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# ANALYSIS OF THE ELECTRO-OCULOGRAMS OF A SERIES OF NORMAL SUBJECTS*

## ROLE OF THE LENS IN THE DEVELOPMENT OF THE STANDING POTENTIAL

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IN previous papers, a description has been given of the way in which the eye movement potential can be used as a clinical test of retinal function (the electro-oculogram, EOG). A detailed theoretical and practical account of the proposed clinical test has been given (Arden, Barrada, and Kelsey, 1962) and previous work has been reviewed. In this paper the results of tests upon normal eyes will be analysed, though some of the findings have already been briefly mentioned. The results described below were obtained over a period of 15 months, during which time the routine work was undertaken by more than one person, and the exact procedure of the clinical test was evolved. By analysis of the results it is therefore possible to discover how modifications of technique (both deliberate variations, and those due to the individual peculiarities of the experimenter) can affect the values obtained in the test. Such an analysis not only enables one to decide whether the findings in diseased eyes depart significantly from the normal, but will also help to guide other workers in the elaboration of similar tests. In addition, the normal subjects have included a series of uniocular aphakics. From the point of view of the EOG, which is a test of retinal function, these eyes may be considered normal, but their investigation has permitted further analysis of the possible contribution of the lens to the standing potential of the human eye.

## Methods

(*a*) *Subjects*.—The analysis is concerned with the results obtained on 91 eyes, which have been divided into two groups: 39 preliminary experiments were performed upon our colleagues at the Institute of Ophthalmology, and 52 results were obtained in patients drawn from the special clinics of the Institute. All the subjects had normal visual acuity, full fields, no cardiovascular disease, and in most cases no history of any disease involving the eye, apart from fourteen patients with uniocular aphakia. In these there was no history of myopia, vision was normal after correction, and the fields were full, the lens having been removed after trauma involving the anterior segment only, the operation having been successful and uncomplicated. Six cases were diagnosed as suffering from functional nervous disorders (hysteria, behavioural defects) and two from central lesions.

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(*b*) *Clinical Test.*—This was carried out as already described (Arden, Barrada, and Kelsey, 1962). The standing potential was measured for 22 to 26 minutes, and during this period the eye was dark-adapted for 12 min. The test was carried out with the following modifications: the preliminary experiments were all carried out by one of us (G.B.A.) and in them the subjects gazed at an illuminated wall; the retinal illumination was less than 350 troland; the 2nd group of patients were nearly all tested by a different person (A.B.) and looked at a viewing box, so that retinal illumination was approximately 3,000 troland.

(*c*) *Measurements.*—The following measurements were made from the graphs:

(*i*) The time from the beginning of dark adaptation until the potential reached its lowest value (dark trough time).

(*ii*) The potential at that moment (trough potential, in $\mu$V/degree of eye rotation).

(*iii*) The time from the beginning of re-illumination until the potential reached its maximum value (light peak time).

(*iv*) The magnitude of the potential at that moment ($\mu$V/degree of eye rotation).

(*v*) The percentage increase in potential, *i.e.* $\frac{\text{peak potential}}{\text{trough potential}} \times 100$

This last value is subsequently called the "ratio".

## Results

The main analysis is concerned with 52 results, which were obtained from patients with normal eyes, under precisely the same conditions as those who had retinal pathology.

Peak and Trough Potentials.—The frequency-distribution histograms of the potentials are shown in Fig. 1.

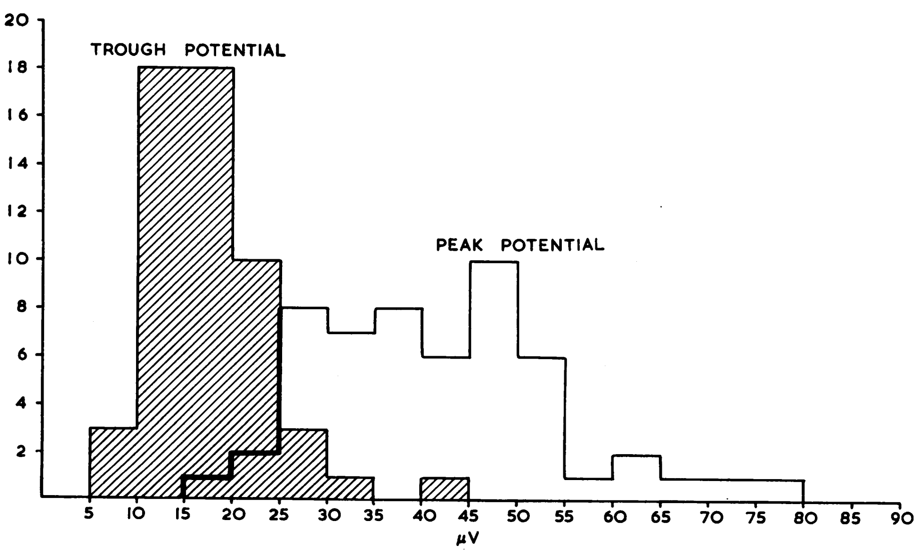


Fig. 1.—Histograms of minimal and maximal potentials recorded. Note wide range, overlap, and skew distribution.

