hydrodynamic model to include the collective effects on the formation of high-density states in nuclear matter in high energy heavy-ion collisions. In such collisions it is possible for nuclear matter to be compressed momentarily to very high densities, and this could have a considerable effect on the rate of pion production. The high densities are associated with high temperatures, and these can result in pion condensation in just the same way as a gas is ionised with the liberation of electrons when its temperature and pressure are raised. The probability of pion formation can be calculated from statistical theory assuming thermodynamic equilibrium between the pion and nucleon components. In a later paper they reformulated the theory relativistically and evaluated the rate of pion production quantum mechanically.

In particular they calculated the effect of the condensation of zero-momentum pions, and found that this might be appreciable at incident energies of 120 to 440 MeV per nucleon, reaching a peak at an incident energy of about 220 MeV per nucleon. They estimate that as many pions as 0.4 per nucleon may be produced and allowing for those that do not escape from the nucleus gives a result in agreement with the experimental results.

These calculations are still in an early stage, but it is notable that they give results similar to those found experimentally, while those based on the independent particle model are far too low. This indicates that some new process is taking place in energetic collisions between heavy ions, and this should be a strong stimulus to further experimental and theoretical work. □

The oddity of blue

from J. D. Mollon

A working party was held in Cambridge in 12-14 July, 1977 to discuss the anomalies presented by the 'blue mechanism' of man's colour vision. The meeting was held at the Kenneth Craik Laboratory, an interdisciplinary laboratory for sensory science, recently founded by the Departments of Physiology and Experimental Psychology, and was supported by a grant from the Cambridge Philosophical Society.

THE first stage of man's colour vision is relatively well understood. It is generally held that there are just three classes of retinal cone, each sensitive to a broad band of the spectrum; and that all our varied experience of hue depends on the comparison, by later neural mechanisms, of the outputs of these receptor cells, each of which is individually colour blind. However, it is increasingly difficult to neglect a catalogue of signs that the blue-sensitive receptor system differs from the green and red-sensitive systems. By special sensory experiments it is possible to study our visual capacities when stimuli are detected only by blue cones and the 'blue mechanism' defined by these experiments turns out to have many odd properties. Moreover, the blue mechanism is disproportionately vulnerable to retinal disease. The working party was held to attempt to sort out these anomalies.

From the discussions emerged three explanatory principles that may account for most of the anomalies of the blue mechanism. Firstly, there are probably rather few blue-sensitive cones. This might explain the poor quantum efficiency and the poor spatial resolution that characterise the blue mechanism as well as the fact that normal observers when matching very small or brief targets resemble the rare class of congenitally colour-blind observers ('tritanopes') who seem to lack blue cones. H. G. Sperling (University of Texas) presented evidence for the relative rarity of blue cones in the baboon retina: measuring the light-induced reduction of nitroblue tetrazolium chloride in the ellipsoids of cones, he found that the putative blue cones (those that stain strongly when exposed to blue light) constitute 12% of the total population of cones over much of the retina and are arranged in a regular mosaic. D. MacLeod, M. Hayhoe and D. Williams (University of California) have demonstrated sharp local variations in the threshold sensitivity of the blue mechanism within an individual human fovea. They also confirmed the finding of Willmer that the very centre of the fovea essentially lacks the blue mechanism. Correspondingly Sperling's measurements suggest that the proportion of blue cones falls to 3–4% at the centre of the fovea.

A second explanatory hypothesis is that signals from blue cones have access only to the 'chromatically opponent' pathways of the visual system, which are thought to carry information about colour. P. Gouras and E. Zrenner (National Institutes of Health, Bethesda) have detected blue-cone inputs in only one class of retinal ganglion cell, which are characterised by tonic responses to blue light and off-responses to long wavelengths. P. Whittle (University of Cambridge) tackled the related and vexed, question of whether the blue cones contribute to brightness as well as to hue: presenting to one eye a flash detectable only by blue clones and to the other a white flash on a white field, he found that some subjects were able to equate the two flashes in brightness while others found the task meaningless.

If indeed signals from blue cones are transmitted only by chromatically opponent pathways, it might be expected that the sensitivity of the psychophysically-defined blue mechanism would be controlled not only by photons absorbed directly in the blue cones but also by signals from long-wavelength cones. E. N. Pugh Jr (University of Pennsylvania) and P. G. Polden and J. D. Mollon (University of Cambridge) suggested that a further group of anomalies could be explained if to the second explanatory hypothesis was added a third assumption: an attenuation of the blue-cone signal occurs at the opponent site and this attenuation depends on the difference of the short and long-wavelength inputs, being minimal when the difference is minimal (and when perhaps our sensation is neither blue nor yellow).

With the two assumptions it seemed possible to explain several phenomena discussed in detail at the meeting: the super-additivity of short and long-wavelength fields in reducing the sensitivity of the blue mechanism (Pugh); a newly-reported and paradoxical increase in the sensitivity of the blue mechanism when yellow light is added to a blue adapting field so as to render the composite field brighter but achromatic (Polden and Mollon); the inflexion that is seen in the threshold-*versus*-intensity function for blue targets on long-wavelength fields (W. S. Stiles); apparent saturation of the blue mechanism (Mollon and Polden); and anomalies of light and dark adaptation (Stiles), such as 'transient tritanopia', the strange loss of sensitivity to blue targets that is found after a long-wavelength adapting field has been turned off and that has now been demonstrated at the ganglion cell level by Gouras and Zrenner and at the level of the b-wave of the electroretinogram by D. van Norren (Institute for Perception, Soesterberg).

