The papers summarized in this report have been selected to convey as general an impression as possible of the lines of advance at present active in the study of visual processes. In two of the topics covered many of the papers were discussed in the sessions associated with Sections 1 and 9 of this Volume.

In the investigation of visual processes in man, the earliest experiments involved the presentation of a luminous pattern to the subject and the study of his response. Since the experimenter is another man, there are no fundamental difficulties of communication and very many varieties of experiments can be carried out with great facility. Much has been learnt by such methods and much remains to be learnt; they are in all cases the touchstone or validity of results obtained by other methods. This basic psychophysical method is exemplified by the papers of Walraven (Photochemical and nervous adaptation effects in human colour vision), Kanavetz (Influence of the level of illumination on the action of the optic and motor analysers) and Gunter, Blakeslee and Feigenson (Colour vision in primates).

Walraven describes investigations of colour appearance and spectral sensitivity of the human eye at very high levels of illumination and finds varieties of adaptation, characterized as photochemical on the one hand and nervous on the other, which support both the Young–Helmholtz and the Hering concepts. Explanation of the course of recovery from high levels of adaptation requires that information on chromaticness and on luminance must be transmitted separately from retina to brain.

Kanavetz presents a study of the effect of illumination level and pattern (e.g. glare sources) on the performance by humans of two tasks simultaneously, one being visual, the other mechanical. In most studies of this type so far made, the interest is in the increased sensitivity of the visual task to level of illumination due to the simultaneous performance of the mechanical task. Kanavetz finds and investigates
the effect of level of illumination on the mechanical task. He surmises that there is a direct effect of light on the central nervous system, though it is hard to imagine any effect except indirectly via the visual pathway.

Günther, Blakeslee and Feigenson go beyond the field of comparatively easy inter-human communication and develop methods suited to experiments with near-human subjects, namely primates of the genus *cebus*. The lack of full speech communication and the fact that the subject is passive, with no mental participation in the aim of the experiment, introduces difficulties which some workers regard as insuperable. It is fortunate, however, that this council of despair is by no means universally shared. The present authors have designed their experiments with great care to overcome the difficulty of exploring an unknown type of colour vision entirely on the basis of behaviour (procuring food by one action selected from three possible actions). A wide range of Munsell chips were used to provide coloured and neutral stimuli in such a way that no assumptions had to be made on the basis of human colour vision, for example of the particular grey which matched the given colour in luminance. As the authors point out, these surface-colour stimuli may be criticized on the basis of reduced specificity compared with the spectral stimuli used by earlier workers, but they regard the defect as being overcome by the procedures used. It must be borne in mind, however, that as the chips were not individually measured by spectrophotometry over the u.v., visible and infra-red regions, there is a remote possibility of the animals responding to radiation outside the human visible spectrum. Results indicated that most of the monkeys were colour deficients, not colour blind, as judged by human standards. They varied as follows: one near dichromatic, one protanomalous and four deuteranomalous, but these classifications cannot yet be assumed to correspond accurately with those of human colour vision.

A paper by Milne and Milne (Stabilization of the visual field) introduces the first stage of departure from purely behavioural and response studies; behaviour is observed, but as movement of body parts, not as a psychological response. The authors present a very complete survey of eye movements in relation to body posture in all animals in which such movements are found (vertebrates, cephalopod molluscs, brachyuran and macruran decapods, stomatopods). The survey is completed by their own observations on the genera *Caiman*, *Constrictor*, *Hemidactylus*, *Bufo*, *Rana*, *Pseudotriton*, *Necturus*,
Carcharius, Sepioteuthis, Ocypode, Podophthalmus, Homarus and Gonodactylus. In all cases, the primary purpose of cyclorotation of the eye would seem to be stabilization of the visual image. By analogy with human experience, it may be supposed that this gives the greatest ease of recognition of pattern in the external field. This may well be of greater importance the more instinctive the grade of behaviour, but there are plenty of animals with highly instinctive behaviour which do not show stabilization of the visual field.

