ash, iodine, nitrogen, mannitol and alginic acid contents determined. It is of interest to note that the results recorded for 1946 are comparable with those obtained for 1945; indicating that the results may be approximately reproducible in subsequent seasons.

Another problem of much scientific and technical importance is a study of the variation in the composition of the sub-littoral seaweeds with depth of immersion. So far, the results obtained substantiate the hypothesis that, consequent upon depth of immersion, there is a decrease in light intensity affecting the photosynthetic processes, which is reflected in the composition of the weeds.

The above programmes of research and development have been approved by the Board of Management under the chairmanship of Sir Steven Bilsland, who is also chairman of the Scottish Council (Development and Industry), as well as by the three specialist Advisory Committees, Algological, Chemical and Engineering. At the official opening of the Institute, Sir Steven emphasized that Scottish seaweed could provide an industry worth £15,000,000 per annum. Of this sum one third would go to collectors. In all, 90 per cent would be spent in Scotland and only 10 per cent outside Scotland.

Thus, for the first time, there has been sponsored in Great Britain an organisation set up to develop an industry based on waste, indigenous, natural products. It is interesting and suggestive to recall that it is now more than sixty years ago (1884) since Stanford, employed in the Scotch kelp industry, first discovered algin and some of the substances contained therein—calcium, magnesium and sodium in combination with the new alginic acid.

H. R. Fletcher

MECHANISM OF COLOUR VISION

ALTHOUGH some references were made to visual investigations carried out for the Forces during the War, the International Conference on Colour Vision held at Cambridge during July 28–August 2 was concerned mainly with the fundamental problem of how the visual mechanism works and, in particular, with the apparatus by which differences of colour are perceived.

R. Granit (Stockholm) reviewed the outstanding new development in this field, the work which he and his school have carried out on the electrical response of single fibres of the optic nerves of experimental animals such as the frog, cat, snake, etc. The response is picked up by applying a micro-electrode to the retina of an eye from which cornea and lens have been removed. Potential spikes generated between the micro-electrode and a second electrode, placed usually at the back of the bulb, may occur only on illuminating the retina (pure on-elements), or only on cutting-off the illumination (pure off-elements), or after both these operations (on-off-elements). But in every case a spectral sensitivity curve for the element which the micro-electrode has contacted can be measured by finding the smallest energy of various wave-lengths which just suffices to elicit a minimal characteristic response. Certain signs, for example, a single spike response at the threshold, enable the experimenter to decide whether the micro-electrode is in contact with the fibre of a single ganglion cell.

The following types of spectral sensitivity curve are obtained: (*a*) *scotopic dominator*, a broad curve which by its shape and position in the spectrum and by its appearance in rod retinæ and under conditions of dark-adaptation can be attributed to ganglion cells associated with end-organs for which visual purple (or for freshwater fish, visual violet) is the photosensitive substance; (*b*) *photopic dominator*, another broad curve, obtained with light-adapted and predominantly cone retinæ, which is displaced some 60–70 mμ towards the red compared with the scotopic dominator of the same retina (when this can be recorded); (*c*) *modulator curves*, comparatively narrow curves obtained with light-adapted retinæ and located at various points of the spectrum from about 440 to 610 mμ, possibly in groups in the red, green and blue regions; (*d*) *composite curves*, which can be regarded as the 'summation' of a dominator and a modulator or of two modulators.

From replies to questions on the relative frequency with which dominator and modulator curves are obtained, it appeared that perhaps one in twenty curves (presumably for light-adapted retinæ) would be of modulator type. A new worker in this field, de Vries (Groningen) reported that he had had no difficulty in obtaining dominator curves, but had not yet observed a modulator curve.

Some criticism was expressed of Granit's second method of obtaining modulator curves, the method of selective adaptation. The modulator curve is derived by taking at each wave-length the difference between (*a*) the sensitivity (reciprocal threshold energy) of an element after strong adaptation to coloured light, and (*b*) the reduced sensitivity of the same element in the fully dark-adapted state, that is, the dark-adapted sensitivity reduced by a constant factor so chosen that the difference in question is zero at some wave-length and is nowhere negative. One of several assumptions underlying this procedure is that both rods and 'modulator receptors' are connected to the ganglion cell, the fibre of which is in contact with the micro-electrode, and that the effects of radiational quanta absorbed in rods and modulator receptors are summed at the threshold just as if they were all absorbed by a single end-organ.