There is a very great range in the potentials recorded in the diagram shown in Fig. 1. In the trough potentials, the range is 5·55 to 27·0 $\mu V/°$, while the corresponding figures for the peaks are 15·3 to 66·7 $\mu V/°$. It is also quite obvious that the distributions of the potentials are skewed, especially the peaks, and it is not therefore very rewarding to apply statistical methods to the crude data. The potentials are, however, rather large. In Table I, a summary is given of the eye movement potentials reported by ourselves and by other workers; there seem to be two groups, those who find the eye movement potential to be about 20 $\mu V/°$ and those who find it to be 5 $\mu V/°$ or less. These latter authors have all used large electrodes, or have placed them far from the canthi, and it seems reasonable to assume that the low potentials recorded are related to this fact. On the other hand, the standard deviation of the potentials recorded by some of these workers is

TABLE I

| Authors | Electrodes | Potential ($\mu V/°$) Range | Mean | S.D. | Experimental Conditions |
|---|---|---|---|---|---|
| Arden, Barrada, and Kelsey (1962) | Silver balls<br>Uniocular | 5·55–27·0<br>15·3–66·7 | 16·03<br>40·63 | 10·9<br>12·6 | Dark trough } High illumination<br>Light peak } series |
| | | 6·0–34·0<br>14·0–80·0 | 16·14<br>36·7 | 5·6<br>4·4 | Dark trough } Low illumination<br>Light peak } series |
| Kolder (1959) | Silver wire<br>Bitemporal | 12–35<br>24–61 | 19·7<br>36·8 | approx.<br>7 | Dark trough } 20 lux.<br>Light peak } |
| | | 10–24<br>29–55 | 17·9<br>39·6 | approx.<br>7 | Dark trough } 200 lux.<br>Light peak } |
| | | 12–22<br>24–61 | 17·1<br>41·4 | approx.<br>10 | Dark trough } 4,000 lux.<br>Light peak } |
| François, Verriest, and de Rouck. (1955, 1956a, b) | Small silver plates<br>Uniocular, placed on lower lid margin | 1·32–4·8<br>1·5–2·75 | 3·35<br>2·50 | 0·5<br>0·3 | General illumination } Calculated from<br>Dark trough } figures of "extreme version". |
| Ten Doesschate and Ten Doesschate (1957) | E.E.G. | — | 2·60<br>3·8 | — | Dark trough } Results from<br>Light peak } one subject |
| Shackel (1960) | Suction<br>Bitemporal, placed with a special device | 10–30 | 19·3 | 4·9 | Illumination not investigated |
| Miles (1939) | Metal foil | 7–80 | 30 | 10 | Average of several figures<br>Significant increase in potential on light adaptation |
| Kris (1958) | Silver wires<br>Uniocular | | approx.<br>20 | | Large changes on illumination |
| Hoffman, Wellman, and Carmichael (1939) | Special solder<br>Bitemporal, near canthi | 13–31 (Uniocular potentials approx. 3/4 of these values) | 18·5 | 7·5 | Calculated from graphs on eight subjects |
| Leksell (1939) | Large suction cup<br>Bitemporal | 10·4–12·5 | | | |
| Lion and Powsner (1950) | Large silver<br>Placed on temples remote from eyes | | approx.<br>5 | | |
| Gabersek (1960) | E.E.G. Bitemporal | | < 5 $\mu V$. | | |
| Mowrer, Ruch, and Miller (1936) | Dimes<br>Uniocular | 7–10 | | | |

rather less than in the present work in spite of the fact that random errors will be much more effective in increasing the scatter when small signals are being amplified. It therefore seems that the less the recorded potential, the less its apparent variation.

DISTRIBUTION OF RATIOS.—These are shown in Fig. 2. The ordinary frequency distribution histogram (Fig. 2*a*) is markedly skewed. The extreme values are 191 and 382 per cent. (mean 252·4 per cent.). Any attempt to perform a statistical analysis on such data would be greatly facilitated if they were normally distributed, and fortunately, this can be approximately achieved by converting each figure into a logarithmic fraction of the mean *i.e.* ($\log x - \log \bar{x}$). The frequency distribution histogram obtained by this simple transformation is shown in Fig. 2 (*b*). The data for the peak and trough potentials may be expressed in a similar way, and this reveals another

