news and views

Hypercomplexities in the visual cortex

from J. Anthony Movshon

In their pioneering studies of information processing in the visual cortex of cats and monkeys, Hubel and Wiesel (*J. Physiol.* **160,** 106; 1962; *J. Neurophysiol.* **28,** 229; 1965; *J. Physiol.* **195,** 215; 1968) distinguished three major classes of neurone by recording single-unit responses to slits, edges and spots of light. 'Simple' and 'complex' cells are selectively sensitive to the orientation and, often, the direction of movement of visual contours; they differ from one another in details of the organisation and size of their receptive fields. 'Hypercomplex' cells add to orientation and direction selectivity a preference for the length of stimulating visual contours: their responses are reduced or abolished by elongating an optimally-oriented contour beyond a limited area of the receptive field. Originally, the properties of hypercomplex cells were thought to be generally similar to those of complex cells. Their excitatory inputs were held to derive from one or a few complex cells with superimposed receptive fields, while their length-specificity was thought to result from the inhibitory influence of other complex cells with displaced receptive fields.

The need to modify this scheme was first suggested by Dreher (*Invest. Ophthalmol.* **11,** 355; 1972), who found that hypercomplex cells in the primary visual cortex (area 17) could be divided into two groups according to their general similarity to either simple or complex cells. Both groups share the defining property of hypercomplex cells—length specificity—but otherwise resemble one or the other of the principal cell types. The clarity of the situation was further reduced by the observation in a number of laboratories studying both cat and monkey visual cortex that it is difficult on quantitative grounds to justify a separation of one group of cortical cells on the basis of length specificity alone. The extent of the reduction in response with increases in stimulus length varies for all cell types, and the distribution of length-specificity is not obviously bimodal (Schiller *et al. J. Neurophysiol.* **39,** 1288; 1976; Gilbert *J. Physiol.* **268,** 391; 1977; Rose *J. Physiol.* **271,** 1; 1977).

Nonetheless, it is possible to distinguish a group of cells (which may or may not form a truly separate class) whose responses are totally or near-totally abolished by increases in stimulus length. These neurones, which are most often found in the superficial layers of the visual cortex (Gilbert *J. Physiol.* **268,** 391; 1977). have recently been studied in the cat by Sillito and his colleagues, using a combination of electrophysiological and pharmacological techniques (Sillito & Versiani *J. Physiol.* **273,** 775; 1977; Sillito *J. Physiol.* **273,** 791; 1977).

Sillito uses a multi-barrelled micropipette electrode; electrical activity can be recorded from single neurones through the central barrel, while the additional barrels (usually four) are used for the iontophoretically-controlled microapplication of specific drugs to the region near the electrode tip (this area is roughly 100 μm across, and thus usually includes the neurone being recorded from but few, if any, others) (Hess *et al. Expl Brain Res.* **22,** 415; 1975). The most interesting of the agents used by Sillito is bicuculline, which antagonises the action of γ-aminobutyric acid (GABA), a substance known to act as an inhibitory neurotransmitter in the visual cortex (Iversen *et al. J. Physiol.* **212,** 519; 1971; Sillito *J. Physiol.* **250,** 287; 1975). By comparing neuronal responses to visual stimuli in the presence and absence of bicuculline, it is possible to infer the contribution of excitatory and inhibitory mechanisms to particular receptive field properties. While these techniques are to some degree imperfect (two problems being the uncertain diffusion of the drugs and the possible action of bicuculline-resistant inhibitory neurotransmitters), Sillito has previously demonstrated their usefulness in studies of the factors influencing orientation and direction selectivity in the visual cortex (*J. Physiol.* **250,** 305; 1975; *J. Physiol.* **271,** 699; 1977); the results of his studies of hypercomplex cells are in many ways more striking.

Under Hubel and Wiesel's original scheme, abolishing the inhibitory inputs to a hypercomplex cell should leave its orientation and direction selectivity unaltered, since these properties should derive from the excitatory influence of a few complex cells. The cell's length-specificity, which should be derived from inhibitory influences, would be expected to disappear. Sillito's results are in almost direct contradiction to this prediction: he finds that the application of bicuculline totally abolishes hypercomplex cells' orientation specificity, while only partially altering their length specificity; direction specificity is apparently unaffected by bicuculline. In other experiments, involving the application of D,L-homocysteic acid (which artificially induces a spontaneous discharge in normally silent cells, against which reductions in firing rate can be observed), Sillito demonstrates that at least a part of hypercomplex cells' length specificity is due to active inhibition at some stage in the visual pathway, but his overall results suggest a very different scheme from that of Hubel and Wiesel.

It seems that hypercomplex cells must receive their excitatory input from cells lacking orientation selectivity, but possessing some degree of both direction and length specificity. Sillito suggests that the neurones responsible may be the large pyramidal neurones located deeper in the cortex, which are known to project primarily to subcortical visual structures but which often send recurrent collateral projections into the upper cortical layers. These neurones are a special subgroup of complex cells lacking pronounced orientation selectivity but having both direction selectivity and a preference for shorter stimuli (Palmer & Rosenquist *Brain Res.* **67,** 27; 1974; Gilbert *J. Physiol.* **268,** 391; 1977). Under this scheme, two of the basic properties of hypercomplex cells—direction and length specificity—would in large part be due to the properties of their excitatory inputs, while their orien-

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tation selectivity would be provided and their length specificity enhanced by intracortical inhibitory inputs. This model is not entirely satisfactory in that hypercomplex cells generally have rather small receptive fields while the deep-layer complex cells proposed as their prime excitatory input have very large receptive fields, but it nevertheless forces a reevaluation of current thinking about interneuronal interactions in the visual cortex. Another unresolved problem posed by these results is the degree to which the inhibitory influences identified in hypercomplex cells may be identified with the rather generalised and potent intracortical inhibitory influences identified using various techniques (Blakemore & Tobin *Expl Brain Res.* **15,** 439; 1972; Bishop *et al. J. Physiol.* **231,** 31; 1973; Creutzfeldt *et al. Expl Brain Res.* **21,** 251; 1974; Hess *et al. Expl Brain Res.* **22,** 415; 1975).

In any case, it is becoming increasingly difficult to conceive of the visual cortex as a straightforward relay system of neurones interconnected by hierarchically ordered excitatory connections which determine the bulk of neuronal properties there. Rather, it is clear that the visual response properties of most neurones depend on subtle interactions within an intricate system of more and less specific excitatory and inhibitory influences, whose cooperative details determine most aspects of neuronal behaviour. □