Pirenne (London) and others found this latter assumption difficult to accept. Apart from the difficulty of justification, however, the procedure used leads to modulator curves for the cat's retina which are very similar to those obtained for other retinæ by the direct method.

Certain main trends relating the on-or-off character of an element with its spectral response and other properties had been observed. Thus pure on-elements were strongly predominant in pure rod retinæ, while pure off-elements were common in retinæ having no rods. Taking as standard the spectral sensitivity curve corresponding to light absorption by visual purple, Granit and Tansley (Birmingham) found that off-responses, particularly those from pure off-elements, were in general relatively red-sensitive, but on-responses, if they deviated at all, did so in the direction of blue-sensitivity. From these and similar results Granit was led to group together rods, on-effects and blue-sensitivity on one hand, cones, off-effects, inhibition and red-sensitivity on the other.

In the latest micro-electrode work, Granit and Gernandt (Stockholm) had found that if, instead of illuminating the retina, a polarizing current of about 0·1 mA. was passed through it, on-elements gave an on effect and off-elements an off effect for one

direction of the polarizing current and the reverse effects when the current was reversed. On-off-elements behaved to the polarizing current either like on-elements or like off-elements, depending on the relative strengths of their on- and off-responses to the ordinary light stimulus. The effect of a polarizing current on the spectral sensitivity curve of an element was expressed by taking at each wavelength the *ratio* of the light thresholds with and without polarizing current. The ratio curves so obtained show peaks and depressions at various parts of the spectrum, different for different current directions and for elements of different type. These peaks and depressions are assimilated to the modulator curves obtained by the method of selective adaptation. In Granit's view the polarization method provides the most satisfactory way of determining modulators. The bearing of the polarization results on the question of inhibition in the neural network of the retina was also discussed by Granit.

A paper by Polyak (Chicago) on retinal structure and colour vision was read by Le Gros Clark (Oxford). Le Gros Clark also summarized the evidence for his interesting suggestion that conduction from the central retina is mediated by three-fibre units, the respective fibres terminating in corresponding cell layers of the lateral geniculate body, and that this triplicity is closely related to the trichromatic basis of colour vision. One supporting observation was obtained from a war-time experiment in which monkeys kept in red light for some weeks showed, in two out of three animals, a degeneration of the cell layers associated by other evidence with the 'blue' mechanism. Oddly enough, this presumed atrophy by disuse affected mainly the layer of 'blue' cells receiving crossed fibres. Two of the main points made by Polyak were that in the extrafoveal retina the ganglion cells are generally connected through bipolars to both rod and cone end-organs, and that in the central fovea the end-organs are structurally indistinguishable, although connected in different ways through bipolars to the ganglion cells.

The latter conclusion cuts across the hypothesis recently developed by Willmer (Cambridge), according to which the end-organs of the central fovea are of two kinds, cones and non-adapting or day rods. Willmer suggested that the staining reactions used by Polyak to identify rods might pick out only those which have the capacity of accumulating visual purple in the dark and might fail for day-rods. Willmer, after summarizing the phylogenetic argument for his hypothesis, presented some new sensory measurements on the luminosity curves of colour-blinds obtained with small test fields in the central fovea. Under these conditions, normal trichromats behave like dichromats (tritanopic), while dichromats are reduced to monochromats. The differences in the luminosity curves of various colour-defectives were correlated by Willmer with the several possible end-organ-ganglion cell systems consistent with his hypothesis. Also the actual shapes of the curves were related to the absorption curves of rhodopsin and iodopsin.

In the discussion, this last step was strongly criticized for the same kind of reason as already noted in connexion with Granit's derivation of modulator curves by selective adaptation. In fact, one main impression from the Conference was that workers on vision have been prone to take differences of experimental curves or to apply other mathematical manipulations to their data without a proper discussion of the kind of summation, inhibition or other process which is automatically assumed to occur in the organism whenever particular mathematical methods are applied.