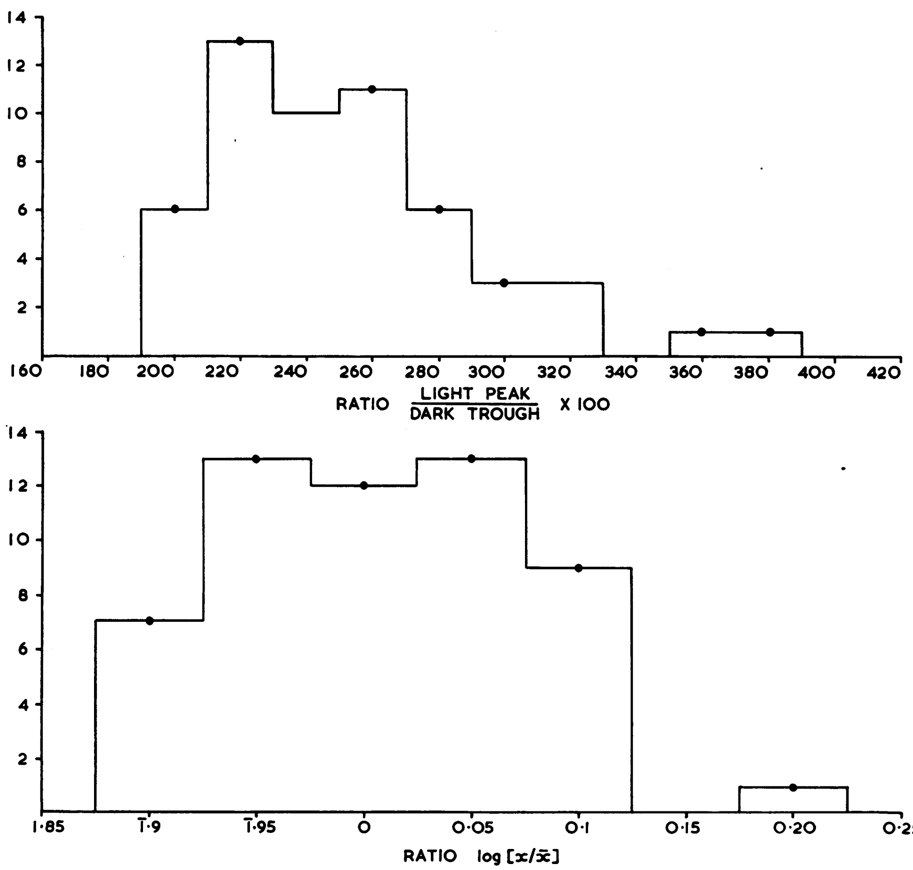


FIG. 2.—Histograms of ratios. Upper, linear plot. Lower, logarithmic transformation approximates to normal distribution.

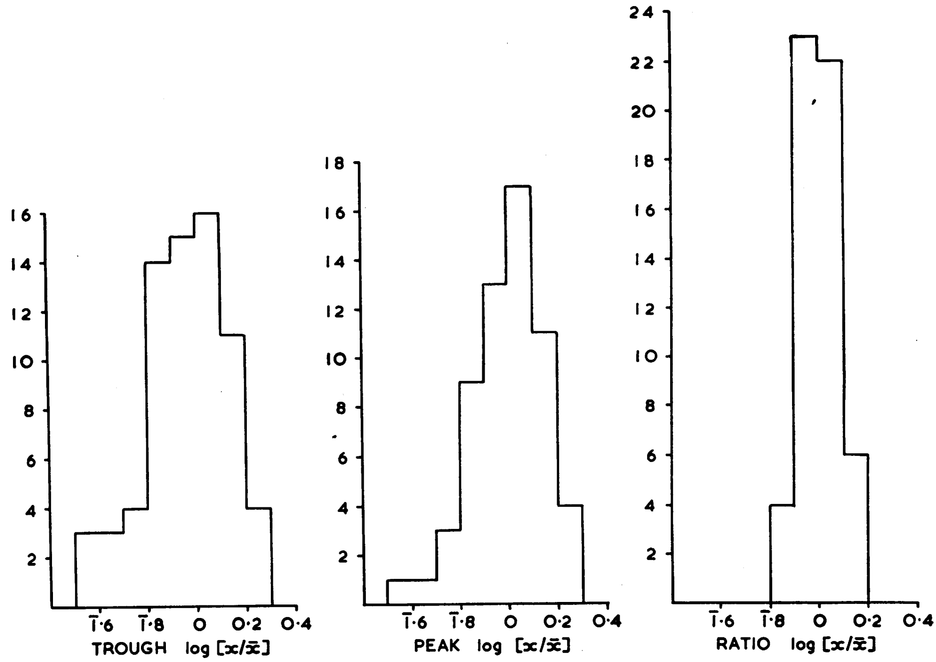


FIG. 3.—Histograms of troughs, peaks, and ratios. Note smaller variation of ratios.

aspect of the data (Fig. 3). It can be seen that the distribution of peaks and troughs is much more variable than for the ratios.

CORRELATION BETWEEN TROUGHS AND PEAKS.—Fig. 3 implies that there is a good correlation between troughs and peaks, and that this is the case can be seen from Fig. 4 (opposite), in which trough potential (ordinate) is plotted against peak potential for the 52 results. The regression line drawn in the Figure is the one calculated from the data. Note that the regression is linear, over the potential range covered by the experiments.

CORRELATION BETWEEN TROUGH POTENTIAL AND RATIO.—Fig. 5 (overleaf) shows that there is no obvious relationship between the two variables, and statistical analysis confirms this belief. The coefficient of correlation is small. It is therefore possible to conclude that the actual potential recorded does not influence the ratio. The positioning of the electrode and the type of electrode are the major causes of variation of potential. The Figure shows that the electrodes do not influence the clinical test, which is merely concerned with the relative change of potential caused by alteration of illumination. This is a formal proof of the assumption previously made (Arden and Kelsey, 1962a,b—and many others) that the EOG potential and its alterations are caused by changes in the direction and magnitude of a generating dipole.