The papers in the next group relate to various aspects of visual pigments: Ripps and Weale (Partial bleaching of pigments in the normal human fovea), Bridges (Distribution and relationships of vitamin A2-based pigments in fishes), Beatty (Metamorphosis of the visual system in Pacific salmon), Cope (Decay of photogenerated eye melanin free radicals described by the Elovich equation, as derived from a theory of activated electron transport across a liquid–solid interface) and Curtis, Pitt and Howell (Formation of an artificial photolabile pigment from opsin and 4-ketoretinaldehyde). The first hint of the presence of photosensitive pigments in the eyes of animals came in 1851 (Müller) and was followed in due course by actual extractions of visual purple from human eyes. Of recent years, elaborations and refinements have proliferated in all directions, well represented in the papers just listed.

Ripps and Weale contribute a study of visual pigments in situ in the human fovea by the technique of direct retinal reflectometry first used qualitatively by Aebielsdorf in 1897 and finally developed with considerable quantitative precision by Rushton and by Weale independently in the years 1953–4. These in situ studies are still difficult and it remains necessary to deduce the properties of the retinal pigments by differential and selective bleaching. The present paper examines the relation between the measured quantities, differential densities and the topography of pigment distribution in the retinal elements. Certain theoretical predictions can be made which are accurate within experimental error for the chlorolabe curves, but show marked discrepancies for the erythrolabe curves, although experimental reasons are advanced to explain the latter. A critical comparison is also made with the results of Marks and of Brown and Wald on excised retinas. Here, again, discrepancies are found which are traced to experimental uncertainties in the use of excised retinas.

In the early years, investigations of visual pigments extracted from
retinae and investigated *in vitro* were confined to 'visual purple', an omnibus and imprecise term which could include any visual pigment. From the early 1930's onwards there has been a parabolic explosion of investigations of visual pigments by extraction methods. One aspect of this domain of visual research has been the extensive cataloguing of pigments from both vertebrates and invertebrates, most of the detailed work so far being from the first phylum. Fishes have been very popular in providing the raw material and our two papers by Bridges and by Beatty draw on this.

Bridges, on the basis of results from thirty-three species of fish belonging to fifteen families, finds that there is a marked clustering of pigments at two wavelength maxima (534 and 523-5 nm) with few exceptions. Whether this is due to functional selection from a close series of possible maxima, or to the existence of only a limited number of more widely spaced maxima, is uncertain as yet. There is slight, but inconclusive, evidence in favour of the first alternative. Whatever may be the truth, however, in regard to availability of pigments, there is strong correlation between habitat and pigment pattern: freshwater, wavelength maxima at 543, 534 or 523 nm; marine, or marine *cum* freshwater, maxima at 523 or 511 nm. Of still greater interest is the existence of species with pairs of pigments. This strongly implies some form of colour vision, in the sense of potential colour discrimination, and has the further interesting feature of variation correlated with season and environment.

Beatty presents results on variation of 'colour' sense in fishes correlated with stages of the life cycle. Five species are described. In all cases the rhodopsin/porphyrropsin ratio varies through life, but in different ways according to species.

Cope deals with a substance not hitherto considered as having any visual function, namely, the melanin granules in which the retinal receptors are more or less embedded. Quoting, 'The electron spin resonance spectra which we occasionally observed in our rod and cone preparations turned out to be derived from a contamination with melanin.' The precise visual function of the melanin granules has not yet been ascertained, although it is surmised that it is metabolic, perhaps a factor in the formation and supply of the visual pigments of the rods and cones. Apart from this question, the kinetics of decay of light-generated melanin radicles led the author to apply the principles of solid state physics to the quantitative prediction of the decay curves. The result was successful and introduces a new concept of the kinetics
of biological processes in terms of electron transport in particulate systems.

Curtis, Pitt and Howell report an experiment in which something very similar to a natural visual pigment was produced in vitro by partial synthesis. 4-Oxo-retinaldehyde was synthesized, isomerized and added to cattle opsin with formation of a pigment similar in a general way to the natural visual pigments. When appropriate feeding experiments were performed with rats, however, by substituting retinoic acid or 4-oxo-retinaldehyde for vitamin A, no visual pigment was formed and the animals became blind with typically degenerate retinae. The authors discuss this negative result, but without making any definite progress in elucidation. Successful experiments of this sort would be expected to add considerably to our knowledge of the basic photochemistry of vision.

