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A STUDY OF THE VISUAL SYSTEM BY THE CORRELATION OF LIGHT STIMULI AND EVOKED ELECTRICAL RESPONSES

A thesis presented for the Ph.D. degree of the University of London by David Regan

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A B S T R A C T

A new method of investigating vision is described in which the potential difference (p.d.) evoked by a sinusoidally modulated light stimulus is correlated with the stimulus. An analogue computing system has been developed which will detect and measure the phase-locked p.d. evoked at stimulus frequency (synchronous response) in the presence of noise and non-synchronous response of up to 30 times signal amplitude.

The stimulation system enables the stimulus frequency, peak retinal illumination and stimulated retinal area to be held constant. It is found that under these stimulus conditions the visual system attains a steady-state mode of response between about 16 and 80 seconds from onset of stimulation.

In this steady state, the phase lag of the synchronous response in the electroencephalogram (E.E.G.) is proportional to stimulus frequency. This is interpreted as indicating an apparent time latency of synchronous response which is independent of stimulus frequency. The apparent latency for equal brightness stimuli is different for different colours. The blue-green latency is longer than the red latency. The minimum latency is in the yellow. The apparent latency is also a function of stimulus intensity. It is proportional to the logarithm of retinal illumination for high stimulus intensities in the blue and green. For yellow there is little variation with intensity. The apparent latency versus wavelength graph is therefore similar to the saturation versus wavelength graph and the changes with intensity are similar. If apparent latency correlates with saturation, the

latency for a white stimulus should be less than that of a yellow stimulus of equal brightness. It was found that the white latency lay between the yellow and blue-green values.

During the initial 16-20 seconds of stimulation, a response is obtained which is larger than the final steady-state response. The amplitude rises linearly and the fall is sudden. It is proposed that the effect is little dependent on rod activity, and a central neural mechanism is postulated.

Beating observed in the records is attributed to intrinsic α activity. It is argued that the observed steady-state synchronous response is a true evoked response which is independent of α activity, and that the freqneucy of the α activity is independent of the light stimulus, and of the synchronous response.

Measurements of the electroretinogram (E.R.G.) reveal a synchronous evoked response. It is shown to be unlikely that the E.E.G. response is a spread of the E.R.G., and unlikely that the E.R.G. response plays a part in the transmission of colour information to cortex.

The advantages and disadvantages of the apparatus relative to summation devices is discussed. It is suggested that the steady-stat response of the visual system, which is attained by using the stimulation technique described here, is a novel and simple mode of functioning which might reveal basic mechanisms not evident when other stimulus conditions are employed.

I N T R O D U C T I O N

Colour mixture data and the trichromatic theory of vision.

Colour vision has been investigated by colour matching. In this technique no attempt is made to describe or measure sensations such as hue or subjective brightness. Instead data is obtained in terms of the physical stimuli used, and expressed in either power units or photometric units. In many types of experiment the observer adjusts two stimuli until the sensations they produce are indistinguishable. Physical measurements of the stimuli then enable deductions to be made concerning the physiological processes produced by the stimuli.

Colour matching measurements were carried out separately by W.D.Wright (refs.1,2) and J.Guild (ref.3), using instruments which in accuracy precision and freedom from stray light were considerably in advance of previous designs. The stimulus was chosen to be bipartite 2^{o} foveally viewed field. A test stimulus in one half of the field was matched in colour and brightness by a mixture of three stimuli in the other half. It was found possible to use either three pure spectral matching stimuli or three impure filtered stimuli, providing that the energy distribution of the impure stimuli were known and that no one stimulus could be matched by a mixture of the other two. Fields larger than about 3^{o} often have a non uniform appearance. This is due to macular pigmentation, and to desaturation caused by rod vision. A 2^{o} stimulus field was chosen in order to avoid such effects. In W,D.Wright's colorimeter the stimuli were obtained by forming a spectrum by means of a prism, and positioning roof prism reflectors at the required wavelengths in the spectrum. The bandwidths used were between 2 mμ in the blue and 6 m μ in the

red.

The units of red, green and blue stimulation can be obtained by matching an internationally agreed white, and defining the colorimetric amounts of the three stimuli to be equal. An alternative system, introduced by W.D.Wright, is to match the three stimuli against a spectral 5825 $\mathring{A}$ and a spectral 4940 $\mathring{A}$. This system has the advantage of clearly separating the effects of macular pigmentation, and variations of receptor properties. By performing matches through what was effectively an equal energy spectrum, the amounts of the three matching stimuli through the spectrum were obtained. When plotted against the wavelength of the test stimulus, these data constituted the spectral mixture curves for the three particular matching stimuli used.

It was found that colour matches made by a group of observers, whose colour vision was not defective, did not show differences much greater than could be attributed to variations in lens or macular pigmentation though small receptor variations were found. For a 2^{o} foveal stimulus it was never necessary to employ more than three matching stimuli, whose choice was arbitrary, so long as no one of the stimuli could be matched by the other two. Matches did not break down over a wide range of retinal illuminations, were accurately repeatable from day to day, and were little affected by the state of retinal adaptation. It was found that colour matching date in terms of one set of three matching stimuli could be expressed in terms of another set, by the use of definite algebraic transformations. In addition, if a stimulus C_1 were matched by a mixture M_1, and C_2 by M_2 then it was found that the matches were additive, i.e. $(C_1 + C_2)$ would be matched by $(M_1 + M_2)$.

This date applied to the specific experimental conditions viz. a 2^{o} centrally viewed stimulus field. Other field sizes or

locations may exhibit different characteristics. For example a small (20') foveal stimulus exhibits tritanopic-like defects of colour vision.

Stiles developed a colorimeter which employed spectral stimuli (ref. 4). Between 4900 Å and 6500 Å the retinal illumination was about 500 trolands. Colour matching data were obtained for 2° and 10° fields. A non-uniform appearance of the field was observed for the 10° field, attributable to macular pigmentation. When the gaze was fixed on the centre of the field, however, little difficulty was experienced in making colour matches.

Only minor differences were found between colour matching data for the 2° and 10° stimulus fields.

Some rod participation was evident for the 10° stimulus in the extreme red at the lower illuminations (100 trolands). Apart from differences between the 2° and 10° data which could be attributed to macular pigmentation, there were differences which appeared to be due to differences between foveal and parafoveal colour mechanisms. Stiles suggested that on going from 5700 Å to 6250 Å, the "blue" parafoveal mechanism becomes relatively more sensitive than the foveal "blue" mechanism, while for the "green" and "red" mechanism the reverse effect occurs.

The facts set out above indicate that for a 2° foveal stimulus, colour information is restricted to three channels at some level which is probably peripheral. This gives support to the Young - Helmholtz theory of colour vision which states that there are three types of foveal cone, one having its maximum sensitivity in the red,

one in the green and one in the blue.

Dominators and modulators.

By "retinal element" is meant the single fibre or ganglion cell from which a microelectrode recording is made.

For individual retinal elements in the retinae of cats, frogs and other animals, Granit and Donner measured the threshold sensitivity in the dark adapted state for different wavelengths throughout the spectrum (ref.5). Often broad band curves were obtained which were described as "dominators". Granit considered these curves to relate to photopic and scotopic brightness sensitivities. They exhibited the Parkinje shift, indicating that visual pigments in addition to visual purple were involved. Selective adaptation to coloured lights revealed narrow band sensitivity curves, described as "modulators". These were suggested to underly wavelength discrimination. The wavelength of the peak sensitivity of a modulator varied, but in general fell into one of three distinct spectral regions. Granit regarded this as support for the Young-Helmholtz theory of vision, suggesting that statistical averages of modulator responses would result in trichromatic vision.

Retinal Densitometry.

Direct evidence for the existence of cone pigments in man has been obtained by Rushton (refs.6a,6b,6c,7). He passed a monochromatic test light into the eye via the nasal half of the pupil. After passing twice through the retina, some twenty-thousandth part of the light returned through the other half of the pupil. Rushton measured the reflectivity of the dark adapted fovea at several

wavelengths for a normal observer. He then repeated the experiment after bleaching the retina with red light. The change in reflectivity at each wavelength was plotted against the wavelength. On the assumption that the red-absorbing visual pigment was predominantly affected by the red bleaching light, the graph was interpreted as indicating the difference in absorbtion between the red pigment and any coloured products of bleaching (difference spectrum). The reflectivity measurements were repeated after a bleaching with blue-green light. The additional changes in reflectivity observed were attributed to the bleaching of an additional green-absorbing pigment. It was not found possible to detect a blue-absorbing pigment, but a sufficient explanation would be its very low concentration.

Only a single pigment was found in the fovea of a subject suffering from protanopia. In this defect of colour vision a loss of red-green discrimination is accompanied by a reduced sensitivity to red. The difference spectrum of the pigment detected was similar to the visual sensitivity curve measured psychophysically in the protanope, and the regeneration of pigment after bleaching followed a similar course to the recovery of visual sensitivity. This strongly suggested that the pigment detected was the pigment responsible for vision in the protanope. The green-absorbing pigment in the normal had a similar difference spectrum. Only one pigment (green-absorbing) was found in the deuteranopic subject. In this defect of colour vision red-green discrimination is lost, but red sensitivity does not appear to be affected. As with the protanope, the pigment detected appeared to be the pigment involved in deuteranopic vision.

Rushton's reflectivity measurements therefore provide support for the Young-Helmholtz theory of colour vision in so far as he has measured the difference spectra of two foveal pigments simultaneously present in the normal eye, and associated them with similar difference spectra of the single pigments of dichromatic observers. These dichromat pigments he showed had difference spectra which paralleled psychophysically measured visual sensitivities of the subjects.

Processing of the information available at the photoreceptors.

The restriction of colour channels to three at the level of the photoreceptors does not preclude the processing of information at higher levels, as proposed in various zone theories of colour vision. A zone theory might postulate for example that colour information is restricted to three channels at the level of the photoreceptors, but that at a higher level (zone) the information is rearranged into four channels. No additional information can result from the processing of information available at photoreceptor level, but such a theory would account for the uniqueness of yellow sensation, and for the subjective red-green and yellow-blue opponent colourappearances.

Electrophysiological evidence that processing of information takes place progressively at higher levels in the cat is described by Wiesel and Hubel (refs.8,9). The simple retinal "on" or "off" responses to a light stimulus (ref.10) are processed, until at the cortical level an individual cell responds for example to only a light

strip in a unique position and at a unique angle, or to only a moving light strip located anywhere in a limited retinal area.

Micropipettes were employed as electrodes by Svaetichin and MacNichols to measure responses to light in the retinae of teleost fishes (ref.11). The trains of impulses which are observed as a result of light stimuli when the electrode tip is located in the layer of ganglion cell bodies or axons were not obtained when the electrode penetrated more deeply into the retina. Instead there was a much slower electrical response which was given the name "Spotential". Svaetichin and MacNichols considered that this arose in the bipolar cell region. In some records the polarity of the response reversed midway through the spectrum, exhibiting a maximum of one polarity in the yellow, and a maximum of the other polarity in the blue. Other records from the same retina showed a reversal at a different point in the spectrum, with opposite maxima in the red and green. Another type of recording showed no reversal, and a sensitivity maximum in the 500 - 600 mμ region. Svaetichin and MacNichols interpreted their results as showing opponent colour red-green and yellow-blue responses suggestive of the Hering opponent colour theory of colour vision (ref.12), and a luminosity mechanism separate from the colour discriminating mechanism. The interpretation is put forward that these responses are elaborations of the simpler photo-receptor responses.

Later work suggested that the S potential might arise not in the nerve cells, but as a consequence of some metabolic interaction between glia cells and nerve cells (ref.13).

A possible anatomical basis for the colour channels was described by Polyak who observed three types of neural connections to cones. He considered that these may play a part in trichromatic vision (ref.14)

The variation of perceptual latency with wavelength.

Kleitman and Pieron investigated the build up of apparent brightness by determining the flash duration necessary in order that the level of a relatively stable sensation produced by a 1 second stimulus be passed. (ref.15) Using filtered coloured stimuli they found the rate of rise of sensation to be in the order red, green, blue andwhite for the fovea. However their interpretation has been questioned, and the suggestion made that the measurements are merely of the relative effectiveness of flashes of different durations.

The spike frequencies of retinal elements in the cat produced by light stimuli of different wavelengths.

Donner investigated whether the presence of receptors in the cat's retina other than those charged with visual purple could be signalled by a frequency code of a single retinal element (ref.5). If this were not so, the spike frequency versus time graphs for all retinal elements could be made identical by adjusting the intensities of the variously coloured stimuli so that the visual purple would absorb equal amounts of energy for all stimuli. This was found to be impossible for many elements, which exhibited a rate of rise of spike frequency for the off-effect dependent on the wavelength of the light stimulus. For 6000 $\mathring{A}$ the maximum spike frequency occurred 0.03 seconds after the light was cut off, for 5200 $\mathring{A}$ after 0.17 seconds

and for 4600 Å after 0.24 seconds. Spike frequencies at these moments were measured for stimuli throughout the spectrum, and graphs resulted which were similar in appearance to the spectral mixture curves measured psychophysically in man.

On the other hand it may be that single fibre records do not include the full range of information on which colour perceptions are based. Measurements on the transmission of energy through retinal receptors reveal that the receptors possess waveguide properties. Enoch illuminated human receptors with white light and found coloured distributions of light within individual receptors, which altered with the angle of incidence and varied from receptor to receptor. (ref.16). In order that the performance of the visual pigments may be separated from the variation from receptor to receptor it seems likely that an averaging process is performed over a large number of receptors.

The stabilised retinal image.

Methods have been developed whereby an image can be made to remain stationary on the retina. The subjective effects resulting from this stabilisation suggest locations for the mechanisms underlying colour discrimination, and form additional experimental data which must be satisfied by any theory of vision.

Ditchburn described a technique of compensating eye movements with an optical system in which the image is reflected by a small mirror on a contact lens. (refs. 17,18). In a method due to Riggs, the target is carried on the contact lens. (ref.19).

It appears that the motion of the image across the retina is

essential for the sensory function of the eye. When the image is stabilised, it soon fades to leave a featureless field. After a time the image regenerates and is visible to the observer, in whole or in part, for a fraction of the time of observation. This fraction depends on the content and character of the image. The effect of stabilisation on colour perception was described as a rapid desaturation.

Using a 1^{o} circular bipartite stimulus field of constant luminance (1 ft. lambert)Clowes investigated the effect of stabilisation on colour differences between the two halves of the field. (ref.20). He reported a fusion of colours, leaving a field of uniform luminance. This effect never occurred when stimuli were on opposite sides of 5900 $\mathring{A}$, in accord with the findings of McCree (see below). Desaturation was marked for all colours, and was greatest for green. There was a partial or total fade out of all colours, the greatest effect being for green.

Similar effects can be produced by intense voluntary fixation even in the fovea. (refs. 21,22,23). McCree found that, for voluntary fixation of a square bipartite 80' foveal field, the colour in the two halves fused after about 0.4 seconds, providing that there was an exact brightness match. For a weak stimulus of less than 60 trolands retinal illumination, any two spectral colours could be fused. For a higher retinal illumination of 830 trolands, two colours could be fused providing they were on the same side of 5900 $\mathring{A}$. A rapid desaturation of all colours was measured, and found to be insufficient to account for the colour confusion. McCree considered that the necessity for an exact brightness match when producing colour fusion

indicated a linkage somewhere in the visual system between the mechanisms underlying colour fusion and brightness equality. This linkage must be located above retinal level, since dividing the field between the two eyes did not alter the effect.

Chapter 2. THE FREQUENCY CODE

The correlation of brightness sensation and impulse frequency.

The Ferry-Porter law, which states that the flicker fusion frequency is proportional to the log. of retinal illumination holds in man over a wide range of illuminations. By using a microelectrode technique it is possible to measure the flicker fusion frequency for an individual retinal element, as being that frequency at which each flash is no longer followed by a separate outburst of spikes. Eroth found in the cat's retina that the flicker fusion frequency was proportional to the spike frequency just before fusion occurred. (ref.5). This suggested that in man there might be a correlation between impulse frequency and the log. of retinal illumination, thus forming a physiological basis for Weber's law.

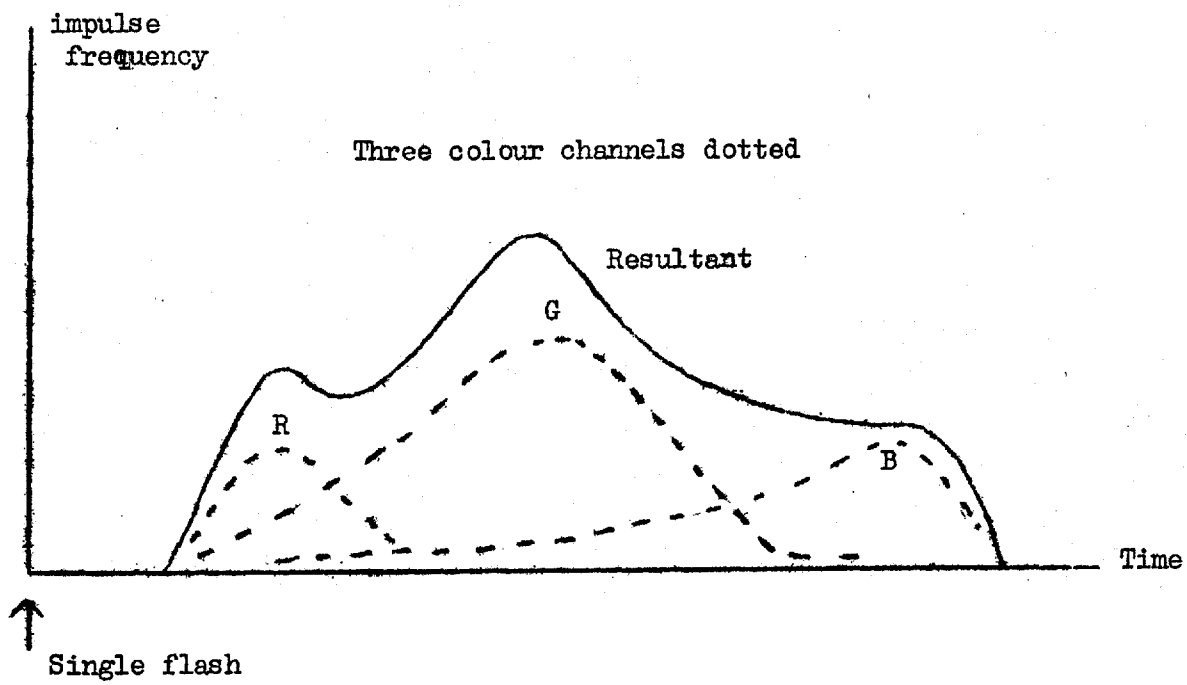
The suggested correlation of colour sensation and the rate of change of impulse frequency.

An account is given below of the hypothesis which led to the design and execution of the experiments which form the basis of this thesis. It can be stated at this point that the results of the experiments were such as to cast doubt on the hypothesis in its original form. As will be seen in Chapter 8, attempts were made to modify the hypothesis on the basis of the new data.

From a consideration of Donner's data for the cat, the hypothesis was evolved that in man colour information might be carried in the form of the rate of change of impulse frequency which results from any change in retinal illumination.

A failure in colour vision would therefore be predicted if the light intensity falling on individual photoreceptors were constant, since most retinal elements respond only to the onset or cessation of stimulation in some part of their receptive field. (ref.10). This is in accord with the experimental results of stabilising the retinal image mechanically or voluntarily which are described in Chapter I.

The hypothetical response to a single flash is indicated in the diagram.



The colour perceived would correlate with the relative heights of the three peaks, and the brightness of the flash would correlate with the average impulse frequency. It would, therefore, be possible for three colour channels and a luminosity channel to be located in a single nerve fibre.

This method of transfer of colour information would probably hold only at retinal level, since at the level of the lateral geniculate body there is some evidence that the three colour channels are anatomically separate. (refs. 24, 25, 26).

CHAPTER 3 THE METHOD OF INVESTIGATION

When electrodes are attached to the scalp in the occipital region, an electrical activity can be recorded (E.E.G.) Rhythmic, wave like potential changes which were called " α rhythms" by Berger are the most prominent feature of brain activity. Since Berger's original work, brain rhythms have been subclassified on the basis of frequency and amplitude, and on functional correlation. Activity in the range 8 - 13 c.p.s is called α rhythm. Theta rhythms are in the range 4-7 c.p.s. and are typically found in the parietal and temporal regions. They are associated with childhood and emotional stress in some adults. Delta rhythms are in the range 1-3.5 c.p.s., and are associated with deep sleep in normal adults, with infancy, and with organic brain disease. Beta rhythms, which have frequencies higher than 14 c.p.s are generally associated with activation and tension. (ref. 27, p.284).

The function of the α rhythm

It has been suggested that the movements of the focus of the α rhythm which are experimentally observed reveal a scanning process. An interaction between the scanning process and the rhythmic volleys of impulses produced by a uniform flickering visual field has been put forward as the cause of the subjective illusions of mottled moving patterns seen under such conditions. Such interactions might also account for the aberrations of colour vision which are indicated by the Ishihara plates when they are viewed by flickering light. (ref.28). There is some evidence that the α rhythm acts as a

gating mechanism for efferent signals. Some workers have concluded that there is a tendency for voluntary movements to be synchronised with the α rhythm. (refs. 29,30,31). In their experiments attempts were made to establish a statistical correlation between the phase of the α cycle and the initiation of voluntary movements. However it is difficult to ensure that the subject has no clue of the α phase. After a statistical analysis of his results Lansing considered the shortest and the longest visuomotor reaction times in some subjects to fall approximately 50 milliseconds apart on opposite phases of the α cycle (ref.32). However this finding did not apply to all subjects investigated and was not always reproducible in any individual subject. The visibility of a line viewed by intermittent illumination was found statistically to point with fair confidence to a heightened acuity when the flicker frequency was the same as the α frequency. (ref. 33).

The effects produced in the E.E.G. by a flashing light.

According to W.G.Walter, on observing a flashing light two separate effects are produced in the E.E.G. (ref.27).

(a) When the flash rate is approximately the same as the α frequency there is a synchronisation of the α rhythm, which becomes locked in phase to the flashes.

(b) A true evoked response is produced. There is often a flash frequency for which the evoked response shows a well defined maximum. This frequency is not necessarily the dominant frequency of the resting α rhythm, but is generally related to one of the α components.

W.G.Walter states that the α rhythm can be identified by its characteristic phase relations. This could be done, for example, by the use of his toposcope. In this apparatus the amplified signal from each electrode pair on the scalp is applied to separate cathode ray tubes. Each tube's time base is a spiral at a repetition frequency which is a sub-multiple of the α frequency. The amplitude of the E.E.G. signal modulates the spot intensity, so that the α activity appears as localised bright regions on the tube faces. The α rhythm characteristics are described as:-

(i) Usually the maximum potential change is earlier in the anterior region than in the occiput.

(ii) Often, for any one region, the α waves for transverse electrodes lead by 90^{o} the α waves for longitudinally placed electrodes

The true evoked potential does not exhibit these characteristics, and has a definite latent period behind the stimulus.

This distinction between α locking and a true evoked response would seem to be indefinite, since the characteristics peculiar to the α rhythm ((i) and (ii) above) are not described as being applicable to all subjects, nor true at all times for any particular subject.

The proposed experimental approach.

The author proposed to use the evoked response to light stimuli in an attempt to measure the hypothetical differences in the rate of change of impulse frequency produced by stimuli of different colours. The further aim was then to measure the characteristics of the observer's colour vision by purely electrophysiological means, without the use of any psychophysical measurements.

It was already established over a rather limited range of frequencies, that if a light flashing at a frequency f is observed, the E.E.G. contains a component at the frequency f. It is proposed to refer to the sinusoidal component in the evoked response which is at the stimulus repetition frequency f as the "synchronous component" of the evoked response, so as to distinguish it from any other harmonics which might be present.

The assumption was made that for a sinusoidally modulated stimulus of constant frequency and constant peak retinal illumination, the synchronous component lags the stimulus by a constant time τ (the latency), even if its amplitude fluctuates, or if the total E.E.G amplitude fluctuates to a large extent.

Some evidence to support this a priori supposition was found in evoked potentials recorded by W.G.Walter et al. (ref.34). Some of the records showed a rather steady amplitude of evoked response at constant flash frequency for short flashes, although many other records exhibited considerable variation. However no real attempt had been made to ensure constancy of flash frequency nor constancy of retinal illumination over a prolonged period.

It was envisaged that if driving of the α rhythm was all that could be recorded, there would be a constant phase relation between the α rhythm and the volleys of impulses arriving at cortex. If this phase relation were independent of frequency over a range of a few c.p.s., variation of frequency would reveal a change in phase relative to stimulus, which could be attributed to the transmission time between photoreceptors and cortex.

The suggested effect of a variation of stimulus frequency.

The phase lag of the synchronous component behind the flashes should be given by:-

$$\phi = k + 360\, f \tau$$

where k° allows for any phase shifts occurring between photoreceptors and electrodes which are not due to the latency τ seconds. If the stimulus frequency f is altered, then there should be a change in the observed phase lag ϕ° where:-

$$\frac{\delta \phi}{360\, \delta f} = \tau$$ providing that k is not a function of f.

By varying f, any ambiguity of a whole number of cycles is removed, and location of the zero of phase is unnecessary.

For a sinusoidal modulation of retinal illumination, the impulse frequency due to each photopigment should vary sinusoidally, with a phase lag characteristic of the particular photopigment. The resulting impulse frequency, being the vector sum of the three contributions should also vary sinusoidally, and have a phase determined by the relative contributions of the three pigments.

The experiment therefore was to carry out measurements of $\frac{\delta \phi}{360\, \delta f}$ for a series of colours of photometrically equal intensities, and also to measure the change of ϕ for each colour with intensity.

Pilot experiment at the Maudsley Hospital using pen recorders.

Short white high intensity flashes illuminating almost the whole of both retinae were employed. E.E.G. signals from scalp

electrodes in the occipital region were amplified and drove recording pens. One recording channel was connected to a photocell in the path of the stimulating flashes so as to provide a record of the stimuli. Direct measurements were made from the records. The distance on the record between the photocell's response to each flash, and the peak of the immediately following E.E.G. wave was measured. The corresponding phase lag was calculated, and assumed to be composed of a constant term, plus a term dependent on the latency of the E.E.G. response. Measurements were made at several flash frequencies in order to isolate the part of the phase lag dependent on latency. At any one flash frequency, variations of phase lag behind individual flashes appeared considerable, but on average an approximately linear phase lag versus frequency graph was plotted, indicating an apparent latency of about 100 milliseconds. Errors were very large, mainly due to much non-synchronous activity.

The main experiment at the Northern Polytechnic.

Attempts were made to design high Q filters in order to separate the synchronous component from the total E.E.G, but no satisfactory compromise could be reached between the high Q required for good selectivity, and the dependence of the phase shift caused by the filter on frequency in the neighbourhood of resonance. Accurate phase measurements on the E.E.G. would have necessitated a degree of stabilisation of stimulus frequency which could not be attained at all easily.

Another approach was to make use of the orthoganality of sinusoids in a well known method of harmonic analysis (ref. 35).

If the p.d. at the electrodes is a repetitive function of time (t), it can be expressed as a series, for example:-

$$\psi(t) = A^{1}\sin\left(\frac{\pi}{2}ft - \phi^{1}\right) + A^{11}\sin\left(\pi ft - \phi^{11}\right) + \text{--} + \boxed{A\sin\left(2\pi ft - \phi\right)}$$

$$+ A_1\sin\left(\frac{5\pi}{2}ft - \phi_1\right) + A_2\sin\left(\frac{6\pi}{2}ft - \phi_2\right) + \text{---}$$

this term is the synchronous component of the evoked p.d.

In the term representing the synchronous component, ϕ is the phase lag and A is its amplitude.

It can be shown that:-

$$\frac{\int \psi(t)\sin(2\pi\ ft)dt}{\int \psi(t)\cos(2\pi\ ft)dt} = \tan\phi$$

where the integration is over the longest period in the expansion.

Also:-

$$A = \sqrt{\left[\int \psi(t)\sin(2\pi ft)dt\right]^{2} + \left[\int \psi(t)\cos(2\pi ft)dt\right]^{2}}$$

CHAPTER 4 APPARATUS

A method was required of performing in analogue form the mathematical operations described above. It was preferable that the apparatus should perform the analysis while the subject was still connected to the recorder, so that the experimenter could recognise and repeat a crucial measurement, or manipulate the experimental variables, perhaps to accentuate some trend which might develop. With the analysis performed during the experiment rather than subsequently, it would be possible to extract much more information before new variables were introduced by the passage of time.
A block diagram of the apparatus can be found at the end of this thesis (diagram 1)

The amplitude of the synchronous evoked E.E.G. response.

The amplitude of the synchronous E.E.G. response was found to be up to 6 microvolts peak-to-peak. Usually it lay between 2 and 4 microvolts peak-to-peak. It was buried in random noise and unwanted signal of 10 to 30 times its amplitude.

Electrodes

In the early stages of the work, electrodes were used consisting of saline-soaked pads tied to silver-silver chloride rods, which were held onto the scalp by means of a rubber net. These electrodes were found liable to movement, so another standard technique using stick-on electrodes was adopted. Stick-on electrodes are silver domes of about 1 cm. diameter, to which flexible leads are connected.

Before every recording session they are cleaned and chlorided in order to form a silver-silver chloride electrode so that polarisation effects are avoided. The dome is then attached to a de-greased region of the scalp by the use of collodion glue. While the glue is being applied, the electrode is held onto the scalp by engaging the shoulder of a small brass rod in a hole in the centre of the electrode. Round the brass rod are several small tubes through which air can be forced by a compressor, so as to speed the drying process. A syringe with a blunted needle is then used to inject conducting jelly through the hole in the electrode. Inter-electrode resistance is measured with an Avometer. The syringe needle is then abraded gently on the scalp under the electrodes until interelectrode resistances are all less than 2000 ohms. The electrode leads are then plugged into numbered sockets in a distribution box. Coloured markers on each end of each lead enable rapid selection of any desired set of electrodes.

A low inter-electrode resistance is essential to minimise the capacitive pick-up of electrical interference at the input grids of the preamplifier. On the other hand this renders the amplifier more susceptible to magnetic interference, and to minimise this the large transformers and chokes of the arc lamp rectifier are located in the next room. Other apparatus containing transformers is placed as far as possible from the electrodes.

p.d. amplifier.

The a.c. coupled p.d. amplifier has a maximum p.d. gain of 2×10^7. I am indebted to Professor G.D.Dawson for the circuit of this amplifier. The input impedance is 2×10^7 ohms, grid-to-grid.

This high value ensures that the inter-electrode resistance is swamped so that it has a negligible effect on the measured p.d. A balanced input discriminates against in-phase unwanted signal at the electrodes, such as electrical mains interference. The preamplifier is installed in a separate screened compartment within the chassis. A first assembly of the circuit gave trouble with valve base noise, so "flying lead" valves were subsequently used. The valves are enclosed in screening cans, and mounted on rubber to avoid microphony. Polystyrene capacitors are used in the preamplifier on account of their very high leakage resistance; polyester capacitors are suitable elsewhere. High quality carbon film resistors are used in the preamplifier, so that resistor noise should be as low as practicable. (ref.36). Triodes are employed throughout rather than pentodes, to avoid the partition noise characteristic of pentodes.

H.T. supplies are derived from batteries, and valve heaters are powered by accumulators. This is partly to avoid mains ripple, and partly as a safety precaution.

In practice by far the greatest source of unwanted signal is found to be attributable to intrinsic brain activity. Nevertheless it was felt worthwhile to minimise all sources of random noise, so that the maximum amplifier gain possible could be employed without driving the apparatus beyond its linear region. Amplifier noise was measured, and found to be equivalent to about 2 microvolts peak-to-peak at the input grids.

Current amplifier.

The current amplifier supplies the multipliers with a current which represents the E.E.G. voltage signal in analogue form. A circuit diagram is given at the end of this thesis (diagram 2).

The p.d. amplifier drives a single E.C.C. 82 triode, which feeds an OC 72 transistor (Tr.1). This drives an OC 35 power transistor (Tr.2). The two-transistor current amplifier is d.c. coupled, since a rather large current of 200 milliamps maximum is required by the Hall effect multipliers. The voltage swing required to drive 200 mA through the 20 ohms resistance of the two multiplier coils in series necessitates a 24 volt power supply, which is obtained by the use of car batteries.

A difficulty with d.c. amplifiers is the drift with time of the gain and the zero. To minimise drift arising from changes in the temperature of the transistors, they are mounted on large heat sinks. Drift arising from temperature rises of resistors is minimised by using resistors of up to 40 watts nominal dissipation. Sufficiently high wattage ratings to minimise drift were found by trial and error. The 24 volt supply used is sufficiently high to allow negative feedback via the emitter resistor of Tr.2, and to allow a large potential drop across the load resistors of Tr.1. and Tr.2. The use of accumulators, which can provide high currents, enable small values of R_1, R_2 and R_3 to be used. All these factors contribute to good thermal stability.

It was found impracticable to use a rectified d.c. supply, since with d.c. coupling and a heavy current drain, the unavoidable small percentage ripple in the supply volts resulted in a percentage

ripple in the current through the multipliers so large as to be unacceptable.

The current biassing of Tr.1 is controlled by the variable R_1, which varies the p.d. across R_3, the base resistor, and so controls the base current. This in turn controls the biassing of Tr.2 so as to set its collector current to such a value that there is zero p.d. across the multiplier coils when there is zero input to Tr.1. This is monitored by the centre reading meter M2. The tapping on the 24 volt supply was chosen so that a 280 milliamp swing of coil current is possible without the occurrence of clipping or bottoming. A twin beam C.R.O. was employed to compare the output current waveform through the coils, with the voltage waveform of a sinusoidal balanced input which was fed to the p.d. amplifier from the alternator via an attenuator. A graph of input p.d. versus the current through the multiplier was plotted, and found to be linear up to 200 milliamps R.M.S. to within the $\pm 2\%$ accuracy of the Avometers used to measure current and voltage.

An Avometer (M1 diagram 2) was installed to monitor coil current, and to check that it does not exceed the limit of linear operation of the apparatus (see page 40). During E.E.G. recordings this is ensured by an initial setting of the gain of the p.d. amplifier.

Multiplication.

A circuit diagram of the multiplier circuits is given at the end of this thesis (diagram 2).

Each Hall effect multiplier core consists of a germanium wafer (plate) through which a current I_1 passes. The wafer is

located in a field of magnetic induction $\underline{B}$ produced by the flow of current $\underline{I_2}$ through a coil. In accordance with the Hall effect, an e.m.f. of magnitude e is generated across the wafer perpendicularly to $\underline{I_1}$ and $\underline{B}$ where:-

$$e \propto I_1 B$$

since $B \propto I_2$

$$e \propto I_1 I_2$$

Thus the device will generate an output e.m.f. proportional to the product of any two variables, providing the variables can be represented in analogue form as currents.