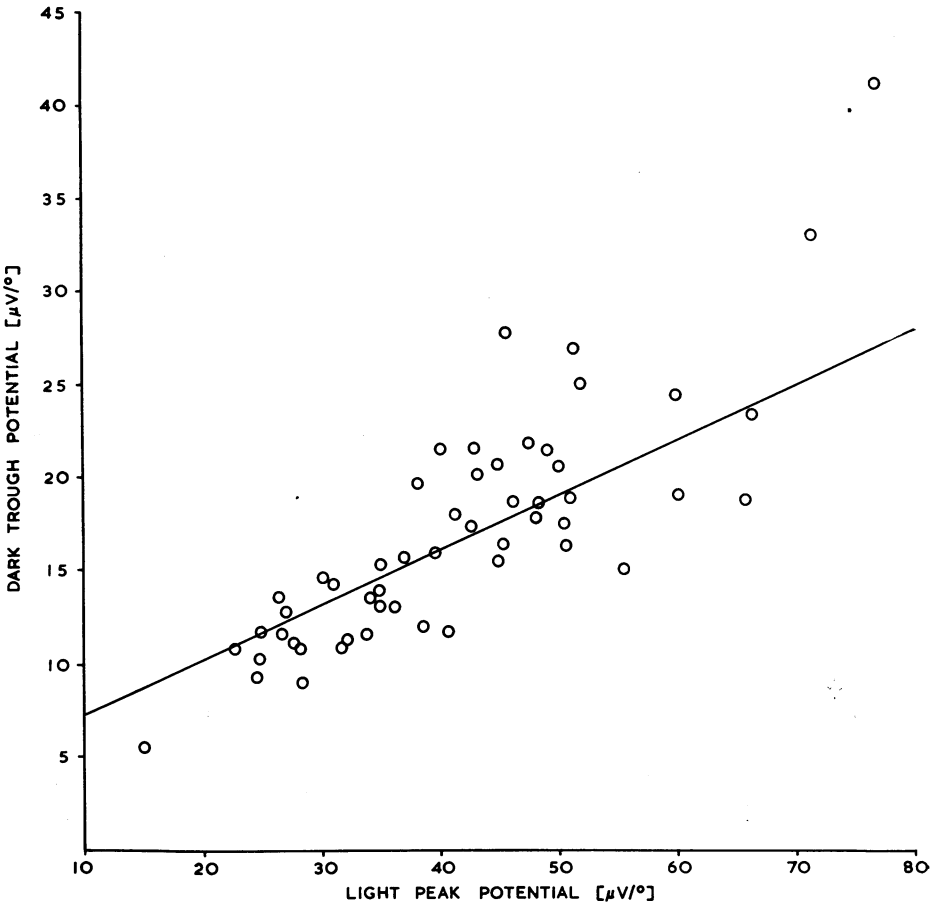


FIG. 4.—Correlation between light peak and dark trough potentials. Note good linear correlation.

CORRELATION OF RATIOS WITH AGE.—A small, significant ($p > 0 \cdot 05$) negative correlation between age and ratio has been established, though the number of results is rather small (Fig. 6, overleaf). No correlation has, however been found between peak or trough potential and age. This result is unlike that reported by Shackel (1960), who found a correlation between the general level of potential and age (the experimental conditions controlled the level of illumination, but fixed potential levels were not achieved). In Shackel's experiments (in which bitemporal recording was used, the nasal electrode being more difficult to place), the electrode positions were apparently much more carefully controlled than in this work and a much more homogeneous group of subjects was investigated. It seems likely that our failure to detect correlations between age and potential may be due to the variability in the actual potentials recorded, but on the other hand, the correlation Shackel observed might equally be due to the fact, demonstrated by

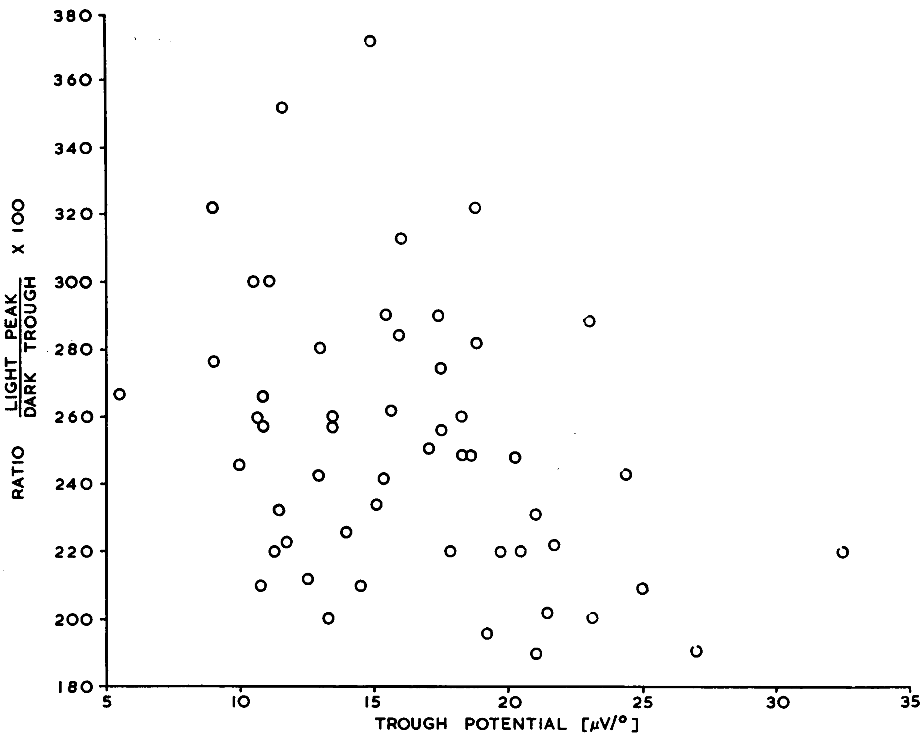


FIG. 5.—Correlation between ratio and trough potential. The scatter diagram shows the correlation to be very poor.

