AN INVESTIGATION OF THE FOVEAL, MACULAR, AND PERIPHERAL REGIONS OF THE RETINA.



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The writer wishes to express his appreciation to Dr. Frank Allen, for suggesting the problem and for aiding in it's solution with much advice, and also for the many pleasant and instructing hours spent in his company.

In a thesis submitted to the University of Manitoba in 1927, R.A.Blair working under the direction of Dr. Frank Allen, noted that foveal vision was inhibited or enhanced, depending on the condition of the peripheral regions of the retina.

He used tubes that were opaque to light and found that when he viewed a postion of a fairly bright surface, with one eye looking through the tube, and the other without the tube, the spot seen through the tube was brighter than the patch seen with the other eye. Also the reverse was true; if the tube was translucent and illuminated by a bright light, the patch seen through it was darker than that seen with the other eye.

The object of the present research is to fully investigate this enhancement and inhibition using white and colored light.

HISTORY & THEORY.

It is perhaps best, to discuss first in some detail, the construction of the eye and the processes of vision, so as to clarify the various facts that may be brought out in the work.

The act of seeing may be divided for discussion into three processes:

- (1) The stimulus
- (2) The receptor organs
- (3) The transference of the sensation to the brain.

The stimulus consists of radiation in the ether which are thought to be transverse vibrations. Those which affect the eye to give color and form have wave lengths roughly between 7000 Angstroms and 4000 Angstroms. They constitute the visible spectrum. When they fall upon the eye they are transferred through the eyeball to the retina, and in some manner, unknown, excite certain elements of the retina to give rise to the sensation of vision which is transferred by the mechanism of the optic nerve to the brain.

The history of the three processes is long and varied. From the times in early history, when the ancients were trying to make up their minds, as to

whether the light emanated from the eye itself and fell on the object, or whether the light emanated from the object and fell on the eye, or whether the light came from an external source and along with the two aforementioned conditions gave rise to vision - - - on through the ages men have given their lives to the study of this most intricate and interesting problem.

The eye was dissected and the various parts were studied to find what functions they performed in the act of seeing. Newton discovered that white light could be broken up into it's respective colored components, and that these components could be added to each other again to give white light. Then through the years, various theories of colour vision arose. Today there are hundreds of these in existence, of which two or three are most universally accepted, and these will be discussed later.

We know that the stimulus consists of vibrations in the ether. Waves of different frequency give rise to different colour sensations.

Without these wave trains of light, sight is impossible.

DIAGRAM OF THE EYE

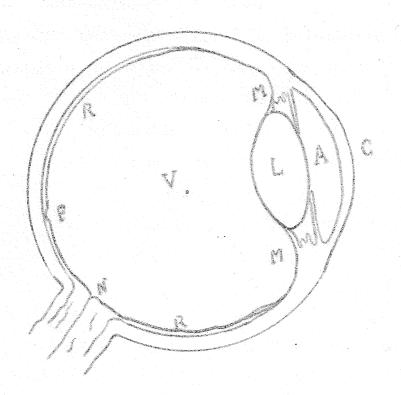
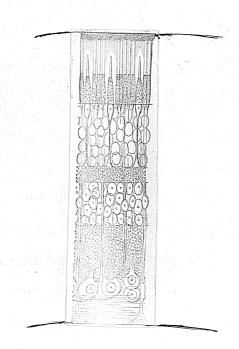


DIAGRAM OF THE RETINA.



The construction of the eye is also fairly well known now. We shall now digress from the history of the subject, to enter into the various details of the construction of the eye, and the various roles that the different parts play in the act of seeing.

The eye is globular in shape, with a central opening in the front which is covered by a slightly protuberant transparent medium, called the cornea (C in the accompanying diagram). Back of this is the crystalline lens L, a biconvex gelatinous looking substance which can be distorted by pressure and whose convexity may be altered by the supporting muscles MM. Between the lens and the cornea is a watery looking liquid A, called the aqueous humour. It constitutes by it's shape a concave-convex lens. The remainder of the globe is filled with the so-called "vitreous body" V, a jelly-like transparent substance which plays some part in the refraction of the rays of light.

Lining more than half the back of the eye is the retina or perceptive membrane. It is, on the average, about 1/100th of an inch thick, and consists of a number of distinct layers (see diagram #2). It is thickest at the back of the eye. At N

(diagram #1), where the optic nerve enters it is white in color, and a little towards the centre it is yellow. This called the macula litae, or yellow spot, and is the seat of most distinct vision. In the centre of this spot is a small depression where certain of the layers of the retina are missing and where the nerve fibres are turned out of their paths. This is the fovea centralis, the point of most acute vision.

The retina is composed of nerve fibres, gang, lion cells and nuclei, and certain distinct elements which are called from their shapes, rods and cones. They are thought to be the real organs of vision, a supposition which is well born out by the fact that the spot N, where the optic nerve enters is free from rods and cones, and is found to be blind.

The various layers of the retina as they occur starting at the back of the eye and working in-wards towards the centre of the eyeball are (see diagram #2):

(1) The layer of rods and cones. The rods are cylindrical in shape, from .063 to .081 mm. in length and .0018 mm in diameter, made of a substance of high index of refraction. They are arranged close together, projecting radially from the retina.

Their outer knobs end abruptly. Inwardly they continue as fine fibres which pass into the next layer.

The cones are shorter and thicker than the rods (except at the macula), and are composed of a similar substance. At the macula there are no rods at all but the cones are longer and mor rod-like in appearance and "evidently partake of the nature of rods as well as cones to some extent".

- (2,3,4,5,6) The next five layers of the retina are composed of cells and nuclear layers and most likely continue the nerve processes through to the outer or
- (7) fibrous layer. from the spot N, the optic nerve branches out into a large network of nerve fibres, which cover the whole front of the retina except at the yellow spot, where they are diverted from their paths, probably so that the light may reach the fovea with the least amount of transmission. They are likely united with the processes of the ganglion cells.²

When light strikes the retina it passes through all the layers till it falls on the layer of rods

¹ Parson's Col. Vis., pg. 12, footnote 2. 2 Helmholtz Phys. Op. trans. 3rd ed. Vol. 1 pg. 26 ft. note 1.

and cones, where it is absorbed to a great degree. The stimulus which it arouses in the is passed out again through the nerve processes attached to them, through all the layers and through the nerve fibres into the optic nerve, whence it is transferred to the brain.