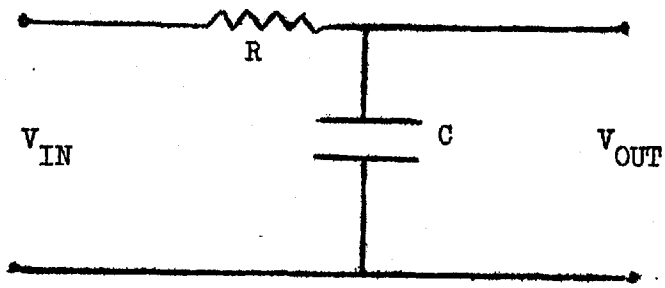
Any asymmetry in the assembly of the wafer is balanced electrically by feeding a fraction of the output back to the plate input by means of a 1000 ohm potentiometer.

The p.d. and current amplifiers pass through the plates a current I, which has the same waveform as the E.E.G. An alternator, which is driven by gearing at the modulation frequency of the light stimulus, drives through the multiplier plates currents which are accurately in quadrature, and equal in magnitude (rejection limits: $\pm \frac{1}{2}^{o}$: for equality of outputs $\pm \frac{1}{2}\%$). Stepped resistors in series, with each plate enable the plate currents to be set to be as large as possible over any particular speed range. The multipliers differ both in plate input resistance, and in output e.m.f. for a given input current. They are balanced by the adjustment of 10 ohm rheostats in the plate circuits so that the same input voltage applied to either plate results in identical outputs (with equal coil currents.)

Integration

Analogue integration is performed by shunt capacitors and series resistors. One or two 45,000 μF. electrolytic capacitors, and a series of stepped resistors can be selected for each multiplier output, enabling the time constant to be varied from 0.5 to 200 seconds.

If, in the circuit below, an input e.m.f. V_{IN} is applied, the capacitor charges through a resistance R.



The equation of the circuit is:-

$$\frac{dV_{OUT}}{dt} = \frac{I}{C} = \frac{V_{IN} - V_{OUT}}{RC}$$

If the time constant, RC, is much longer than t, the period of application of V_{IN}, then the final V_{OUT} will be much less than V_{IN}. Hence, approximately:-

$$\frac{dV_{OUT}}{dt} = \frac{V_{IN}}{RC} \quad \therefore \quad V_{OUT} = \frac{V_{IN}}{RC} t$$

So that in general for an input pulse of arbitrary shape, the peak output p.d. is proportional to the area under the pulse (i.e. under the e.m.f. versus time graph), providing that RC $\gg$ pulse length.

The time constant used experimentally in the E.E.G. measurements was usually 15 seconds. It is shown above that the R.C. integrating circuit will integrate pulses whose duration is much less than 15 seconds. However, a synchronous input signal to the analogue computer produces a d.c. output. The R.C. circuit above will not act as an integrator to this output. Instead the capacitor will charge through the resistance R, and the p.d. across C (V_{OUT}) will change according to the equation

$$V_{OUT} = V_{IN}\left(1 - e^{-t/RC}\right)$$

and will tend to a constant value equal to V_{IN} .

Thus the "integrating circuit" acts as an integrator only for pulses of duration much less than 15 seconds. Most of the noise and unwanted signal falls into this category. For the d.c.output of the required synchronous input signal the "integrating circuit" does not integrate at all.

Display of integrated multiplier outputs.

A Leeds-Northrup two pen recording potentiometer is fed by the two multiplier output p.d's via the integrators. The full span of the instrument is 10 millivolts for each pen, and the response time 1 second. The paper speed is 1" per 7.5 seconds. The pens are electrically set to centre zero by the adjustment of two separate external arrangements of a potential divider across a battery. The resistance R in diagram 3 was chosen to be small, so that the pen biassing should be little altered on changing the time constant controls or operating the "reduce span" control.

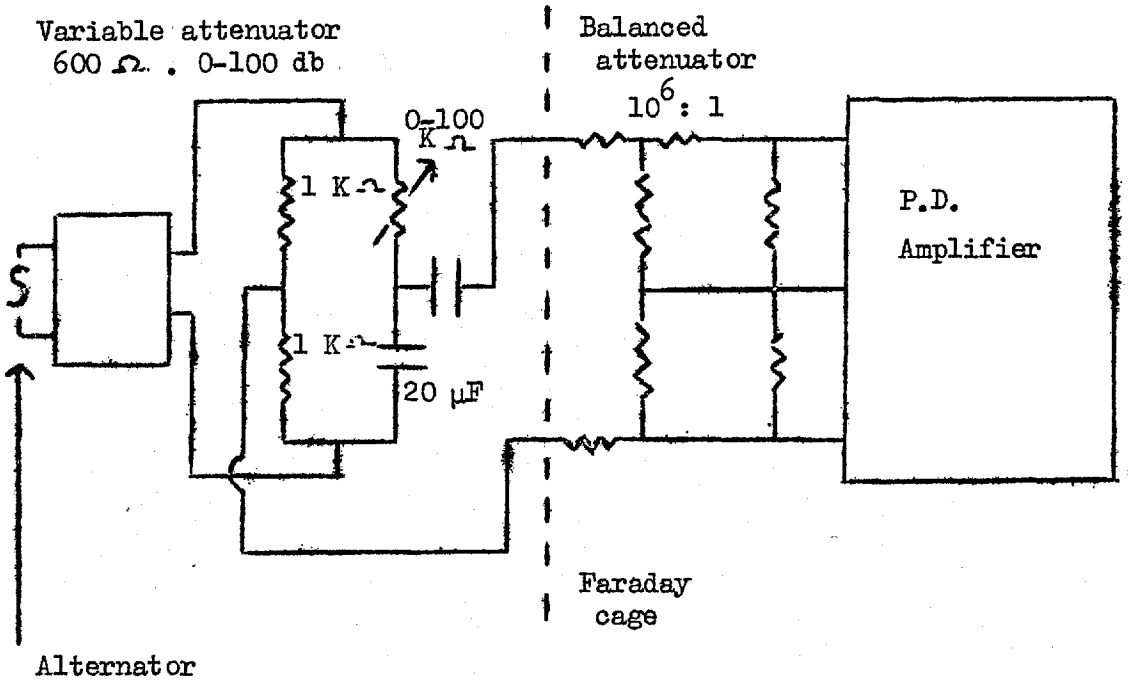
The reduce span controls shown in diagram 3 act as potential dividers across the multiplier outputs. They enable the output p.d. to either or both of the pens to be reduced by a predetermined factor of about 2. This can be done rapidly during an E.E.G. observation if it is seen that a pen is about to leave the edge of the paper.

A synchronous calibration signal was obtained from the alternator, and applied via attenuators to the p.d. amplifier. The reduce span switches were operated and the "reduce span" factor measured. It was also confirmed that the operation of one reduce span control did not affect the other pen, nor did it affect the reading of phase angle or amplitude indicated by the combined readings.

The 5 millivolts pen biassing is also applied across the electrolytic capacitors in the integrating circuits, thus providing the required d.c. polarisation. (diagram 3).

Calibration of analysing circuits.

The synchronous sinusoidal signal from the alternator was passed through the R-C variable phase shifting circuit shown, then through an attenuator so as to provide a balanced synchronous signal to the p.d. amplifier.



The apparatus was calibrated for phase measurements against a Dawe transistorised phase meter. A 20 microvolts peak-to-peak signal with low noise (2 μv p-p) was used. The readings agreed to within the calibration accuracy of the phase meter (± 3%). A calibration graph can be found on page 36 . At the frequencies used in the E.E.G. experiments a ± 3% error is equivalent to

approximately $\pm$ 0.8 milliseconds.

Sinusoidal noise derived from an audio frequency oscillator was added to the signal, after removing the phase meter, which was not able to operate with other than sinusoidal input. When the noise frequency was very close to the signal frequency beating made readings impossible, but with frequencies separated by at least 1 c.p.s. the effect of raising noise amplitude to about 35 times signal amplitude, while simultaneously exceeding the design limits of the multipliers, was to cause errors in phase measurements of about 10^{o}, and about 35% errors in amplitude measurements. The effects on the accuracy of the analogue computer of noise amplitude and frequency are illustrated on pages 39 and 40.

At a constant frequency and phase shift, signal amplitude was plotted against $\sqrt{(\text{deflection of pen 1})^2 + (\text{deflection of pen 2})^2}$ and was found to be linear to within the $\pm$ 2% accuracy of the voltmeter used to measure the amplitude of the input signal. A calibration graph can be found on page 37.

A phase lag versus frequency graph for the apparatus alone gave a linear plot over the range 11-17 c.p.s. The slope indicated an apparent time lag for the amplifiers of about 12 milliseconds.

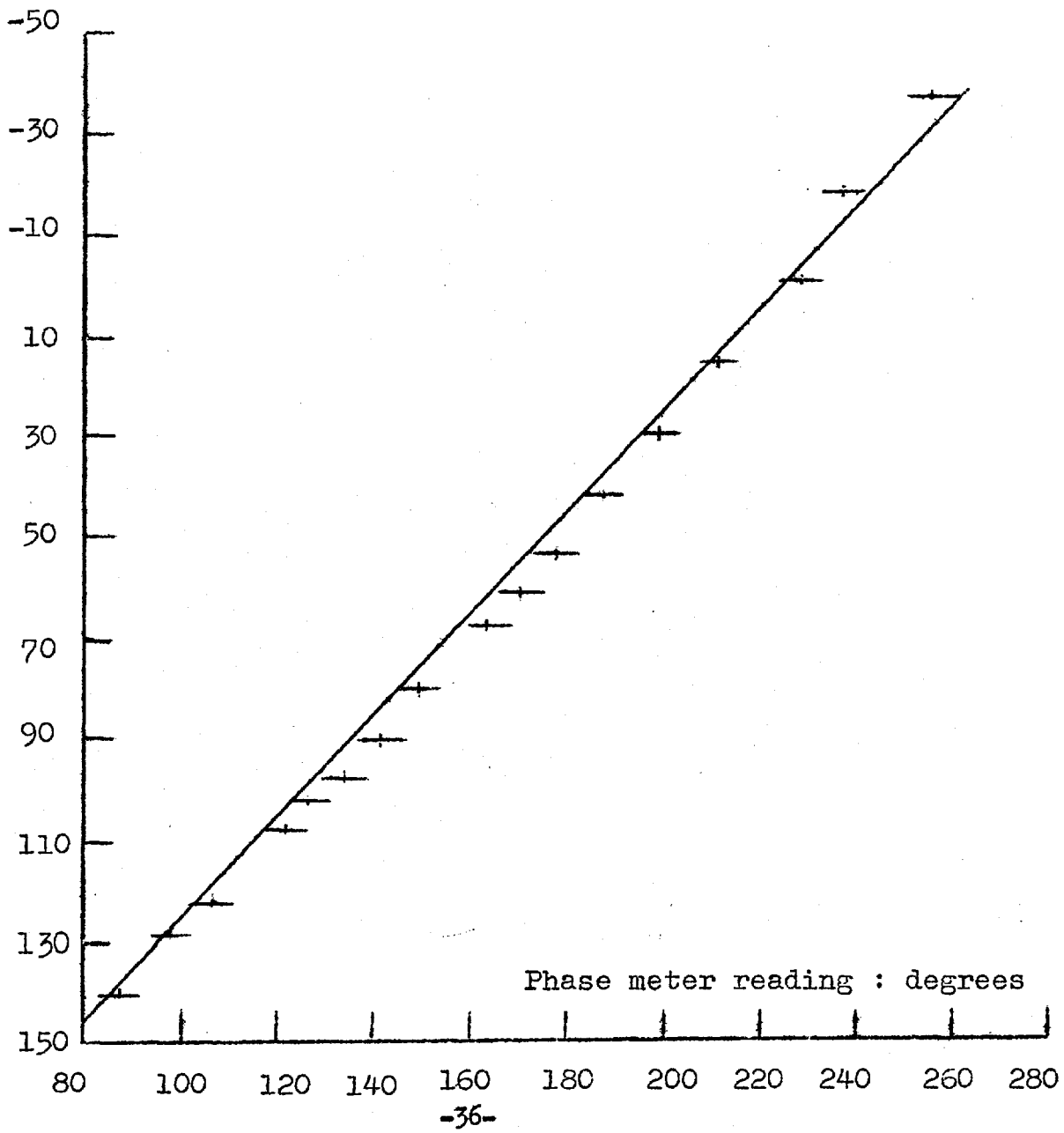
Noise Rejection

The basis of the method described in this thesis for selecting a signal from a large noise background is the ordered relation of stimulus and response, in contrast to the random relation between stimulus and noise. Specifically, it is only the synchronous component of the evoked response which is phase locked to, and at the

CALIBRATION OF ANALOGUE
COMPUTER AGAINST DAWE PHASE
METER. FREQUENCY 10 c.p.s.

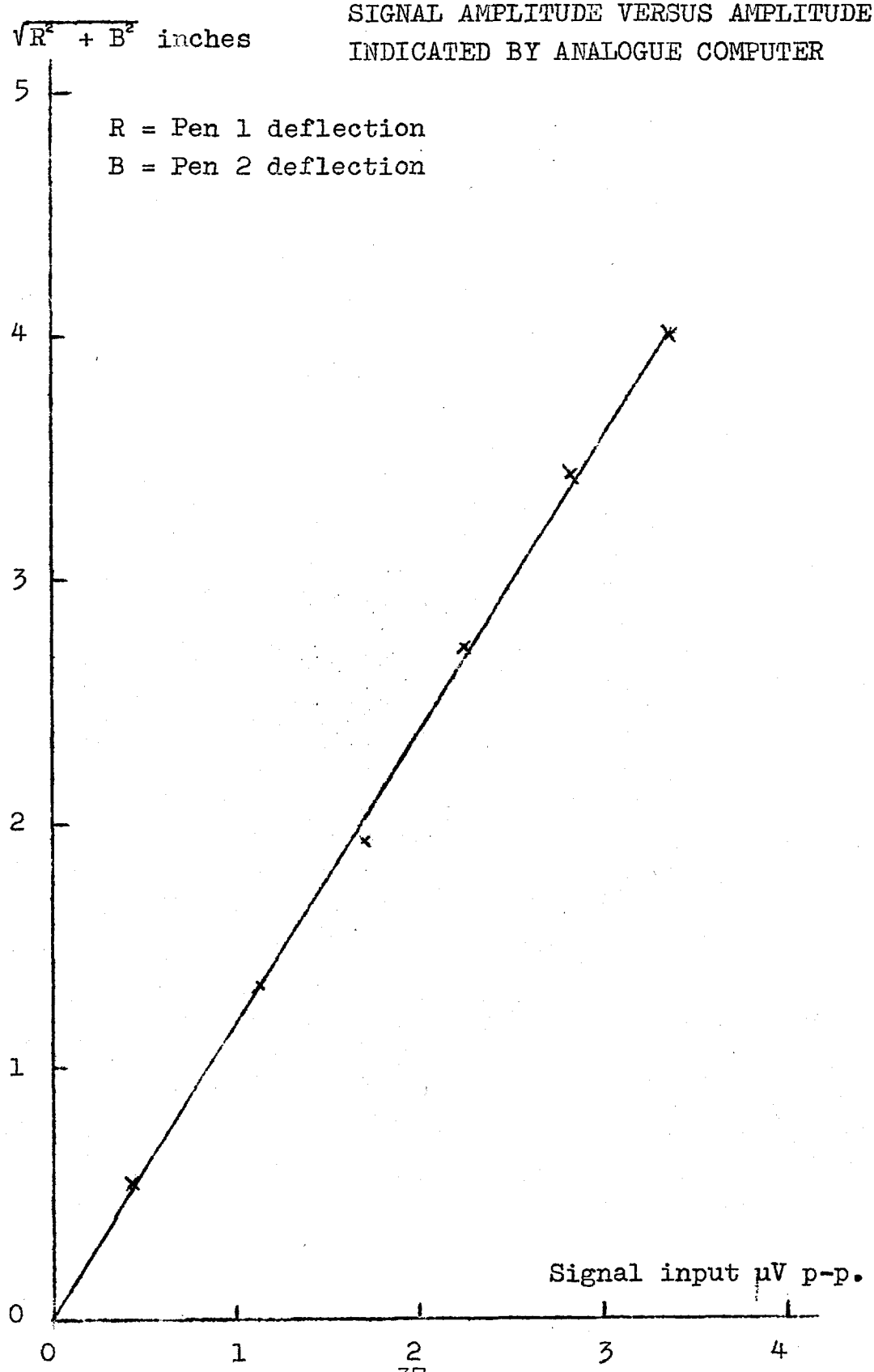
Horizontal lines indicate error of phase meter.
The 45° line is drawn.

Phase lag recorded by
analogue computer in
degrees : arbitrary zero



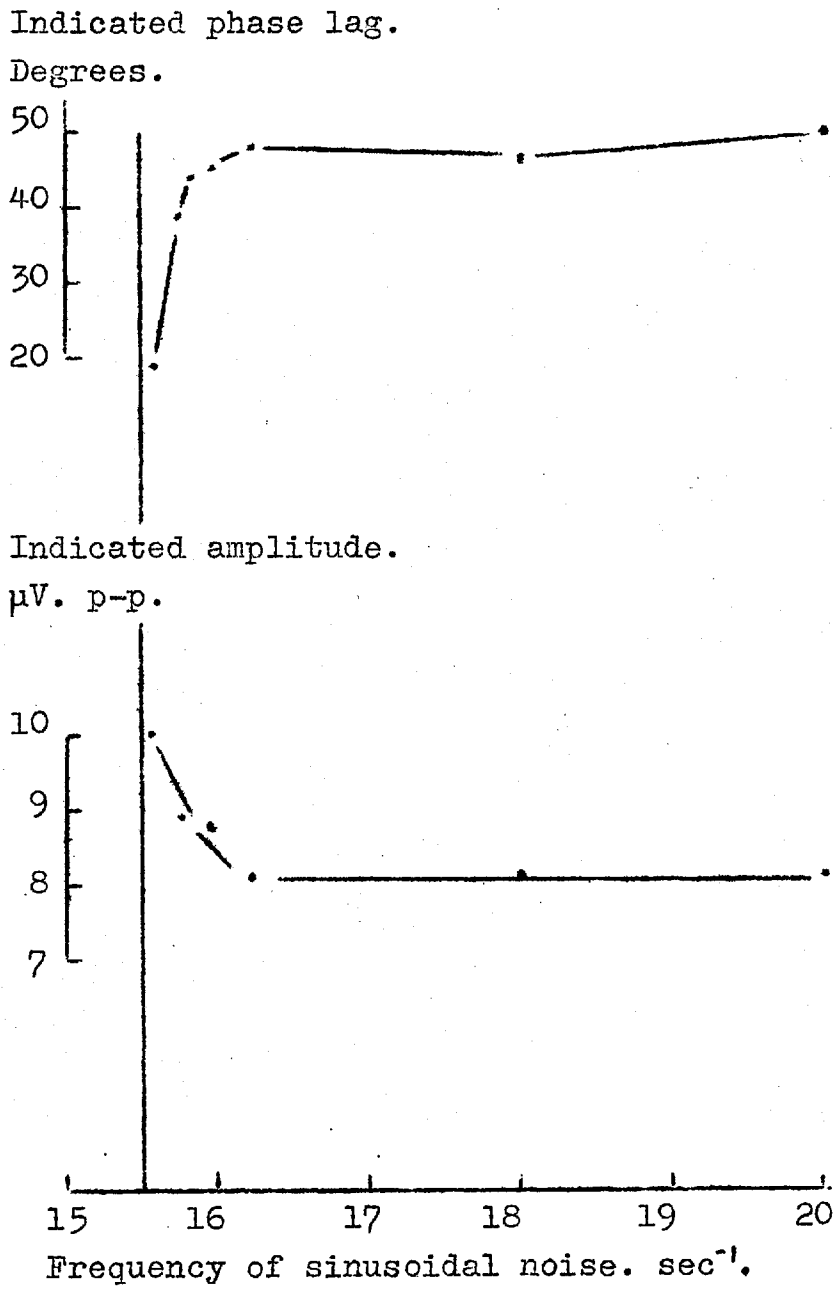
CALIBRATION

SIGNAL AMPLITUDE VERSUS AMPLITUDE INDICATED BY ANALOGUE COMPUTER



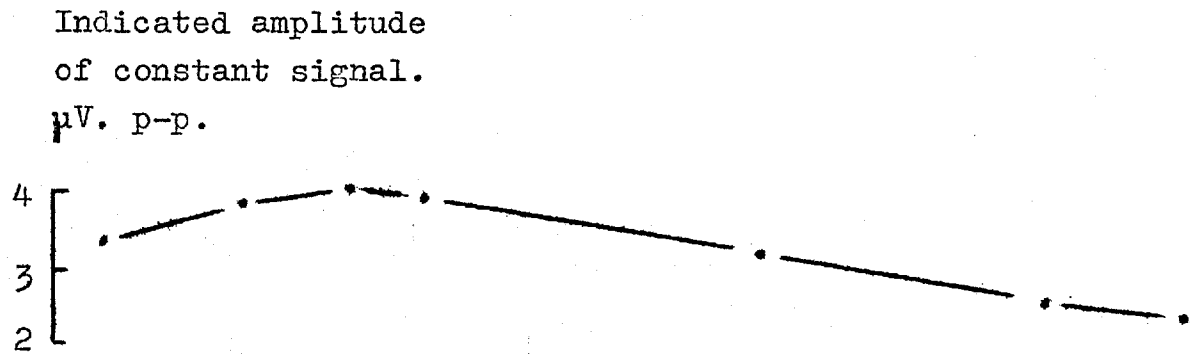
THE EFFECT OF NOISE FREQUENCY ON THE MEASUREMENT OF THE AMPLITUDE AND PHASE LAG OF A CONSTANT SIGNAL

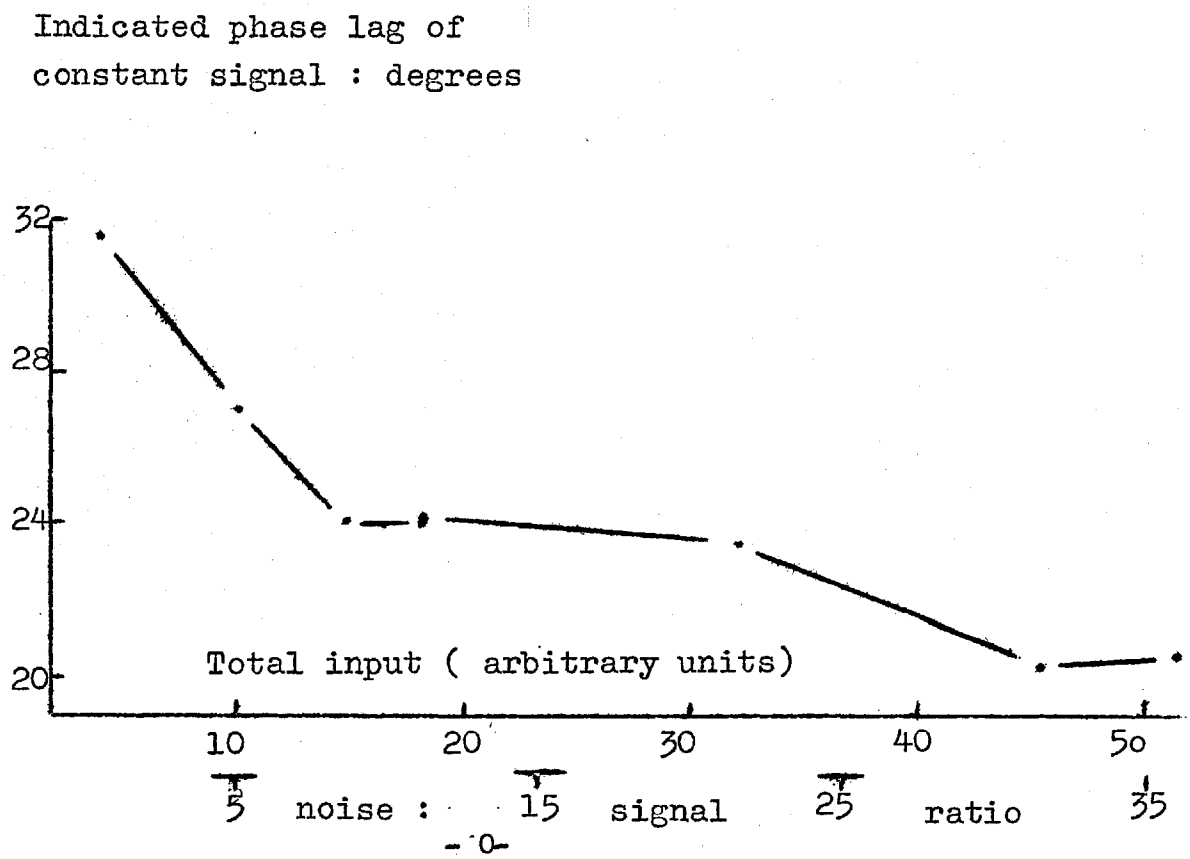
SIGNAL : 15.5 c.p.s. of amplitude 7.8 μV. p-p.
NOISE : amplitude 14 μV. p-p of variable frequency.



THE EFFECT OF THE TOTAL INPUT TO THE AMPLIFIERS ON THE MEASUREMENT OF THE AMPLITUDE AND PHASE LAG OF A CONSTANT SIGNAL.

Constant noise frequency = 20 c.p.s.
Constant signal: 3.7 μV p-p 15.5 c.p.s.





same frequency as the light modulation. The longer the signal remains fixed relative to the stimulus, the greater may be the discrimination against noise.

Constancy of the signal-stimulus relationship is found to be very dependent on the observer's fixation. If head or eye movements occur, the eye pupil will move. This will cause an alteration of effective retinal stimulation due to the Stiles-Crawford effect, or possibly a cutting off of part of the beam. Eye movements also cause stimulation of fresh areas of retina of varying light adaptations and the result is a varying signal. The technique's dependence on good fixation was not realised at first, and many trials were required before a suitable time constant for the integrating circuits could be established. Until this stage had been reached it was not possible to tell whether the apparatus would work at all. The time constant must be sufficiently long so that the high amplitude beating of the analysing circuits with the intrinsic brain rhythms is rejected in favour of the constant synchronous evoked response. If the time constant is too long however, fixation cannot be maintained, so that the signal varies and is confused with the noise.

The starting point of the experiments was the standard method of evoking a large photic response, which is to use very bright short flashes, so large as to stimulate almost the whole of both retinae.

The highest retinal illumination is obtained with Maxwellian view, but field size is limited by aberrations, particularly spherical aberration. Its effect is that light from the outer zones of the lens misses the artificial pupil, so that the field appears to be

of uneven luminance. It seemed likely that at high retinal illuminations it would be better to aim at higher field sizes than still higher intensities, since the impulse frequency along a ganglion cell axon is proportional to the log. of stimulus intensity. (ref. 5, p.284). If the evoked response in the E.E.G. varies with the number of impulses in a synchronised volley reaching the cortex, the effect of a doubling in field size would be equivalent to a tenfold increase in intensity. Although this line of reasoning seemed crude, it suggested that the initial experiment should be made with a large field size. Accordingly the eye lens was formed of a well corrected camera objective of f number 2.5 and clear aperture 3 inches, in combination with a moulded aspheric condenser lens of 4.5 inches clear aperture and f number 0.9. Unfortunately the largest interference filters obtainable were only 2 inches in diameter, so with the beam limited in this way a field size of about 22^{o} was the maximum obtainable. Aberrations were troublesome, since the aspheric lens was not working under the conditions for which it was designed. In addition, the cone of light was of high angle with such a large field. Thus the eye pupil had to be placed and maintained in position with greater accuracy than for smaller field sizes. It seemed that on balance the better fixation possible with a 16^{o} field was preferable to the greater effective stimulation of the larger field.

The light source.

The image of the brightest region of a 500 watt d.c. Xenon arc is focussed onto a 2 m.m. artificial pupil (diagram 1). The eye lens is observed in Maxwellian view. It is a general property of optical systems that, even when absorption and scattering losses are ignored, the maximum luninance of a retinal image is equal to the source luminance. (ref. 37, p.152.) For a 2 m.m. artificial pupil, requirements of high retinal illumination mean that a source of maximum luminance rather than maximum luminous intensity should be selected. The 500 watt d.c. Xenon arc lamp was chosen as providing the highest luminance (about 20,000 cd.per cm^2. over a 2 m.m. diameter circle) without being of impractically high power dissipation. The characteristic stability of position of the Xenon arc is essential if the luminous flux through the 2 m.m. pupil is to remain constant. Bloomed lenses are used so that light losses and scatter are minimised.

A large robust lamphouse was designed to afford containment in the event of explosion of the lamp. The ends of the lamp are held in loosely fitting caps, and location is by a single weak spring in the lower cap. Thus there is little danger of mechanical stress, with consequent explosion risk, due to thermal expansion. The upper cap was carefully designed so that the lamp could be installed without putting any mechanical strain on it. The caps are joined by a non-conducting U shaped bar, made partly of metal, and partly of P.T.F.E. Design calculations on heat transfer through the rod indicated that it was necessary to shield the P.T.F.E. section from direct radiation

in order to prevent the production of poisonous fumes by overheating of the P.T.F.E. The whole lamp assembly can be rotated and moved in a horizontal plane by sliding. A screw-and-plunger enables fine vertical adjustments to be made from the outside, while the lamp is running. For all positions of the lamp there are no gaps through which ultraviolet light could escape. The lamp is cooled through a length of 3 inch diameter flexible steel tubing, connected from the top of the lamphouse to an extractor fan in the next room. Air enters at the bottom of the lamphouse through a slit covered by a light trap. Starting is by application of a 40,000 volt radiofrequency pulse. The starter unit is mounted close to the lamphouse in order to avoid losses in the leads. The high voltage lead is a brass rod, led in through the centre of a 4 inch diameter P.T.F.E. disc, which provides electrical insulation. Design calculations showed that the expected temperature drop across the disc would not result in dangerously high P.T.F.E. temperatures. A toughened Chance OC 22 infra red filter is loosely mounted immediately before the first lens. To enable this filter to be examined frequently for any signs of cracking, a movable disc and examination port are provided on the lamphouse.

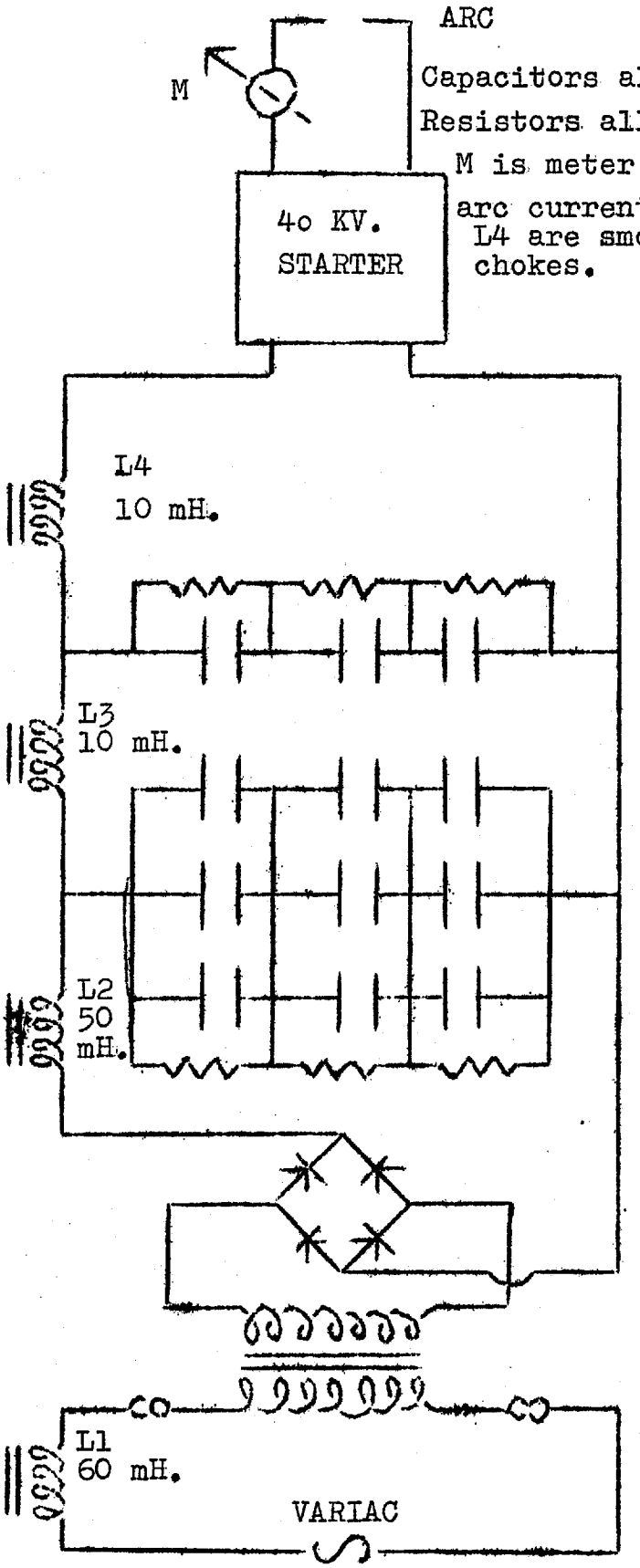
It was experimentally found that for reliable striking of the arc after application of the 40,000 volt pulse it was necessary that the source of d.c. power should provide an open circuit p.d. of about 120 volts. Immediately on striking, this output p.d. must fall to its running value of 22 volts at 22 amps. When running, the light output is required to be very steady so that the modulation

should be purely sinusoidal. Since the fluctuations of luminance are much greater than the fluctuations of current producing them, the ripple content of the arc current must be less than 0.1%. Also it is characteristic of an arc that its resistance falls with increasing current. If it were connected to a constant voltage generator the current would therefore rise until the lamp was destroyed.

A circuit diagram of the rectifier which was eventually designed and constructed is given on the next page. Stabilisation of the arc was installed on the a.c. side rather than the d.c. side, since much less power is dissipated by this arrangement. Any tendency for the arc current to rise results in a rise of input alternating current, and hence an increase in the voltage drop across the 60 mH. input chokes. This reduces the input voltage to the rectifer, hence opposing the original change. Smoothing is by choke input filter. Twelve separate 5000 microfarad capacitors are used so that their rated d.c. voltage is not exceeded during the short interval before striking when the output p.d. is 120 volts, nor the a.c. ripple rating exceeded during prolonged running. Each is shunted by a 22 k ohm resistor, since unequal leakage resistances would otherwise result in an unequal division of d.c. voltage across the series capacitors.

It was found that the lamp became progressively more difficult to strike as it aged, and also that the arc current tended to fluctuate slightly. Accordingly, the rectifier supply was via an 8 amp. Variac. A heavy shunt and 3m.A. meter were calibrated against a sub-standard ammeter so that arc current could be monitored during

BALLASTED AND SMOOTHED XENON ARC SUPPLY



Capacitors all 5000MF.
Resistors all 22 K.ohms
M is meter to monitor arc current. L2,L3, L4 are smoothing chokes.

every session and maintained constant by use of the Variac.

The Photomultiplier.

About 10% of the light flux passes through a mirror into a photomultiplier housing. The tube is a Mazda 27 M1, and is supplied by an A.E.I. E.H.T unit. This is operated at voltages between 400 and 800 depending on the colour filter used. An Avo measures the current through the potentiometer chain, thereby monitoring the E.H.T. supply.

The dynode current was measured for various constant values of arc current in order to investigate whether there were any short term fluctuations in light output of the order of 0.5-10 seconds (the rectifier supply ripple had been designed to be less than 0.1%). The apparatus used could detect fluctuations of about 2%. No fluctuations of this magnitude were observed.