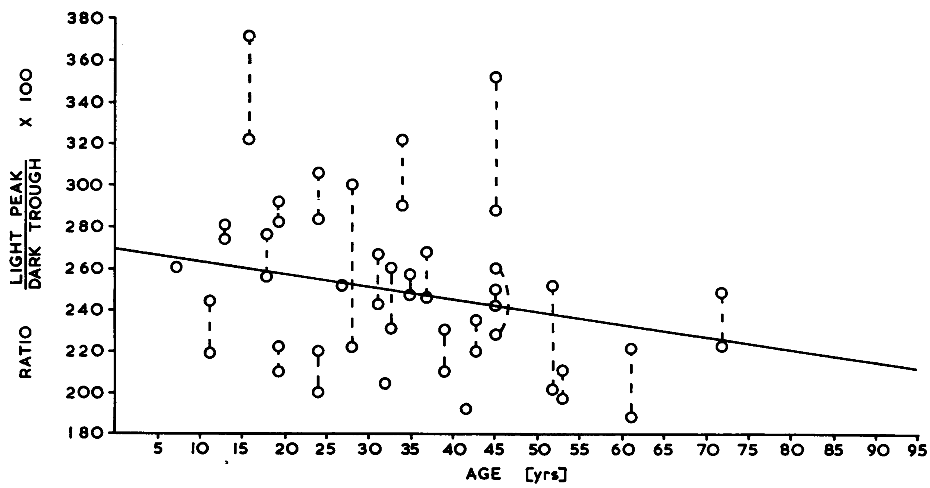


FIG. 6.—Correlation between ratio and age. There is a significant negative correlation. The dotted lines join values obtained in the two eyes of the same subject.

Fig. 6, that the light rise is greater in younger people. It is impossible to draw any conclusion from this correlation. In older subjects there might be a decreased retinal illumination, caused by a reduction in pupillary aperture, or a loss of transparency of the ocular media. However the decreased light rise could also be due to a direct effect of ageing on the potential generators.

CORRELATIONS BETWEEN RIGHT AND LEFT EYES.—Since both eyes of the same subject were investigated, it is possible to discover how closely the results obtained in the two eyes resemble each other. There is a very highly significant correlation, not only between the ratios (which might be expected) but also between the actual peak and trough potentials in the right and left eyes (Table II).

TABLE II

CORRELATIONS BETWEEN FUNCTIONS MEASURED

| Variables | No. | R. | Significance |
|---|---|---|---|
| Peak potential/Trough potential | 52 | ·635 | > 1 per cent |
| Ratio/Age | 52 | ·297 | > 5 per cent, < 1 per cent. |
| Trough potential/Ratio | 52 | ·149 | Not significant |
| Trough potential/Age | 52 | ·0275 | Not significant |
| Peak potential/Age | 52 | ·004 | Not significant |
| Ratios Right eye/Left eye | 31 | ·804 | > 1 per cent. |
| Troughs Right eye/Left eye | 31 | ·730 | > 1 per cent. |
| Peaks Right eye/Left eye | 31 | ·604 | > 1 per cent. |

The implication of this finding is that the right eye electrodes were placed in the same positions relative to the globe as were the left eye electrodes, but that the electrode positioning varied from patient to patient. The experimenter always tried to place the electrode in the same place relative to the canthi, so that the high coefficients of correlation between the potentials recorded in the right and left eyes express the fact that this aim was to a large extent realized, and also that most people's faces are symmetrical about the sagittal plane. The differences between *individuals* must therefore be due to the experimenter putting the electrodes in widely differing places in different subjects, or to individual differences in the bony structure of the face, or to a real difference in the amplitude of the generating dipoles from person to person. This last source is most unlikely to account for more than a small part of the individual variation, which has a range of nearly 500 per cent.

SECOND GROUP OF NORMALS.—This group was investigated by one or us who took part in only five of the experiments reported above. The only difference between the two groups is the intensity of illumination used to re-illuminate the retina. This variable does not affect the magnitude of the trough potentials (Table III), the mean value of which was 16·14 μV/°. This figure is almost identical with the value obtained by a different person in the major investigation (16·03 μV/°). The actual fixing of the electrodes is highly subjective, and it is scarcely to be expected that two experimenters would employ exactly the same criteria (which they must have done from the identity of the trough means) unless there was some restraint upon their choice of electrode position. Such a restraint is provided by the size of the electrode mounting, and the adhesive plaster used to stick the electrodes on the skin, and the results make it likely that, in fact, electrode placement was fairly accurate, the big scatter of potentials recorded being due to individual differences in the shape of the orbit.