The third process in seeing is the one about which least is known. That is the part which deals with the transference of the stimulus from the retina to the brain. By the very fact that it deals with brain, we can see that a study of the conditions and methods of transference would be difficult, as it is almost impossible to take into account all the many factors which go towards making up a sensation received by the brain. And, in fact, in spite of the many brilliant men that have studied this portion of the work, the laws which have been formulated are mostly empirical, and merely show the relationship between the intensity of the stimulus and the regulting sensation in the brain.

However, one fact seems to stand out with remarkable clarity in most of the laws governing the action of the senses; they all show a logarithmic relationship between the intensity of the stimulus and the resulting sensation, and indeed

that is what we shall find in the various laws (in the form of graphs) which are found to hold in this thesis. This agrees well with Dr. Frank Allen's findings in the entire field of cutaneous sensations.

To explain why black and white and certain combinations of colours were used in this work, and also why this type of apparatus was used, we shall now insert a short dissertation on colours, considered from the physiological standpoint, and on the flicker phenomenon as applied to this type of research.

Colours as perceived by us, may be divided (for purposes of discussion only) into two classes - toned, and untoned.

The untoned colours are black, white and the shades of grey between them.

The toned colours are all the other colours of the spectrum.

There are two views held about black as a positive colour:

- (1) The view held by most physicists, that black is merely the absence of light.
- (2) The other view, that is held by many physiclegists is that black is truly a positive sensation, and is as much a colour as yellow or red.

It is true that a deeper black is known than that which is seen by eyes carefully shaded from the light, which would tend to show that the second view is most likely the truer one.

We find certain of the toned colours, that when perceived together in a definite ratio, give the sensation of white light. The colours making up these pairs are known as complementary colours.

In certain physiological experiments, black and white bear to each other the same sort of relationship as do complementary colours. This point is illustrated very neatly in the following work, where the same type of curve results from using black and white as from blue and yellow which are complementary toned colours.

The Flicker Phenomenon. It is well known that is a succession of stimuli follow one another with sufficient rapidity the resulting sensation appears to be a continuous one, and not intermittent as it actually is. When a short single stimulus is given to the eye, the resulting sensation is not an equally single short one, but consist of " a series of pulses of sensation of diminishing intensity, rapidly succeeding one another". 1

Parson's Col. Vis. Pg. 89 footnote 2.

When a series of short stimuli are given to the eye in rapid succession, the sensation curve of the succeeding stimuli are superimposed on the primary and tend to keep it oscillating about a mean value. If the oscillations are above a certain critical value in frequency, the sensation is a continuous one; if below the critical value, the sensation of flicker is obtained.

The periphery of the eye has an inhibitory effect on the acuity of foveal vision. The stronger the stimulus which the periphery receives the greater the inhibition of foveal vision. This effect may be illustrated as follows: Look through an opaque tube with one eye, leaving the other eye open. and fix both eyes on a bright surface. It will be noticed that the spot seen through the tube is much brighter than the patch seen with the other eve. The tube in this case is merely a device for allowing light to fall only on and around a small area in the centre of the retina at the fovea, the greater part of the periphery receiving little or no light. The acuity of foveal vision in this eye is then increased. By varying the dimensions of the tube, various areas of different sizes may be illuminated and the brightness of the

patch seen, varies correspondingly as the periphery receives more or less light.

If the tube, instead of being opaque, is translucent, and a strong light is allowed to fall on it, the opposite effect will be noticed. The periphery in this case will be receiving more than it's usual amount of light, due to refractions and reflections in the tube, and it's inhibitory effect on the fovea will be correspondingly greater.

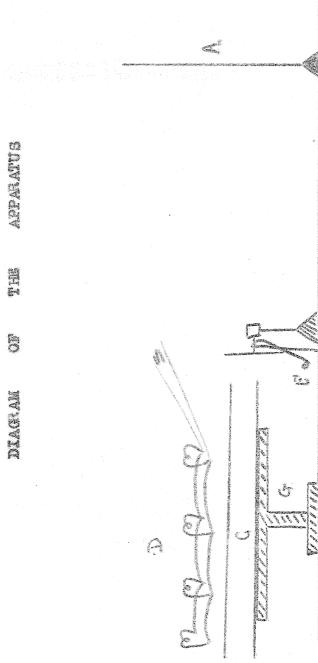
These effects were first investigated by
H.A.Blair as mentioned earlier. He, however, merely performed a few preliminary experiments on the
magnitude of the effect. It will be the aim of
this work to show the effect of illuminating
various areas of the eye around the foves, by
the above and similar methods; the effect of
relative luminosity on tube and field; and to
investigate the phenomenon as applied to toned
celours.

SPICIPIO NOTES

It was found that on using a translucent tube which was strongly illuminated (giving the dark patch as previously mentioned), and a flicker apparatus being but into the field to give a black and white flicker, that at the critical framency, when the sensation of flicker just disappeared, a deep black spot was seen through the tube. This epot was much more intensely black than the ordinary blackness of a light proof room. This then was used as the end point in the course of the work, and the end points were determined for yorious conditions of the eye. The critical frequency was then plotted against the logarithm of the area of the eye illuminated. The apparatus was simple to begin with, but with continual refinements, more and more accurate results were obtained to give finally the logarithmic relationship which was found to exist between the area of the eye illuminated and the sensitivity of the eye, as measured by the epicotister method (flicker apparatus). We shall follow the work from the first attempt, showing the refinements as they were added and the improvements in the results obtained.

APPARATUS & METHOD.