Long term changes in light output were measured by visual photometry (see below). The smallest change which could be revealed by this method was 0.14 log units. For the 22 amps constant arc current employed no change of light output exceeding 0.14 log units was observed over a period of about 1 hour, nor over a period of about 2 months in which about 40 hours running had occurred.

Modulation of retinal illumination.

The intensity of a parallel beam is sinusoidally modulated by a combination of a stationary and a rotating polaroid.

The light beam, linearly polarised by the fixed polaroid, and of intensity I_1 falls on the rotating polaroid so that at any instant

the angle between the incident electric vector E_1 and the transmission direction of the polaroid is θ . If absorbtion is ignored, the magnitude of the transmitted vector is $E_1 \cos \theta$. When the polaroid rotates steadily f times per second, the transmitted intensity is I, where:-

$$I = I_1 \cos^2 \theta = \frac{I}{2}1(1 - \cos 2\theta) = \frac{I}{2}1 \ (1 - \cos [4\pi ft])$$

The intensity of the transmitted beam is therefore sinusoidally modulated, and for good quality polaroid is almost 100%. This modulation is at twice rotation frequency, and is equivalent to a sinusoidal variation of peak $\frac{I}{2}1$ superposed on a steady level of $\frac{I}{2}1$.

Modulation frequencies are chosen that are not related harmonically to mains frequency, so that there can be no synchronous interference caused by nearby apparatus running at a sub-multiple of mains frequency.

Neutral filters.

The intensity of the stimulus light can be varied by sliding Chance neutral density filters in and out of the beam. A range of 5 log. units is available in 0.14 log. unit steps.

Photometry.

A calibrated and aged 1000 watt tungsten lamp is underrun to give a colour temperature of 2854 ^{o}K. MgO is smoked onto a white painted sector, which is rotated by a variable speed motor controlled by the observer. The sector is placed so that flicker photometry

can be used to measure the retinal illumination produced by each colour filter. It was found that a photometric match could most easily be reached by reducing the field size to 5^{o}. Matches made in this way were found to be satisfactory when the field size was increased to 16^{o}. The day to day scatter of the matches for any particular colour filter was found to be of the order of the smallest neutral density filter used i.e. 0.14 log units.

Stabilisation of the speed of polaroid rotation (diagram 4)

A d.c. permanent magnet motor is used to drive the polaroid and magnet alternator via a gear train. Its speed is stabilised by negative feedback of the alternator's output to the motor power supply.

The collector of an OC 35 power transistor (Tr.2 in diagram 4) is connected via the motor armature coil to a rectified and smoothed 35 volt supply. Tr.2 is mounted on a heat sink, and some emitter resistor feedback is provided to obtain thermal stability. The collector current, and hence motor speed are adjusted by the fine control of a helical rheostat which varies the base current of Tr.2. The motor speed is stabilised by negative feedback as follows. The a.c. voltage output of the alternator is proportional to motor speed. Since stabilisation is required at speeds for which the alternator's output is insufficient to operate a silicon rectifier, the alternator's output is amplified by a single d.c. coupled OC 35 transistor (Tr.1). This feeds a full wave rectifier bridge, whose

smoothed output is arranged to supply negative feedback to be base of Tr.2.

Measurement and monitoring of modulation frequency.

An a.c. signal at the modulation frequency is obtained from a modified Magslip Receiver. This consists of coils which surround a piece of magnetic material which is mounted on a shaft. An auxiliary coil makes possible a d.c. polarisation of the magnetic material. When the shaft is rotated, sinusoidal e.m.f.'s are generated across the coils at the frequency of the shaft rotation.

This alternating e.m.f. is applied to the X plates of a C.R.O. The alternating e.m.f. from a low frequency oscillator is applied to the Y plates, and the motor speed set by adjusting motor current until the Lissajou figure is stationary.

The low frequency oscillator used was a master electricity meter. This gives exceptional stability of frequency ($\pm$ 0.1%) and can be easily calibrated by the use of a stop clock. It consists of a selected domestic electricity meter, essentially a wattmeter, which registers watts by the speed of rotation of a disc. The disc interrupts a light beam which falls on a photocell whose output frequency is proportional to the wattage. The volts coil to the wattmeter is supplied by a constant voltage transformer in order to safeguard against variations of mains voltage. The current in the current coil is measured by an Avometer which is calibrated in terms of meter output frequency, measured by means of a stopclock. Frequent checks of the calibration have shown it to remain constant

to within at least 0.5%. It was found in practice that the experimenter could maintain the stimulus modulation frequency constant during a $1\frac{1}{2}$ minute observation to $\pm$ 0.2 c.p.s.

Colour filters.

Interference filters are used. The halfwidths vary between 80 Å and 120 Å. It would have been desirable both from the point of view of having a sharper cut-off, and also a reduced bandwidth, to select stimuli by means of a single or double monochromator system, but insufficient space was available. Had spectral stimuli been used it would have been possible to establish in more detail the form of the dip in the τ^{-1} versus λ graph (diagrams 5,6).

Chapter 5. OBSERVATIONAL CONDITIONS

The observer lies face downwards in a Faraday cage. Entry is by two doors constructed so as to ensure good electrical continuity and screening when closed. The construction is of a Dexion framework covered by perforated zinc sheet. Sections of zinc were either soldered and screwed together, or screwed with a large overlap. The p.d. amplifier is located inside the cage. The observer's position is partly determined by the accommodation available, and partly chosen to provide relaxation and consequent minimum interference from muscle potentials.

Pads support the observers shoulders. The head is supported by an adjustable padded semicircle, and by padding round the vertical eyepiece. Two fixation crosses locate the eye pupil directly above the 2 m.m. exit pupil, and also ensure that the visual axis of the eye is along the axis of the optical system. This is done by keeping the eye in such a position that there is no parallax between the crosses. The purpose is to maintain stimulation of a fixed region of the retina, and to avoid other variations of effective stimulation which might arise due to the Stiles-Crawford effect. The field is circular and of about 16° subtense with a dark surround.

The accuracy of a particular reading is limited by the steadiness of the observer's fixation. The accuracy of a set of readings is limited by the precision with which the eye is returned to the same position over the exit pupil for each reading.

Before each reading the experimenter checks the Xenon arc current,

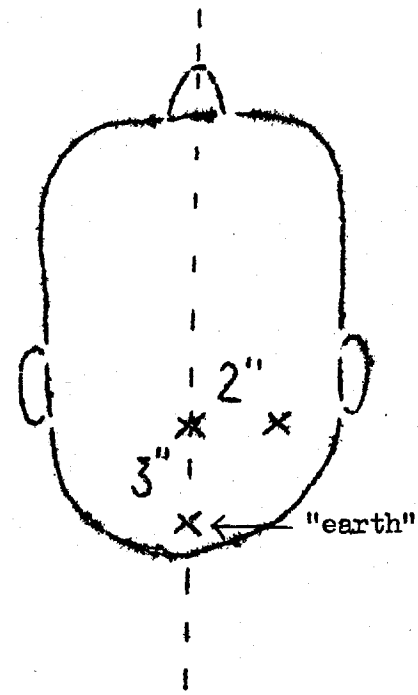
sets the oscillator frequency, and adjusts the motor speed until the Lissajou figure is stationary. The pens are allowed to reach a steady level with the shutter closed and the polaroid rotating while the observer is in position. This enables the synchronous magnetic interference arising from the alternator to be measured. To minimise this interference, the electrode leads are twisted together, and taken away vertically. The shutter is then opened and the observer breathes shallowly, or not at all. It is found that the only effect of breathing during an observation is a type of irregularity in the recording attributable to shifts in the eye position produced by chest movements.

In the later experiments this procedure was modified as a result of an improvement in the apparatus designed to reduce synchronous magnetic interference. The motor and magslip receiver assembly was installed in the next room, about 12 feet from the electrodes, and drove the polaroid via an automobile speedometer cable. It was found that even when running at a steady speed, the driving cable was twisted through a large angle. The magslip alternator was therefore installed immediately under the polaroid, and driven from the polaroid by means of a chain and sprocket arrangement. In this way a constant phase relationship between polaroid and alternator was ensured, while still enabling the alternator to be magnetically screened by enclosing it in a mumetal box.

During an observation the experimenter is silent. He notes the maximum reading of input current to the multiplier coils to ensure that the E.E.G. voltages are neither driving the apparatus

beyond its linear region, nor causing blocking of the amplifiers. At the same time he monitors the stimulus modulation frequency by glancing at the Lissajou figure. The observer's unused eye is left open in dim illumination. Three minutes recovery in dim illumination is allowed between readings. This was found to be sufficient to obtain repeatable readings. Latency measurements are taken from the constant part of recordings, between approximately 16 to 80 seconds from onset of stimulation.

Many electrode placements were tried. The arrangement shown is found to give a comparatively large signal, combined with minimum beats with intrinsic rhythmical activity in the E.E.G., and was used throughout the experiments.



CHAPTER 6 SUMMARY OF RESULTS

1. INITIAL TRANSIENT OF SYNCHRONOUS EVOKED E.E.G. RESPONSE

On stimulating the central retina with a 16° circular stimulus field which is sinusoidally modulated, a transient synchronous evoked response is observed in the E.E.G. during the first 16-20 seconds. The stimulus field has a dark surround. The effect has been observed for stimulus modulation frequencies between 11 and 16 c.p.s.,(diagrams 7,8), and for retinal illuminations between 1,000 and 500,000 trolands peak. The amplitude of the synchronous response varies with the time t from onset of stimulation as approximately (A + Bt) where A and B are constants. The phase lag is constant within the limits of error ($\pm 5^{\circ}$). The effect has been observed for stimulus wavelengths from 4337 $\mathring{A}$ to 6335 $\mathring{A}$. The total number of definite observations exceeds 90. Absence of the effect has been found to be attributable to poor initial fixation, or alterations in stimulus frequency.

2. STEADY-STATE SYNCHRONOUS EVOKED E.E.G RESPONSE

After 16-20 seconds the synchronous response to a stimulus of constant frequency and peak retinal illumination falls suddenly to an amplitude which remains constant. The apparent latency also remains constant. (Experimental variation during a single observation: $\pm 4^{\circ}$ in phase i.e. $\pm$ 1 millisecond approximately in apparent latency: $\pm$ 10% in amplitude). See diagrams 8,10,11,12,13. This effect has been observed for stimulus intensities between

1000 and 500,000 trolands peak and for stimulus wavelengths between 4337 $\mathring{A}$ and 6335 $\mathring{A}$. The effect is observed even when the total E.E.G. output reaches 20 times the amplitude of the synchronous response. Constancy holds till at least 80 seconds after onset of stimulation. The total number of observations of this effect exceeds 100. The predominant contribution to fluctuations observed in the amplitude of the synchronous response after 20 seconds is found to be attributable to changes in the stimulated retinal region caused by eye flicks, or to changes in effective stimulus intensity caused by movements of the eye pupil over the exit pupil.

3. THE VARIATION OF THE PHASE LAG OF THE SYNCHRONOUS EVOKED E.E.G. RESPONSE WITH STIMULUS MODULATION FREQUENCY.

The phase lag of the synchronous evoked response behind the stimulus has been measured for the steady state response between about 20 and 80 seconds after onset of stimulation. The phase lag (ϕ) is found to vary linearly with the stimulus modulation frequency (f) over a range of at least 5 to 29 c.p.s (diagram 14). An attempt was made to find the accuracy to which linearity can be said to hold. It was assumed that $\phi \propto f^n$, and a graph was plotted of $\log_{10} \phi$ versus $\log_{10} f$ using the data of diagram 14. It was found that n was equal to 1.1 ± 0.3.

Since beating with α activity becomes troublesome when f is near the α frequency, and since difficulties of fixation or poor reproducibility of measurement was experienced near f = 17 c.p.s. it was decided to restrict latency measurements to 11-16.5 c.p.s.

The data of diagram 17 was plotted in log-log. form and with the assumption of $\phi \propto f^n$, n was found to be 0.92 ± 0.8. So over the restricted frequency range used in latency measurements linearity could be assumed to hold to about 8%.

4. THE VARIATION OF APPARENT LATENCY WITH STIMULUS WAVELENGTH.

The linear ϕ versus f graph is interpreted as indicating an apparent latency of the synchronous response behind stimulus frequency (τ' seconds) which does not vary with stimulus frequency between 5 and 29 c.p.s., within experimental error. τ' varies in a specific manner with stimulus wavelength for stimuli of equal retinal illuminations. τ' has a minimum in the region of 5900 $\mathring{A}$, so that τ' is not a monotonic function of λ, and is therefore unlikely to be the only correlate of colour information at the cortical level (for example a τ' of 120 milliseconds corresponds to either yellow-green or red for 50,000 trolands illumination).

5. THE CORRELATION OF APPARENT LATENCY WITH SATURATION.

The apparent latency for a white (5500 ^{o}K) stimulus of equal retinal illumination to the coloured stimuli is less than the longest (blue-green) latencies, and longer than the shortest (yellow) latencies for restricted spectral regions. If τ' was the correlate of saturation, the white latency would be expected to be shorter than the yellow latency. It is concluded therefore that τ' does not correlate with saturation.

6. THE VARIATION OF APPARENT LATENCY WITH STIMULUS INTENSITY.

It is proposed that:- For a 4387 Å or 4577 Å stimulus the apparent latency τ' is inversely proportional to log.(stimulus intensity) for intensities above about 12,000 trolands peak. Below this intensity τ' tends towards a value independent of intensity. For a 5449 Å stimulus the transition occurs around 200,000 trolands peak. For a yellow stimulus τ' has little variation with intensity.

Experimental data.

For a given stimulus wavelength, the phase lag of the synchronous evoked component of the E.E.G., (ϕ), has been measured for a constant stimulus frequency of 14.9 c.p.s. It is found that ϕ varies in a specific manner with stimulus intensity (diagrams 18,20, 22, 24, 26, 28). For stimuli centred on 4387 Å and 4577 Å, the phase lag is found to be inversely proportional to the log of stimulus intensity down to about 12,000 trolands peak. Below this intensity, the phase lag tends towards a value which is independent of intensity. For a 5449 Å stimulus, the transition occurs around 200,000 trolands peak.

In the yellow, ϕ has little variation with intensity. The interpretation of the ϕ versus intensity curves which is offered here, is that the variation of ϕ with intensity is due to a variation of apparent latency(τ') with intensity. It might be objected that the hypothetical part of the phase lag, k (which is not due to the real latency τ seconds) is dependent on intensity (see pages 77 and 80 for a discussion of k).

An attempt was made to check the interpretation of the ϕ versus intensity graphs by calculating from the change in ϕ the expected values of apparent latency τ' for various stimulus intensities, and then measuring τ' directly at these intensities. The direct measurement was made by plotting ϕ versus stimulus frequency f at constant intensity.

The interpretation was confirmed within the limits of experimental error, but since a small quantity (35 milliseconds) was being measured as the difference of two large quantities (two values of τ'), each with an error of $\pm$ 15 milliseconds, the check was very crude.

It should be pointed out that changes of τ' with intensity obtained from the ϕ versus intensity graphs are much more precise, since the small change in τ' is obtained directly, rather than as a difference of large quantities.

7. THE DISTINCTION BETWEEN THE SYNCHRONOUS EVOKED P.D., AND INTRINSIC BRAIN ACTIVITY.

When E.E.G. records are made using occipital electrodes, beats are observed to occur between the analysing frequency and a fixed non-synchronous frequency (see page 90). The non-synchronous frequency is identified as the α frequency. The synchronous evoked response appears to be independent of α activity. Conversely, α activity appears to be independent of whether the light stimulus is off or on, and independent of stimulus frequency. Measurements could not be taken when the stimulus frequency was less than about 0.5 c.p.s. removed from α frequency, since the beating became so slow that the analysing apparatus failed to reject it. These conclusions

are based on about 30 observations.

These effects can be seen in diagrams 10 - 13, but not very clearly. The reason is that electrodes were placed so as to minimise beating. In this session the placement of electrodes was successful in this respect.

E. R. G. RESULTS

Measurements were made of the synchronous component of the evoked E.R.G. response. Electrodes were placed above and below the stimulated eye as illustrated on page 84 . The small amplitude of the synchronous E.R.G. responses obtained, coupled with the very poor signal to noise ratios, meant that E.R.G. measurements were not so reliable as the E.E.G. measurements, so that only the general trends of E.R.G. results can be regarded with confidence.

8. THE SYNCHRONOUS E.R.G. RESPONSE.

After about 20 seconds from onset of stimulation there is a synchronous E.R.G. component, which remains constant in amplitude and phase lag till at least 80 seconds from onset of stimulation. The variation during a single observation was, at best, $\pm 10^{o}$ in phase i.e. $\pm$ 3 milliseconds approximately in latency and $\pm$ 15% in amplitude. It was not possible to ascertain whether these variations were physiological or due to noise, and fixation variations.

9. THE AMPLITUDES OF THE SYNCHRONOUS COMPONENTS OF THE RESPONSES EVOKED IN THE E.R.G AND E.E.G. BY IDENTICAL STIMULI.

The steady-state synchronous component of the E.R.G. recorded from electrodes placed above and below the stimulated eye lies between 0.5 and 1 microvolt peak-peak. The steady-state synchronous component of the evoked E.E.G. response recorded from occpital electrodes lies between 1 and 5 microvolts peak-peak. Measurements were made between retinal illuminations of 1000 and 500,000 trolands peak and for stimulus wavelengths between 4337 $\mathring{A}$ and 6335 $\mathring{A}$. The E.R.G. response was always found to be less than the E.R.G. response for identical stimuli.

10. THE VARIATION WITH STIMULUS FRE UENCY OF THE PHASE LAG OF THE SYNCHRONOUS E.R.G. RESPONSE.

The variation with stimulus frequency of the phase lag of the synchronous E.R.G. response has been measured for the steady-state response between about 20 and 80 seconds from the onset of stimulation. The phase lag versus frequency graph is linear over the range 9 to 16 c.p.s. for a λ = 4337 $\mathring{A}$ stimulus. This was the only stimulus wavelength for which measurable records could be obtained (diagram 16.)

11. BEATS ARE NOT SEEN IN E.R.G. RECORDS.

This conclusion is based on a total of about 30 records.

12. APPARENT LATENCIES OF THE SYNCHRONOUS E.R.G. AND E.E.G. RESPONSES FOR IDENTICAL STIMULI.

For a blue stimulus centred on λ = 4337 $\mathring{A}$, the linear phase lag versus stimulus frequency graph was interpreted as indicating

an apparent latency τ' seconds for the synchronous E.R.G. response which is independent of frequency for the range investigated (9 - 16 c.p.s.). The graph is shown in diagram 16 and can be compared with the variation of phase lag with frequency in the E.E.G. for an identical stimulus, recorded using occipital electrodes. shown in diagram 15. The apparent latencies of 165 $\pm$ 15 milliseconds and 165 $\pm$ 20 milliseconds are identical within the limits of experimental error.

13. THE VARIATION OF THE APPARENT LATENCY OF THE SYNCHRONOUS E.R.G. RESPONSE WITH STIMULUS INTENSITY.

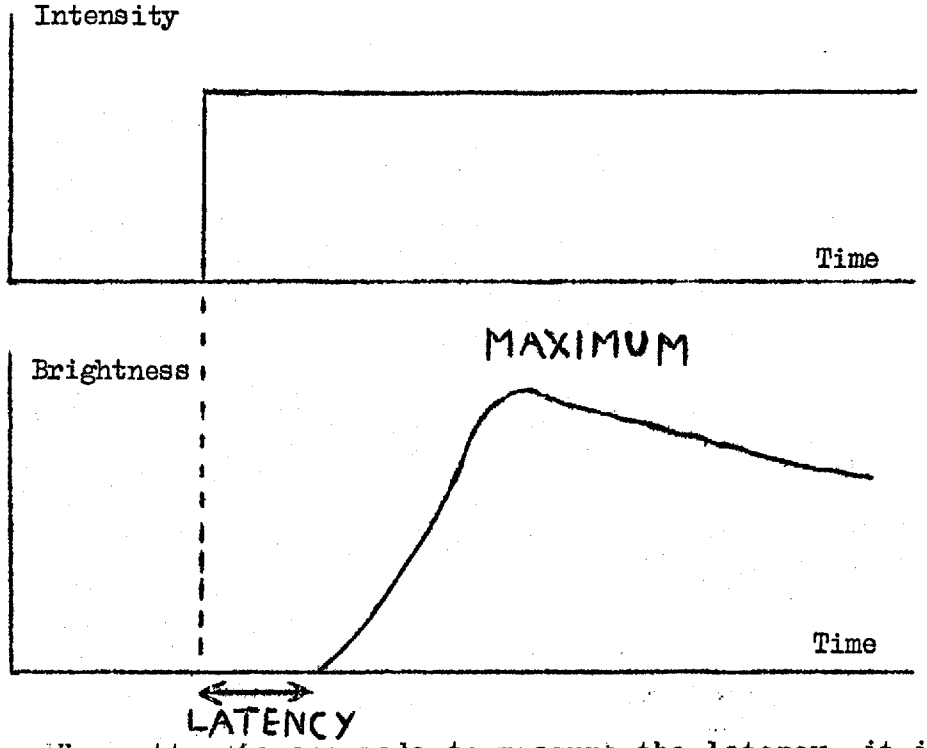
For a stimulus centred on λ = 4337 $\mathring{A}$ the apparent latency of the synchronous E.R.G. component increases as the intensity is reduced over a range of 50,000 to about 5,000 trolands.

CHAPTER 7 COMPARISON OF RESULTS WITH RELATED DATA

Measurements of perceptual latency

(1) Variation of latency with intensity.

When a test field with dark surround is suddenly and brightly illuminated, the course of the brightness sensation is of the form indicated below.



When attempts are made to measure the latency, it is often dubious whether the quantity measured is the latency, the latency of the maximum, or some intermediate time. There are large differences in stimulus size, intensity and the state of adaptation used in different investigations. Results differ considerably, but there is general agreement that latency falls as stimulus intensity is increased.

Experiments date from Exner in 1868. Early work is summarised by Bills (ref.37).

Pieron (ref.38) used the masking of a variable dim flash by a subsequent bright flash. He observed both flashes with the same eye. The criterion on which timing was based was a yes-no judgement of whether the first flash was visible. He found a difference of about 87 milliseconds between foveal cones and extrafoveal rods at high intensities by an extrapolation from lower intensities using the empirical formula:-

$$t = \frac{a}{i^n} + k$$

where t = latency difference
i = intensity
a,k,n = constants

However, the distinction between rods and cones was made by stimulation using red and blue filters. This would be effective only at low intensities (ref.39). Pieron also used motor reaction time measurements to investigate latency (ref.38). As with the masking technique, only the intensity dependent part of latency can be investigated. A criticism is that the efferent part of the response might also have a latency variable with intensity.

Arden and Weale (ref.39) presented a circular white field to each eye, the right of constant intensity and the left variable. The interval between the flashes was adjusted so that the perceptions were simultaneous. The criterion of simultaneity was the absence of apparent movement from one flash to the other. The binocular technique was preferred to the method of presenting both flashes to the same eye in order to avoid flicker effects.

Parafoveal measurements were performed with a 2.7' test field, and a 2.7' foveal constant field. At an illumination of about 0.12 trolands, the latent period difference was about 100 milliseconds for one observer, falling to about 25 milliseconds when the illumination was raised by 4 log. units. For another observer the latency difference fell from about 150 milliseconds to about 35 milliseconds over the same range. With a foveal 2.7' test field, and foveal 2.7' constant field the latency difference varied much less with intensity, and was always less than 30 milliseconds. At the highest intensities, the latency of the test patch showed a slight rise with intensity.

Roufs (ref.40) also used as a criterion of simultaneity the absence of apparent movement between two flashes. He used a 1^{o} circular field on a dark background, centrally viewed, and found no significant difference between monocular and binocular presentation. The method of subjective concurrence of a flash and a 400 millisecond tone of 1000 c.p.s., and the method of motor reaction time were also used. Except for one observer, all three methods gave results which fitted the formula

$$t - t_o = - T \log_e \frac{E}{E_o}$$

over the range 10 to 1000 trolands retinal illumination, where t and t_o are the perception delays of retinal illuminations of E and E_o trolands, and T is a constant of about 10 milliseconds. This held for both white (Xenon) and red (Neon) light. The results showed that the difference between reaction time and perception delay

in the range considered is almost independent of stimulus intensity.

If an oscillating pendulum is viewed binocularly with one eye covered by a neutral density filter, the path of the bob appears to be elliptical. This illusion was first described by Pulfrich. The explanation is often given that different retinal illuminations in the two eyes result in different perceptual latencies. Banister used the effect to measure the variation of perceptual latency with intensity (ref.41). Over the range investigated the latency difference between the eyes fell from about 18 milliseconds to about 5 milliseconds, at first rapidly, then levelling off as the intensity difference was varied over a 20:1 range.

If a light stimulus is suddenly switched on, the amplitude of the α rhythm is found to be suddenly reduced (α blocking). Bernhard measured the latency of α blocking caused by a 37^{o} white stimulus field (ref.42). He obtained results similar to those of Arden and Weale for the parafovea over a similar range of intensities. Measurements were made of the latency of the E.R.G. picked up from a corneal electrode. These supported the view that the increase in α blocking time as stimulus intensity decreased was mainly due to peripheral processes. The motor reaction time was measured simultaneously with the α blocking time. Bernhard concluded that the motor reaction occurred later than the α blocking. On the other hand the data on which Bernhard bases his judgement of the instant of initiation of the motor reaction involves an assumption about the unknown duration of the efferent part of the reaction. A rather small error in this would invalidate his conclusion.

Bates found the α blocking to be influenced by instructions given to the subject and that it had a closer correlation with times of discriminitive reactions than with simple reaction times (ref.43).

The author's measurements on the latency of the synchronous component of the evoked E.E.G. response reveal a relationship of the form $\tau' \propto \log$ (retinal illumination) for blue and green stimuli at high illuminations. Roufs found a similar logarithmic relationship for a 1^{o} foveal field at much lower retinal illuminations. The constant "T" in his formula which he found to be about 10 milliseconds, is 10-14 millisecs in the author's E.E.G. results. For lower retinal illuminations, the apparent latency τ' tends towards a constant value. For yellow stimuli there is little variation of τ' with intensity. However, the field size of 16^{o} is not comparable with Rouf's, nor Arden and Weale's conditions, nor is the greater part of the intensity range covered. Arden and Weale's results showed that the 16^{o} field would include regions whose latencies exhibited widely different dependences on intensity.

The variation of latency with colour.

Using a just noticeable difference technique with a 2^{o} foveal field Bills measured sensory latency (to maximum sensation) for various colours at three different levels of illumination (ref.32).

Assuming a 6 m.m. diameter pupil, the levels of retinal illumination were about 2, 4.5 and 36 trolands. Neither field size nor intensities are comparable with the conditions under which the synchronous evoked response was measured, but there is agreement

on a minimum value of latency in the yellow, and a decrease of latency with illumination for all colours except yellow, which shows little variation.

Kleitman and Pierons work is described in Chapter I. They found the build up of sensation in the order of red most rapid, then green then blue then white. Pieron used a similar technique to investigate the build up of saturation. He found the same order of events. (ref.44). The method is open to the objection that it does not in fact measure latency, but the relative effectiveness of flashes of different lengths. These measurements were for the fovea at much lower intensities than the E.E.G. measurements. Measurements on peripheral regions gave quitedifferent values of latency, and a different variation with intensity, indicating that results for widely different field sizes are not comparable. Pieron also measured reaction times for different coloured stimuli which had been adjusted to equal brightness. He found a longer time for blue than for red (ref.45).

Walraven and Leebeck, following De Lange (ref.46, 47, 48) used a 2^{o} foveal field and 100% sinusoidally modulated coloured stimuli of 2 trolands retinal illumination. (ref.49). Two stimuli of different colours illuminated the same retinal area alternately. Their relative phase was varied about 180^{o} until luminance flicker disappeared, indicating that the perceptions were exactly in anti-phase. They found a relative phase shift between the two perceptions which varied with frequency , so as to enable the calculation of a latency difference of about 30 milliseconds between the fundamental

red and green systems of Pitt, the red system being slower. The reduction of latency in the yellow indicated by the author's results was not found. However their data applied to a 2^{o} foveal region and much lower retinal illumination.

Lennox and Madsen recorded the electrical response to coloured flashes at the primary optic cortex and cornea of the anaethetised cat. (ref.50). For both cortical and retinal responses the amplitude rose and the latency fell with intensity. The colour of the stimulus affected the shape, amplitude and latency of the cortical response. Cortical responses were usually evoked at intensities ten times lower than those required to give a measurable retinal response, and the retinal latency was usually longer than the cortical. When the intensities of the stimuli were adjusted to give equal retinal latencies, the latency of the cortical response was longer for blue than for either green, yellow or red. For stimuli of equal energy, the cortical latency was shortest for responses to green and yellow, and a little longer for blue and red.

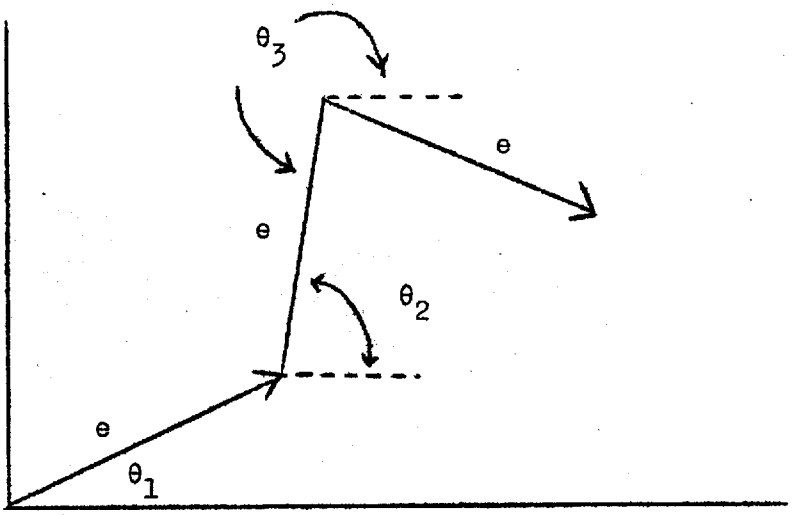
CHAPTER 8 DISCUSSION OF TECHNIQUE AND RESULTS

The method of rejection of unwanted signal.

It has been described how the sin(ωt) and cos(ωt) multiplying terms are generated by an alternator, which is driven by gears from a shaft on which the rotating polaroid is mounted. The polaroid produces the sinusoidal modulation of the light stimulus. Therefore, if the synchronous component of the evoked response is locked in phase to, and has the same frequency as the light modulation, it is similarly locked to the alternator. So it is only the synchronous component in the E.E.G that gives a d.c. output from the multipliers. All other components give a.c. outputs. The resistors and capacitors in the integrating circuits constitute a.c. potential dividers, whilst the d.c. outputs are fed to the recording potentiometers almost unattenuated. A time constant of 15 seconds is often used, obtained by means of a 330 ohm resistor and 45,000 microfarad capacitor. For noise of 1 second period, for example, the arrangement attenuates in a ratio of about 100:1 relative to the d.c. signal. For higher noise frequencies, the rejection is proportionately better.

The technique described in this thesis is designed to detect a synchronous signal buried in random noise, and in the presence of other unwanted nonsynchronous signals which may be related to stimulus. The technique is analogous to the well-known summation or averaging technique.

In summation methods , each successive identical stimulus synchronises an averaging sweep, so that the desired responses add in phase. The sum of N equal signals of amplitude E will be NE, and the average E, if each signal occurs exactly the same time after each successive stimulus. Activity unrelated to stimulus (i.e. noise) will sum out of phase, and thus average out.



The sum of N equal noise pulses of amplitude e can be calculated using Pythagoras theorem (see diagram), and is given by

$$\sqrt{\left[\sum_{i=1}^{N} (e_i \cos \theta_i)\right]^2 + \left[\sum_{i=1}^{N} (e_i \sin \theta_i)\right]^2}$$

$$= \sqrt{\sum_{i=1}^{N} e_i^2 + \sum_{i=1}^{N} \sum_{\substack{s=1 \\ s \neq i}}^{N} e_i\, e_s\, (\cos \theta_i \cos \theta_s + \sin \theta_i \sin \theta_s)}$$

If the phases of the noise pulses vary randomly, the θ's will be as often negative as positive, and the second summation will be zero. The sum of N pulses will be $\sqrt{N}$ e, and the average $\frac{e}{\sqrt{N}}$

Thus by averaging N responses, the signal to noise ratio is improved from $\frac{E}{e}$ to $\frac{\sqrt{N}\ E}{e}$.

It is in a somewhat similar manner that the technique described in this thesis improves the signal to noise ratio in the E.E.G. by using the fact that only the required synchronous component of the E.E.G. is at the same frequency as the stimulus, and bears a non-random phase relation to it.

The upper trace in diagram 9 is a direct E.E.G. record before and during a typical stimulation with a sinusoidally modulated 16^{o} light stimulus. The lower row of dots indicates the onset and frequency of the sinnusoidal light stimuli. The synchronous evoked component in the upper trace which is hidden by noise, and by α activity, is at the same frequency as the lower row of dots. The hidden synchronous component is here about 5 microvolts peak-to-peak, and on this scale would be represented by a sinusoidal trace of about 2 m.m. peak-to-peak. This can just be discerned visually in parts of the upper trace. It can be seen however that bursts of α activity occur before, and during stimulation.

Diagram 9 should be compared with diagrams 10 to 13 and diagram 8. These are records made before and during a stimulation similar

to the stimulation of diagram 9, but the raw E.E.G. has been processed by the analogue computer so as to reveal the synchronous component of the evoked response, and reject all else. The steady deflections of the pens from their centre-zero is caused by the synchronous response. The bursts of α activity are revealed by the much attenuated beating with the alternator visible on the record before and after stimulation.

Elimination of artifacts

A check was often made that the response of the analysing apparatus was caused by an evoked p.d., and was not due to electric or magnetic interference.

The fixed polaroid was suddenly rotated through an angle of 90°. The effect of this manoevre was to shift the phase of the stimulus modulation through 180° with respect to the alternator, while leaving all electric and magnetic sources of interference unaltered. If the pen deflections were in fact due to an evoked synchronous response, both pens would immediately start to cross the centre zero position, and assume new positions with deflections of the opposite sign, but the same magnitude, as initially.

At no point in the apparatus does the light beam strike surfaces which could introduce photoelectric p.d's into the analysing circuits.

Features of the technique

The use of a 2 m.m. exit pupil, careful fixation, steady lamp output and stabilised motor speed ensure that the stimulus

is of constant peak retinal illumination and constant frequency. It is also sinusoidal, and so any frequency-dependent effects may be examined separately, rather than confusing the picture as they do with non-sinusoidal stimuli. The light adaptation of the illuminated region of the retina closely corresponds to the steady level which would be produced by a constant light of $\frac{1}{2}$ (peak retinal illumination). The stimulus is therefore very simple, and after the initial 16-20 seconds, transient effects are absent from the photoreceptor-electrodes system (which then attains a steady state.) The apparatus selects only that component of the evoked response which is at the stimulus frequency.