Other contributors independently provided results pointing to the second and third hypotheses. Thus R. Boynton (University of California), using pairs of stimuli equated for their effects on both red and green cones and therefore discriminated only by blue cones, has found that such discriminations are impaired by red,

J. D. Mollon is a lecturer in Experimental Psychology at the University of Cambridge.

yellow or green fields that have relatively little effect on the blue cones themselves; long-wavelength fields of different wavelength but of the same luminance produce equal losses of discrimination even though their direct effects on the blue cones are very different. M. Alpern and F. Zwas (University of Michigan) have measured the sensitivity of the blue mechanism to adapting beams passing through different points of the pupil and find that the point of entry for best effect is different for short and long wavelength stimuli, suggesting that more than one class of receptor is involved. They add a fresh anomaly to the catalogue: unlike the other cones, the blue cones have their maximal directional and spectral sensitivities at the same wavelength.

Inherited and acquired losses of the blue mechanism may not necessarily result from a loss of blue cones. van Norren demonstrated a blue-cone signal in the electroretinogram of congenital tritanopes; and E. King-Smith, F. Zisman and S. K. Bhargava (University of Manchester) have found that the loss of blue sensitivity in disease is greater for flashes on a yellow field than for flashes on a white field, a result that they relate to the second and third assumptions above.

Lampbrush chromosomes brought up to date

from J. O. Bishop

Nearly 100 years after the discovery of lampbrush chromosomes by Walter Flemming in 1882, what is believed to be the first meeting exclusively devoted to them was held at Maria Laach, in the Eifel in West Germany on May 12–15, 1977. The meeting was arranged by Dr Werner Kunz, University of Düsseldorf, and sponsored by the Deutsche Forschungsgemeinschaft.

DURING the first meiotic division of oogenesis segregation of the chromosomes is suspended, in some organisms for months, after the pairing of homologous bivalents and the formation of chiasmata. The oocyte increases greatly in size and it is reasonable to suppose that, whatever the programme for early embryogenesis, some of its most vital components are laid down at this time. The chromosomes become greatly extended and take up the characteristic lampbrush form in which a chromosome axis, condensed chromomeres and extended lateral loops are all clearly distinguishable in the light microscope.

One feature in particular makes lampbrush chromosomes uniquely interesting. The lateral loops are very actively transcribed. RNA complexed with proteins accumulates on the loops. The form of the RNP complexes and their relationship to the loop vary from one loop to another. This, and the fixed positions of the loops on the axis, makes it possible in some cases to identify the same loop in different oocytes. The RNA products of particular loops can sometimes be identified, and the same loop can be studied at different stages in oogenesis.

Given that a massive increase in the size of the oocyte is necessary, it seems likely that the formation of lampbrush chromosomes is designed to make this possible. The lampbrush form perhaps optimises transcriptional efficiency. On the other hand, since the bivalents are arrested in the process of segregating, perhaps only the parts required for transcription are extended, while the remainder of the chromosome is maintained in a more condensed form. A completely different class of hypotheses is based on the idea that the cell is taking advantage of the growing phase to perform some laborious operation on the chromosomes, such as repair or reconstruction, and that the lampbrush morphology is the result. Of course, these explanations are not mutually exclusive.

It quickly emerged at the meeting that the basis for current thinking about lampbrush chromosomes was laid down between 1950 and 1960, largely due to the work of H. G. Callan in St. Andrews and J. G. Gall at Yale and Minnesota. It was shown that each loop is based on a single extended DNA duplex. When adjacent chromomeres are separated by physical stress, both remain attached to the ends of the intervening loop, suggesting that there is no disruption of the linear continuity of the chromosomal DNA at the junctions of loops and chromomeres. This widely accepted interpretation requires that the pair of chromomeres lying at the base of a loop must be held together by secondary forces. During the 1950s extensive descriptions of lampbrush chromosome sets were published, and genetic polymorphism of loop morphology was discovered. The latter is a strong indication that lampbrush chromosome structure is at least partly determined by the DNA involved.

(from the left) O. Hess, H. G. Callan and E. H. Davidson in discussion.

Transcription

Study of the structure of lampbrush chromosomes is now intimately bound up with inferences as to patterns of transcription. Electron microscope studies of partially deproteinised preparations (O. L. Miller, University of Virginia, Charlottesville) reveal arrays of RNA fibres emanating from a series of polymerase molecules arranged along the loop. In many cases the lengths of the fibres increase regularly along the loop, and this is very reasonably taken to reflect progressive synthesis. Recent autoradiographic studies on *T. c. carnifex* loops that carry histone-specific RNA (see below) are interpreted to show that transcription is initiated before the histone DNA sequences, proceeds through them and continues beyond, with the histone-specifying sequences being cleaved from the transcripts before transcription ends (Callan). Electron microscope studies of loop-associated RNP particles (J. Sommerville, St Andrews) show them to be composed of surprisingly uniform 20-nm particles. The considerably different appearance of the RNP on different loops is apparently due to differences in the quantity and arrangement of these units.

All the evidence available supports the long-standing idea that the lateral loops are transcribed but the chromomeres and the axis are not. Structures with the appearance of transcription complexes are found only on the loops. Antibody to *Drosophila melanogaster* B-form RNA polymerase binds to the loops, but not to the axis or, apparently, to the chromomeres (E. K. F. Bautz; M. Jamrich, Heidelberg).

Provisionally, a transcription unit can be defined as occupying approximately the region between the shortest and the longest fibres observed in an array of transcription complexes (polymerase+fibril). The arrangement of

J. O. Bishop is in the Department of Genetics at the University of Edinburgh.