The original apparatus consisted of a number of tubes 12 inches long and varying in diameter from 1 inch to 2 inches. They were made of celluloid and covered with one layer of thin white tissue paper. They were held in position C on a support G (figure #3), and were lighted by four 60 watt Mazda frosted lamps D, in parallel on an A.C. 110 volt circuit. A, was a white screen placed about 2 feet from the end of the tube. Directly in front of the end of the tube was an epicotister arrangement, consisting of a sectored disk attached to a direct current motor, the speed of which could be adjusted by means of a hand brake E. The disk had two open and two closed sectors of 900 each. Thus when the motor was running at a constant speed the disk gave equal periods of light and darkness. The motor had a counter attachment on the shaft, with a metal pointer extending about 14 inches from it. This pointer made contact with a metal spring every 50 revolutions of the counter. The pointer and spring were put into a circuit with one arm of a chronograph, and a clock which made a contact every } second was put into a circuit with the other arm of the chronograph. When the critical speed of revol-



B DIAGRAM uits into operation was depressed and a record was taken for a period of 4 or 5 seconds. From this record the duration of a single impulse to the eye could be easily calculated. We plotted the inverse of this, that is the number of impulses per second which were given to the eye to give a steady sensation.

The area of the eye which was illuminated could be calculated since A, B and C in the relationship

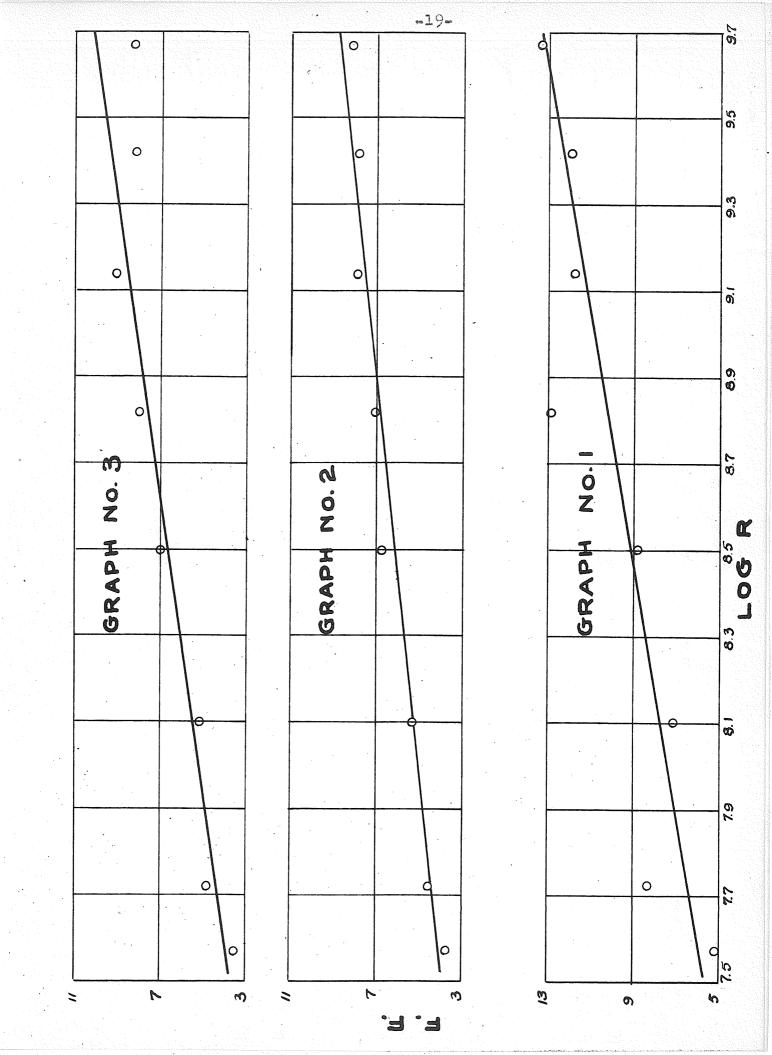
were known; where A is the area of the end of the tube. B is the distance from the end of the tube to the eye (i.e. the length of the tube) and C is the distance from the front of the eye to the retina, and D is the area of the retina illuminated. The above relationship holds since light is propagated in straight lines (over these distances).

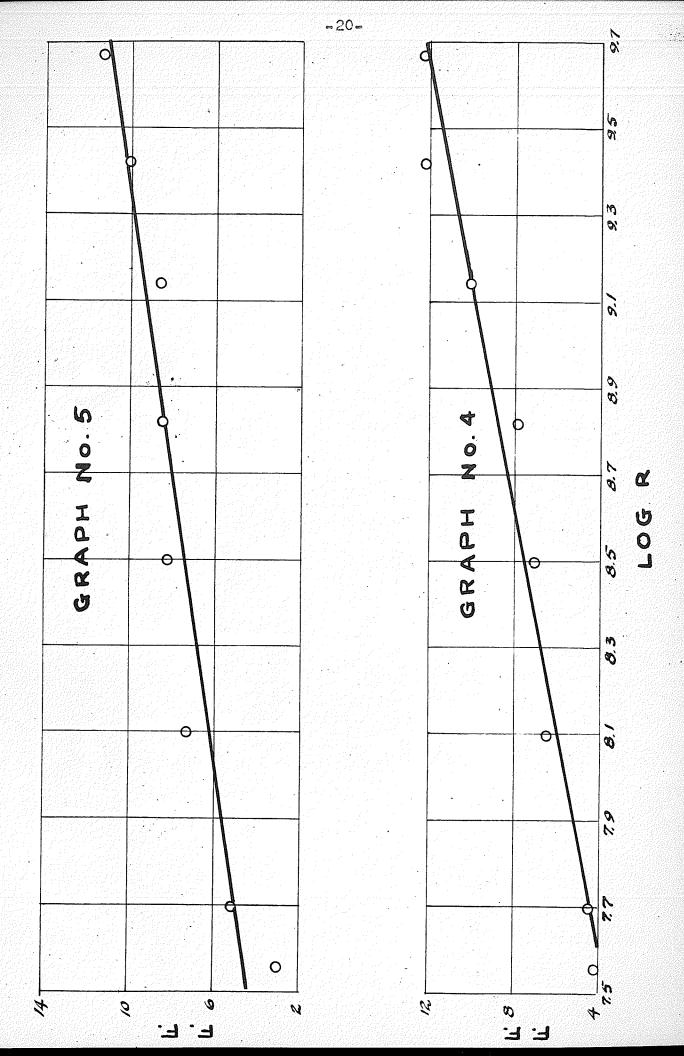
During the cours of the entire work that follows the investigator was careful to see that the eye was in a normal condition at the beginning of each reading. By normal is meant that condition that the eye is in during the course of an ordinary day. Readings were taken only between 10A.M. and 3 P.M. They were taken in a dark room, but between each reading the eyes