By employing a long train of identical sinusoidally modulated stimuli at a precisely maintained frequency it was hoped to cause the human visual system between photoreceptors and scalp electrodes to function in a steady-state condition. It is found experimentally that from about 16 seconds to at least 80 seconds after the onset of stimulation this is true to within $\pm$ 10% of the amplitude of the synchronous evoked component and $\pm$ 1 milliseconds in its latency (page 55). This steady state functioning which is independent of large fluctuations in intrinsic brain activity (page 55) is rather different from the type of functioning produced by a single flash, the response to which is often analysed by the use of summation techniques. So it might be envisaged that a study of this carefully induced steady state functioning might be complementary to the "single shot" studies. It might possibly reveal details of the underlying physiological mechanisms of brightness and colour

vision operating in the conditions of complex patterned visual fields encountered in everyday vision, which may not be evident in the quite different "single shot" stimulus conditions.

Support for this view can be adduced from the experiments of Armington (ref.51). He used rectangular wave flashes of an 8^{o} stimulus field of constant peak intensity. The stimulus was viewed through a 1 m.m. artificial pupil. Fifty occipital and retinal responses were averaged for various intensity levels at a flash rate of 2 per second. Although retinal responses showed comparatively little percentage variation, the main features of the occipital responses were complexity of waveform, and variability of amplitude and waveform. The variation of the occipital response with intensity was also complex, and variable. Armington desired that responses to successive flashes should not overlap, and showed that to be the case at 2 flashes per second.

In the author's technique it is the average response that is measured. Variations between successive responses, other than long-term changes, are lost. So it cannot be decided here whether the variability observed in responses to widely separated flashes is reduced when successive responses interact, or whether the author's apparatus has rejected any variations.

It should be pointed out that summation techniques are not restricted to "single-short" stimuli. They could be used in steady-state conditions also, and with some advantages over the author's technique.

It might be expected that the technique described in this thesis would give simpler results than techniques in which more variables are involved such as eye pupil diameter, stimulus waveform, the waveform of the evoked response, and level of light adaptation of the retina.

It has been already mentioned that the technique described here is analogous in some respects to the well known technique of summation. An advantageous feature though, is the clear on-line presentation of changes in the evoked response. For example, the initial stages of the computer output are immediately seen during the progress of the experiment to be caused by a systematic change in the synchronous signal, rather than being due to noise or nonsynchronous signal. This would not be so obvious if the steady accumulation of responses were being observed, although of course the information would be available. Further analysis of the data though, would be required to reveal such features. Again, a short-term high amplitude change in synchronous signal is immediately seen on-line using the present technique. This sort of effect would easily be averaged out and lost when using a summation technique. A further advantage is that any regularities in the noise are evident. For example, the beating between the α rhythm and alternator frequency enables deductions to be made concerning the nature of the synchronous response.

A disadvantage of the technique when compared to summation techniques is that there is no information available about the waveform of the evoked response. However this is merely a limitation

of the present apparatus, since a simple modification would make waveform data available. Low amplitude, short-term signal changes cannot be examined when the present technique is employed. For example, if the integration time is reduced in an attempt to make a direct examination of the early stages of the synchronous component, noise rejection is so impaired that the records are unintelligible. This measurement could easily be carried out using summation apparatus. A further limitation when compared with summation methods which separately store each response to each stimulus flash is that any variations in the responses to successive flashes are lost.

The intepretation of the measured phase lag.

In the equations:-

$$\phi = k + 360\, f \qquad \phi^{\circ} = \text{phase lag}$$

$$\tau' = \frac{\phi}{360\,\delta f} = \tau + \frac{\delta k}{360\,\delta f} \qquad \tau \text{ secs} = \text{latency of synchronous component}$$

k° is any phase shift, not due to the latency τ, occurring between the photoreceptors and the electrodes. If k varies linearly with frequency over the range investigated, the measured $\frac{\delta \phi}{360\,\delta f}$ would include a contribution $\frac{\delta k}{360\,\delta f}$ indistinguishable from τ. The quantity $\frac{\delta \phi}{360\,\delta f} = \tau'$ will therefore be referred to as the apparent latency.

However if k varied nonlinearly with f, the measured phase lag versus frequency graph would be nonlinear. This was not found so over the range 11 - 16 c.p.s., and in fact over the range 5-29 c.p.s. This suggests that k varies slightly, if at all, with f.

The significance of τ'

The objection could be made, that by arbitrary adjustment of the relative intensities of the stimuli the shape of the τ' versus λ curve could be altered. However it can be seen by reference to the phase lag versus intensity graphs that this is only true to a very limited extent. At a retinal illumination of 500,000 trolands peak for all stimuli, the dip in the yellow is still pronounced. If stimuli were independently adjusted between 500,000 trolands peak and 1,000 trolands peak, it would still not be possible to obtain equal values of τ' for all colours.

Under the conditions of observation, viz. good fixation over about 80 seconds and high retinal illumination, it is possible that colour vision would be grossly disturbed. In particular, McCree's results show saturation and wavelength discrimination to be affected by voluntary fixation for a high proportion of observers. The author is particularly susceptible to this effect. (author is observer D.R. ref. 22). In addition, when retinal illumination passes a certain value, different for each wavelength, saturation starts to fall with increasing illumination. At the highest illuminations used by the author there was a subjective impression that desaturation was almost complete. One might expect that the mechanisms underlying colour discrimination were almost inactive during observations at the highest intensities (500,000 trolands.) On the other hand the τ' versus intensity graphs are interpreted to mean that the τ' versus λ curve at 500,000 trolands peak is similar, though with a less pronounced dip in the yellow, to the 1,000 trolands

peak curve. The maximum level at which standard colour matching data has been obtained in the N.P.L. measurements is 1000 trolands (ref.52). Also, it has been found that although colour matches break down at glare levels of adaptation, they still hold at 1,000 trolands (ref.2). This suggests that the lowest intensities used in the present investigations were not such as to disturb colour vision.

Since τ' is not a monotonic function of λ, it does not appear possible that it could be the only means of transferring colour information from photoreceptors to cortex.

The measuring technique selects only that component of the total evoked response which is at stimulus frequency. The complete response could contain other harmonics and sub-harmonics, such that the waveform of the evoked response might form an additional channel capable of carrying hue data. This hypothesis could be investigated by a simple development of the apparatus described, which simultaneously analysed at a series of harmonics and sub-harmonics of the stimulus frequency.

The τ' versus λ curve bears a resemblance to the saturation versus λ curve for spectral stimuli measured by Martin Warburton and Morgan for a 2° field of about 30 trolands retinal illumination. (ref. 2, p.162). In addition, an increase of intensity to very high levels reduces the saturation of spectral stimuli. This effect was very noticeable during the present observations. The τ' versus λ curve shows analogous effects (diagram 6). The similarity of the graphs suggested that a measurement should be made on a white stimulus, adjusted to the same retinal illumination as the colours

already investigated. If a short τ' did correlate with a low saturation, it was to be expected that white would have a τ' less than yellow. The apparatus was modified, and measurements carried out on a white of about 5500 ^{o}K colour temperature. (diagram 17). The τ' was found to be intermediate between the yellow and the blue-green-red values. Thus the suggested correlation between τ' and saturation was not supported, and the experiment suggested that the synchronous component measured for a white stimulus was simply the vector sum of responses to all colours.

The initial stage of the synchronous component of the evoked p.d.

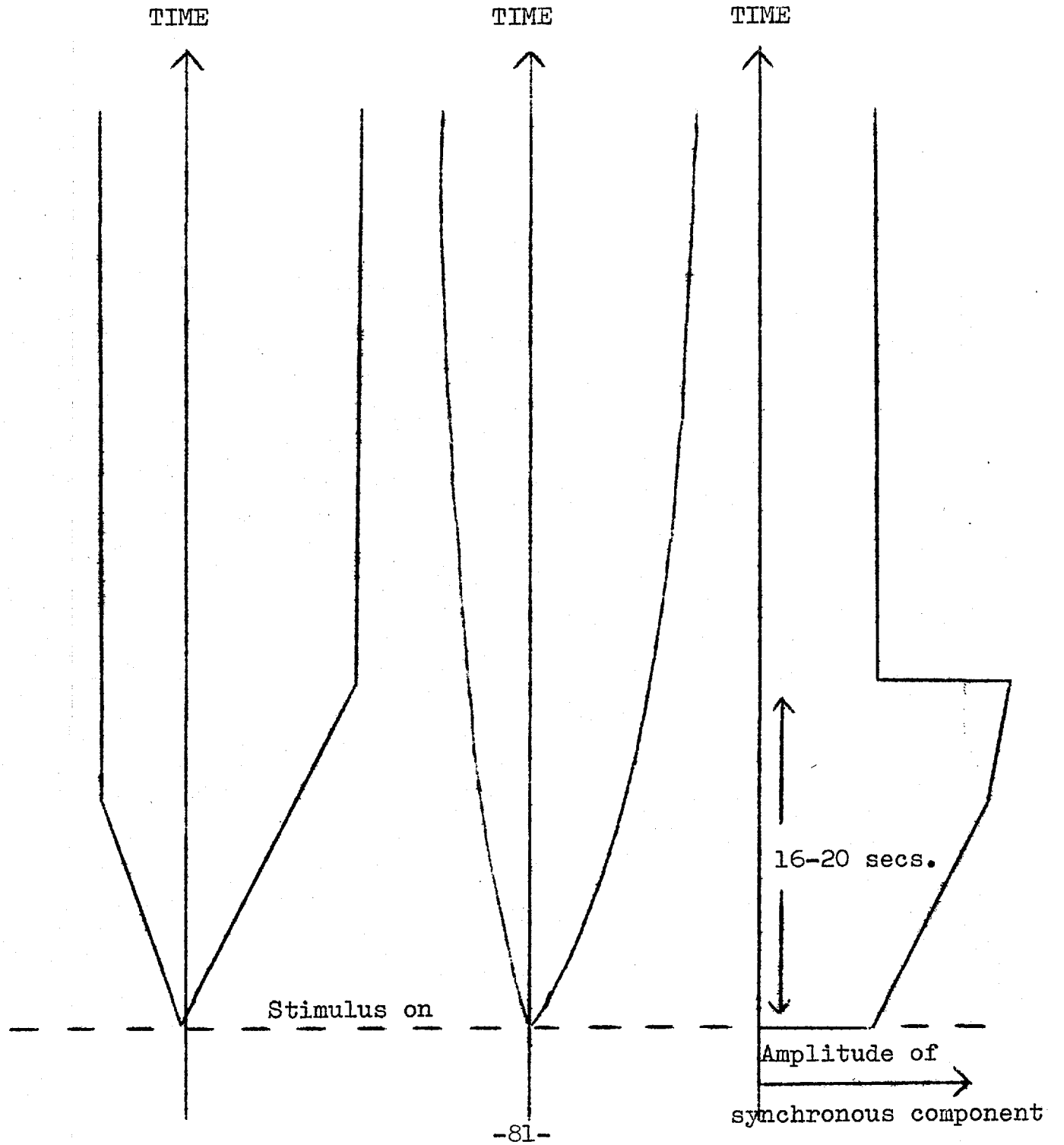
For the first 16-20 seconds of stimulation the records indicate a much larger response than the final steady level. This was most pronounced when the eye and head were held still from the onset of stimulation. The large response appears to fall to the steady level quite suddenly (diagram 7,8). The analogue computer output appears to be of the form (a) in the diagram on page 81 , whereas a steady input gives shape (b). Curve (c) is the suggested variation with time of signal amplitude at the electrodes, which would produce the observed record (b).

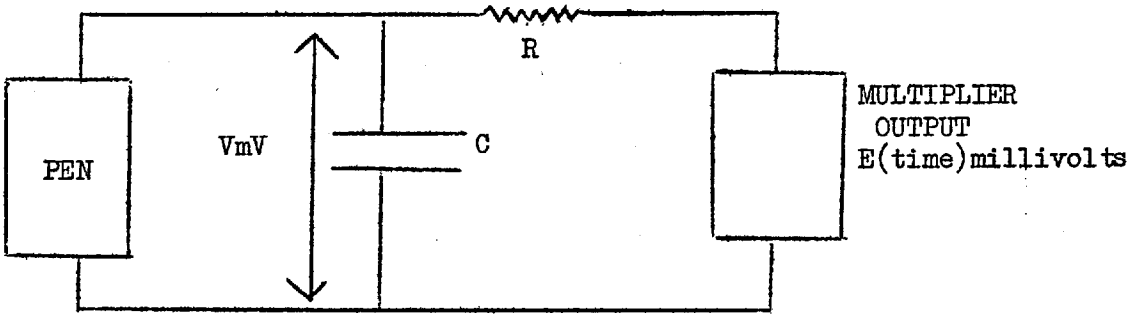
Recordings were made at shorter time constants, in an attempt to measure directly the early stages of the response, but the efficiency of noise rejection was reduced to such an extent that results were inconclusive.

(a) Record of output of analogue computer with E.E.G. input as in diagram 8. (idealised)

(b) Record of output of analogue computer when calibration input of steady amplitude supplied.

(c) Suggested time course of synchronous component in E.E.G. to produce (a) (idealised).





The pen deflection is proportional to V , the p.d. across C.

If q is the charge on the capacitor at any instant:-

$$\frac{q}{C} + R\left(\frac{dq}{dt}\right) = E$$

Now $V = \frac{q}{C}$

$$\therefore\ V + RC\left(\frac{dV}{dt}\right) = E$$

It is found, experimentally that $V = mt$ where m = constant, for the first 16-20 seconds after onset of stimulation.

Therefore $mt + RCm = E$ for the first 16-20 seconds.

In the initial stage, then, the output of each multiplier, and hence the signal at the electrodes is of the form $A + Bt$ where A and B are constants. Calculations were made on the record of diagram 8 and the results are those illustrated on page 81. In many records the kink in the amplitude time curve on page 81 did not occur. This may have been due to a shift in fixation.

The variation with time of the amplitude of the synchronous component during the initial 16-20 seconds is completely different from what might be expected from measurements on the time course of light adaptation.

W.D.Wright used a binocular matching technique to investigate the progress with time of light adaptation. (ref. 2, p.222). Results for a centrally viewed 5^{o} adapting field of 8,000 trolands and a $1^{o} \times 2^{o}$ test patch of 150 trolands showed a rapid loss of sensitivity over about the first 20 seconds, then a levelling off which almost reached completion after 100 seconds.

A similar form of reduction of the amplitude of the synchronous component of the evoked response is not found. Instead, as described above, it continues to rise rather than fall, for the first 16-20 seconds, and then exhibits a sudden fall to a level which then remains constant. This occurs even at 1000 trolands peak, corresponding to a steady level of light adaptation of 500 trolands, which is comparable with the intensities used by Wright. On the other hand, the $2^{o} \times 1^{o}$ field used by Wright is quite different from the 16^{o} field used by the author. The 16^{o} field stimulates, in particular, a large number of rods.

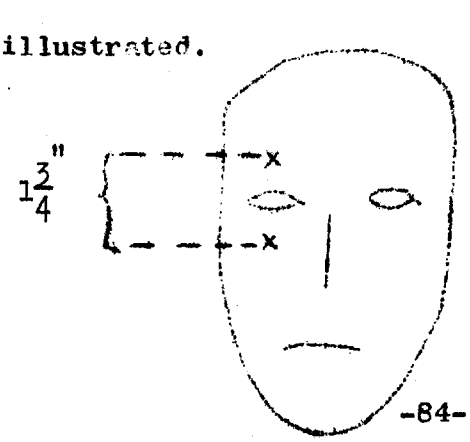
However the initial transient stage of the synchronous response appears similar in form for all colours, and for levels between 1000 trolands peak and 500,000 trolands peak.

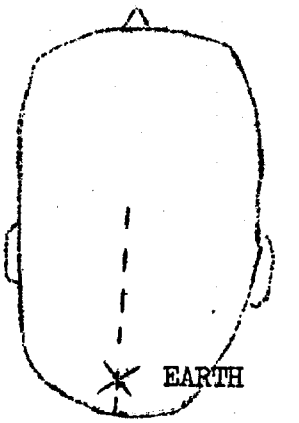
Now when the spectral sensitivity of a 2^{o} foveally viewed region is measured psychophysically for very low light intensities, a curve peaking at about 510 $m\mu$ is obtained, which is characteristic of rod functioning. As the light intensity is increased, the peak of sensitivity shifts towards the red, and at very high intensities is located around 560 $m\mu$. This curve is characteristic of cone function. The shift is called the Purkinje shift,

and suggests that as the light intensity rises, rod activity is not increasing at the same rate as cone activity. Instead the activity of the rods is being depressed relative to cone activity to an extent which increases as light intensity rises. So at high intensities, and particularly in the red, there is evidence that rod activity is much reduced. Since the initial stages of the synchronous component are observed to be similar for all colours, and from 1000 to 500,000 trolands peak retinal illumination, it is suggested here that this initial large transient response may be quite unconnected with rod activity. Since the transient response also appears to have little correlation with the temporal course of light adaptation, and since the fall to the final steady-state amplitude clearly occurs very suddenly, a central neural adaptation process is postulated. No pronounced subjective effects paralleling this electrophysiological transient were noticed in any of about 90 observations of the effect. Some subjective change at the 16-20 seconds mark might have been expected.

Measurements on the E.R.G.

Measurements were made on the synchronous evoked component of the E.R.G., using electrodes placed near the stimulated eye as illustrated.





This placement was found to give the lowest noise and largest signal of the electrode placements tested. The initial reason for attempting E.R.G. measurements was to investigate whether the synchronous component of the E.E.G., being of amplitude only 1 to 4 microvolts peak-to-peak, could be due to a spread backwards of a large E.R.G. (typically up to 100 microvolts.)

It was found experimentally that the synchronous component of the E.R.G. was 0.5 to 2 microvolts peak-to-peak.

This amplitude of E.R.G. response is much smaller than has been described in the literature. The small response may be due to the light adaptation produced by a sinusoidally modulated stimuli. The short flashes often employed do not result in such a high level of light adaptation. Other factors leading to a small response may be the rather small 16^{o} stimuli field, and to not using a corneal electrode.

Using a corneal wick electrode E.D.Adrian recorded the E.R.G. in response to short, widely separated flashes. (ref.53). He found that the individual responses to a series of flashes was reduced when the flash rate exceeded about 10 per second. Adaptation to quite small light intensities also reduced the E.R.G. response. For example, the response to a 30 f.- c. flash was reduced 2 to 3 times by a 2 f. - c. background. Granda used a circuit timed to the flash frequency in order to improve the signal to noise ratio. (ref.54). For a 25% - 75% light to dark ratio in a 60^{o} stimulus field he recorded evoked potential differences up to 30 microvolts peak-to-peak for all colours. At 35 flashes

per second, where he considered the photopic response would predominate, he found stimuli of equal retinal illuminations to give responses of similar amplitudes throughout the spectrum. However he did not measure the response waveform, nor the latency, so this result does not demonstrate that the E.R.G. does not carry colour information. Armington et al. averaged the responses to each of a series of flashes, (ref.55). The light source was a ribbon filament tungsten lamp. Measurements were carried out for a series of intensities, colours, and stimulus field sizes. The waveform of the response was found to vary with stimulus wavelength. The amplitude of the evoked p.d. was greatly increased at higher field sizes. Maximum spectral sensitivity was in the blue-green. For a 16^{o} stimulus field, for example, the response to an orange flash reached 18 microvolts at 18 flashes per second. At 5 flashes per second the response to blue reached 80 microvolts. For a 3^{o} foveal field up to 4 microvolts was recorded for orange, and 20 microvolts for blue. A corneal electrode was used.

Difficulty was caused in the present work by the poor signal to noise ratios encountered, which were never better than 40 - 60 times more noise than signal. In addition, eye movements produced large pulses, which at times caused blocking of the amplifiers. It was found necessary to use a 30 second time constant, instead of the 15 second setting used in the E.E.G measurements so as to improve noise rejection. Fixation difficulties were thereby increased.

Intepretation of E.R.G. measurements.

With the amplification required for measurement of the small E.R.G. signals, the noise level was so great that the apparatus was often operating beyond its limit of linear phase and amplitude recording. (page 40). The E.R.G. measurements are therefore not so reliable as the E.E.G. measurements, and little confidence should be placed in anything but their general trends.

However it does seem established, that using the electrode placements shown above, the synchronous E.R.G. component is smaller in amplitude than the synchronous E.E.G. component produced by an identical 16^{o} stimulus. This has been found to hold for sinusoidal stimulus intensities from 1000 trolands peak to 500,000 trolands peak, and for stimulus wavelengths from 4337 $\mathring{A}$ to 6337 $\mathring{A}$. If the 0.5 to 2 microvolts p. - p. E.R.G response had been as large as the 2 to 6 microvolts synchronous E.E.G. component, the amplification could have been reduced so that the apparatus would not have been driven beyond its linear region.

This suggests that the E.E.G. is not due to a backwards spread of the E.R.G. The reliability of E.R.G. latency measurement is not sufficient to enable many further deductions to be made, and in fact it cannot be said with certainty that the synchronous E.R.G. component detected is not due to a forward spread of the E.E.G.

A blue stimulus centred on 4337 $\mathring{A}$ gave a sufficiently large response to enable the apparent latency of the synchronous E.R.G. component to be measured as 165 $\pm$ 15 milliseconds, and compared with an apparent latency of the synchronous E.E.G. component of

165 $\pm$ 20 milliseconds. (diagrams 15, 16). Both measurements were made during the same recording session.

In so far as the E.R.G. data is reliable, this result indicates that for a 16^{o}, λ = 4337 $\mathring{A}$ stimulus, the synchronous response in the E.E.G. measurements using occipital electrodes occurs simultaneously within the limits of error with the synchronous response in the E.R.G. recorded using electrodes $\frac{1}{2}$" above and below the stimulated eye. If the E.R.G. response played a role in the transmission of colour information to cortex there would be expected to be a latency difference between E.R.G. and E.E.G. corresponding to the transmission time from retina to cortex. So it appears that the synchronous evoked component of the E.R.G. detected by the apparatus is unlikely to play a part in the transmission of colour information to cortex. It should be emphasized however that the reliability of the E.R.G. data is questionable.

Discussion of the quantity measured in the E.E.G. experiments.

The arousal of the synchronous evoked component of the E.E.G. would seem to occur some time after the arrival at cortex of the first impulses.

Using an averaging technique, Cobb and Dawson found the latency of first arrival at cortex to be about 25 milliseconds for short white isolated flashes. (ref. 56). Assuming that the pupil diameter returned to about 6 m.m. between flashes, the integrated retinal illumination was about 10,000 troland.seconds, and the peak illumination was about 10^{8} trolands. With an 80 times reduction in intensity, the latency was increased to about 30-35 milliseconds.

The author's results were obtained at an integrated retinal illumination (per modulation cycle) of 1500 troland.seconds, with a peak of about 50,000 trolands, but the correlation of physiological stimulus intensities of an isolated short flash, and one of a long train of sinusoidal 50 - 100 millisecond flashes is of dubious validity.

Cobb and Dawson found the largest component of the response to a single isolated flash to occur with a latency of 90 - 100 milliseconds, and to be of magnitude 5 - 10 microvolts. For a 16^{o} white stimulus the amplitude of the synchronous component is 2 - 6 microvolts peak-to-peak, and latency about 165 milliseconds, for a stimulus intensity much less than that used by Cobb and Dawson as described above. An increase in stimulus intensity so as to bring the integrated retinal illumination of each flash to the level used by Cobb and Dawson would reduce the apparent latency to about 130 milliseconds.

A tentative identification is made of the synchronous component with the largest component in the single flash response. However it is likely that interaction would occur between the responses to successive flashes at some or all levels, so that the form of the evoked response to a single isolated flash might be quite different to the response to a sinusoidal flash which was one of a long series of identical flashes.

The distinction between the synchroncus component of the evoked response in the E.E.G., α locking and intrinsic α activity.

The interpretation is advanced that for stimulus modulation frequencies separated by at least about 0.5 c.p.s from the α frequency, the synchronous evoked response is a true evoked p.d., in that its amplitude and latency are independent of the amplitude of the α activity, and independent of the difference between stimulus frequency and α frequency. Also that the α frequency is independent of whether the 16^{o} sinusoidally modulated light stimulus is on or off, and independent of the stimulus frequency, providing that it is at least 0.5 c.p.s. removed from the α frequency. So the α activity is separate from the mechanisms underlying the synchronous evoked response to a 16^{o} stimulus over the frequency range investigated (9 - 17 c.p.s.) providing that the frequency difference exceeds 0.5 c.p.s.

Experimental Evidence

In the analysing apparatus, the amplified E.E.G. is multiplied separately by sine (ωt) and cosine (ωt) where $\omega = 2\pi f$ (stimulus modulation frequency f). Any periodic signal in the E.E.G at a frequency f^{1} which differs from the stimulus modulation frequency will cause beating at frequency $(f - f^{1})$. The beating will be attenuated to an extent dependent on the time constant of the integrating circuits.

Such beating can be seen in diagrams 10 - 13. These are records of the outputs of the analogue computer before and during light stimulation. Table 1 shows the beat frequency measured from

such records, and the calculated frequency of the non-synchronous signal in the E.E.G. which produced the beats. It can be seen that to within ± 0.2 c.p.s. the frequency of the non-synchronous signal is unaffected by whether the light stimulus is on or off. To within ± 0.2 c.p.s. the non-synchronous frequency is unaffected by stimulus frequency. Since the stimulus frequency is constant to ± 0.2 c.p.s these are within the limits of experimental error. Table 2 summarises the results of other calculations such as that given in Table 1.

TABLE 1

16° SINUSOIDALLY MODULATED, 50,000 TROLAND(PEAK) WHITE STIMULUS				
ANALYSIS & MODULATION FREQUENCY. c.p.s	BEAT FREQUENCY c.p.s		NONSYNCHRONOUS FREQ.c.p.s	
	STIMULUS ON	STIMULUS OFF	STIMULUS ON	STIMULUS OFF
16.3	6.7	6.7	9.6	9.6
14.9	5.1	5.3	9.8	9.6
12.5	2.9	3.1	9.6	9.4
11.9	2.0	2.0	9.9	9.9

TABLE 2

STIMULUS WAVELENGTH	FOR VARIOUS STIMULUS FREQUENCIES, NONSYNCHRONOUS FREQUENCY. c.p.s. FOR STIMULUS ON OR OFF.	
	ON	OFF
5780 Å	9.3 ± 0.1	9.2 ± 0.2
5885 Å	9.7 ± 0.2	9.6 ± 0.3

An attempt was made to investigate the nature of the non-synchronous signal. Immediately after the measurements of beat frequency given in Table 1, the observers α frequency was measured before, and during light stimulation by using an A.E.I. pen writing oscillograph. The α frequency before stimulation was found to be 9.7 ± 0.1 c.p.s and during stimulation 9.8 ± 0.3 c.p.s as compared with 9.6 ± 0.3 c.p.s. given in Table 1 for the frequency of the nonsynchronous signal. Additional evidence that the nonsynchronous signal is the intrinsic α activity is that beating occurs in bursts in a similar manner to the α activity.

It can be seen in diagrams 10 - 13 that the d.c. level of the pens does not appear to be affected by the bursts of beats i.e. by the bursts of α activity. The d.c. levels of the pens were measured over a time equal to the duration of a burst before the burst, and after the burst. The ratio of the amplitude of the synchronous response during the burst to the amplitude before the burst was calculated, and also the ratio of the amplitude after the

burst to the amplitude before the burst. This was done for a total of 24 bursts. If there is no systematic change in synchronous response before, during and after a burst these ratios should average out to unity. The ratios were on average, (after allowing for the time constant) :- amplitude during burst: amplitude before burst = 1.01, and amplitude after burst: amplitude before burst = 0.93. So it can be concluded that to at least 7% the amplitude of the synchronous response is unaffected by the amplitude of α activity. A similar calculation showed that the tangent of the phase lag is unaffected to at least 8% by the amplitude of α activity.

Attempts were made to see whether the synchronous component and α activities were still independent, when the stimulus frequency was separated by less than about 0.5 c.p.s. from the α frequency. Beating was found to be of such low frequency that it passed through the integrating circuits with little attenuation so that results were unintelligible. Also it was found that the $\pm$ 0.2 c.p.s. constancy of stimulus frequency was insufficiently precise so that the difference between stimulus and α frequencies was subject to large percentage fluctuations during the experiment.

SUMMARY

An optical stimulator has been constructed, which will produce a sinusoidally modulated stimulus of constant peak retinal illumination and modulation frequency.

An analogue computer has been developed which is designed to detect any evoked component in the E.E.G. which is at stimulus frequency, in the presence of a large background of noise and unwanted signal.

Such a component (synchronous component) has been detected, and found to have a constant amplitude and phase lag from about 16 to 80 seconds from the onset of stimulation.

During this steady-state regime the amplitude and phase lag of the synchronous response have been measured for various stimulus frequencies. The phase lag is proportional to stimulus frequency. This is interpreted as indicating an apparent latency τ' milliseconds of the synchronous component, which is independent of frequency.

For a constant modulation frequency the phase lag (and hence apparent latency) is inversely proportional to the logarithm of retinal illumination at high intensities for blue and green stimuli. At low intensities the apparent latency tends towards a constant. For a yellow stimulus there is little variation with intensity.

For stimuli of different colours, but the same retinal illumination, the apparent latency is longer for blue and green than for red, and least for yellow. This effect is accentuated at low intensities, and diminished at high intensities.

The apparent latency for white lies between the values for yellow and blue stimuli of equal retinal illuminations. So apparent latency is unlikely to correlate with saturation.

During the initial 16-20 seconds of stimulation there is a transient synchronous response in the E.E.G. of the form:-

amplitude = $A + Bt$ where A and B are constants.

The amplitude falls suddenly at 16-20 seconds to the steady-state value. Rods are unlikely to play an important role in this effect.

The synchronous response is independent of α activity. Conversely, the α frequency is independent of the light stimulus. Therefore the synchronous response is a true evoked p.d.

Electrodes above and below the stimulated eye were used to make E.R.G. measurements. Reliability was adversely affected by poor signal to noise ratios. However, the amplitude of the synchronous E.R.G. component can be said to be less than the amplitude of the synchronous E.E.G. component for identical stimuli. For a blue stimulus, the apparent latency for E.R.G and E.E.G. synchronous components were equal. Therefore the E.E.G. synchronous component is unlikely to be a spread backwards of the E.R.G. Also, the synchronous E.R.G. component is unlikely to play a part in the transmission of colour information to cortex.

REFERENCES

reference number

1. W.D.WRIGHT (1928) Trans. Op. Soc. 30, 141
2. W.D.WRIGHT (1946) Researches on Normal and Defective Colour Vision.
3. J.GUILD (1931) Phil. Trans. Roy.Soc. 230A, 149
4. W.S.STILES (1955) Physical Society Yearbook pp.44-65
5. R.GRANIT (1955) Receptors and Sensory Perception. Yale Univ.Press.
6a. W.RUSHTON (1963) J.Physiol. 168, 345
6b. W.RUSHTON (1963) J.Physiol. 168, 360
6c. W.RUSHTON (1963) J.Physiol. 168, 374
7. W.RUSHTON (1962) Sci.Amer. 207, 5, 120
8. D.H. HUBEL (1963) J.O.S.A. 53, 1, 58-66
9. D.H. HUBEL (1963) Sci.Amer. 209, 5, 54
10. S.W.KUFFLER (1953) J.Neurophysiol. 16, 37
11. G. SVAETICHIN and E.F.MacNICHOL Jr. Annals of N.Y. Ac. of Sciences 74, 385-404
12. J.H.PARSONS (1924) Colour Vision. Cambs.Univ.Press.
13. T.TOMITA (1963) J.O.S.A. 53, 1, 49.
14. S.L.POLYAK (1941) The Retina. Univ. of Chicago Press.
15. N.KLEITMAN and H.PIERON (1925) Comptes Rendus, Acad. des Sciences, Paris, 180, 393-6
16. J.M.ENOCH (1961) J.O.S.A. 51, 1122
17. R.W.DITCHBURN and D.K. FENDER (1955) Optica Acta 2, 128
18. R.W.DITCHBURN (1955) Optica Acta, 1, 171
19. L.A.RIGGS and S.U.TULUNAY (1959) J.O.S.A. 9, 741-745
20. M.B.CLOWES (1962) Optica Acta 9, 65-68
21. K.J. McCREE (1960) Optica Acta 7, 281-290
22. K.J. McCREE (1960) Optica Acta 7, 317-323
23. K.J. McCREE (1958) Thesis. Univ. of London.
24. W.E. Le GROS CLARK and G.B.PENMAN (1933) Proc.Roy.Soc. 114B, 291
25. W.E. Le GROS CLARK (1942) Trans.Ophth.Soc. of U.K. 62, 229
26. W.E. Le GROS CLARK and L.CHACKO Nature 160, 123

reference number

27. HANDBOOK of PHYSIOLOGY Vol. 1.

28. W.G.WALTER (1956) Nature London 177, 710

29. G.O.KIBBLER et al. (1949) Nature, London 164, 171

30. G.O.KIBBLER and D.RICHTER (1950) E.E.G and Clin. Neurophysiol. 2, 227

31. J.A.V. BATES (1950) E.E.G and Clin.Neurophysiol 2, 227

32. R.W.LANSING (1957) E.E.G and Clin.Neurophysiol. 9, 497

33. D.H.FENDER and S.MAYNE (1960) Optica Acta 7, 129-135

34. W.G.WALTER et al.(1946) Nature, Lond. 158, 540

35. MUIRHEAD PUBLICATION E - 1000 p.38.

36. G.W. DUMMER (1956) Fixed Resistors : Pitman

37. W.T.WALSH (1958) Photometry : Constable

37a. M.A.BILLS (1920) Psychol. Monographs. Vol. 28, 1 - 101

38. H.PIERON (1925) Annee Psychol. 26, 1-30

39. B.G.ARDEN and R.A.WEALE (1954) Proc.Roy.Soc. 142B, 258-267

40. J.A.ROUFS (1963) Vision Research 3, 81-91

41. H.BANISTER (1932) Discussion on Vision at Imperial College. Pub. by Phys.Soc.

42. C.G. BERNHARD (1940) Acta Physiol.Scand. Vol.1. suppl.1

43. H.PIERON The Sensations : London, F.Muller (1952)

44. H.PIERON (1932) Discussion on Vision at Imperial College. Pub. by Phys.Soc.

45. H.PIERON (1932) C.R.Soc. Biol. Paris 111, 380-382

46. H. de LANGE Dzn. (1952) Physica 18, 935

47. H. de LANGE Dzn. (1958) J.O.S.A. 48, 11, 777-784

48. H. de LANGE Dzn. (1958) J.O.S.A. 48, 11, 784-789

49. P.L.WALRAVEN and H.J.LEEBECK (1964) J.O.S.A. 54, 1, 78

50. M.A.LENNOX and A.MADSEN (1955) J.Neurophysiol. 18, 413

51. J.C. ARMINGTON (1964) Vision Research 4, 179-192

52. W.S.STILES and J.M.BURCH (1959) Optica Acta, 6, 1-26.

53. E.D.ADRIAN (1945). J.Physiol. 104, 84-104

54. A.M.GRANDA (1960) J.O.S.A., 51, 648

55. J.C.ARMINGTON et al. (1961) J.O.S.A., 51, 877-886

56. W.A.COBB and G.D.DAWSON (1960) J.Physiol. 152, 108-121

PHOTOGRAPHS AND DIAGRAMS

Photograph 1. General view of apparatus.