Wald (Harvard) reviewed the considerable knowledge we now have of the rhodopsin–retinene$_1$–vitamin A_1, and the porphyropsin–retinene$_2$–vitamin A_2 photochemical systems of the retina. Morton (Liverpool), who has recently obtained retinene$_1$ in the crystalline state, explained briefly his reasons for attributing to retinene$_2$ a structure differing from retinene$_1$ by one additional conjugated double bond in the ring. The extraction by Bliss (Boston, U.S.A.) of a substance termed cephalopsin, a kind of non-bleaching visual purple, from the eye of the squid raised interesting possibilities. No substantial advance in the difficult problem of extracting from the retina photosensitive substances which might be assigned to cones or to hypothetical end-organs possessing spectral sensitivities of modulator type was reported. Wald showed how measurements of the absolute light threshold in the visible and ultra-violet for parafoveal rod vision and foveal and parafoveal cone vision on normal and aphakic eyes led to determinations of the absorption curves of the macular pigment and of the eye lens. The results were in satisfactory agreement with his direct measurements on preparations from human eyes. The macular pigment could be identified as a xanthophyll, probably ordinary lutein.

Turning to purely sensory studies of colour vision, MacAdam (Rochester, U.S.A.) explained how by the use of Landolt test objects (*a*) of usual type, (*b*) with the broken circle of one colour and the background of different colour but equal brightness, he had succeeded in comparing the visual acuities attributable respectively to pure brightness and pure colour contrast. Taking as standard the relative importance of colour and brightness contrast in determining the observed discrimination in a 2° colorimeter field, colour contrast was found to be much less effective in the acuity observations, which depend on discrimination in small areas. At the other extreme of large non-contiguous areas, colour contrast was much more effective than brightness contrast. As fixation was not controlled in the acuity measurements, the results were not directly comparable with those of Willmer and Wright (London) showing tritanopic colour defect in the central fovea, and, in fact, the loss of colour discrimination was not of this specific type.

Wright considered the recent work on colour matching and discrimination in small fields in his talk on the present status of the trichromatic theory. His general conclusion was that the theory in some form is necessary to explain some of the known facts and, at the same time, it is not inconsistent with much of the remaining data. According to Stiles (Teddington) the observed foveal thresholds of a coloured light patch superimposed on an adapting field of, in general, a different colour are consistent with a classical trichromatic theory and lead to fundamental response curves of König type. But from the threshold recovery curves obtained after extinguishing the adapting field, it appears that the 'blue' mechanism has very different dynamics from the 'green' and 'red' mechanisms, a result already indicated by Wright's studies of colour adaptation by the binocular matching method. The difficulty of reconciling three fundamental response curves which are widely separated in the spectrum (for example, curves of

König type) with the apparent saturations of different spectral colours was enunciated by Hecht (New York), who also raised the problem of the sensations experienced by subjects with one normal and one colour-defective eye.

In the discussion two issues were separated: (*a*) differences in the number of just perceptible colour steps between white and the various spectrum colours; (*b*) the relation between the descriptions of colour sensations given by normals and various types of colour-defectives. Wright argued that attempts to explain (*a*) on the basis of the trichromatic theory, while not without some success, were too mechanistic. On (*b*), it was suggested that the colour names applied by colour-defectives are determined during the development of the individual so as to give, under the conditions of everyday life, the greatest measure of agreement with the names used by colour normals; or, in the case of a single defective eye, maximum agreement between the names which would be applied when the two eyes were used in turn.

Judd (Washington, U.S.A.) found the explanation of the colour sensations experienced by colour-blinds the principal stumbling-block to the interpretation of dichromatic vision on the trichromatic theory. He summarized several alternative views according to which a different form of explanation of colour vision is required for the various stages (photosensitive, substance, receptor, optic nerve, cortex) of the visual process.