R = area of retinal illumination (square inches)

log R	graph 1	graph 2	graph 3
3.5682	5.12	3.64	3.50
3.7075	6.20	4.54	4.76
2.1139	7.05	5.26	5.08
2.4913	8.69	6.66	6.97
2.8208	10.81	6.97	8.00
T.1405	11.76	7.89	9.11
₹.4232	11.93	7.78	8.19
T.6732	13.33	8.10	ै•33

	graph 4	graph 5
3.5682	4.12	2.94
3.7075	4.26	5.13
2.1139	6.45	7.20
2.4913	6.90	8.16
2 .8208	7.84	8.45
ī.1405	10.00	8.51
1.4232	12.20	20.00
T.6732	12.30	11.32





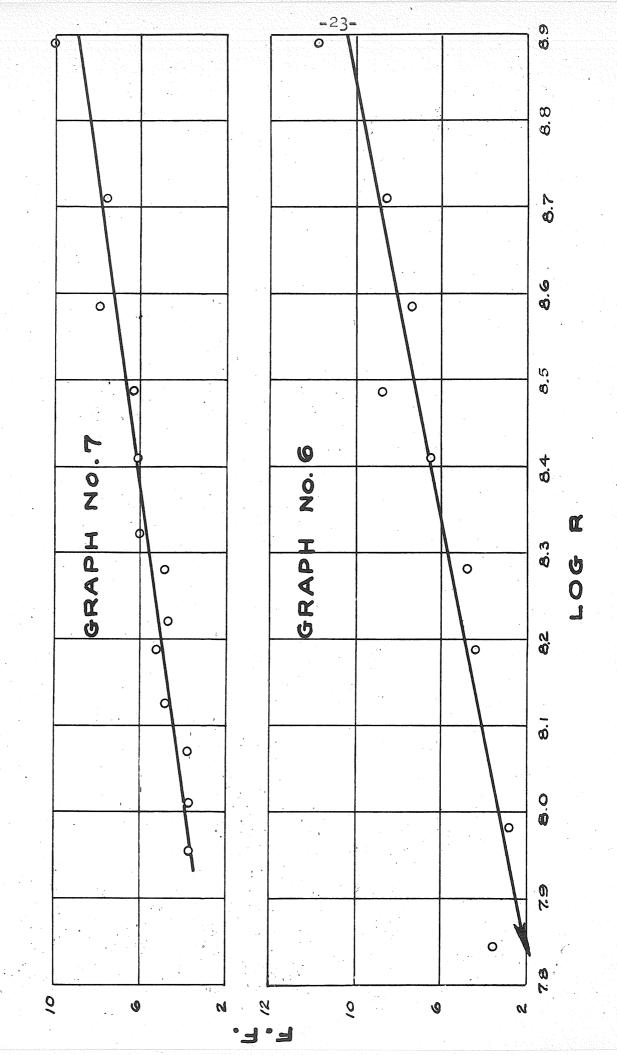
were rested for a period of from 3 to 5 minutes by sitting in a well lighted room and looking around at the walls and furniture, making sure that the eyes were not in direct bright sunlight so as to become abnormally light adapted - or dark adapted by staying in the dark room between readings.

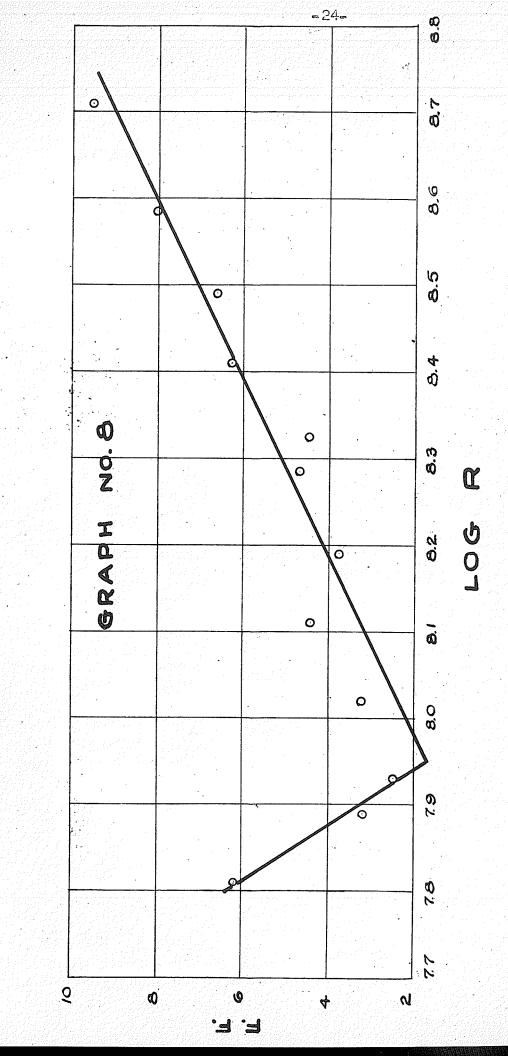
These sets of readings gave graphs numbered 1 to 5, and show a linear relationship between the logarithm of the area illuminated and frequency of flicker (number of impulses per second), that is to say an exponential relationship between the area of the eye illuminated and the critical frequency of flicker. If x denote the area of the retina illuminated and y denote the critical frequency of flicker, then the relationship given by these graphs is

log x = ky (k a constant)
i.e. $x = e^{ky}$ or $x = ce^{y}$ (c = e^{k})