Photograph 2. Optical system.

Photograph 3. Electrode placement for E.E.G. recordings.

diagram number.

1. Block diagram of apparatus.
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3. Integrating circuits.
4. Stabilised variable speed motor supply.
5. Apparent latency versus λ showing errors. 50,000 Trolands peak.
6. Apparent latency versus λ for three retinal illuminations.
7. Output of analogue computer when synchronous calibration signal of frequency 14.9 c.p.s and constant amplitude is applied.
8. Output of analogue computer when electrodes connected to observers scalp and constant frequency, constant amplitude sinusoidally modulated light observed.
9. Direct recording of E.E.G before and during observation of stimulus similar to that in diagrams 8 and 10-13.
10. Output of analogue computer before and during stimulation with sinusoidally modulated light of constant frequency and peak retinal illumination. Frequency 11.4 c.p.s.
11. As diagram 10. Frequency 12.5 c.p.s.
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13. As diagram 10. Frequency 16.3 c.p.s.
14. Phase lag of synchronous evoked component versus stimulus frequency. Range 5-29 c.p.s.
15. Phase lag versus frequency 11-16 c.p.s. λ = 4387. E.E.G.
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17. Phase lag and amplitude versus frequency at constant intensity λ = 4387 Å.
18. Phase lag and amplitude versus intensity at constant frequency λ = 4387 Å.
19. Phase lag and amplitude versus frequency at constant intensity λ = 4577 Å

diagram
number

20. Phase lag and amplitude versus intensity at constant frequency λ = 4577 Å

21. Phase lag and amplitude versus frequency at constant intensity λ = 5449 Å

22. Phase lag and amplitude versus intensity at constant frequency λ = 5449 Å

23. Phase lag and amplitude versus frequency at constant intensity λ = 5780 Å

24. Phase lag and amplitude versus intensity at constant frequency λ = 5780 Å

25. Phase lag and amplitude versus frequency at constant intensity λ = 5885 Å

26. Phase lag and amplitude versus intensity at constant frequency λ = 5885 Å

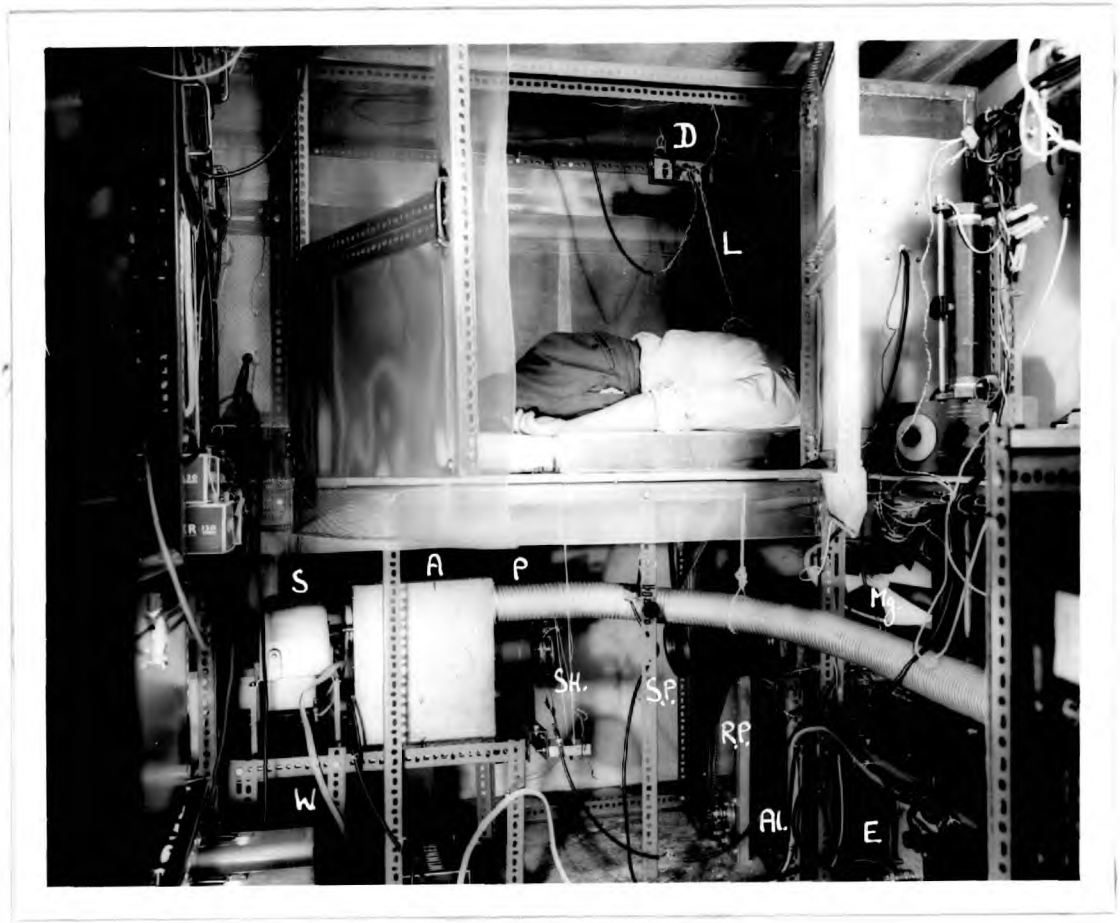
27. Phase lag and amplitude versus frequency at constant intensity λ = 6337 Å

28. Phase lag and amplitude versus ~~frequency~~ intensity at constant ~~intensity~~ frequency λ = 6337 Å

29. Phase lag and amplitude versus frequency. White. E.E.G. constant intensity.

PHOTOGRAPH I

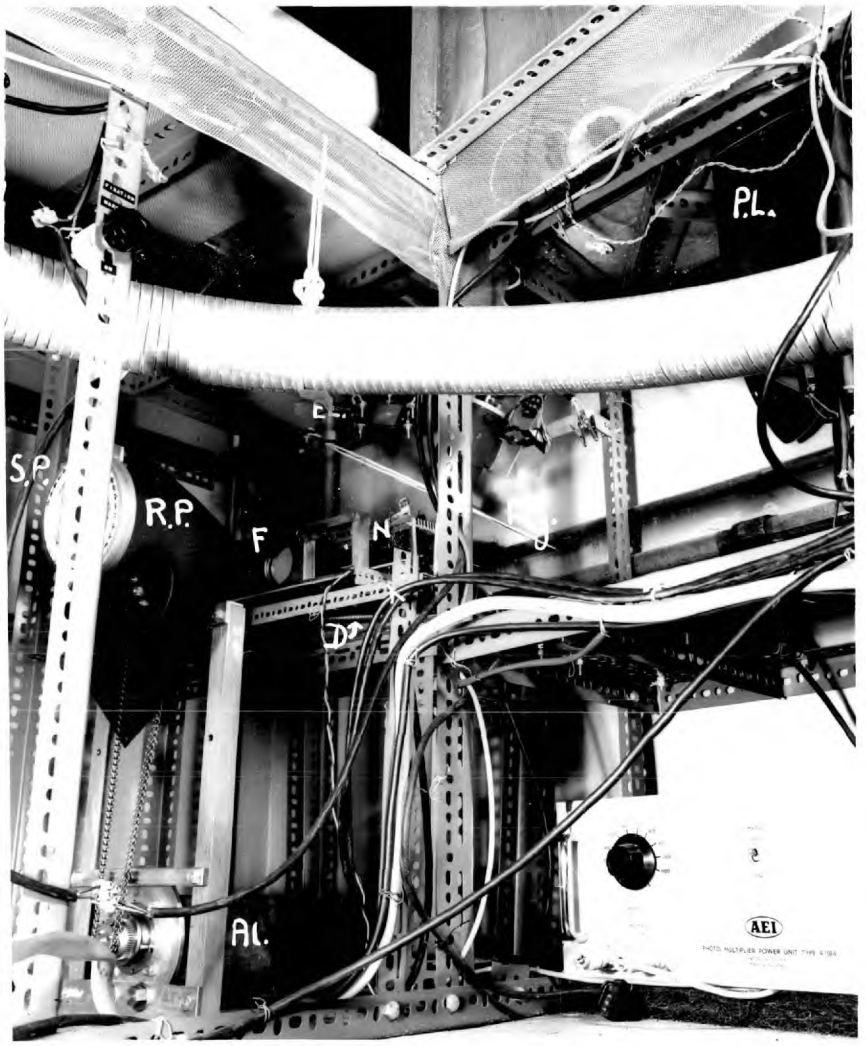
General view of the appratus. Observer in position. Doors to the Faraday cage open.



A - arc lamp housing.
Al. - alternator in mumetal box.
D - distribution box between electrodes and preamplifier.
E - E.H.T. supply to photomultiplier.
L - twisted electrode leads.
Mg. - white MgO sector.
P - air cooling pipe from arc lamp housing.
R.P. - rotating polaroid.
S - 40 KV. arc lamp starter.
SH - shutter.
S.P. - stationary polaroid.
W - 22 amp line from rectifier.

PHOTOGRAPH 2

Detailed view of optical stimulator.



Al. - alternator in mumetal box.

D - flexible drive cable to rotating polaroid from distant motor.

E.L. - eye lens and first fixation cross.

F - colour filter in slider.

Mg. - MgO sector.

N - neutral filters.

P.L. - photometer lamp housing.

R.P. - rotating polaroid.

S.P. - stationary polaroid.

PHOTOGRAPH 3

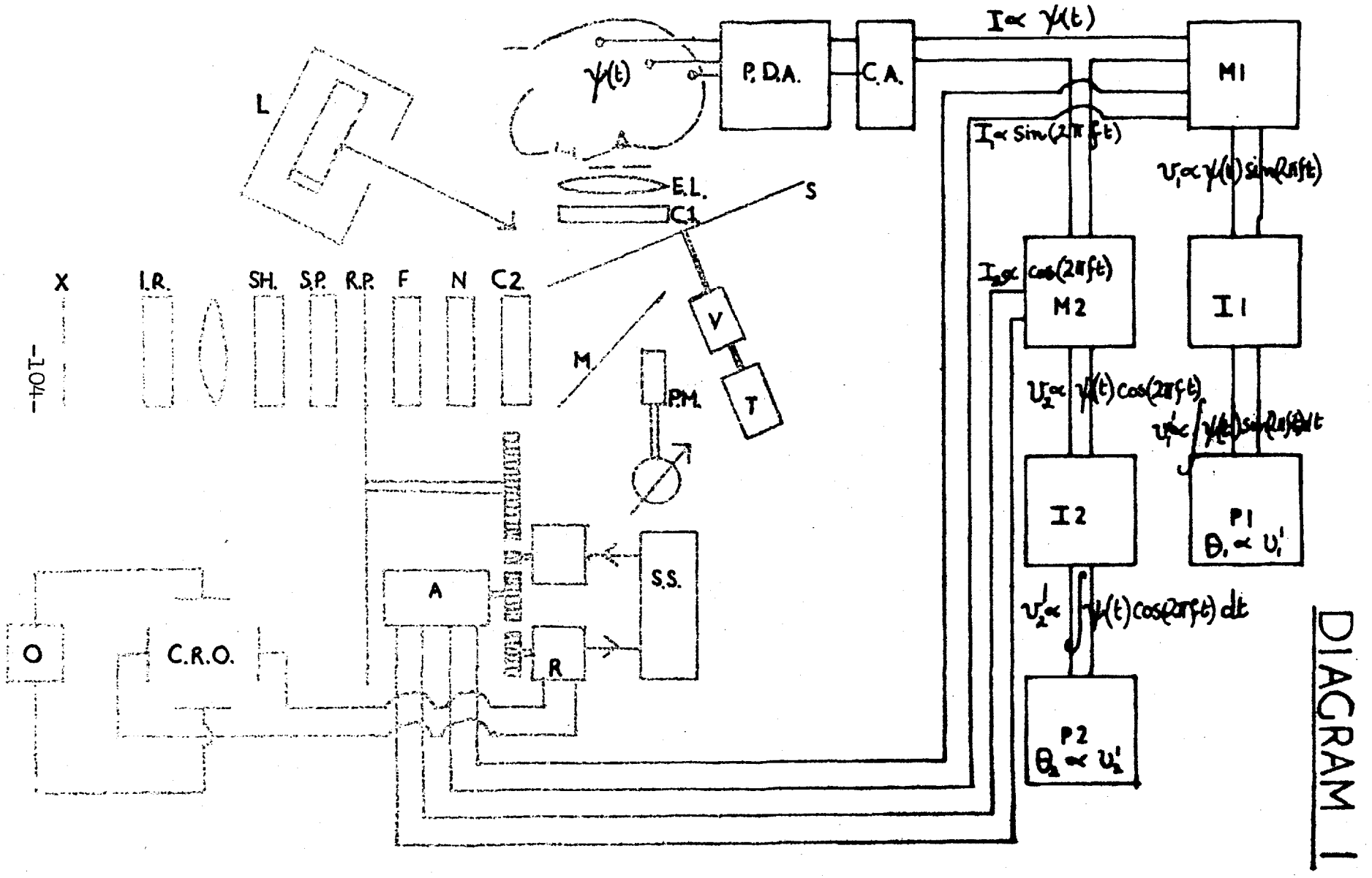
Electrode placement used in E.E.G. measurements.



BLOCK DIAGRAM OF APPARATUS

KEY TO DIAGRAM 1

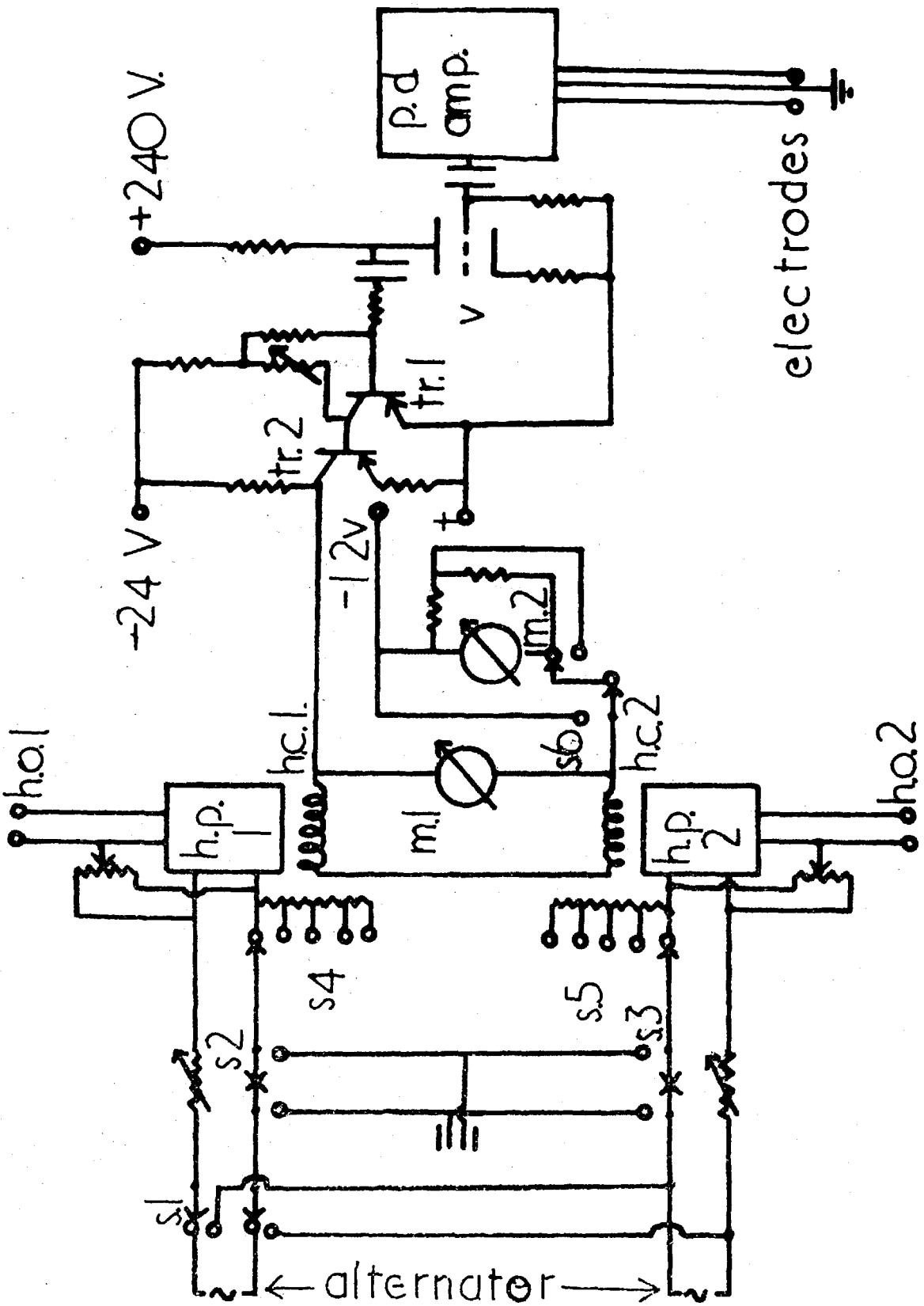
A	MAGSLIP ALTERNATOR
C.1.	FIRST FIXATION CROSS
C.2	SECOND FIXATION CROSS
C.A.	CURRENT AMPLIFIER
E.L.	EYE LENS
F.	COLOUR FILTER
I.1., I.2.	INTEGRATORS
I.R.	INFRA RED FILTER
L	STANDARD LAMP
M.1., M.2	MULTIPLIERS
M	90% REFLECTING MIRROR
N	NEUTRAL DENSITY FILTERS
O	OSCILLATOR
P.1., P.2.	RECORDING POTENTIOMETERS
P.M.	PHOTOMULTIPLIER
R	MAGSLIP RECEIVER
R.P.	ROTATING POLAROID
S	WHITE MgO SECTOR
SH	SHUTTER
S.P.	STATIONARY POLAROID
S.S.	STABALISED MOTOR SPEED SUPPLY
T	TACHOMETER
V	VARIABLE SPEED MOTOR
X	XENON LAMP


L
ψ(t)
P. D.A.
C. A.
I ∝ ψ(t)
M1
I₁ ∝ Sin(2πft)
V₁ ∝ ψ(t) Sin(2πft)
E.L.
C1
S
X
I.R.
SH.
S.P.
R.P.
F
N
C2
M
V
T
P.M.
I₂ ∝ Cos(2πft)
M2
I1
V₂ ∝ ψ(t) Cos(2πft)
V₁' ∝ ψ(t) Sin(2πft) dt
I2
P1
θ₁ ∝ V₁'
V₂' ∝ ψ(t) Cos(2πft) dt
P2
θ₂ ∝ V₂'
A
S.S.
R
O
C.R.O.
DIAGRAM 1

MULTIPLIER INPUT CIRCUITS

h.o.1,2	Hall multiplier outputs 1 and 2
h.p.1,2	Hall multiplier plates 1 and 2
h.c.1, 2	Hall multiplier coils 1 and 2
m1	Avo on 10V a.c. range to monitor coil input current. This is proportional to the E.E.G. voltage input at the electrodes.
m2	d.c. balance. Adjustment of the biassing of the transistor current amplifier ensures that there is zero coil current for zero E.E.G input.
p.d. amp.	potential difference amplifier.
tr 1	transistor OC 72)
tr 2	transistor OC 35) current amplifier
S1	Balance Hall Multipliers
S2,S3	Measure plate currents externally
S4,S5	Adjust plate currents
S6	Meter m2 in or out of circuit
S7	Coarse or fine d.c. balance using m2
V	valve ECC 82

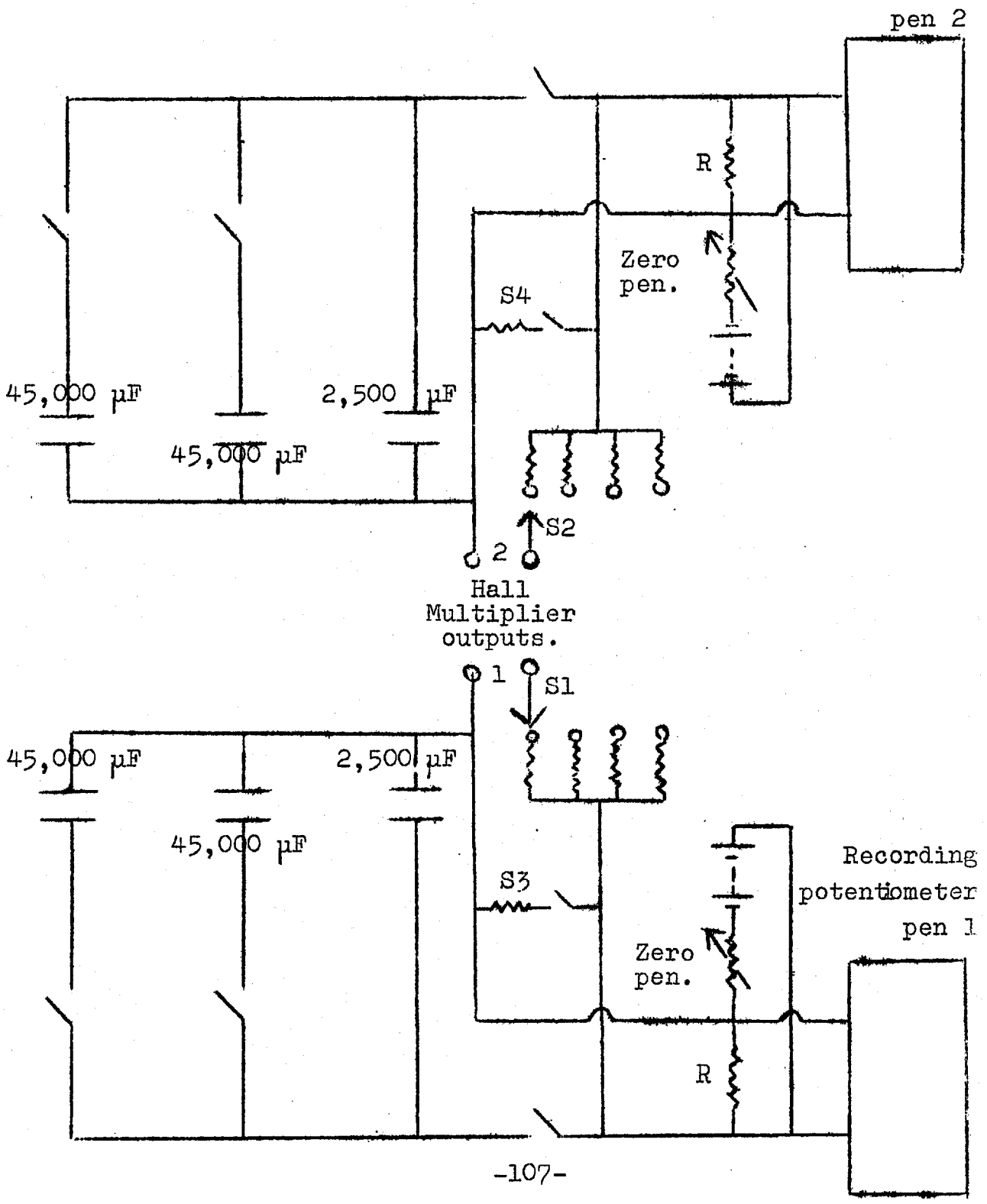
MULTIPLIER INPUT CIRCUITS diag. 2



INTEGRATING CIRCUIT DIAGRAM 3.

S1, S2 : set time constants controls.

S3, S4 : 'reduce span' controls.



STABILISED VARIABLE SPEED MOTOR. DIAGRAM 4.

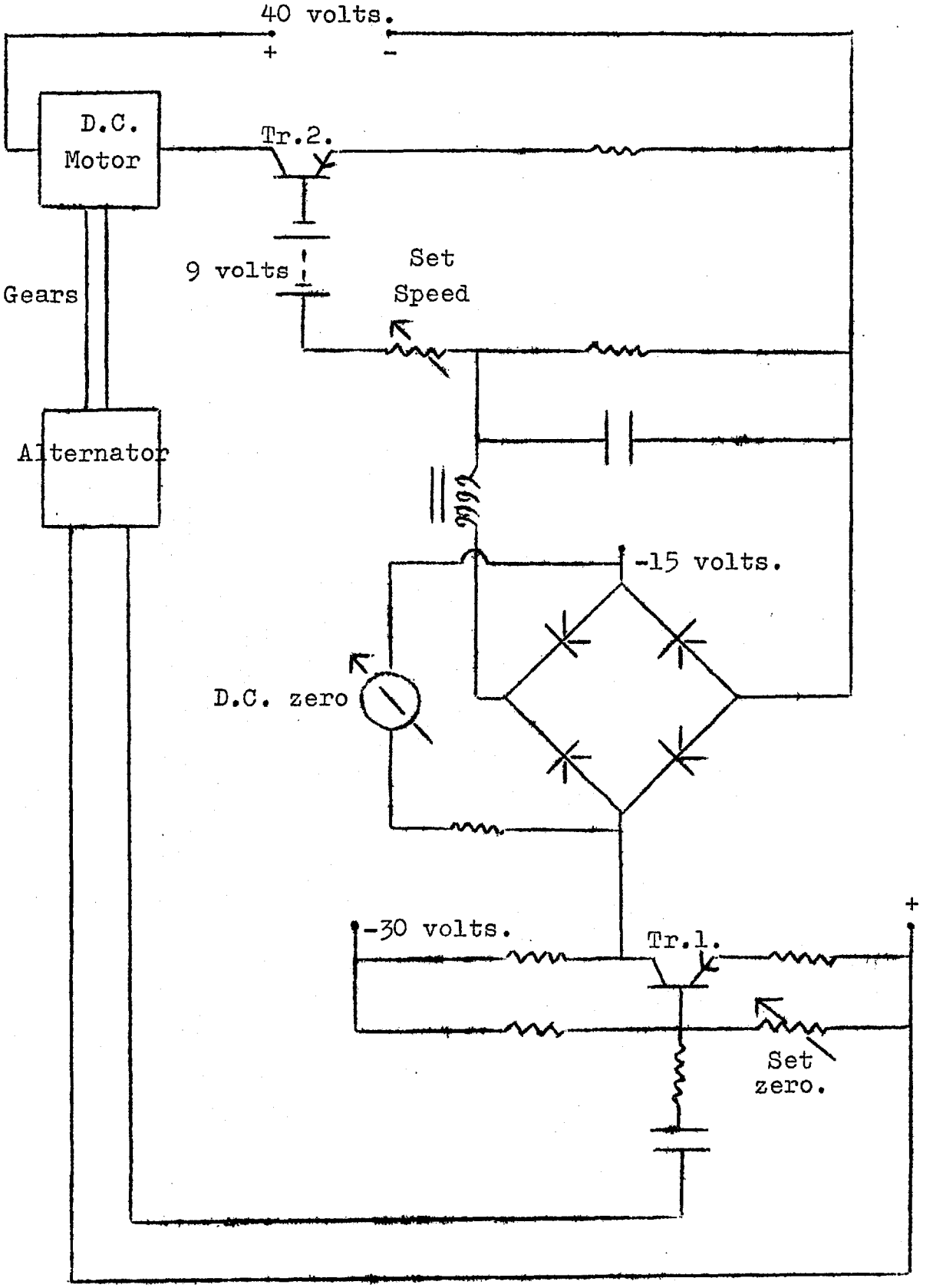


DIAGRAM 5

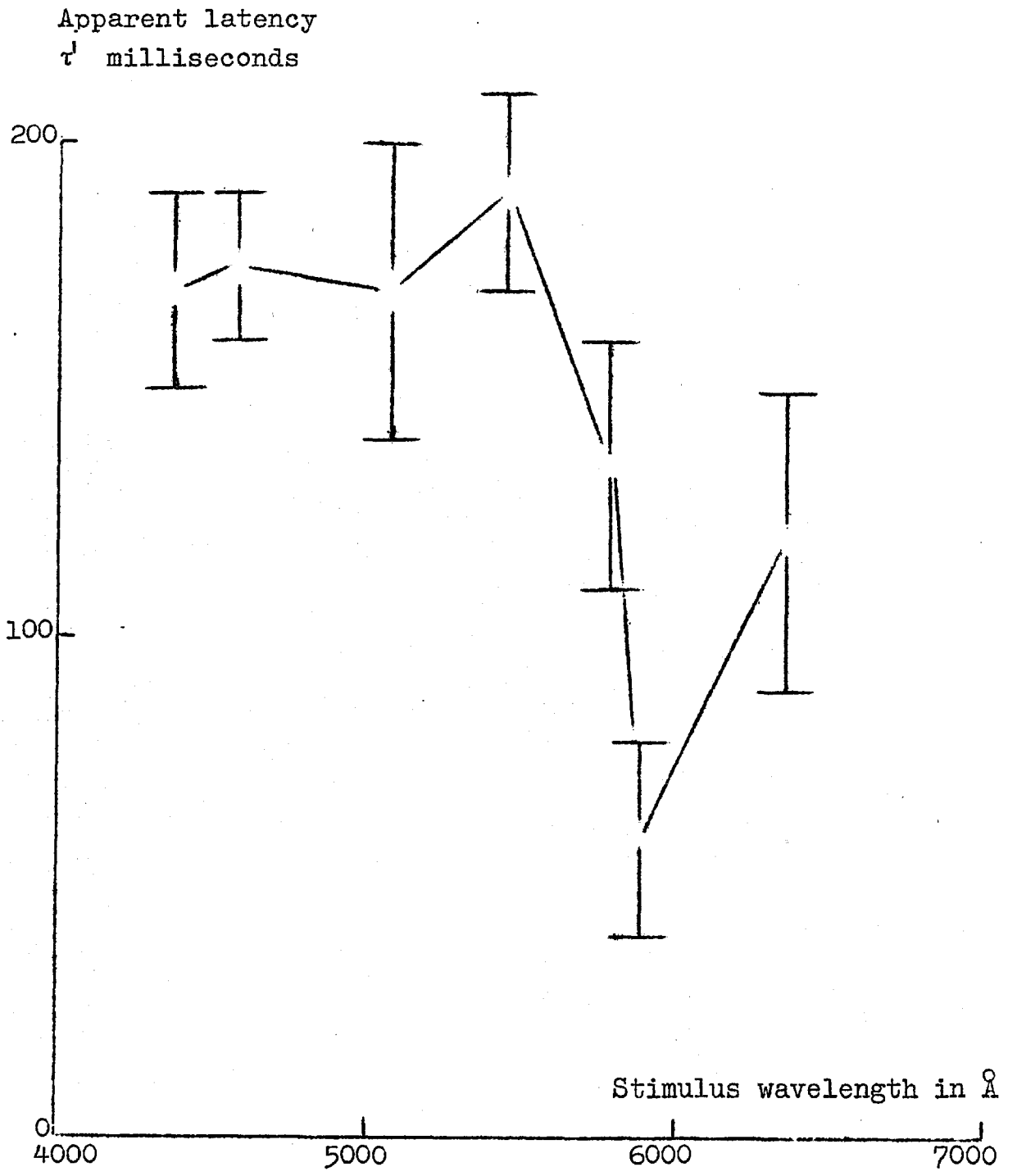
Graph of the apparent latency (τ') of the synchronous evoked E.E.G. response versus stimulus wavelength for stimuli of equal retinal illuminations of 50,000 trolands.

The values of τ' are obtained from the linear phase lag versus stimulus frequency graphs for each individual stimulus wavelength (diagrams 17, 19, 21, 23, 25, 27).

The stimulus is a 16^{o} centrally viewed circular field with dark surround modulated sinusoidally at a frequency of f. c.p.s.

The errors shown are taken from the phase lag versus f graphs for each stimulus and are the maximum errors occurring during the steady state response measured (about 20 to 80 seconds after onset of stimulation.)

DIAGRAM 5.


Apparent latency
τ' milliseconds
200
100
0
4000
5000
6000
7000
Stimulus wavelength in Å

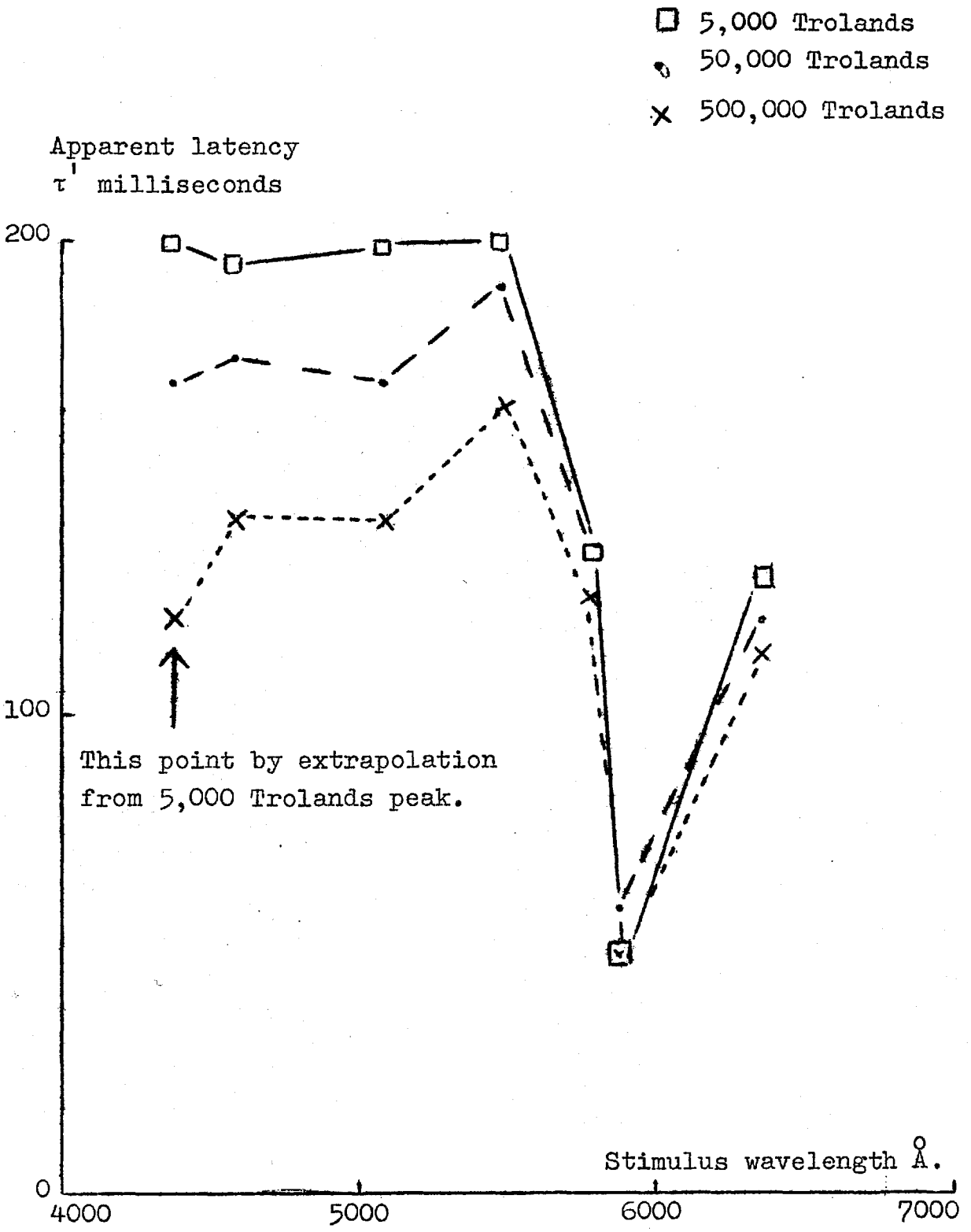
D I A G R A M 6

Graph of the apparent latency of the synchronous component of the evoked E.E.G. response (τ' seconds) versus the wavelength of the stimulus for three different stimulus intensities. Errors are omitted for clarity.

