terminate broadly within layer 4B itself, but these pathways might specifically target different groups of neurons.

Are projection pathways distinguished this way elsewhere in the cerebral cortex? Because a variety of systems in the brain consist of multiple parallel subsystems, the visual cortex is a valuable model, reminding us that anatomy and physiology do indeed have something to do with one another.

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