The system of illuminating the eye was then changed as follows, to see whether there would be any effect on the results:

graph 6		graph 7		
log R	F.F.		F.F.	
3 .740	2.85	3.954	3. 73	
3.785	3.12	2.008	3.70	
3. 845	3.50	2.071	3.77	
3. 982	2.77	2.146	4.82	
2,187	4.34	2.187	5.19	
₹.283	4.76	₹.243	4.65	
2.41 0	6.45	2.283	4.88	
2.48 8	8.69	2.342	6.06	
2.585	7.54	2.409	6.12	
2.711	8.51	2.4 88	6.25	
2887	11.76	2. 585	8.85	
ಚ್ =1	oh 8	2.71 0	7.50	
3.809	6.18	2. 88 7	10.00	
3.888	3.17			
3.958	2.44	By F.F. in this	and the	
2. 043	3.17	following pages of data is meant the number of impulses per second which the eye receives. The graphs were plotted by adding 10 to the characteristic of the log-		
2.110	4.39			
2.1 89	3•73			
₹.286	3.73 4.65			
2.344	4.44	arithm. That is plotted as 7.80	3.009 was	
2.411	6.25			
2.490	6 . 59			
2. 587	8.00			
2.712	9 . 52			



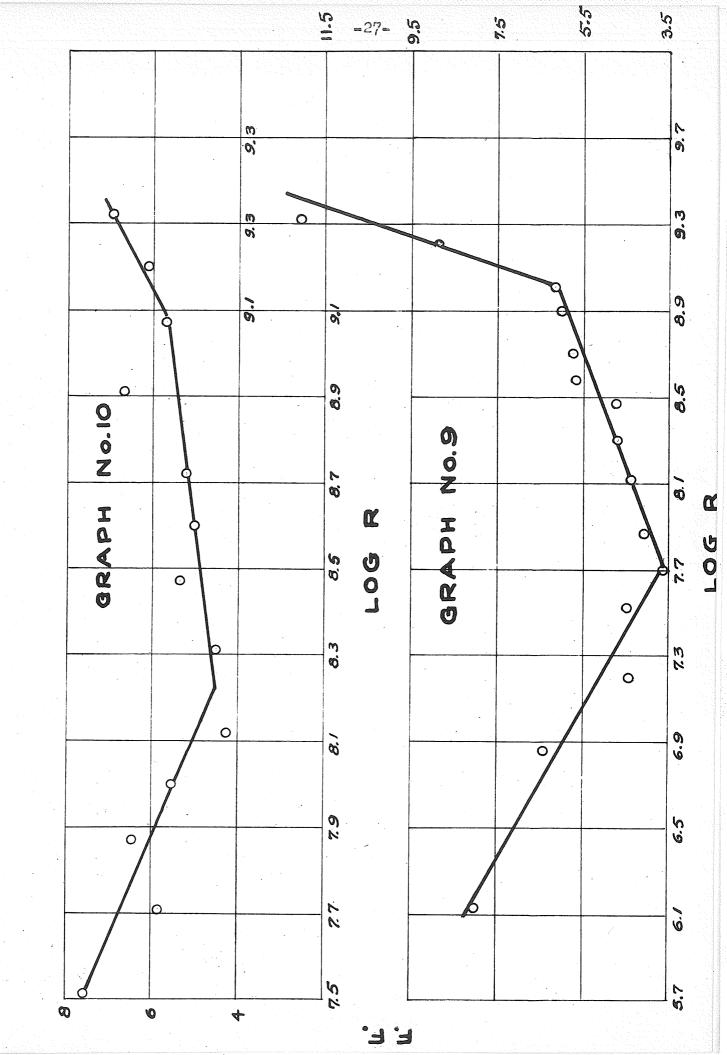


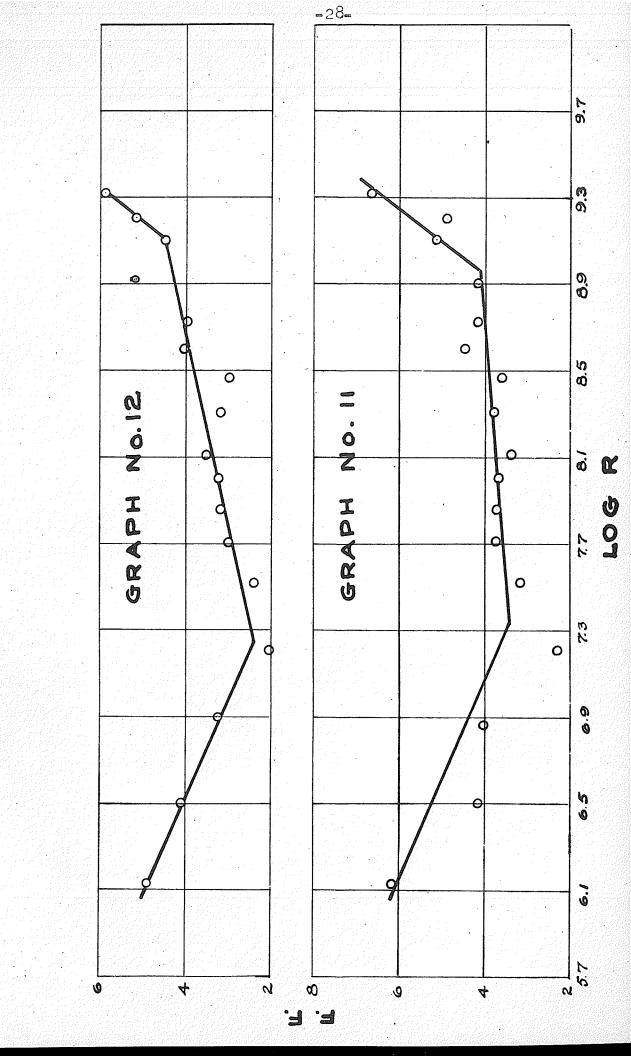
Instead of varying the diameter of the tube (i.e. A in the eq'n on page 17), the length of the tule was varied (i.e. B in that equation), the diameter being kept constant. A & inch diameter tube, 24 inches long, was used. This was marked off into inches for a distance of 20 inches, and the last 3 inches were marked off into 🛊 inches. Then a reading was taken with the 24 inch tube. During the period of rest before the next reading, one inch was cut off the end. A reading was taken with the 23 inch tube, etc.etc. This gave gradually increasing areas of illumination. The results were plotted as before, giving graphs 6,7, and 8. The lines were still straight, but this method was evidently not as accurate as the last, since the points did not lie so closely on the **line.**