The values of τ' for each of the individual stimulus wavelengths for the 50,000 troland intensity level (full line) are obtained from the linear phase lag versus stimulus frequency graphs for the individual wavelengths (diagrams 17, 19, 21, 23, 25, 27).

The values of τ' for the various stimulus wavelengths at intensities of 500,000 and 5,000 trolands are derived from the separate graphs of phase lag versus stimulus intensity (diagrams 18, 20, 22, 24, 26, 28). These graphs are plotted for a constant stimulus frequency and variable stimulus intensity. The observed change in phase lag as stimulus intensity is altered is attributed to a change in latency with stimulus intensity. The values of τ', for intensities other than the 50,000 trolands for which τ' is measured directly, are obtained from these graphs. A note on the interpretation of the graphs can be found on page 58.

DIAGRAM 6.


5,000 Trolands
50,000 Trolands
500,000 Trolands
Apparent latency
τ' milliseconds
200
100
0
This point by extrapolation
from 5,000 Trolands peak.
Stimulus wavelength Å.
4000
5000
6000
7000

D I A G R A M S 7 and 8

Diagram 7 This is a record of the output of the analogue computer when a constant synchronous calibrating signal is applied to the preamplifier. The signal is obtained from the alternator via an attenuator. It is sinusoidal, of amplitude about 5 microvolts peak-to-peak, and frequency 14.9 c.p.s.

The two traces are produced by the pens of the two recording potentiometers P1 (red pen) and P2 (blue pen) in diagram 1. The centre line (marked 5) is the zero line. The final steady deflection of pen 1 from the zero is proportional to $\int$ (input signal)$\sin(2\pi ft)dt$ and the steady deflection of pen 2 is proportional to $\int$(input signal) $\cos(2\pi ft)dt$.

The inch marks on the papers correspond to 7.5 seconds. The time constant of the integrating circuits here is 15 secs. for each pen. The exponential form of rise of the pens' deflections is evident, and is according to the equation for the charging of a capacitor, viz.

$$\text{p.d. across capacitor} = \text{applied p.d.} \left(1 - e^{-t/15}\right)$$

where t is the time (in seconds) elapsed from switching on the signal.

Diagram 8 This is a record of the output of the analogue computer similar to diagram 7. The difference is that here a calibration signal is not used. In this record in input signal is picked up from electrodes placed in the occipital region of

an observer's scalp. At point A he starts to observe a sinusoidally modulated 16^{o} stimulus of retinal illumination about 300,000 trolands and wavelength 5780 $\mathring{A}$. The frequency is held constant at 14.9 $\pm$ 0.2 c.p.s for the duration of the stimulation (about 50 seconds).

The time constant of the integrating circuits is still 15 seconds and the sensitivity is the same as for diagram 7.

The steady deflections of the pens from the centre zero are due to a synchronous signal of constant amplitude and phase lag. Noise and unwanted (nonsynchronous) signal can be seen on the traces. At the electrodes the noise is 15-20 times signal.

It can be seen that the initial stages of the pens' deflection is quite different to diagram 7. Hence the initial stages of the synchronous response are not a constant amplitude signal. The interpretation of this graph is given on pages 80 -84 and is that there is a large initial transient response which suddenly falls to the constant steady-state level after 16-20 seconds.

This initial response has been clearly observed on more than 90 occasions.

DIAGRAM 7

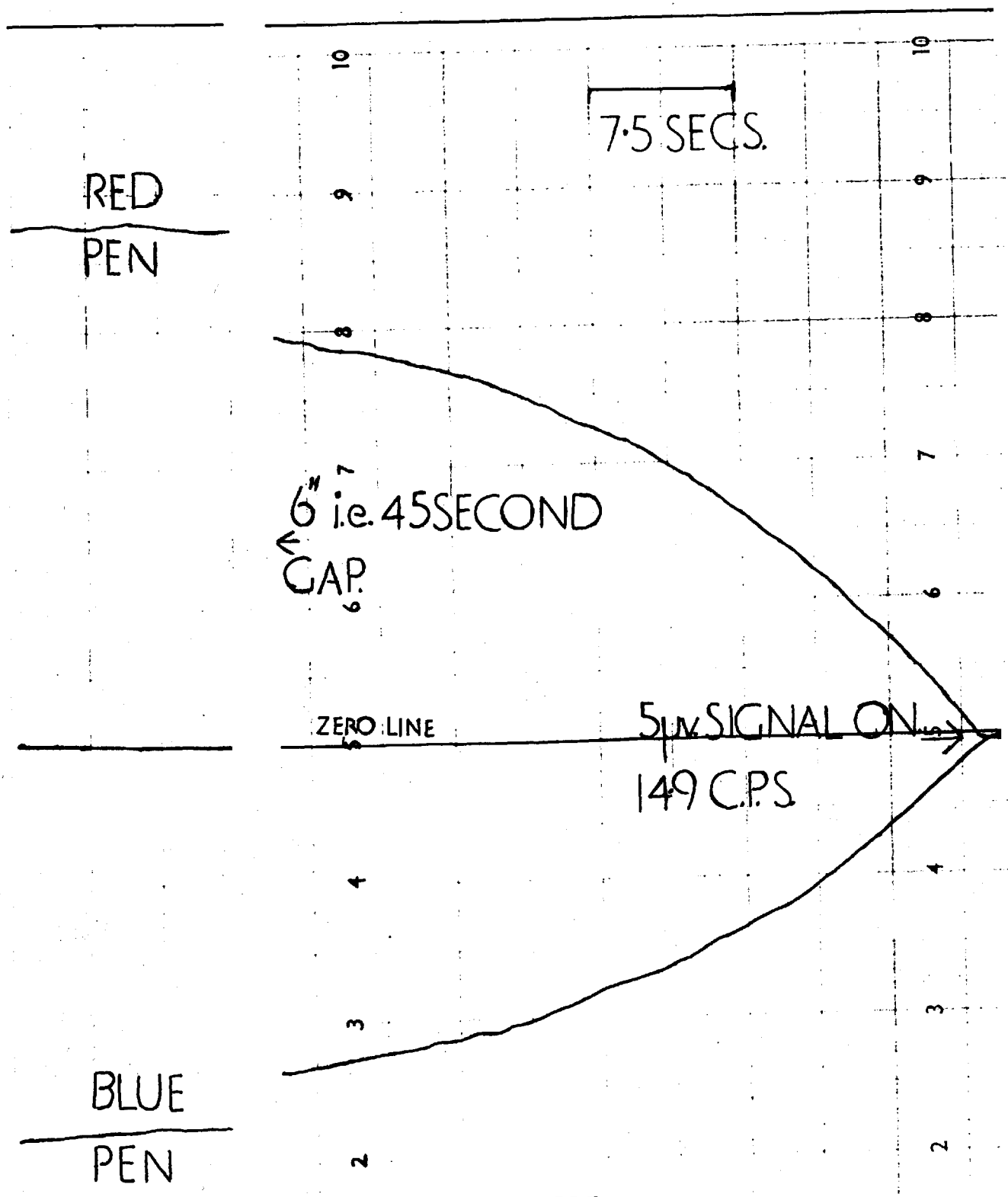
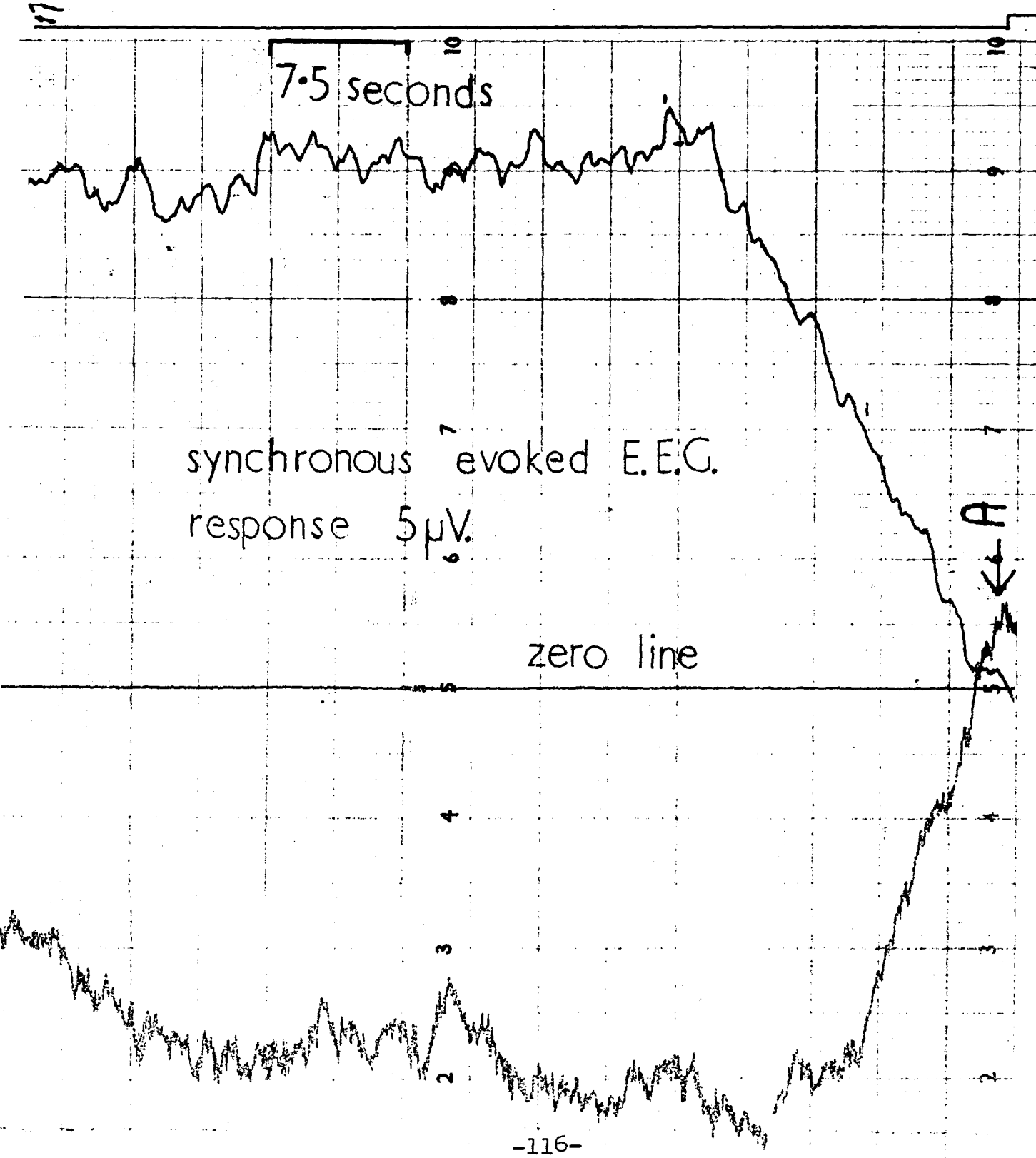

RED
PEN
7·5 SECS.
6" i.e. 45 SECOND
GAP
ZERO LINE
5μv SIGNAL ON
149 C.P.S
BLUE
PEN

diagram 8



D I A G R A M 9

This is a direct recording of the E.E.G. from occipital scalp electrodes, taken with an A.E.I. pen oscillograph. The α activity at 9.6 ± 0.2 c.p.s. can be prominently seen when the subject's eyes are closed. The characteristic fluctuations of amplitude are evident. When the eyes are opened, the α activity can be seen to be immediately much reduced (α blocking).

A sinusoidally modulated 16^{o} light stimulus is marked by a row of dots at stimulus frequency (14.9 c.p.s). A response in the E.E.G. at stimulus frequency is just detectable in the trace, with an applitude of (very approximately) 5 V. p-p. Whether its amplitude or phase remains constant cannot be determined from the trace, as the response is buried in noise, and intrinsic brain activity.

Bursts of α activity of frequency 9.4 ± 0.3 c.p.s can be seen to occur during stimulation.

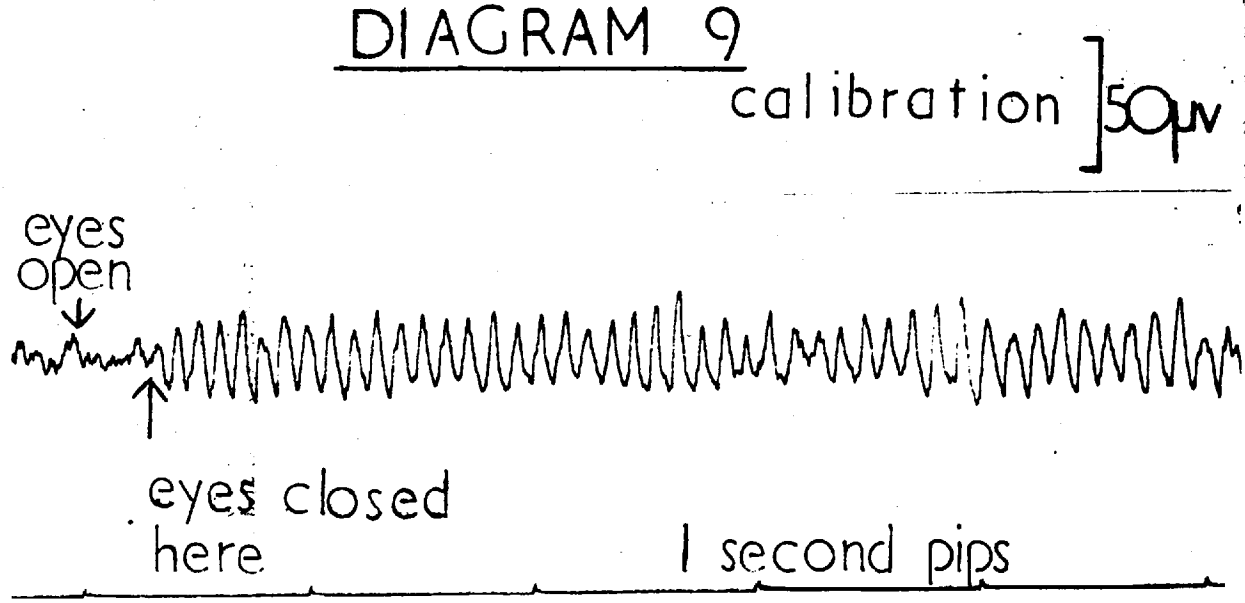
A response in the E.E.G. which is at stimulus frequency, and which is phase - locked to the stimulus will be described as a synchronous response. The analogue computer is designed to detect whether there is a synchronous response buried in the E.E.G., and if so to measure its amplitude and phase lag behind the stimulus.

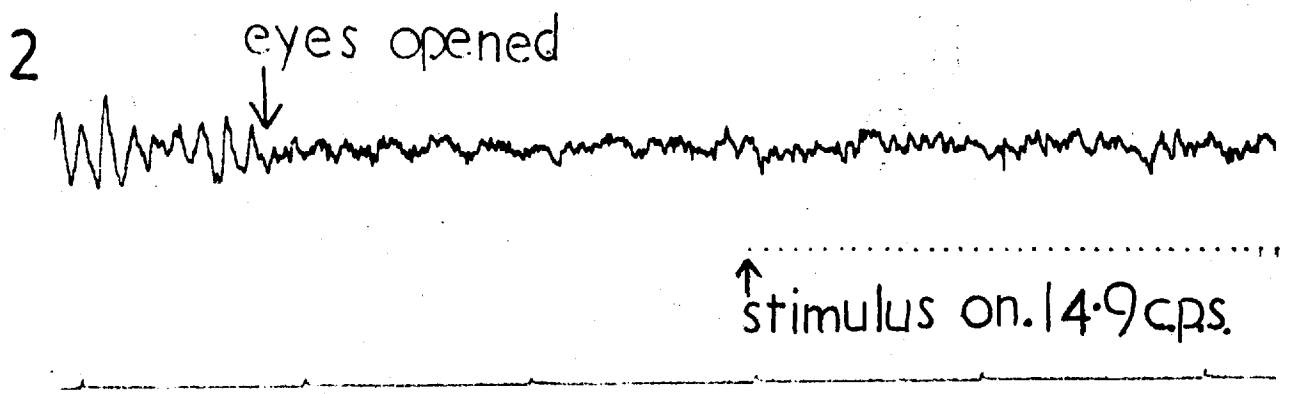
Diagram 9, the raw E.E.G., should be compared with diagrams 8, 10, 11, 12 and 13. These are records of the analogue computer's output before, and during similar stimulations to that of diagram 9.

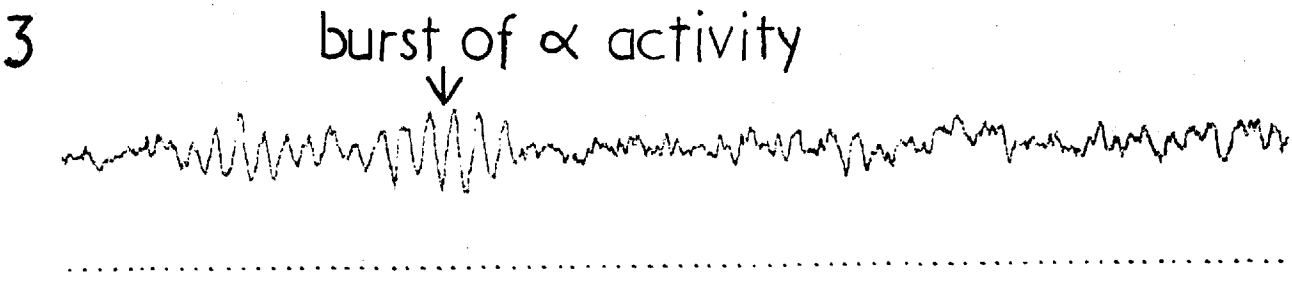
In diagrams 8, 10, 11, 12 and 13 the steady deflections from the centre zero line (marked 5) are produced by the synchronous response. The ripple visible on the computed traces is a much-attenuated beating with the α activity.

It can be seen that the analogue computer clearly detects a synchronous component in the E.E.G., even though the response is buried in noise such that its presence is hardly visible in the raw E.E.G. trace. Furthermore, the computed E.E.G. results show that from about 16 to 80 seconds after onset of stimulation the amplitude of the synchronous response remains constant to $\pm$ 10% and the latency to $\pm$ 1 milliseconds, even though the total E.E.G. activity may reach 20 times the amplitude of the synchronous response.

DIAGRAM 9


calibration] 50μV
eyes open
1
eyes closed here
1 second pips


2
eyes opened
stimulus on. 14·9 cps.


3
burst of ∝ activity

D I A G R A M S 10 - 13

These diagrams illustrate the method by which the phase lag and amplitude of the synchronous component of the evoked E.E.G. response may be measured by the use of the analogue computer , and stimulation technique described in this thesis. They should be compared with diagram 9.

The traces are made by the pens of the recording potentiometers P1 and P2 in diagram 1. Pen 1 gives a steady deflection from the zero (5 line) proportional to $\int \psi(t) \sin (2 \pi ft)dt$ and pen 2 gives a deflection proportional to $\int \psi(t) \cos (2 \pi ft)dt$. Here $\psi(t)$ is the waveform of the total E.E.G signal, and f is the stimulus modulation frequency. A positive deflection is counted to the right of the zero (5) line, a negative deflection to the left. The chart speed is one inch (large square) per 7.5 seconds.

It is described in Chapter 3 how the ratio of the steady deflections is equal to the tangent of the angle of phase lag (ϕ) of the synchronous response behind the stimulus. On each of diagrams 10-13 is a vector diagram illustrating this, and showing how the phase lag (ϕ) increases as the stimulus frequency (f) increases.

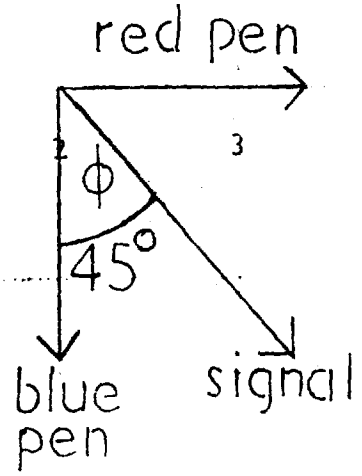
It should be pointed out that this measured phase lag (ϕ) differs from the true phase lag of synchronous response behind stimulus. The difference is an integral number of cycles plus a constant term arising from the constant misalignment of the rotating polaroid.

An additional physiological constant term is discussed in Chapter 8. Any contribution to phase shifts due to the amplifiers is eliminated by calibration. The variation of measured phase lag with frequency is due to an apparent time latency τ' of the synchronous response behind the stimulus.

The amplitude of the synchronous response is proportional to $\sqrt{(\text{deflection of pen 1})^2 + (\text{deflection of pen 2})^2}$. (Chapter 3). The constant of proportionality is obtained by calibration.

The time constant in diagrams 10 - 13 is 30 seconds, rather than 15. The result is that the initial transient produces only a slow initial rise in the traces.

DIAGRAM 10



blue pen
Pen 1

red pen
Pen 2

1 2 3 4 5 6 7 8

1 2 3 4 6 7 8

bursts of beats at approx 2·2 cps.
analyser beating with 11·4 − 2·2 = 9·2 c.p.s.

← stimulus on. Frequency 11·2 c.p.s.

6 7

DIAGRAM II

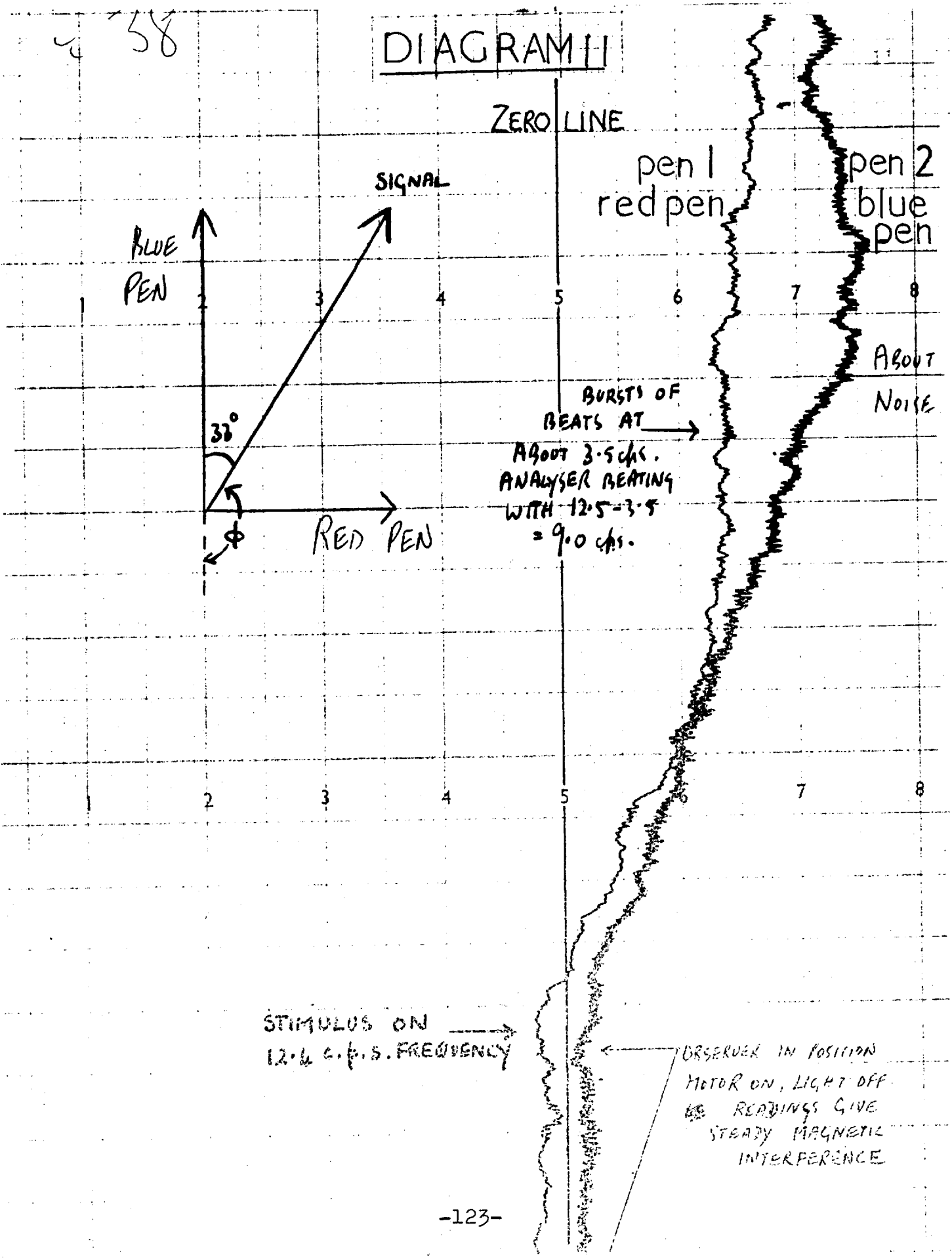
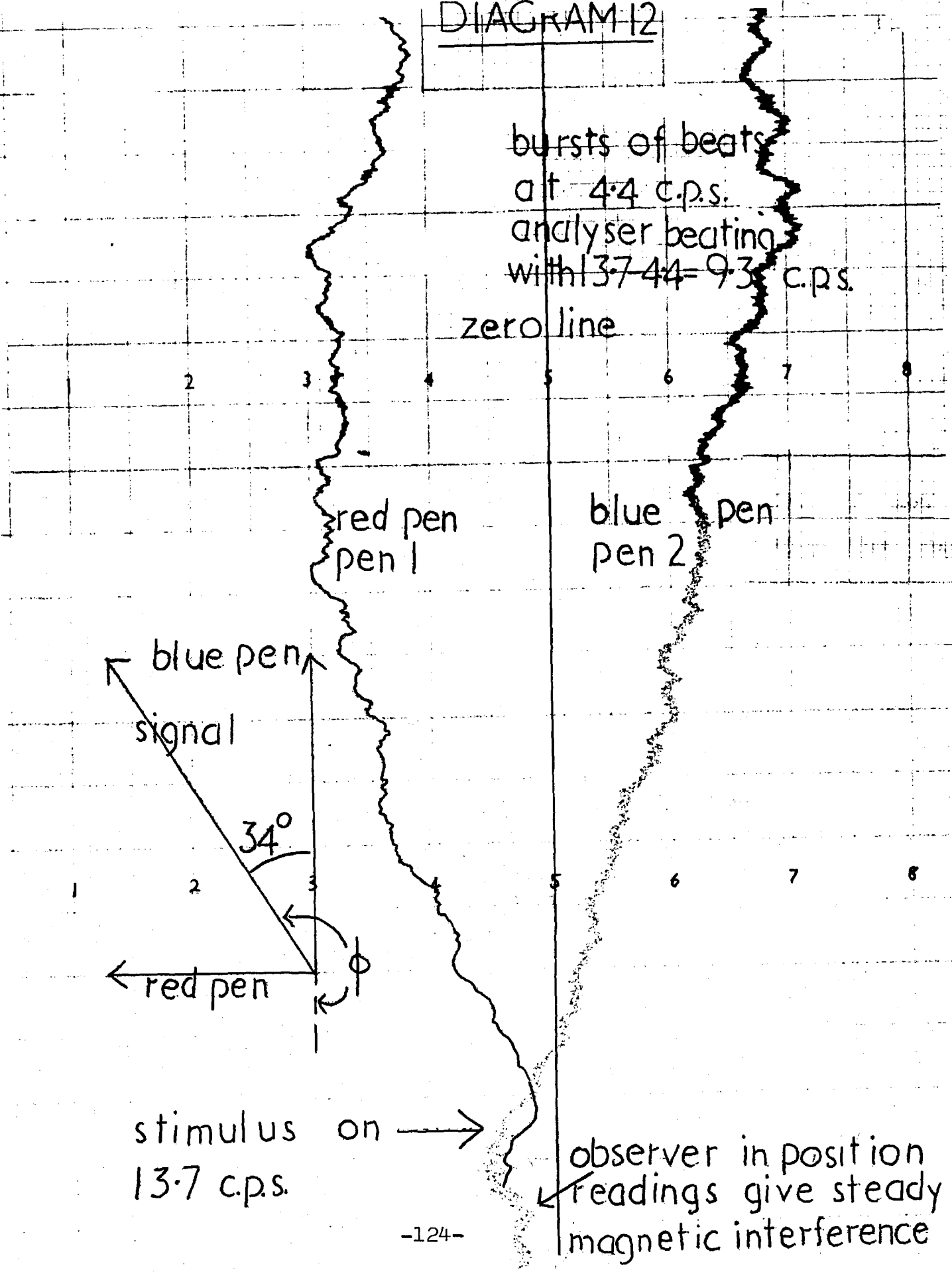
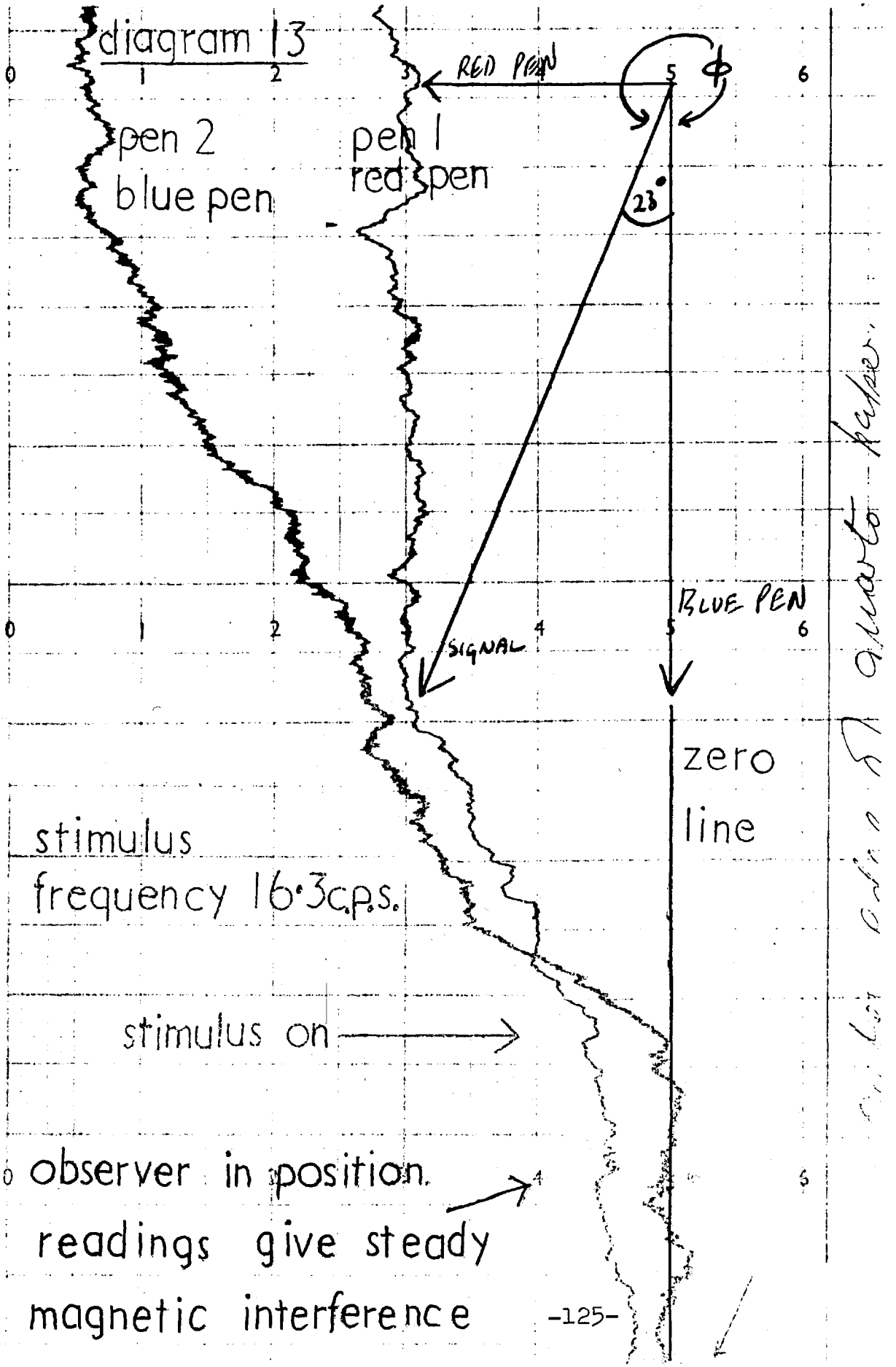

ZERO LINE
pen 1
red pen
pen 2
blue pen
SIGNAL
BLUE PEN
RED PEN
38°
Φ
1
2
3
4
5
6
7
8
ABOUT
NOISE
BURSTS OF BEATS AT
ABOUT 3·5 cps.
ANALYSER BEATING WITH 12·5 - 3·5 = 9·0 cps.
STIMULUS ON
12·4 c.p.s. FREQUENCY
OBSERVER IN POSITION
MOTOR ON, LIGHT OFF
READINGS GIVE STEADY MAGNETIC INTERFERENCE

DIAGRAM 12


bursts of beats
at 4·4 c.p.s.
analyser beating
with 13·7-4·4 = 9·3 c.p.s.
zero line
red pen
pen 1
blue pen
pen 2
blue pen
signal
34°
red pen
stimulus on
13·7 c.p.s.
observer in position
readings give steady
magnetic interference



9/63
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D I A G R A M 14

This graph shows the relation between stimulus modulation frequency for a 16^{o}, λ = 5780 $\mathring{A}$ stimulus field of about 50,000 trolands, and the phase lag of the synchronous evoked E.E.G response behind the stimulus during the steady-state response.

Measurements are made over an extended frequency range of 5 to 29 c.p.s. Measurements were difficult around 9-10 c.p.s. due to slow beating with the α rhythm.

All readings were taken in a single session. The different frequencies were observed, not in a steady progression from high to low frequencies, but by a more random selection.

