

PERSPECTIVES

Reshaping the binding problem of form and motion vision

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The primary visual cortex (or V1) is the first cortical processing stage in primates and receives visual information from the retina via several parallel pathways. Cortical regions beyond V1 are segregated into two major streams: dorsal and ventral. The dorsal route takes information from V1 to the posterior parietal cortex, while the ventral pathway takes a route from V1 to the inferotemporal cortex. The ventral visual stream is tuned for object identification, while the dorsal stream is tuned to detect where objects are located and in which direction they move (Ungerleider & Mishkin, 1982; Ungerleider & Pasternak, 2003). The apparent functional separation between the two paths has created a theoretical challenge. How can the information in the two systems be brought together across cortical space: the visual binding problem (Roskies, 1999).

A good example of this binding problem relates to form and motion processing. It is generally believed that motion direction is coded by the dorsal stream and only combined with form processing from the ventral stream at higher cortical levels (e.g. Oram & Perret, 1994). The segregation into form and motion paths begins in V1 where only certain horizontal layers have been shown to have large proportions of direction-selective cells (Hawken *et al.* 1988). V1 has six layers of neural tissue each being subdivided into functionally distinct sublayers (Fig. 1; Lund, 1988). In primates only layers 4B, 4C α and 6 have been shown to contain a high proportion of direction-selective cells. Layer 4C α receives input from the retina via the dorsal lateral geniculate nucleus and transfers signals to layers 4B and 6, which in turn send

information to the dorsal stream (Movshon & Newsome, 1996). There has been little evidence of highly direction-selective signals being sent to the ventral pathway.

However, the study by Gur & Snodderly (2007) in this issue of *The Journal of Physiology* reveals a new pathway for direction-selective neurons that targets the ventral stream (also see Gur *et al.* 2005). The route begins in the primary visual cortex in sublayer 4C α (Fig. 1) from where it travels a short distance to a neighbouring sublayer, 4C m , which is a thin sheet of cell bodies and dendrites wedged in the middle (m) of layer 4C (Yabuta & Callaway, 1998). The axons of neurons in layer 4C m travel upwards through V1 and innervate direction-selective neurons in layer 3 (Gur & Snodderly, 2007), from where information is sent to the ventral stream (Ungerleider & Pasternak, 2003). It appears that the ventral visual pathway has no need to extract motion information from the dorsal stream across wide reaches of cortical space. Rather, the ventral path is supplied by its own motion input at source. This is significant because trying to combine form and motion signals that have already travelled through many separate cortical areas, each adding variable transmission delays, is a complex task.

Direction-selective neurons in V1 that send motion information to the ventral stream are highly discriminating. They must

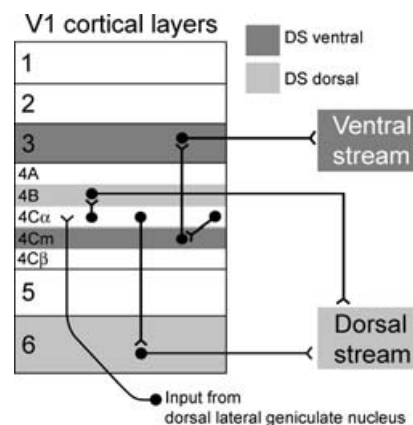


Figure 1. Schematic diagram of the direction-selective (DS) pathways in V1

be activated with a stimulus of exactly the correct orientation, moving in the correct direction and doing so within a very restricted patch of visual space. It is presumed that these cells are involved in fine motion discrimination during fixation, e.g. detecting the movement of facial features. Gur & Snodderly (2007) have also found consistent differences between the directional properties of cells in the other direction-selective V1 layers (4B and 6), which are destined for the dorsal pathway. Taken as a whole it appears that three distinct motion pathways exist in V1, two targeting the dorsal pathway, and one targeting ventral destinations (Fig. 1).

Gur & Snodderly (2007) have uncovered a functional pathway by which directional information reaches the ventral stream without first travelling along the dorsal stream. This finding reduces the spatial binding problem by removing the need to combine form and motion information from widely separate brain regions. A binding issue still remains as form and motion need to be united, but at least this can happen in neighbouring cells that have experienced similar transmission delays.

References

- Gur M, Kagan I & Snodderly DM (2005). *Cereb Cortex* **15**, 1207–1221.
- Gur M & Snodderly DM (2007). *J Physiol* **585**, 383–400.
- Hawken MJ, Parker AJ & Lund JS (1988). *J Neurosci* **8**, 3541–3548.
- Lund JS (1988). *Ann Rev Neurosci* **11**, 253–288.
- Movshon JA & Newsome WT (1996). *J Neurosci* **16**, 7733–7741.
- Oram MW & Perrett DI (1994). *J Cogn Neurosci* **6**, 99–116.
- Roskies AL (1999). *Neuron* **24**, 7–9.
- Ungerleider LG & Mishkin M (1982). In *Analysis of Visual Behavior*, ed. Ingle DJ, Goodale MA & Mansfield RJW, pp. 549–586. MIT Press, Cambridge, MA.
- Ungerleider LG & Pasternak T (2003). In *The Visual Neurosciences*, ed. Chalupa LM & Werner JS, vol. 1, pp. 541–562. MIT Press, Cambridge, MA.
- Yabuta NH & Callaway EM (1998). *J Neurosci* **18**, 9489–9499.