Since there was quite a lot of difficulty in fixing the small diameter tube to fit the eye so that no light crept in around the side, another change was made in the tube arrangement. A 3 inch tube of celluloid was made and covered with tissue paper as before. One end of the tube was fashioned to fit closely to the side of the head and round the eye. The other end was so constructed as to allow flat celluloid disks to be fitted across the end. These disks were also covered with tissue

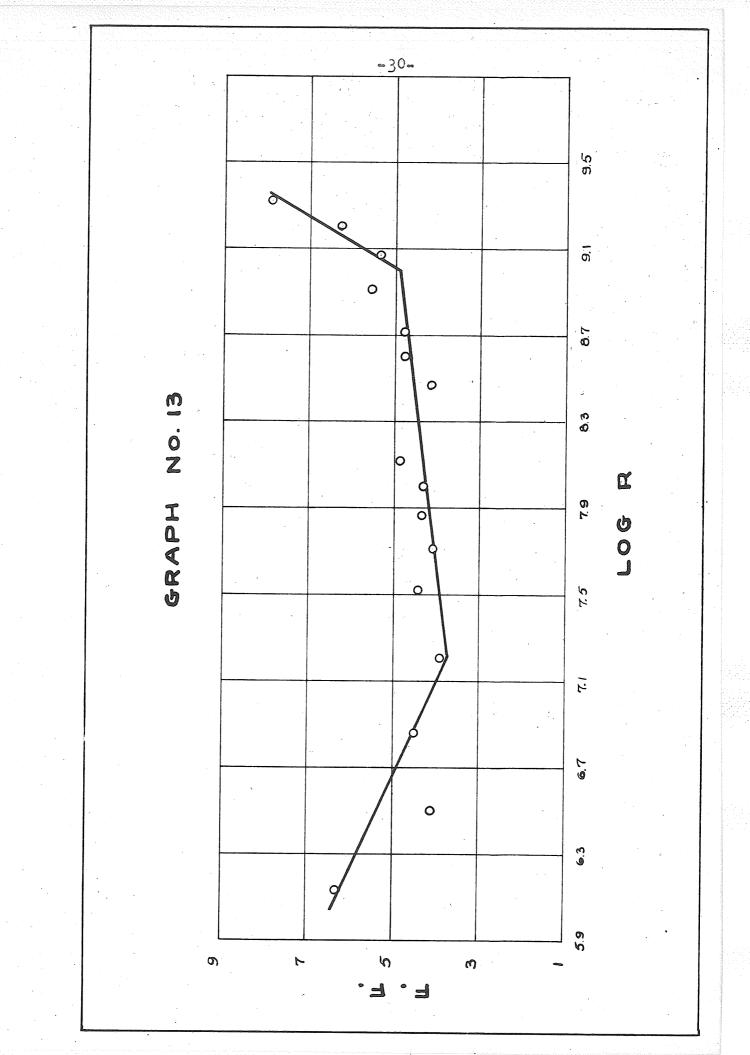
R = area of retinal illumination (square inches).
F.F. = number of impulses per second.

Log R	graph 9	graph 10 F.F.	graph 11 F.F.
4,134	7.89		6.15
7.503			4.16
4. 862	6.38		4.00
3.210	4.39		2,24
3.525	4.44	7.54	3.14
3.709	3.60	5.82	3.70
3.867	4.08	6.45	3.70
2. 001	4,88	5 • 5 5	3.63
2.117	4.35	4.25	3.3 8
2.3 11	4.69	4.49	3.77
5. 469	4.70	5-33	3.57
2.603	5.66	5.00	4.39
2.71 9	5.71	5.21	4.28
2.912	6.00	6.66	4.21
T.071	6.12	5.71	5.12
T.205	8.85	6.12	4.87
T.321	12.07	6.95	6.66





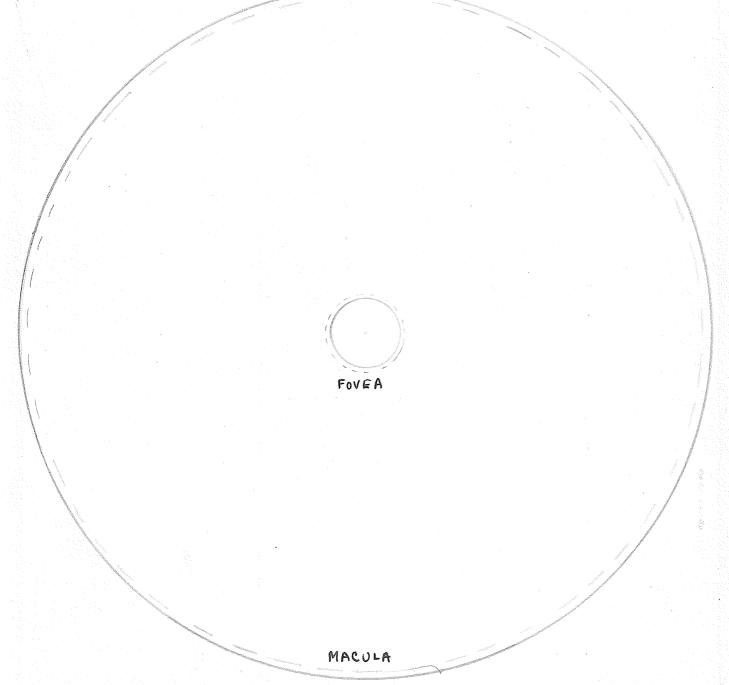
log R	graph 12 F.F.	graph 13 F.F.
7.134	4.88	6.30
4.503	4.04	4,10
4 .862	3.22	4.53
3.210	2.00	2.88
3.515	2.38	4.37
3.709	2.94	4.01
₹.867	3.14	4.34
2.001	3.22	4.32
2.117	3.50	3.87
2.311	3.14	4.02
2.469	2.94	4.13
2.603	4,00	4.76
2.719	3.94	4.78
2.912	5.26	5.53
1.071	4.44	5.35
I.205	5.12	6,24
ī.321	5.88	7.89



paper. Each one had a hole in the centre which was left uncovered. The holes varied from t inch to 2 inches in diameter. This arrangement was virtually equal to tubes of different diameters, as the light came in through the hole in the end, and the retina was illuminated by it over an area exactly equal to the image of the hole at the end of the disk. This arrangement was found to be highly satisfactory, and was used for the remainder of the work. On account of using this system, holes of very small diameter could be accurately made in the disks and therefore very small areas of the eye could be illuminated. The holes were accurately measured by means of a sliding microscope and the areas of the retina illuminated were calculated. This brought these areas down to less than foveal size and enabled the investigation to be completed. The readings taken with this apparatus gave graphs 9 to 12. As can be seen, it was found that instead of the relationship being that shown by a straight line, it was necessary to have three straight lines to fit the points with any degree of satisfaction. Many sets of readings were taken so that it might be sure that there was no possibility of error in this new development. The two end slopes

