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PERSPECTIVES

Colour and form in the early stages of cortical processing

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Over the past decades, the functional role of many cortical regions has been elucidated. Many regions previously labelled as unspecific 'association' cortex have been attributed a specific role, and assigned to one or other of the many systems underlying our mental processes. The trend towards assigning a unique role to specific neuronal populations is also reflected within individual systems: a given function, such as seeing or hearing, is often thought to be achieved by a number of neuronal populations working in parallel, each solving one specific component of the task at hand. This notion has been particularly evident in studies of the visual cortical areas.

Proponents of the 'segregation' hypothesis suggest that an object's physical attributes such as colour, form and motion are analysed by different populations of cortical neurons. In that view, signals related to various attributes are segregated early in the visual pathways, processed separately by a number of dedicated populations of cortical neurons, and recombined at a later stage to yield a coherent percept. The specialized populations of neurons are thought to be segregated into different cortical areas, or into anatomically distinct subregions within a cortical visual area. This view is prevalent in many neuroscience textbooks, and is reflected as well in the concept of 'feature maps' in the computer vision literature.

Other scientists argue that individual neurons must treat more than one visual attribute to achieve a specific goal. For example, a neuronal population dedicated to analysing borders could do so irrespective of the physical attributes defining the border. To achieve this goal, all possible combinations of border attributes must be represented within the population. For example, a neuron in such a population might respond preferentially to a vertical, red–green border. It codes simultaneously for the orientation and the colour of a stimulus. In that view, an object's visual attributes can remain integrated and there is no need to postulate a subsequent stage that recombines segregated signals into a coherent percept.

To decide between these extreme views, much attention has been devoted to the relationship between selectivity for orientation and colour. Specifically, the segregation hypothesis proposes that colour is represented by cells that do not code for orientation, and vice versa (see, for example, Livingstone & Hubel, 1988 or, more recently, Shipp & Zeki, 2002). In that scheme, colour signals reach primary visual cortex (V1) neurons located in clusters (blobs) spanning layers 2 and 3, as revealed by cytochrome oxidase (CO) staining. Several studies reported that neurons within the V1 CO blobs are selective for the colour but not the orientation of a stimulus. Signals processed within the blobs are then sent to specific regions within area V2: the thin stripes revealed by CO staining. Orientation, on the other hand, is represented by neurons located outside of the V1 blobs, and in the interstripe regions of V2.

A number of reports are at odds with that view. Several studies failed to find a segregation of functional properties between cells inside and outside the V1 blobs (as in Leventhal *et al.* 1995). Similarly, the segregation of functional properties between V2 compartments was shown to be considerably weaker than initially reported (Gegenfurtner *et al.* 1996). In fact, neurons selective for orientation and colour were found in all V2 stripes, as well as inside and outside the V1 blobs.

To explain these conflicting results, researchers have argued that some studies based their conclusions on too few neurons, that results obtained in anaesthetized animals might differ from those obtained in awake ones, or that the discrepancies result from the different criteria used to classify cells. The last point is of particular interest, because the schism between proponents of the segregation hypothesis and their opponents largely coincides with methodological differences in the procedures used to classify cells. Researchers relying solely on qualitative criteria (as in Shipp & Zeki, 2002) generally accept the segregation hypothesis. Most studies using quantitative methods agree to reject it.

The careful study by Friedman *et al.* (2003), in this issue of *The Journal of Physiology,* goes a long way towards resolving this debate. The authors record the activity of individual V1 and V2 neurons presented with uniformly coloured figures. They measure each neuron's selectivity for the orientation of an optimally sized bar, and its colour selectivity by flashing optimally oriented coloured bars in its receptive field. In addition, they study the responses evoked by the presence of an edge presented in various positions inside and outside the neuron's receptive field. From these measures, they compute several indices that allow them to quantify a cell's selectivity for orientation, colour and the position of a border. They collect data from large samples of neurons in both V1 (425 neurons) and V2 (417 neurons) of awake animals, and use the same quantitative criteria to characterize neuronal responses in both areas. Therefore, their study does not suffer from any of the weaknesses listed above.

Their results show that, in both V1 and V2, there is no correlation between selectivity for colour and orientation. The lack of correlation is observed irrespective of the particular indices used to quantify the responses. If colour was represented by neurons unselective for orientation, a negative correlation between the indices quantifying these attributes should be observed. Instead, they show that colour-selective neurons uniformly span the full range of orientation selectivity, and vice versa. Similarly, their data show a lack of correlation between a cell's colour selectivity and its ability to signal the position of a border. These results convincingly show that orientation and colour are not treated by separate, independent populations of cortical neurons.

When further research shows that the present results generalize to other visual attributes, current notions of cortical processing will change considerably. The view of the visual cortex as an ensemble of parallel circuits each dedicated to the analysis of a single visual attribute will be replaced by one of task-driven circuits, where the analysis of one physical attribute may never be fully dissociated from that of another.

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