Neurophysiology

Parallel channels and redundant mechanisms in visual cortex

from N.V. Swindale

ALL too rarely, pharmacologists come up with a drug that interferes selectively with a particular pathway or a single well-defined function of the nervous system. Ideally the drug should be easily administered, specific and reversible, but such combinations are not often achieved. One molecule that does seem to satisfy these criteria is the glutamic acid analogue 2-amino-4-phosphonobutyric acid (APB) which has been studied by P.H. Schiller and collaborators and whose latest work is reported on page 824 of this issue[1]. APB blocks the function of a class of retinal ganglion cells, and it is hoped that it will help to determine to what extent the visual system functions as an integrated whole or whether its differrent components are capable of some degree of independent function.

The pathway from retina to brain is divided into parallel channels, each selective for different attributes of the image, such as light intensity, colour and spatial frequency. Each channel consists of neurones of two types, ON and OFF, the former responding only to light levels that are greater than the local average in the image and the latter responding (by an increase in firing rate) to levels that are less than the local average. Thus, ON channels carry information about bright spots or areas in the image and OFF channels do the reverse. This division of labour, which resembles that of the push–pull output stage of an amplifier probably has more than one advantage: it allows cells to have low levels of activity when the retina is in darkness or uniformly illuminated, reducing metabolic requirements, and it effectively doubles the dynamic range over which neurones can signal information about light levels in the retinal image.

The separation between ON and OFF pathways occurs at the synapse between the rod and cone photoreceptors and bipolar cells, the earliest stage in the visual pathway. All photoreceptor cells hyperpolarize in response to light, but the bipolar cells to which they are connected are of two types: ON bipolars that depolarize when the photoreceptor to which they are connected hyperpolarizes, and OFF bipolars that hyperpolarize when the photoreceptor hyperpolarizes. If APB is applied to the retina it hyperpolarizes the ON bipolars, silencing cells post-synaptic to them[2]. The action of APB appears to be the same in retinas from all species of vertebrate, and is specific to all classes of ON channel.

One of the first observations made with the drug[3] was that it did not abolish the antagonistic centre-surround organization of either retinal cells or lateral geniculate nucleus cells to which the retina projects. This means that the inhibitory actions involved in generating the surround must occur entirely within the OFF pathway. The same is probably true for the ON pathway. ON and OFF channels thus remain separate in the retina and the lateral geniculate nucleus, and the pathways do not converge until the inputs reach the visual cortex.

The ability to disable half of the visual system in this way raises obvious questions. Can each half function on its own and, if so, how well? Because an edge normally has both light and dark components, it might be thought that the detection of edges and their orientation (a function of the visual cortex) will depend on the proper functioning of both ON and OFF channels. Blocking the ON channels by applying APB to the retina might be expected to interfere seriously with vision. But it appears that, although APB does have some deleterious effects, they are much less than had been supposed.

The carefully controlled experiments on awake monkeys reported in this issue show that, when treated with APB, the animal cannot detect a light coming on, although it can still detect the onset of a dark spot. Perhaps more relevant is that many visual functions are relatively unimpaired by APB. For example, the report[1] shows that monkeys treated with the drug have qualitatively normal stereopsis when tested with random-dot stereograms and can detect apparent motion in random-dot kinematograms. Both these tasks are normally regarded as rather severe tests of visual performance. Other studies[3] show that cortical neurones in APB-treated animals, although lacking in ON responses, still possess orientation and direction selectivity.

Although interactions between ON and OFF channels are not necessary for the generation of many neuronal-response properties, they do not prove that such interactions do not occur, or that they have no important functional role. A really careful comparison of the properties of cortical cells between normal and APB treated animals has yet to be carried out, and strong interactions betwen ON and OFF inputs to the cortex are known to exist (see, for example, ref.4). It seems

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NEW discoveries of some remarkable Lower Carboniferous fish[1-5] show that they had vast toothed spines apparently suspended directly above their heads. *Stethacanthus*, a 1-m-long shark, now known from nearly complete specimens from Scotland and Montana[1-3], had a remarkable spine shaped like a shaving brush just behind its head. The spine stands nearly vertical and is topped by dozens of small teeth. It is clearly an unwieldy structure and must have had an important function. The spine was present in both males and females, and Zangerl[3] suggests that it was used to scare off potential predators: *Stethacanthus* had a patch of teeth on top of its head as well and, when partially buried in the mud, the two toothed areas would have mimicked a vast gaping mouth, as if of some giant predator. The figure illustrates the possible appearance of the fish[3].

A second stethancanthid, *Falcatus*[4], is a small shark up to 14.5 cm long and has a long, shelf-like spine extending from roots deep in the muscles of the 'shoulder' region to run over the head, like a sunshade. The spine is in two parts, the fixed base and the horizontal portion which slots on to it, and is present only in sexually mature males. Lund[4] suggests that male *Falcatus* sharks aggregated before the breeding season for display–courtship rituals. The third complete Stethacanthid shark, *Damocles*[5], is also small (up to 20 cm long) and differs from *Falcatus* in having a simpler spine with many sharp teeth.

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