GRAPH No. 14

Showing graphically the agreement between the calculated and actual values of the areas of the fovea and macula. The dotted lines give calculated values and the continuous give actual values (as in Helmholtz Phys. Op.)



were carefully investigated to see that the deviation from the middle straight line was warranted,
and also that the points were best fitted to straight lines instead of to some other type of curve.
The five curves while not exactly co-incident, were
nevertheless, so close to being the same, that it
was thought wise to take the mean of the 5 sets
of readings and plot a mean graph (#13). As great
care was taken to see that the eye was as near to
being in the same condition for each reading and for
each set of readings, as possible, it was felt that
this was permissible.

At this point it suddenly occurred to the investigator that there might be some special significance attached to the points where the slopes changed since these points remained the same on the various graphs. When the areas corresponding to these points were calculated they were found to correspond within the limits of experimental error with the areas of the fovea and macula respectively. The relationship between these calculated values and the values obtained from the authors is shown very beautifully by means of diagram #14.

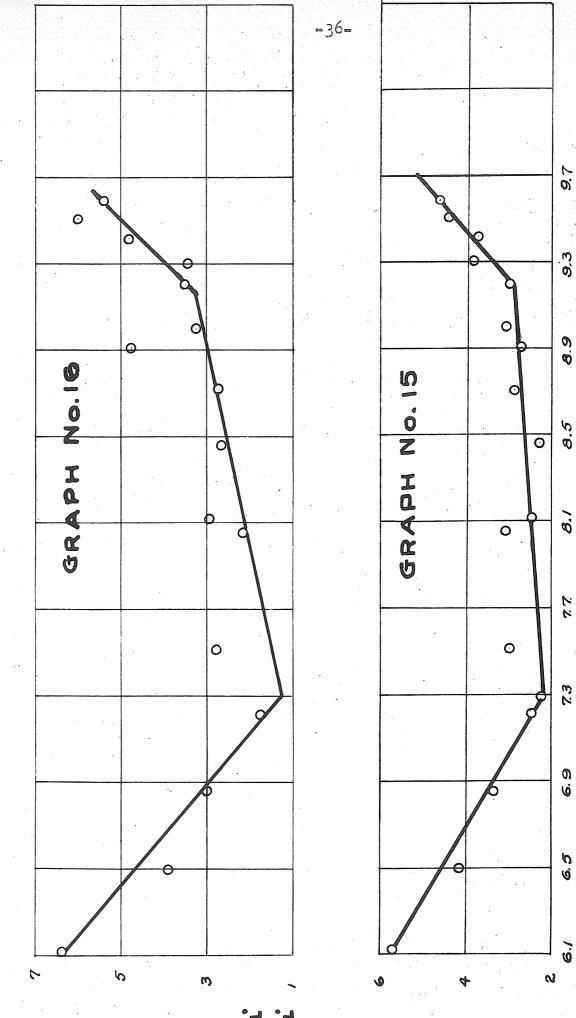
C.Krause & Kollicker in Helmholtz Phys. Op. trans. 3rd ed. Vol. I, pg. 28.

On page 21 there was developed a mathematical law which is derived from the graphs in that section. This law evidently holds here also since we have the same type of curve. The only change is in the slope, i.e. in k, and therefore in c. That is to say c becomes c1, c2, c3 for the first, second and the third branches of the curve respectively. Now since the change occurs just at the points where the areas change from foveal to macular, and from macular to peripheral in size, it is obvious that the constant of the law depends on which part of the retina is doing the work of seeing. That the three processes of seeing in the three different parts of the retina are separate will be brought out later during the discussion of the theories of vision. However, it is clear that this method illustrates very well that there is some change in the manner of seeing as we use one or more of the three parts of the eye.

This concludes the general investigation of the phenomenen, and attention was now turned to investigating what effect, if any, was caused by varying the relative illumination of field and tube.

The ratio at the head of each column gives the number of lights on the tube to the number on the field.

log R	l:1 graph 15 F.F.	2:1 graph 16 F.F.	3:1 graph 17 F.F.
· .		يناهل ور السند	•
I.598	4.54	5.40	4.88
1.515	4.34	6.00	4.44
Ī.423	3.70	4.81	3.44
T.312	3.77	3.41	3.57
T.205	2,98	3.50	3.44
Ī.071	3.03	3.22	3.03
2.912	2.66	4.76	2.70
2.719	2.85	2.70	2.32
2.469	2.27	2.66	2.29
2.11 7	2.43	2.94	2.27
3.867	3.07	2.17	2.38
3.525	2.94	2.74	2.32
3.210	2.43	1.72	2.79
₹.862	3•33	2.98	2.84
平。503	4.16	3.84	2.56
7.134	5.71	6.38	4.54