The data was plotted in log form (not shown) in order to find to what accuracy linearity can be said to hold. It was assumed that:-

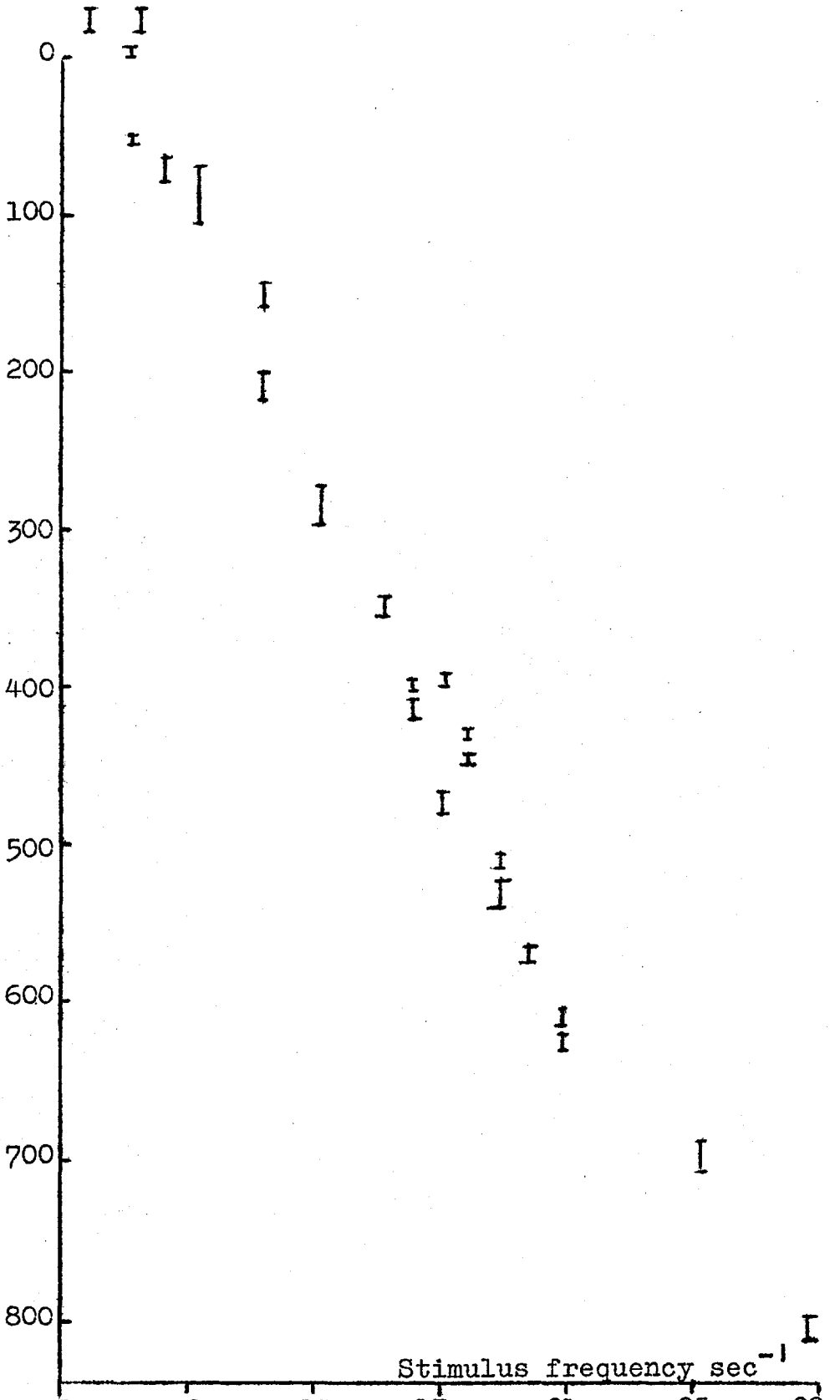
$$\phi \propto f^{n}$$

and log ϕ plotted versus log f. It was found that n = 1.1 $\pm$ 0.3.

All measurements of latency were restricted to an 11-16.5 c.p.s range of stimulus frequencies so as to avoid the high amplitude beating and apparatus inaccuracy at the lower frequencies (see page 27), and the difficulties of reproducibility or fixation experienced around 17 c.p.s.

Phase lag. degrees.
Arbitrary zero.

DIAGRAM 14.



D I A G R A M S 15 and 16

These diagrams show the synchronous evoked response in the E.E.G. (measured using occipital electrodes), and in the E.R.G. (measured using electrodes just above and below the stimulated eye) for identical stimuli.

The stimulus is a 16^{o} circular centrally viewed field of $\lambda = 4387\ \mathring{A}$ which is sinusoidally modulated. The intensity is constant at about 50,000 trolands peak.

Diagram 15

E.E.G. Phase lag of synchronous response versus stimulus frequency. Assuming a linear relation between phase lag and frequency (diagrams 14 and 18), the slope of the line is interpreted as an apparent time latency of synchronous response behind stimulus of $t' = 160 \pm 15$ milliseconds.

Diagram 16.

E.R.G. Phase lag of synchronous response versus stimulus frequency for an identical stimulus to diagram 15.

Assuming a linear relation between phase lag and stimulus frequency, the slope of the line is interpreted as indicating an apparent latency of the synchronous response behind the stimulus of 160 ± 20 milliseconds.

The synchronous E.R.G. responses are small, and the noise level is 40-60 times signal. The apparatus is often driven beyond full load (40 units on page 40). The E.R.G. results are therefore much less reliable than the E.E.G. results.

DIAGRAM 15

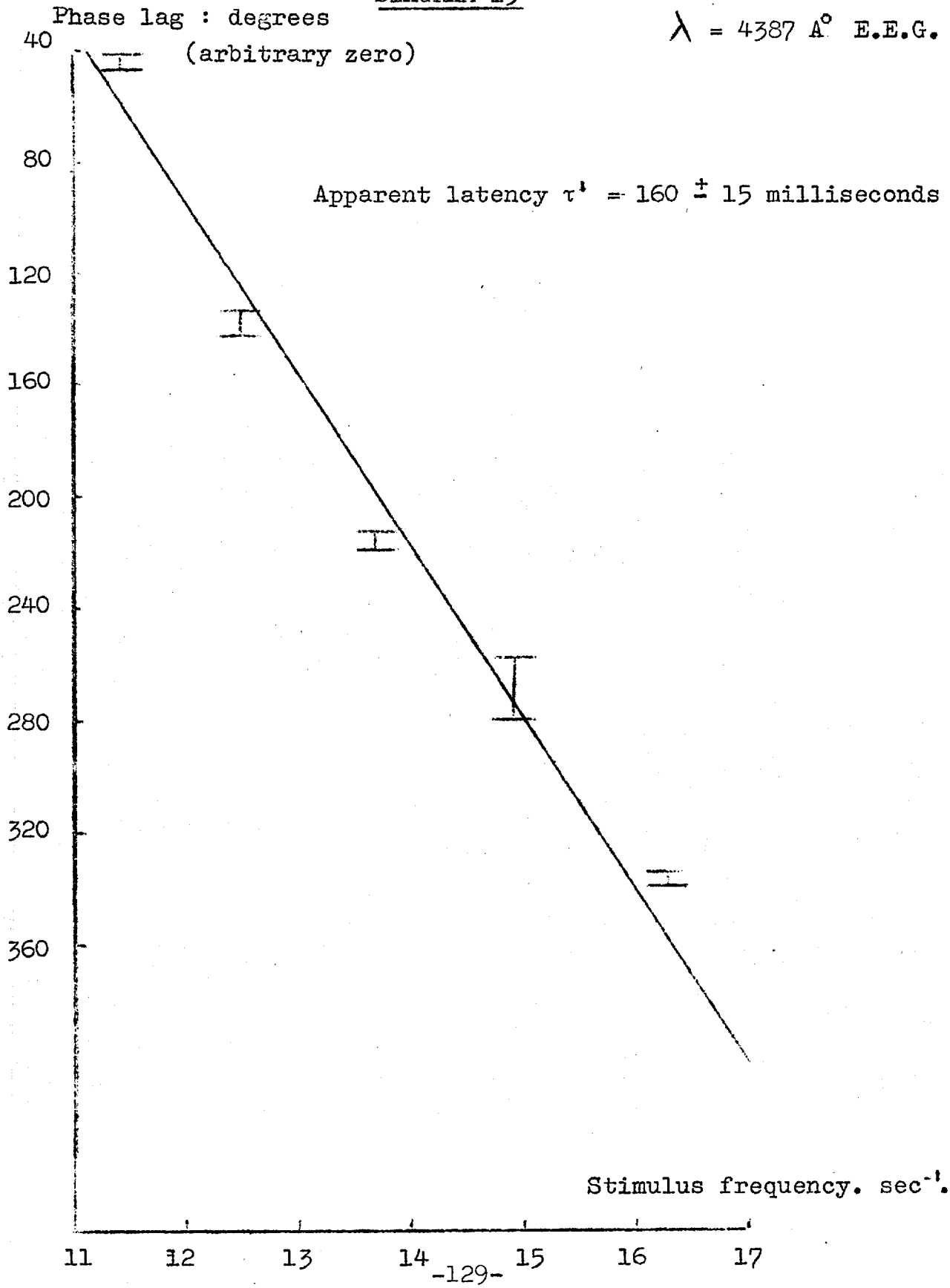
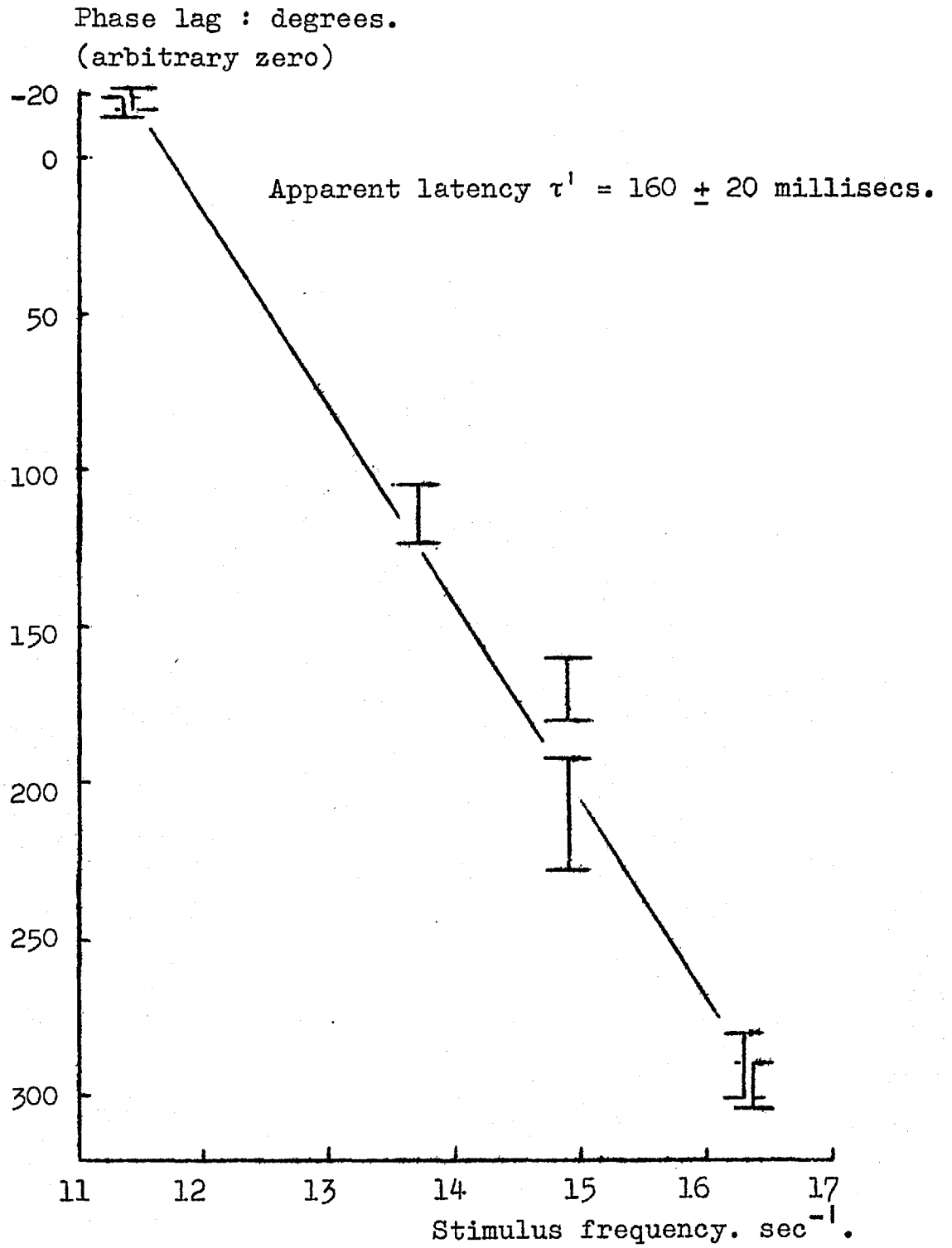

Phase lag : degrees
(arbitrary zero)
λ = 4387 A° E.E.G.
Apparent latency τ' = 160 ± 15 milliseconds
40
80
120
160
200
240
280
320
360
Stimulus frequency. sec⁻¹.
11
12
13
14
15
16
17

DIAGRAM 16. E.R.G.



D I A G R A M 17

E.E.G. λ = 4387 $\mathring{A}$. Retinal illumination about 50,000 trolands peak (light adaptation equivalent to a 25,000 troland constant level). Circular, 16°, centrally viewed, sinusoidally modulated stimulus with dark surround.

In the upper part of the diagram the phase lag of the synchronous response (ϕ) is plotted against stimulus frequency (f).

The data of this graph was replotted in order to find the accuracy to which linearity can be said to hold. It was assumed that:-

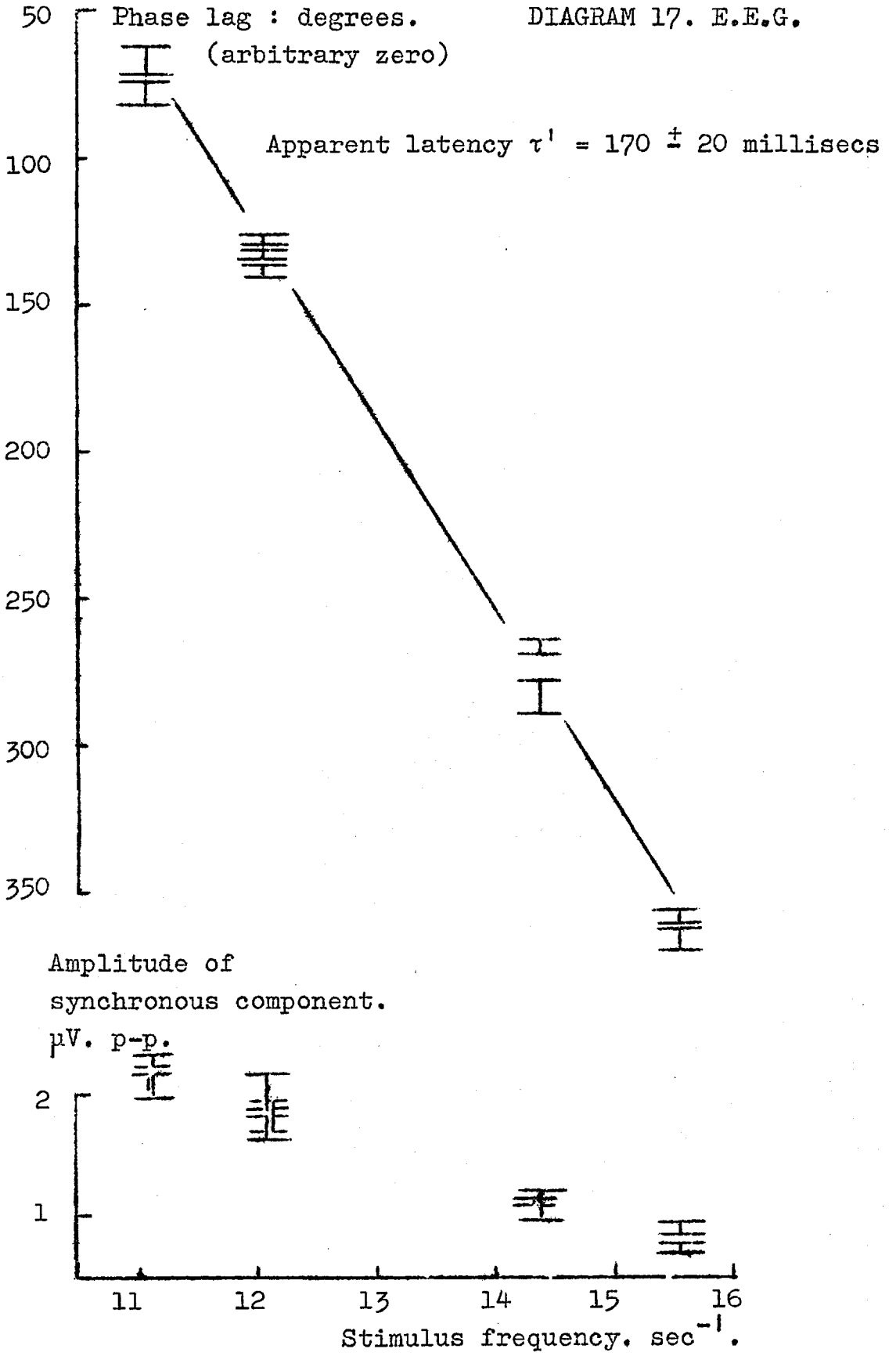
$$\phi \propto f^n$$

It was found that $n = 0.92 \pm 0.8$ over the range f = 11 to 16 c.p.s.

Assuming that $\phi \propto f$, the slope of the line of diagram 15 was interpreted to indicate an apparent latency $\tau' = 170 \pm 20$ milliseconds of the synchronous response behind the stimulus. This latency is independent of stimulus frequency from 11 to 16 c.p.s., to the accuracy with which linearity can be said to hold i.e. $\pm$ 8%.

The lower part of the diagram shows the amplitude of the synchronous response for the various stimulus frequencies. Amplitude is often found to exhibit a rather large % scatter when repeat measurements are made, although the phase repeats well (see diagrams 20-29). Here the amplitude repeats unusually well.

DIAGRAM 17. E.E.G.



D I A G R A M 18

E.E.G. stimulus as for diagram 17.

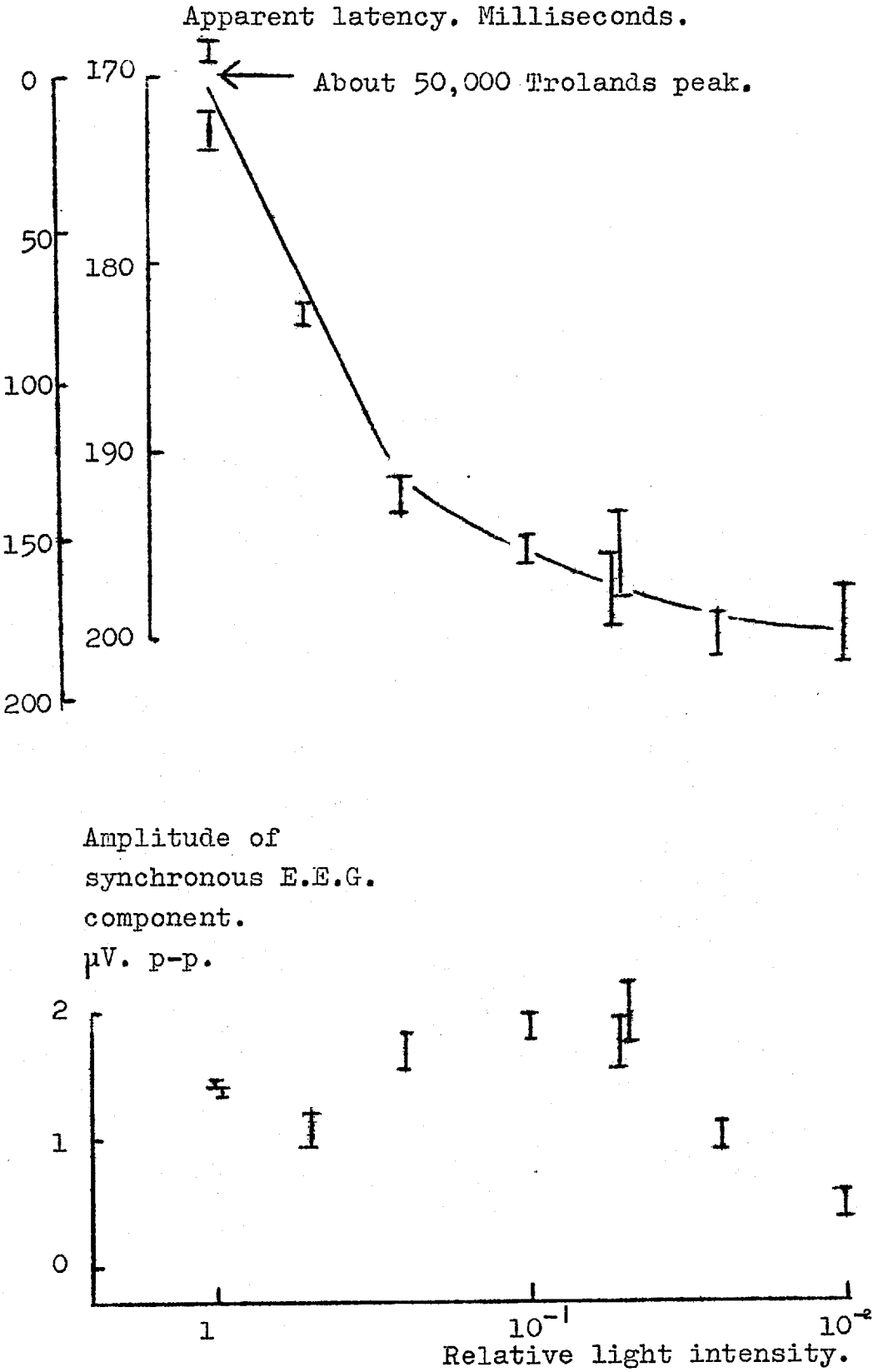
Stimulus frequency constant at 14.9 c.p.s.

In the upper part of this diagram the phase lag of the synchronous response behind the stimulus is plotted versus the stimulus intensity.

The interpretation is that apparent latency increases as stimulus intensity decreases. A discussion of this interpretation is given on page 58.

In the lower part of the diagram, the amplitude of the synchronous response is plotted versus stimulus intensity at constant stimulus frequency.

DIAGRAM 18. E.E.G.



D I A G R A M 19

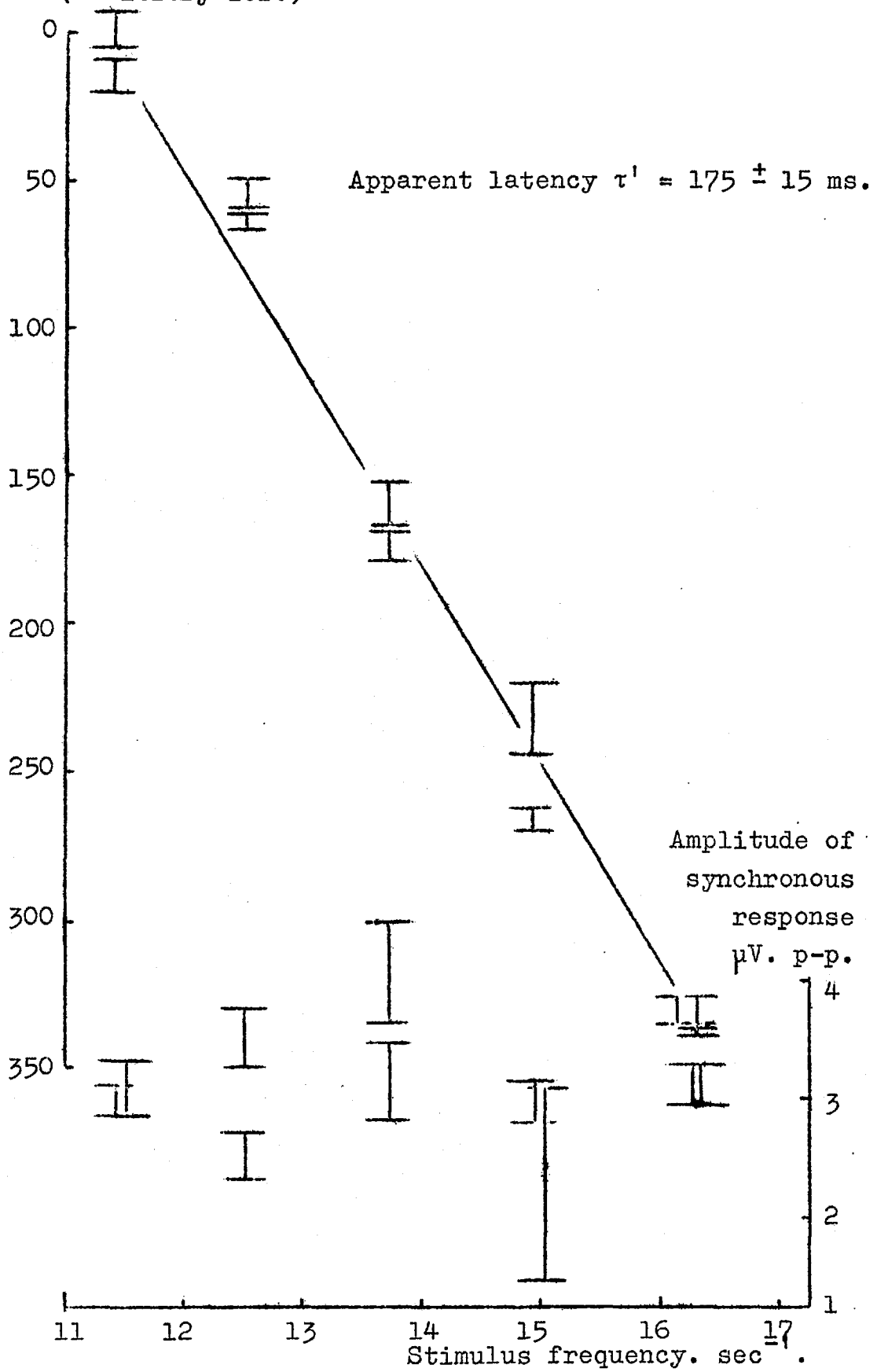
E.E.G. λ = 4577 $\mathring{A}$. Retinal illumination about 50,000 trolands peak (light adaptation equivalent to a 25,000 troland constant level). Circular, 16°, centrally viewed, sinusoidally modulated stimulus with dark surround.

In the upper part of the diagram the phase lag of the synchronous evoked response is plotted against stimulus frequency.

The slope of the line is interpreted to indicate an apparent latency (τ') of 175 $\pm$ 15 milliseconds of the synchronous response behind the stimulus. (see page 77).

The lower part of the diagram shows the amplitude of the synchronous response for the various stimulus frequencies.

DIAGRAM 19. E.E.G.



D I A G R A M 20

E.E.G stimulus as for diagram 19. λ = 4577 Å

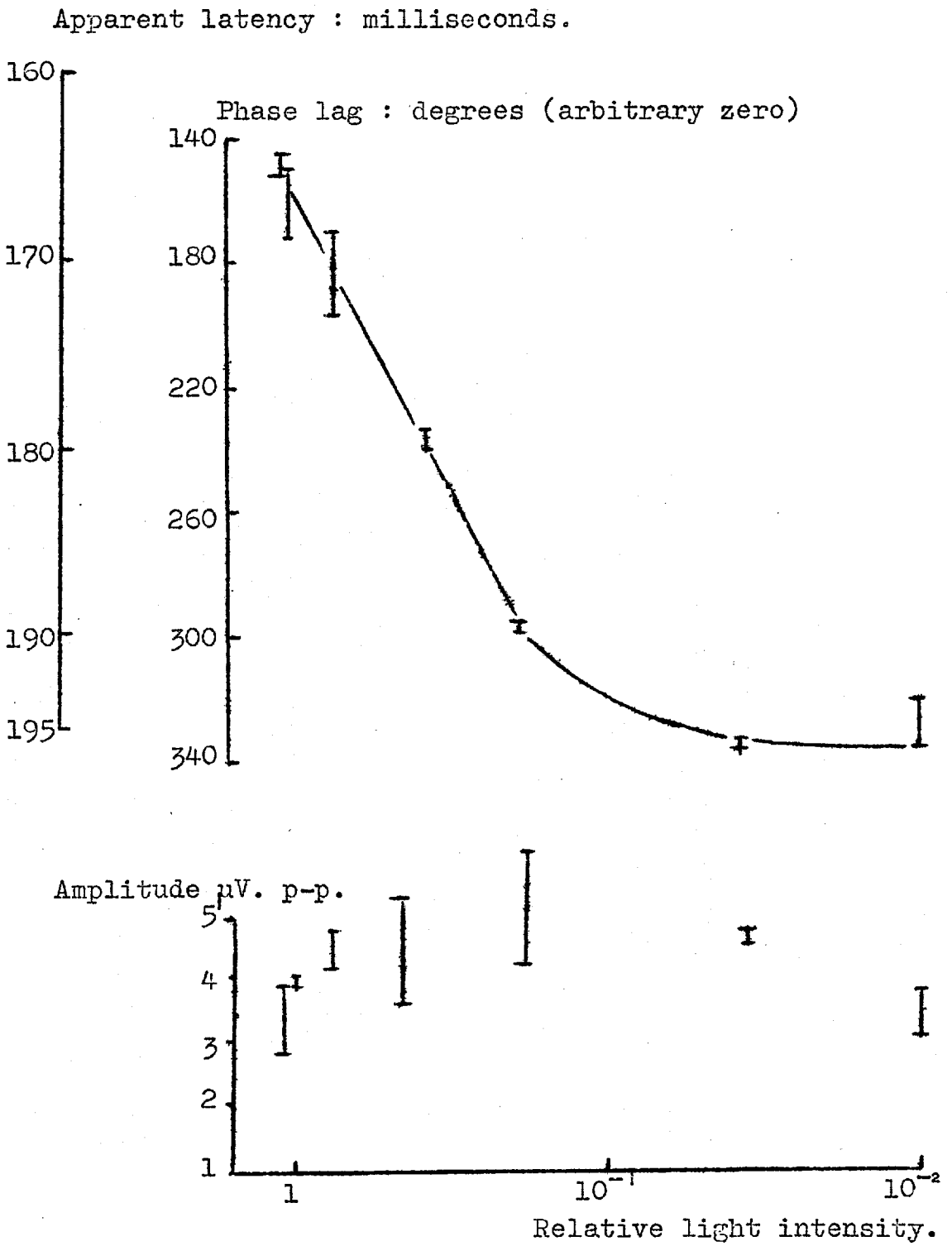
Stimulus frequency constant at 14.9 c.p.s

In the upper part of the diagram the phase lag of the synchronous response behind the stimulus is plotted versus the stimulus intensity.

The interpretation is that apparent latency increases as stimulus intensity decreases (see page 58).

In the lower part of the diagram the amplitude of the synchronous response is plotted versus stimulus intensity at constant stimulus frequency.

DIAGRAM 20 E.E.G.



D I A G R A M 21

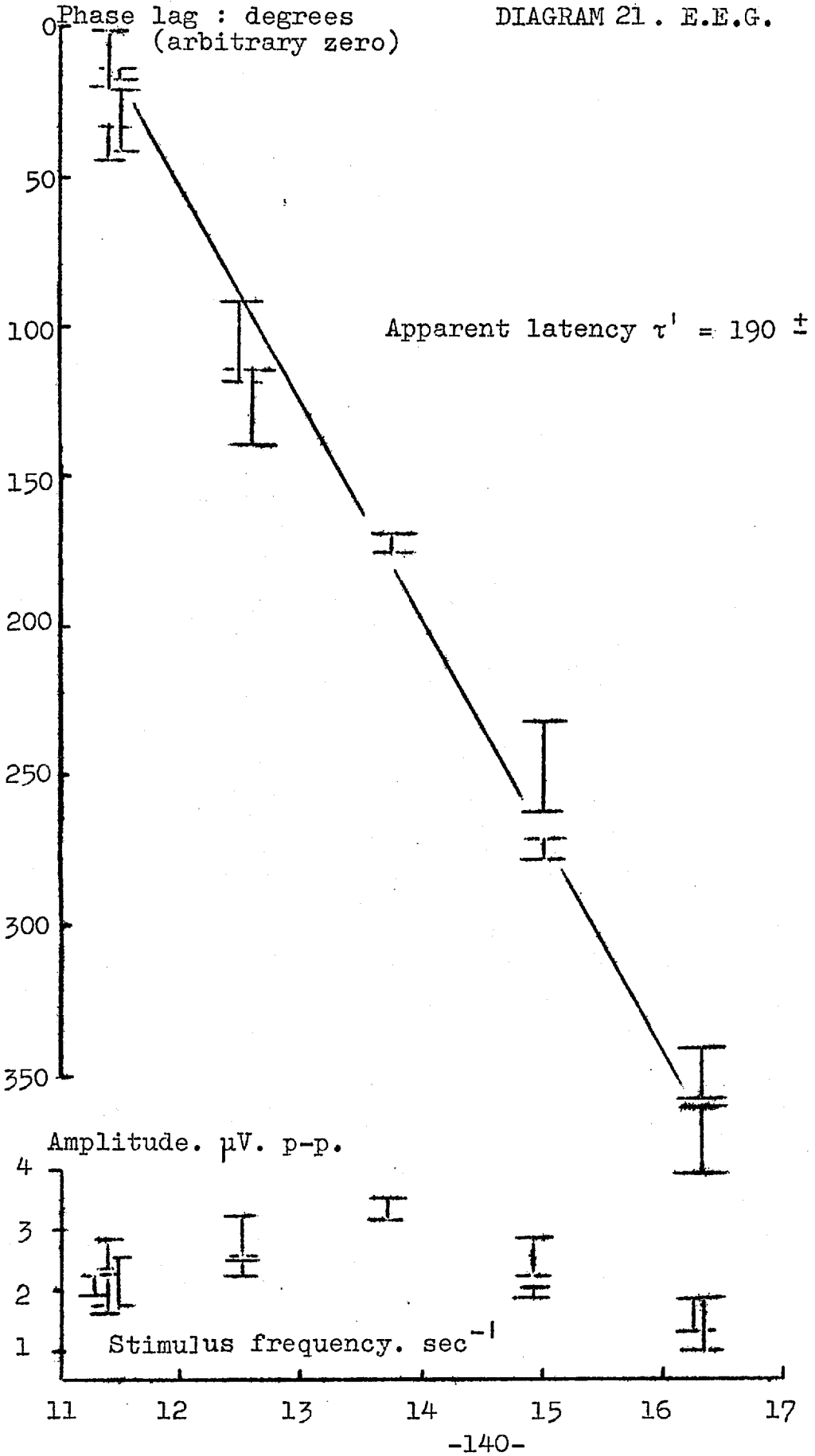
E.E.G. λ = 5449 $\mathring{A}$. Retinal illumination about 50,000 trolands peak (light adaptation equivalent to 25,000 troland constant level). Circular, 16^{o}, centrally viewed, sinusoidally modulated stimulus with dark surround.

In the upper part of the diagram the phase lag of the synchronous response is plotted against stimulus frequency.

The slope of the line is interpreted to indicate an apparent latency τ' of 190 $\pm$ 20 milliseconds of the synchronous response behind the stimulus (see page 77).

The lower part of the diagram shows the amplitude of the synchronous response for the various stimulus frequencies.

DIAGRAM 21 . E.E.G.