TABLE III

NORMAL VALUES OF ELECTRO-OCULOGRAM

| Conditions | No. of Cases | Troughs μV/° | | | Peaks μV/° | | | Ratios $\frac{\text{Peak}}{\text{Trough}} \times 100$ | | | Trough Time (min.) | | | Peak Time (min.) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Mean | S.D. | S.E. | Mean | S.D. | S.E. | Mean | S.D. | S.E. | Mean | S.D. | S.E. | Mean | S.D. | S.E. |
| Normal High Illumination | 52 | 16·03 | 10·9 | 1·5 | 40·63 | 12·6 | 1·74 | 252·3 | 40·71 | 5·6 | 9·66 | 2·4 | 0·34 | 8·85 | 1·00 | 0·15 |
| Normal Low Illumination | 39 | 16·14* | 5·60 | 0·89 | 36·70* | 4·40 | 0·70 | 223† | 23·15 | 3·7 | 10·53* | 1·67 | 0·28 | 7·78† | 1·07 | 0·14 |
| Normal eyes of Unilateral Aphakics | 14 | 18·8 | 7·89 | 2·11 | 43·8 | 12·8 | 3·37 | 235 | 63·42 | 16·9 | | | | | | |
| Aphakic Eyes | 14 | 18·3* | 7·32 | 1·9 | 42·8* | 17·2 | 4·69 | 252* | 43·3 | 11·58 | | | | | | |

* Not significantly different from previous group.
† Significantly different from previous group.

The other point of interest is the ratios recorded in the low illumination group. The mean value is 223 per cent., considerably lower than in the other group. Further, there is a smaller variability between the highest and lowest ratios recorded (Fig. 7, opposite). Part of this may be only apparent, but it seems that only the incidence of large ratios is increased by the higher illumination. It must be remembered, that these experiments were performed with-undilated pupils, and that there is therefore an automatic compensation for the change in light intensity.

The degree of compensation can be calculated. In a series of experiments on the effect of light intensity (Arden and Kelsey, 1962b), subjects were exposed to the viewing box at the same brightness as in the clinical series described above. The retinal illumination was, however, higher because the subjects' pupils were maximally dilated (8 mm.). Under these circumstances the average ratio was 300 per cent. Ratios of 252 per cent. were produced when the output of the viewing box was decreased by 1·1 log units.

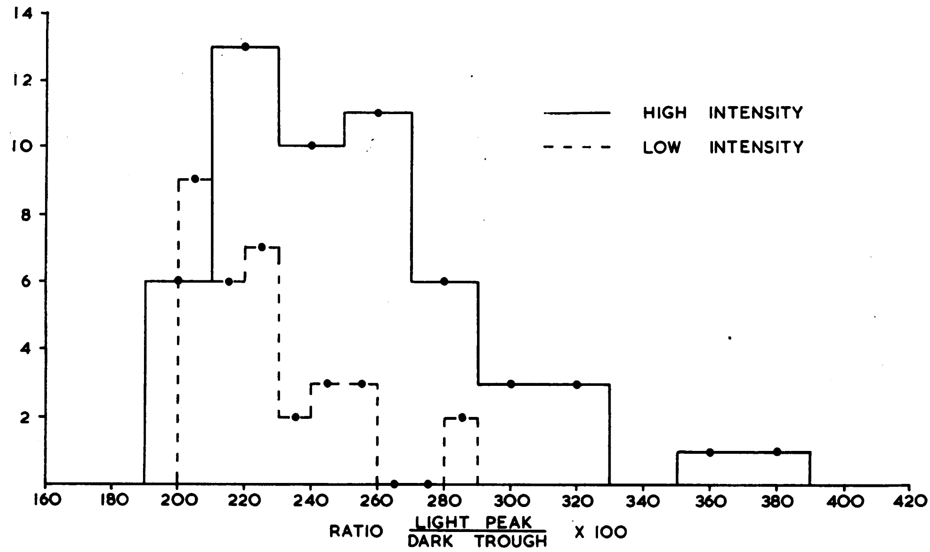


FIG. 7.—Comparison of ratios at two levels of illumination. The scatter is greater in the high illumination series.

Such a retinal illumination would be expected if, in the present series, the patients' pupils contracted to a diameter of 2·48 mm. On many occasions the patients' pupillary diameter was estimated during the course of the test, and was approximately 2 mm., so that the present results are consistent with those of Arden and Kelsey. Similarly, one can make calculations about the retinal illuminations in the two series of experiments reported in this paper. The brightness of the wall was only one-tenth of the viewing box (1 log unit), but the difference in the average ratios corresponds to a difference in retinal illumination of 0·6 log unit. The discrepancy is accounted for if one supposes that when the subjects faced the wall the average pupillary diameter was 4·04 mm., and this value is approximately confirmed by our observations.

PEAK AND TROUGH TIMES.—Table III shows that there is a larger variation in trough timing than in peak time. This might be expected, for the dark trough depends upon the previous history of illumination, which was not controlled. The light peak time is less variable, and in the high intensity series is significantly greater than in the low intensity group.

COMPARISON OF APHAKIC EYES WITH NORMAL.—The relevant data are given in Table III. It can be seen that, in comparison with the normal eyes of the same subjects, there is no difference in trough potentials, and only small insignificant differences between the peak potentials and the ratios, which seem to be larger in the aphakic eyes. It must be recalled that these patients were selected and that in other cases with evidence of damage to the posterior segment, the ratios in the aphakic eyes were abnormally small.