We now come to papers in which results of electrical response measurements are reported: Samsonova (Repercussions of the Purkinje effect on the electrical activity of the human brain) and Scholes (Discrete sub-threshold potentials from insect photoreceptors).

Samsonova's work is in the direction of linking visual response with recorded electrical activity presumed to come from the brain, following the school of thought, at present popular in Russia, that visual performance could eventually be expressed entirely in terms of electrical activity of the brain. The particular aspect investigated by Samsonova is the correlation of the Purkinje effect with recorded electrical activity. Earlier workers have demonstrated response correlation in the electroencephalogram (EEG) with frequency, intensity and duration of a rhythmically interrupted light stimulus and with the intensity of a steady background. Samsonova extends the correlation to the effect of colour, still using an interrupted stimulus of nearly square-wave form. For a chosen frequency of stimulation (40 c/s), the increase in EEG amplitude due to the light stimulus is greater for blue (440 nm) than for red (660 nm) at low intensities (0.4 to 3 lux), but greater for red than for blue at high intensities (greater than 4 lux). In other words, there is a direct correlation with the Purkinje effect, although only demonstrable for intermittent stimulation. The EEG also showed that different frequencies, simultaneously applied, are separately present in the electrical activity of the brain, though not apparent in sensation. It should also be noted that fusion of electrical response occurs at about 160 c/s, much higher than the frequency of
fusion of visual sensation. The general conclusion is that there is a significant correlation between the visual sensations of the Purkinje effect and the electrical responses of the brain, but there are also significant discrepancies, as yet unexplained.

Scholes takes us again to a non-human eye, the compound eye of a locust, and to the study of single-receptor response which modern technique has made possible. Single receptor cells (retinulae) were penetrated by micro-pipette electrodes and the electrical potential outputs were recorded in relation to the incident illumination on a time scale. A pulsed or 'noise' output was obtained, the discrete miniature potential waves, and carefully analysed by several statistical methods. By the first method the waves were treated as elementary Poisson events. Sigmoid response curves were obtained which could be compared with the theoretical curves for various values of $m$-fold coincidences of assumed primary quantum absorptions. The best fit was for $m = 1$, or nearer $m = 1$ than $m = 2$, indicating a single quantum absorption corresponding to a single potential wave. By the second method, the observed frequency distributions of potential waves (per 3-sec interval) can be compared with the predicted distributions for $m = 1$ and $m = 2$. Again, the agreement was best for $m = 1$. Tests of reciprocity of time and intensity of the stimulus flash of light were also made and further confirmed the one-quantum hypothesis. Scholes is careful to point out that his treatment implies that a quantum absorption produces a potential wave, but that it is not a direct demonstration.

Papers by Rosenberg, Aziz and Heck (Photoconduction in $\beta$-carotene—a model for the generation of chromatic 'S' potentials) and by Gutierrez-Costa (A hypothetical-deductive approach to colour perception) may be taken as rounding off this survey by their synthetic approach to the problem of explaining the phenomena of vision.

Rosenberg and his collaborators have investigated the photovoltaic and photoconductive effects for carotenoid pigments in vitro and found them similar to graded receptor potentials in electroretinograms. Chromatic differentiation of response is found to agree closely with the chromatic potentials found in Svaetichin's work in vivo on excised fish retinae; blue light is strongly absorbed and generates only negative potentials (P III), while red light is weakly absorbed and generates only positive potentials (P II). It is further demonstrated that the $\beta$-carotene cell produces a characteristic response to colour rather than wavelength, for example the response to a mixture of long and short wavelengths mimics that to a single intermediate wavelength.
This is the first instance of a photocell which gives a true colour response.

The paper of Gutierrez-Costa is purely theoretical. Assuming three types of receptor unit, each with its characteristic spectral sensitivity function, a formal model of the chromaticity diagram is deduced on the basis of the response ratios from pairs of receptor types. From study of dichromatism and complementarity, a quantitative correspondence with the CIE Chromaticity Diagram is established from which quantitative visual sensitivity functions may be deduced. These turn out to be two simply-shaped curves with maxima at 590 nm and at 540 nm respectively together with a third, more complex, curve with a main maximum at 540 nm and indications of a subsidiary maximum at 500 nm. The deduced mechanism thus contains three types of spectral sensitivity, but these are associated in an unexpected way in three types of receptor.