By measuring the foveal threshold sensitivity through the spectrum, Hecht had deduced that the effective luminosity of an equi-energy spectrum would be, for the protanope, about one half and, for the deuteranope, about three fifths that of the normal. On the assumption that luminosity is the dominant factor in determining differences of visual acuity between normals and colour-defectives, he tested and confirmed this result by acuity measurements on subjects of the three types. de Vries determined the modification in brightness match between green and red stimuli when the matching field was covered by a veiling brightness of red or blue light. The modified matches agreed with those obtained in the absence of the veiling brightness by protanopes and deuteranopes respectively. This result and that of Hecht appear to support the simple theory of dichromatism as the loss of a receptor system.

Pitt (Harrow) developed the interesting suggestion that for protanomalous trichromats only the 'red' fundamental response curve is aberrant, this curve being related to the corresponding normal curve by some modification of form, progressive with increasing anomaly, and perhaps resembling the change of the absorption curve for a layer of increasing thickness. Schouten (Eindhoven) put forward related ideas for both deuteranomalous and protanomalous cases. Hecht questioned the usual interpretation of anomaloscope studies of large groups as showing a continuous transition between the normal and the anomalous. By taking account of the whole range of uncertainty in each subject's setting of the anomaloscope, he concluded that the groups are clearly separable without overlap. Farnsworth (New London, U.S.A.) showed a pseudo-isochromatic chart, which he had designed and made up from Munsell colour patterns, for the detection of tritanomalous subjects, a type which is likely to have escaped earlier tests of colour defect. The genetics of colour vision were not discussed in any detail, but Kalmus (London) made a plea for the study of the colour vision of heterozygous females.

Of the several points raised by Hartridge (London) in developing a polychromatic theory of vision, his use of the negative values in sets of fundamental response curves like those of Wright as an argument for additional receptor mechanisms was not generally acceptable. On the other hand, Dimmick (New London, U.S.A.) and Schouten were sympathetic to certain aspects of the theory, which they consider are in better accord than the usual trichromatic presentation with the psychological analysis of sensation.

Measurements, by a new method, of the chromatic aberration of the eye, which is of particular importance in the recent studies of colour in small fields, were presented by Ivanoff (Paris). His results agreed satisfactorily with other new measurements by American workers. Hecht, Shaer, and Pirenne's notion of quantum fluctuations in the stimulus as the main factor in determining the intrinsic indefiniteness of absolute threshold values was discussed by Van der Velden (Utrecht) and Bouman (Utrecht). By extending the theory to take account of variations of threshold with the area and exposure-time of the test stimulus, they conclude that the absorption of two quanta is sufficient to initiate a response. Hecht reported new work on the effects on the threshold of the size and shape of the test stimulus. He found that the dominant factor is the length of the boundary edge rather than the area.

It was a great pleasure to all present to have the Conference opened by the veteran of the subject, Sir John Parsons.

W. S. Stiles

OBITUARIES

Dr. Ellsworth Huntington

Dr. Ellsworth Huntington, who died recently at the age of seventy-one, was well known for his views on the dominant effect of climate on human affairs. As a student of geography under Prof. W. M. Davis, he spent the years from 1900 to 1906 in the exploration of Asia Minor and Central Asia, his first paper being an account of the Upper Euphrates published in 1902. In Central Asia he was struck by the evidence that large populations formerly inhabited regions now arid and deserted, and from these and other historical studies, including the changes of level of the Caspian Sea, he developed the theory that during the past few thousand years there have been great oscillations of climate. These researches were published in "The Pulse of Asia" in 1907 and aroused much controversy among geographers. In the following years he extended his studies of climatic change to Palestine and North America, and he was one of the pioneers in the measurement of tree-rings as climatic indicators. These researches led him to the view that the ideal climate for human vigour is one of moderate but rapidly fluctuating temperatures, which is best developed in the storm-belts of temperate latitudes; and in "Civilization and Climate" (1915) he compared estimates of the level of existing civilizations in different countries, obtained in various ways, with their level of climatic energy, finding remarkably close agreement. In the same book he extended his studies of the effect of climatic changes on the history of ancient civilizations, including a new version of the decline and fall of the Roman Empire.