## Discussion

The detailed analysis of normal results, which has been presented above, is necessary before one can employ the EOG as a diagnostic test. The analysis will also act as a guide to any other worker who wishes to use the method. In addition, the evaluation of this fairly large series of results has confirmed many of the observations made in earlier papers. Thus, it has been shown that the ratio between dark trough and light peak is independent of the actual measured potential, a statement previously illustrated by a single example (Arden and Kelsey, 1962a). This is proof that the light-induced changes in potential are due to alterations in the magnitude of the retinal potential generators. In addition, it has been firmly established that the ratios vary considerably less than the actual potentials. The finding that the trough potentials measured in the two conditions of illumination are identical, while the peak potentials are not, further demonstrates the fact that the dark trough is not related to intensity of illumination in the same way as is the light peak.

The actual voltages recorded in the test depend largely upon the type of electrode used. The closer the pick-up to the electrical source, the greater the voltage recorded. However, though with small electrodes the traces recorded are more accurate, the results of François, Verriest, and de Rouck (1956) who have conducted the only survey comparable to the present one, show that the variability of the results is not greatly affected by the choice of electrode. The correspondence between the average trough potentials found in this clinic by different workers suggests that the positioning of our electrodes is determined by their shape, and that the scatter of potential values is caused by the subjects' facial differences.

**The "Normal" Values.**—It would be gratifying if it were possible to define precise limits for the normal value of this new test, in particular for the ratio. As is usual, this cannot be done. A very large number of cases would have to be investigated since, for example, we have demonstrated a correlation with age. In addition, the skew distribution of ratios is difficult to treat statistically. The logarithmic transformation (Fig. 2) does produce an approximately normal curve, with a standard deviation of log 0·0687. When this is translated back into linear values, it gives a 5 per cent. confidence limit for values of ratios outside the range 185 and 322 per cent. While this figure excludes some of the higher normal values, no normal eye has given a ratio of less than 191 per cent. Additional reasons can be advanced for distrusting this method of calculation. For example, in the series performed with lower illumination, the average value of the ratios was lower, but there was no case in which it fell below 200 per cent. Again, there is a high correlation between the values obtained in the two eyes of the same person. If a ratio of 300 per cent. is recorded in one eye, the lower limit in the other will be 200 per cent., which is significantly greater than the lower limit of the whole series. In this clinic we have therefore adopted the convention that any ratio of 200 per cent. and under is suspicious, particularly in young persons, or if the condition is uniocular and the ratio in the unaffected eye is high. In such a case, the patient should be seen again. Any value under 185 per cent. is frankly pathological. Abnormally long peak times (over 11 min.) are also noted: they are always associated with low ratios.

**Alteration of Illumination Level.**—In theory, the results of the test should vary considerably with the illumination level. However, in practice, this seems much less important, owing to the automatic compensation of retinal illumination by changes in pupillary diameter. This is rather a good reason for not attempting to dilate the pupils before the test begins, for the light output of the source will inevitably fall off as the tubes age and the surfaces accumulate dust. It is interesting that, although the mean value of the ratios is less at lower illumination, the lower limit found is in fact higher. This shows how difficult it must be to fix a lower limit of normal. It must, however, be remembered that the low illumination series was part of a research investigation, and that the subjects could be prepared more carefully than in later work which was carried out with a somewhat more hurried clinical routine. The smaller scatter may simply reflect a better technique.

**Aphakic Eyes.**—It has been mentioned (Arden, Barrada, and Kelsey, 1962) that retinal detachment and myopia cause a decrease in the ratio, and in view of the higher incidence of detachment in the aphakic eye, it might be supposed that abnormalities might be detected in our series. However, in view of their careful selection, we feel this to be unlikely. The slightly higher ratios found in the aphakics are not significant, but might possibly be attributable to greater retinal illumination caused by loss of the lens or to a partial iridectomy. However, the figures show that the aphakic eyes are to all intents normal. This result has a bearing on the origin and mode of spread of the current field which produces the standing potential. Brindley (1956) has shown that the surfaces of the lens carry an electric charge, and has suggested that this may contribute to the standing potential. This idea is open to the theoretical objection that, if both surfaces are charged, the current flow from one will be opposed by a similar current flowing in the reverse sense from the other; it follows that the lens, being an iso-potential sphere, will not produce a current field detectable by electrodes placed remotely from it. The present results permit a more direct investigation of the problem. The lens may either contribute to (or subtract from) the standing potential, and it may in addition act as a resistance to the flow of current.

However, it is most unlikely to be affected by the alteration in retinal illumination. By measuring peaks, troughs, and ratios, one can therefore discover what electrical effect, if any, the lens possesses. For example, if the lens contributes to the standing potential, the dark trough and light rise potentials will be smaller in the aphakic eye. The reduction will be more obvious for the dark trough, since in these circumstances the contribution of the lens will be proportionately greater. The figures show that it is quite unlikely that the dark trough potentials differ in normal and aphakic eyes and therefore the lens contribution to the standing potential must be very small. (This argument does not take into account any interaction between the hypothetical lens potential and the pigment epithelium potential, but this possibility is so unlikely that it may safely be neglected.) The lens might also act as an electrical resistance to current flow. This possibility can be considered if we admit that the lens resistance is small in comparison with the total, and that the proportion of the standing potential current which actually passes external to the eye is also small. This assumption is very plausible and allows one to neglect any alteration in the work done by the generators of the standing potential as a result of the removal of the lens. In this simplified system, removal of the lens should cause an increase in the measured standing potential, which will be proportionately greater for the dark trough; aphakia should therefore be associated with an unchanged ratio and larger potentials. Since this is not the case (Table III), it can be stated that the lens forms only a small fraction of the resistance in the circuit through which the standing potential generators drive current.