D I A G R A M 22

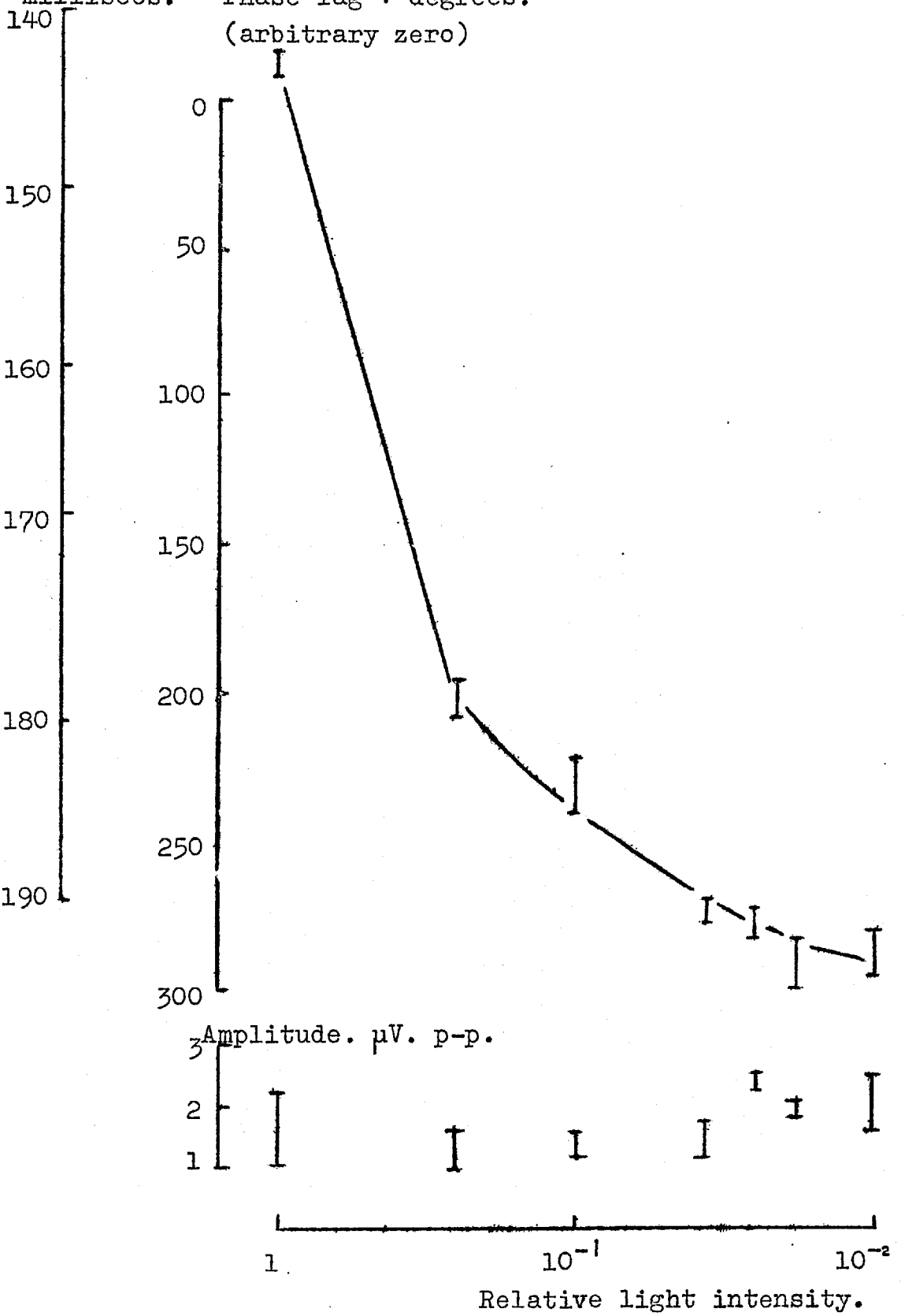
E.E.G. Stimulus as for diagram 21. λ = 5449 Å

Stimulus frequency constant at 14.9 c.p.s.

In the upper part of the diagram the phase lag of the synchronous response behind the stimulus is plotted versus the stimulus intensity.
The interpretation is that apparent latency (τ') increases as stimulus intensity decreases.
A discussion of this interpretation is given on page 58.

In the lower part of the diagram, the amplitude of the synchronous response is plotted versus stimulus intensity at constant stimulus frequency.

DIAGRAM 22. E.E.G.



D I A G R A M 23

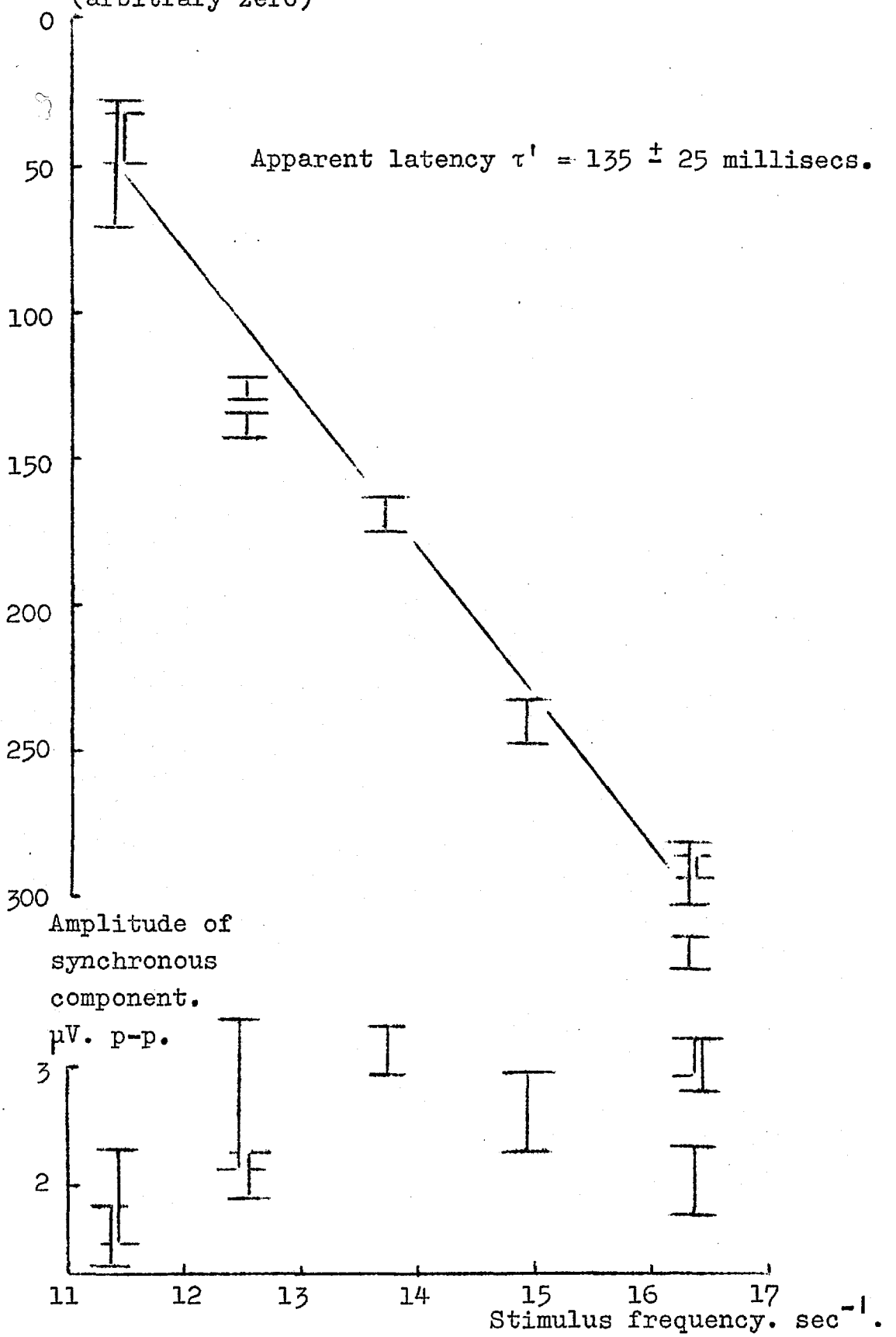
E.E.G. λ = 5780 $\mathring{A}$. Retinal illumination about 50,000 trolands peak (light adaptation equivalent to a 25,000 troland constant level). Circular, 16^{o}, centrally viewed, sinusoidally modulated stimulus with dark surround.

In the upper part of the diagram the phase lag of the synchronous response is plotted against stimulus frequency.

The slope of the line is interpreted to indicate an apparent latency (τ') of 135 $\pm$ 25 milliseconds of the synchronous evoked response behind the stimulus. (see page 77).

The lower part of the diagram shows the amplitude of the synchronous response for the various stimulus frequencies.

DIAGRAM 23. E.E.G.



D I A G R A M 24

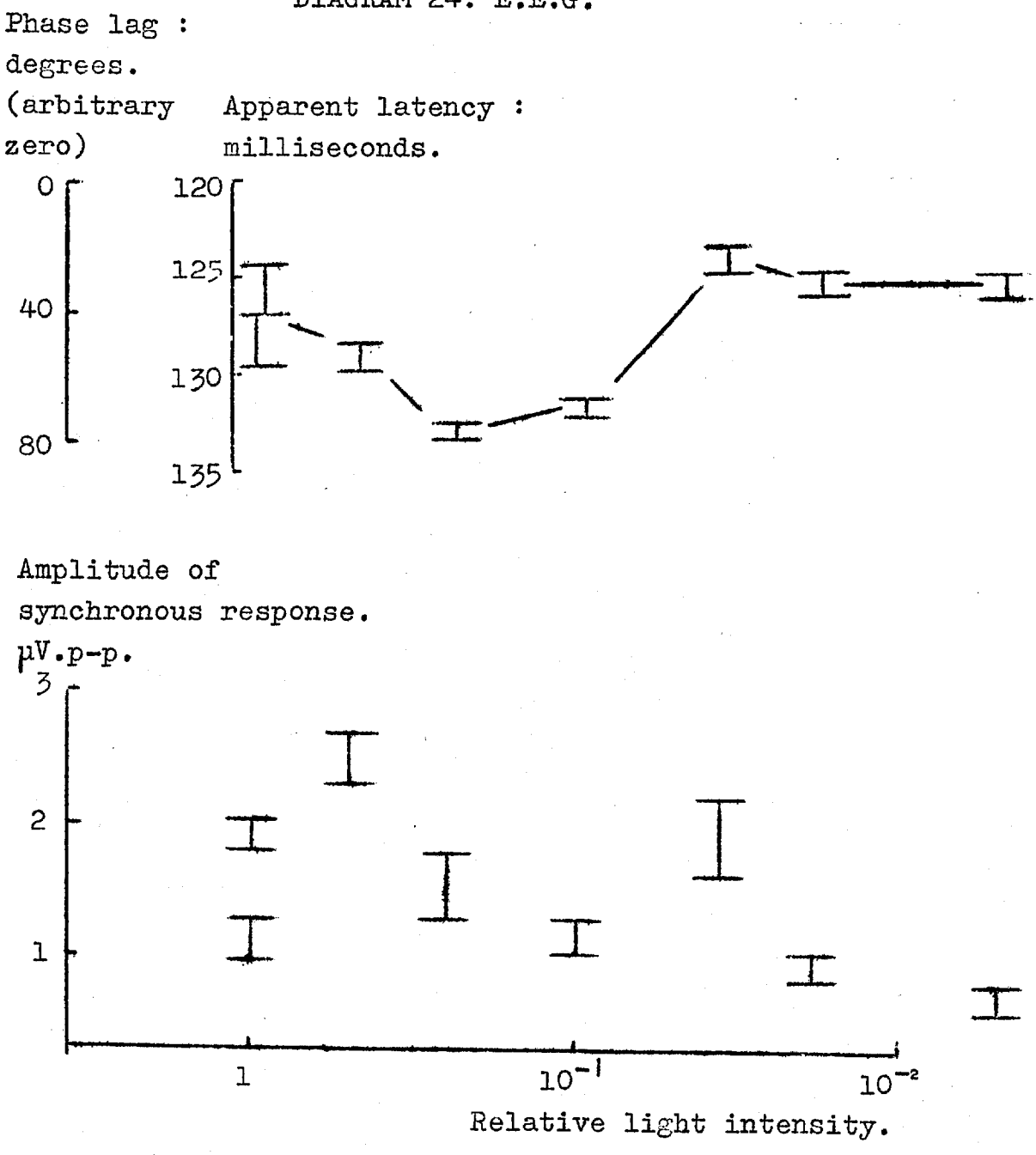
E.E.G. Stimulus as for diagram 23. λ = 5780 $\mathring{A}$

Stimulus frequency constant at 14.9 c.p.s

In the upper part of the diagram the phase lag of the synchronous evoked response behind the stimulus is plotted versus the stimulus intensity.
Any changes of phase lag with stimulus intensity are interpreted as changes in the apparent latency (τ') of the synchronous response (see page 58).
The scatter in the repeat measurements of the phase lag is up to $\pm 20^{o}$ (see diagrams 18, 20, 22, 24, 26, 28). This is attributed mainly to inaccuracy in replacing the eye pupil over the exit pupil. Taking the scatter into account it can be said that the apparent latency for a λ = 5885 $\mathring{A}$ stimulus varies little, if at all, with stimulus intensity between about 570,000 and 5000 trolands peak (equivalent steady intensities about 280,000 and 2500 trolands.

In the lower part of the diagram, the amplitude of the synchronous evoked response is plotted versus stimulus intensity at constant stimulus frequency.

DIAGRAM 24. E.E.G.



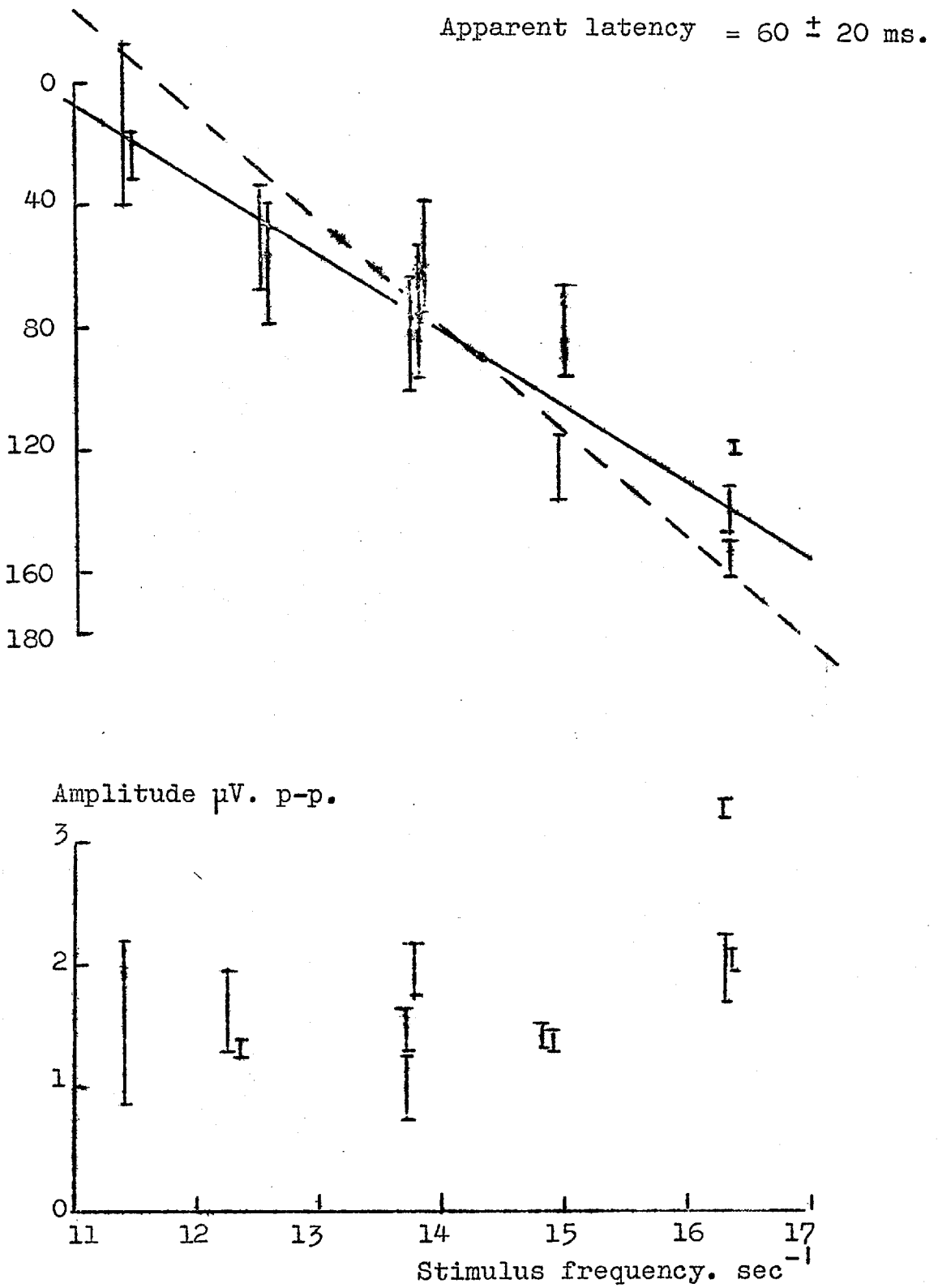
D I A G R A M 25

E.E.G. λ = 5885 Å. Retinal illumination about 50,000 trolands peak (light adaptation equivalent to a 25,000 trolands constant level). Circular, 16°, centrally viewed, sinusoidally modulated stimulus with dark surround.

In the upper part of the diagram the phase lag of the synchronous evoked response is plotted against stimulus frequency.
The slope of the line is interpreted to indicate an apparent latency (τ') of 60 $\pm$ 20 milliseconds of the synchronous response behind the stimulus (see page 77).

The lower part of the diagram shows the amplitude of the synchronous response for the various stimulus frequencies.

DIAGRAM 25. E.E.G.



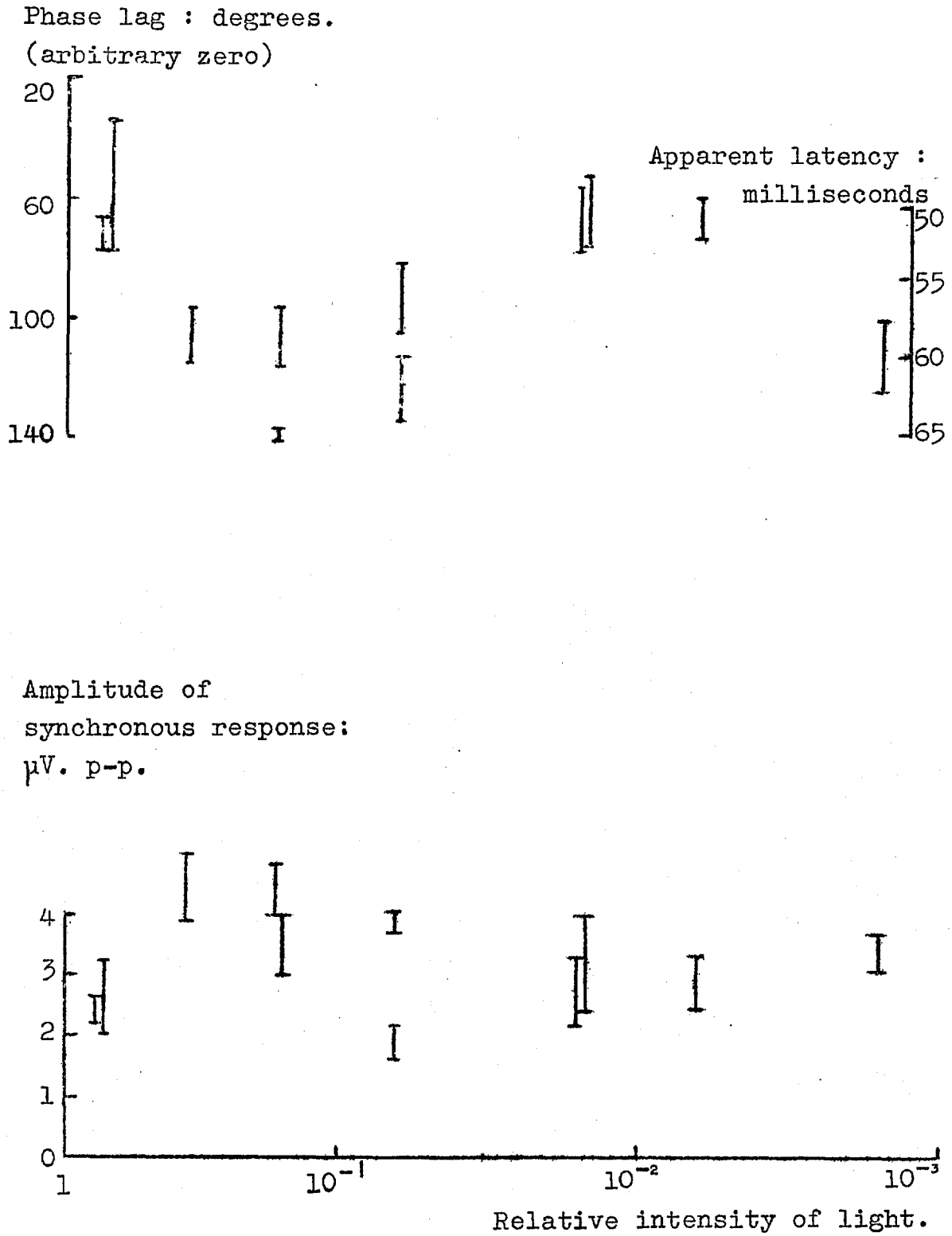
D I A G R A M 26

E.E.G. Stimulus as for diagram 25. λ = 5885 Å.
Stimulus frequency constant at 14.9 c.p.s

In the upper part of the diagram the phase lag of the synchronous evoked response behind the stimulus is plotted versus the stimulus intensity.
Any changes of phase lag with stimulus intensity are interpreted as changes in the apparent latency τ' of the synchronous response. (see page 58)
The scatter of repeat measurements of the phase lag can be seen to be up to $\pm 20^{o}$. This is attributed mainly to inaccuracy in replacing the eye pupil over the exit pupil. Taking this scatter into account it can be said that the apparent latency for a λ = 5885 Å stimulus varies little, if at all, with stimulus intensity between 500,000 trolands peak and 1200 trolands peak (equivalent steady intensities 250,000 and 600 trolands).

In the lower part of the diagram the amplitude of the synchronous evoked response is plotted versus stimulus intensity at constant stimulus frequency.

DIAGRAM 26. E.E.G.



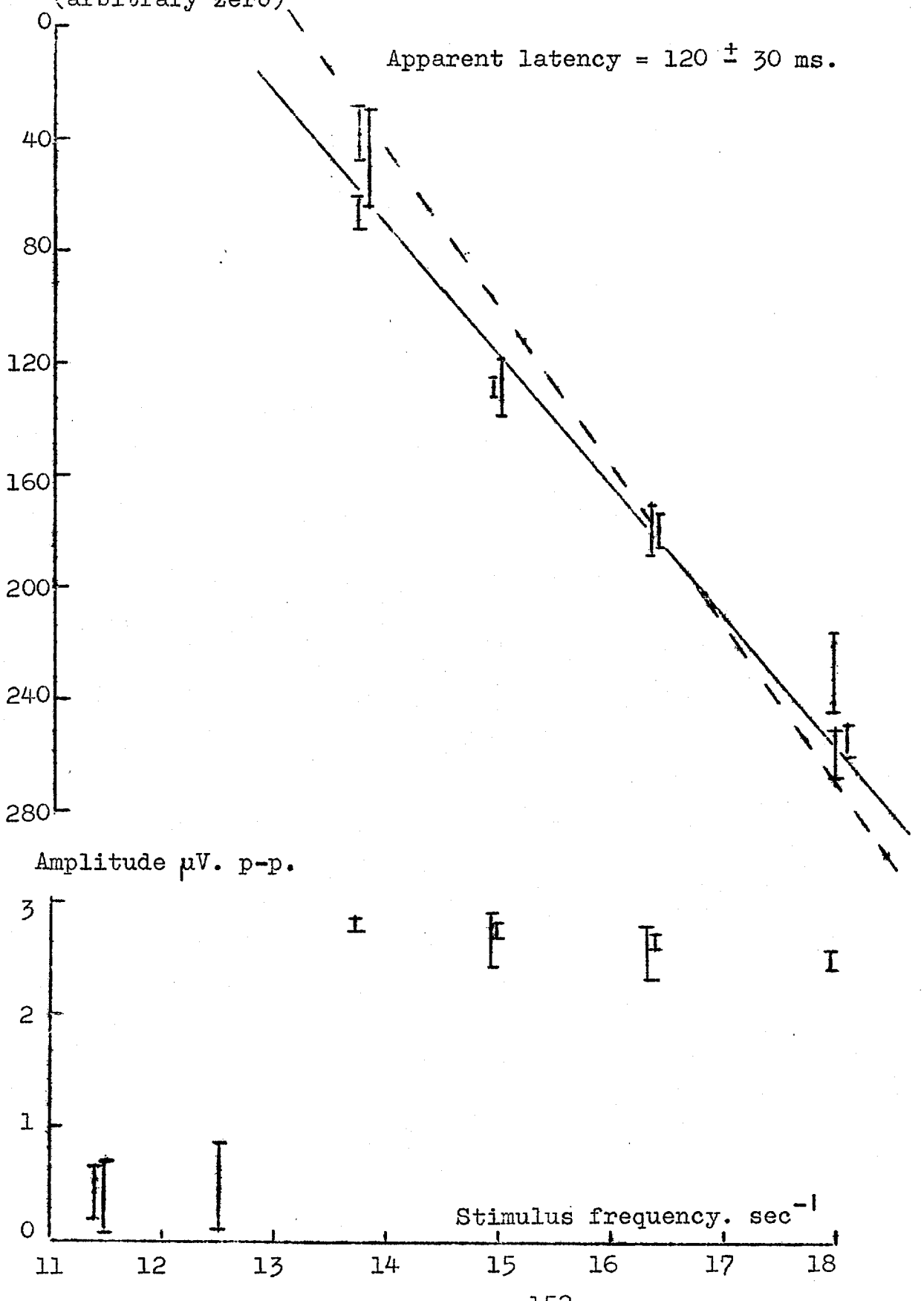
D I A G R A M 27

E.E.G. λ = 6337 $\mathring{A}$. Retinal illumination about 50,000 trolands peak (light adaptation equivalent to a 25,000 troland constant level). Circular, 16°, centrally viewed, sinusoidally modulated stimulus with dark surround.

In the upper part of the diagram, the phase lag of the synchronous evoked response is plotted against stimulus frequency.
The slope of the line is interpreted to indicate an apparent latency (τ') of 120 $\pm$ 30 milliseconds of the synchronous response behind the stimulus (see page 77).

The lower part of the diagram shows the amplitude of the synchronous evoked response for the various stimulus frequencies.

DIAGRAM 27. E.E.G.



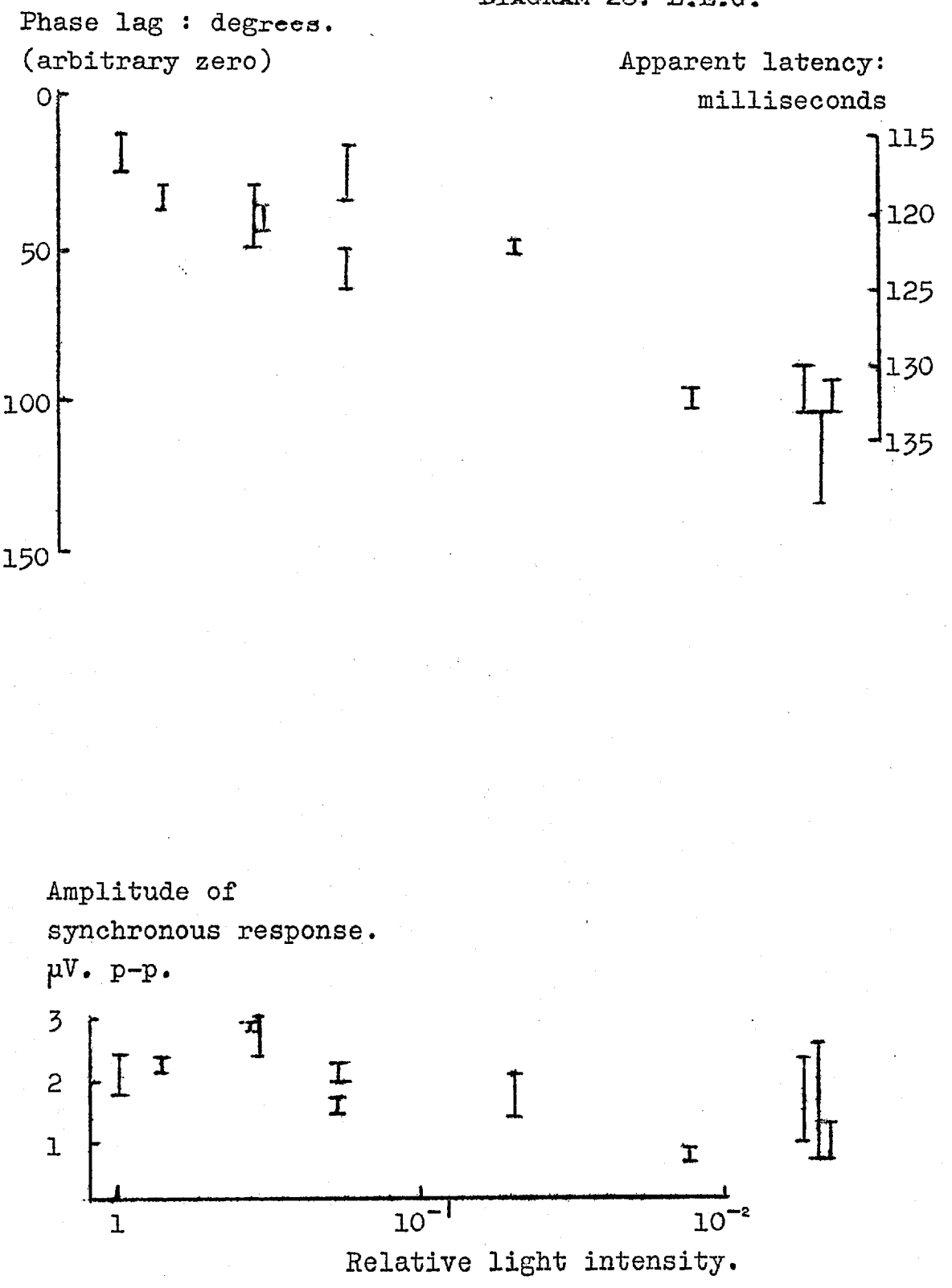
D I A G R A M 28

E.E.G. Stimulus as for diagram 27. λ = 6337 $\mathring{A}$

Stimulus frequency constant at 14.9 c.p.s.

In the upper part of the diagram the phase lag of the synchronous evoked response behind the stimulus is plotted versus the stimulus intensity.
Any changes of phase lag with stimulus intensity are interpreted as changes in the apparent latency τ' of the synchronous response. (see page 58).
The scatter of repeat measurements of the phase lag can be seen to be up to $\pm$ 20°. This is attributed mainly to inaccuracy in replacing the eye pupil over the exit pupil. Taking this scatter into account it can be said that the apparent latency for a λ = 6337 $\mathring{A}$ stimulus varies little with stimulus intensity over a range of about 120,000 to 2500 trolands peak (equivalent steady level about 60,000 to 1200 trolands). However there is a definite trend for apparent latency to increase as stimulus intensity decreases.

DIAGRAM 28. E.E.G.



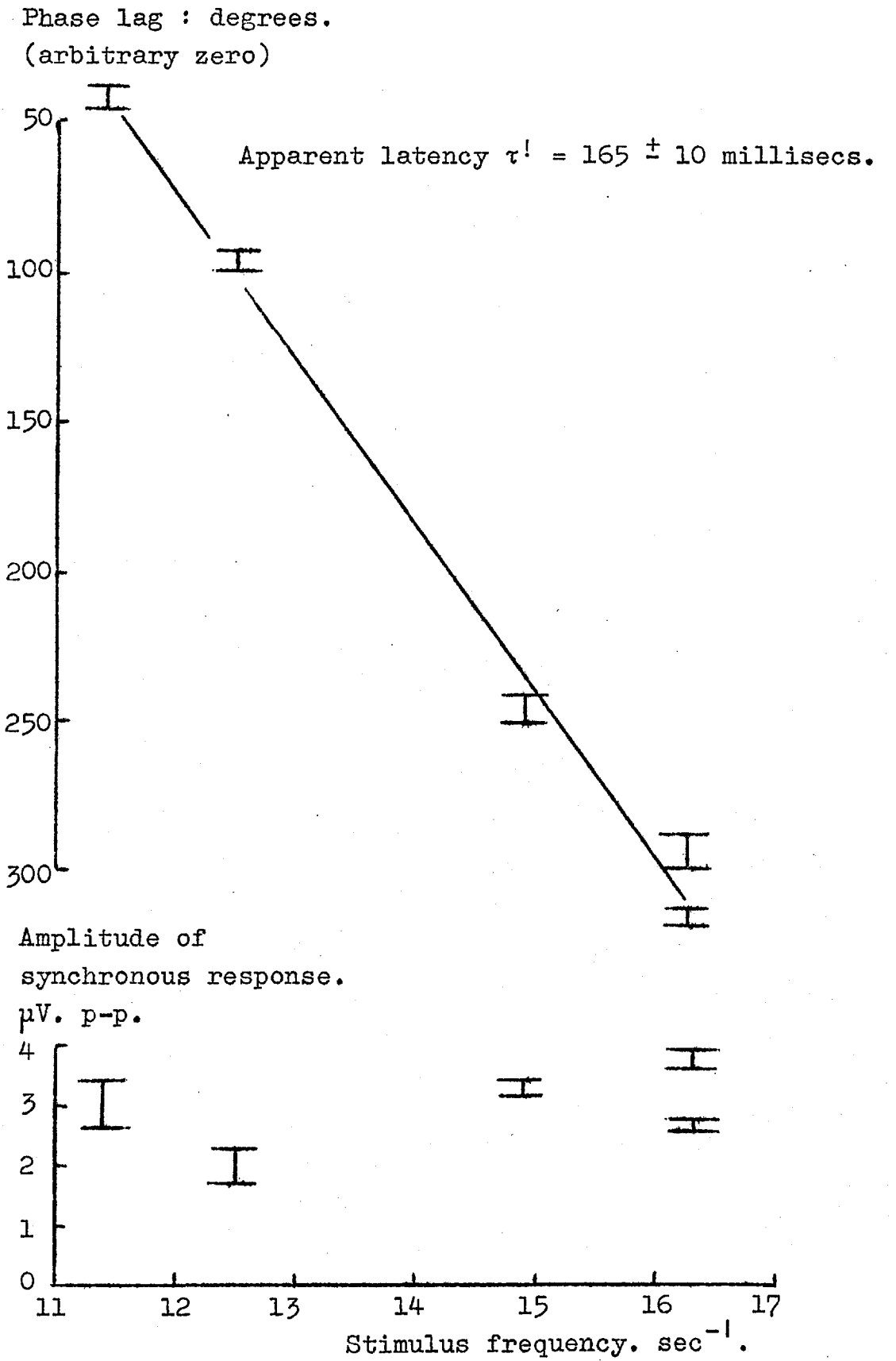
D I A G R A M 29

E.E.G. White, of colour temperature about 5500 ^{o}K. Retinal illumination about 50,000 trolands peak (light adaptation equivalent to a 25,000 troland constant level). Circular, 16^{o}, centrally viewed, sinusoidally modulated stimulus with dark surround.

In the upper part of the diagram the phase lag of the synchronous evoked response is plotted against stimulus frequency.

The slope of the line is interpreted to indicate an apparent latency (τ') of 165 $\pm$ 10 milliseconds of the synchronous response behind the stimulus.

DIAGRAM 29. E.E.G.



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