## Summary

The results of EOGs in normal subjects are analysed and compared with the values obtained for aphakics. The following conclusions are drawn:

(1) The normal ratio is greater than 185 per cent., and usually above 200 per cent.

(2) The potentials recorded depend upon the type of electrode employed. The operator places these in a uniform manner, determined by their shape. The test is independent of the magnitude of the potentials recorded.

(3) Alteration in the retinal illumination employed is partially compensated for by variation in pupillary diameter.

(4) The lens cannot be shown to contribute to the standing potential or to act as an electrical resistance to current flow.

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## APPENDIX

### *Recording situation of the eye movement potential*

The experiments of Fig. 3 demonstrate that, while the potential, measured in terms of $\mu$V per degree of eye rotation, varies greatly from person to person, the ratio $\frac{\text{light peak}}{\text{dark trough}}$ does not.

These observations support the view that the alterations in potential produced by change of illumination are caused by variations in the magnitude of intra-ocular potential generators. The alternative view, that the change in potential is caused by variations in the passive electrical properties of the tissues can be discounted. This may best be understood by reference to the diagram (Fig. 8).

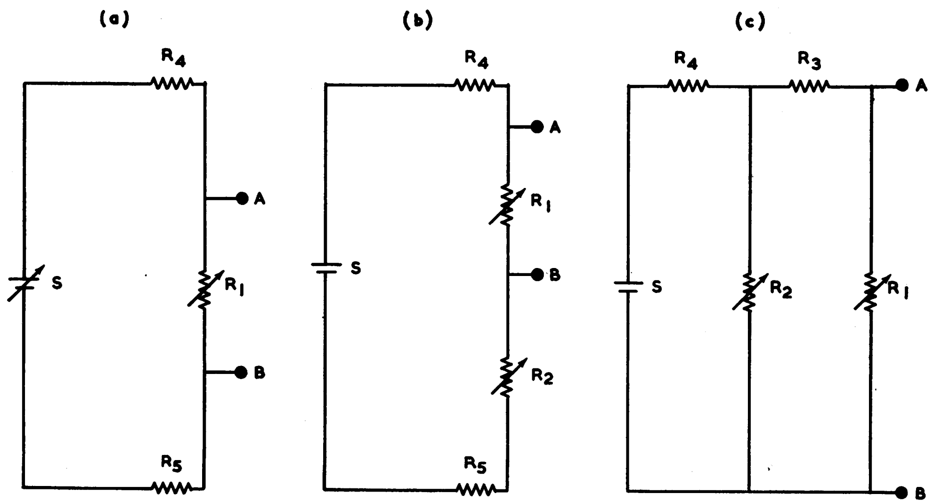


FIG. 8.—Possible recording conditions for the EOG.
(a) assumes that the potential generator, S, varies with illumination.
(b) and (c) assume that S is constant, but that some resistance ($R_2$) varies with retinal illumination.

CIRCUIT (*a*) represents the hypothesis accepted in the text. S is the potential generator, shown as variable, $R_1$ the resistance across which the electrodes A and B record, $R_4$ and $R_5$ additional resistors. Depending upon irrelevant factors, $R_1$ will vary from person to person, while S and the change in it produced by illumination does not.

CIRCUIT (*b*) examines the case in which a variable resistance $R_2$ is placed in series with $R_1$. If *i* represents the current in the circuit at the dark trough, and $i_L$ the current at the light peak, it is required that

$$\frac{i}{i_L} \text{ is constant for all values of } R_1. \quad \quad (1)$$

Now $$i=\frac{S}{R_2+R_1+R_4+R_5} \quad \text{and} \quad i_L=\frac{S}{R_{2L}+R_1+R_4+R_5},$$

$R_{2L}$ being the new resistance of $R_2$ at the light peak. Therefore, unless all the resistors change on light-adaptation and their relative values are precisely fixed, circuit (*b*) can be discounted.

CIRCUIT (*c*) examines the case in which $R_2$ is placed in parallel with the recording resistance $R_1$. Now the voltage between A and B ($_AV_B$) can exceed 10 mV for full version of the eye. If condition (1) above is to be fulfilled, $R_3$ an additional resistance much greater than $R_2$, must be inserted, and also $R_3 \gg\gg R_1$. Hence the voltage across $R_2$ must be much greater than 10 mV., and by similar reasoning S must generate a higher potential still. Since the size of the resistors *in vivo* is unknown, S cannot be calculated exactly, but if $R_3 = 10R_1$, it will be over 100 mV., which is impossible. Since the total corneo-fundal potential is only about 6 mV in the isolated eye, $R_2$ $R_3$ and $R_4$ must be intra-ocular, and since the potential S is developed in the optic axis, $R_3$ must be a high radial resistance across which a potential drop occurs. The only radial resistance in the eye is in the pigment epithelium, the presumed site of generation of the eye movement potential. Circuit (*c*) is therefore most unlikely, though changes in the impedance of the actual generator S might account for the apparent alteration in magnitude of the potential.

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