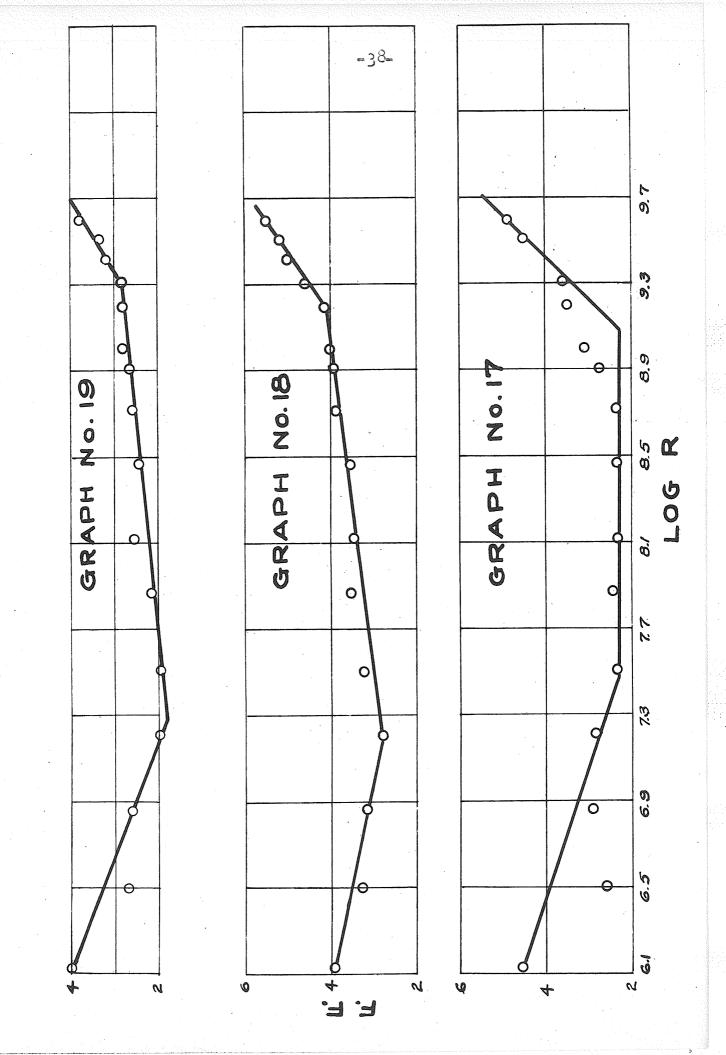


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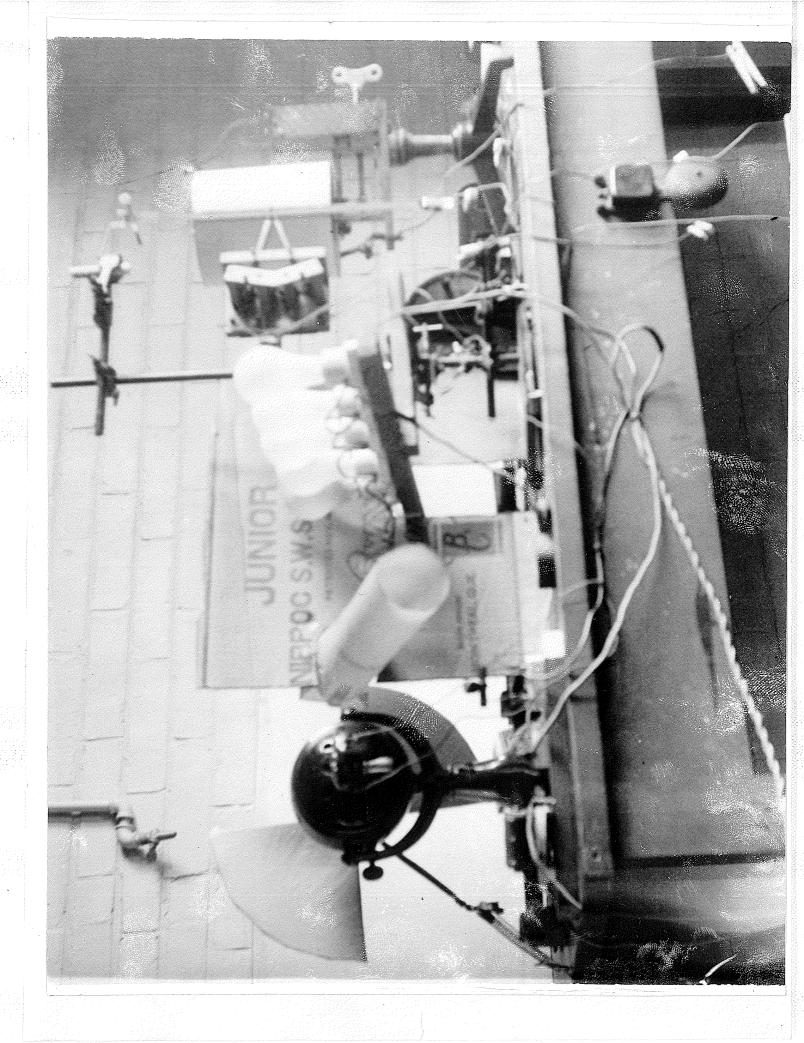
log R	4:1 graph 18 F.F.	5:1 graph 19 F.F.
* 48 **	# * # *	
1.598	4.49	3.84
1.515	4.17	3.39
Ī. 423	3.96	3.22
1.312	3.54	2.81
T. 205	3.14	2.81
1.071	3.03	2.82
2.912	2.94	2.66
2.719	2.85	2.59
2.469	2.50	2.46
2.117	2.40	2.56
3.867	2.50	2.15
3.515	2.22	1.90
3.210	1.73	1.94
4.862	2.10	2.59
4.503	2.27	2.66
4.134	2.94	4.08

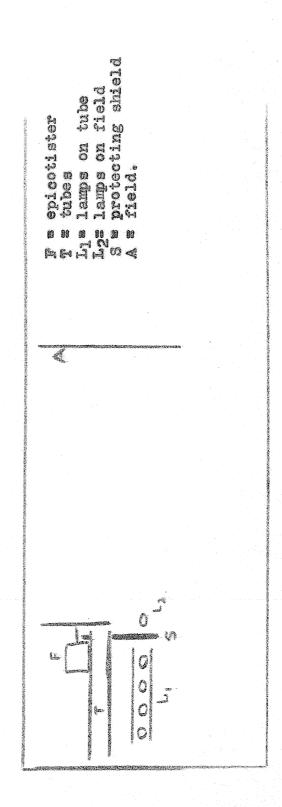


ON TUBE AND FIELD.

Accompanying is a photograph and also a diagram of the new set up of the apparatus. A cardboard screen was placed so that the light falling on the tube could be altered without altering the illumination of the field. It had a hole cut into the side so that the tube was held up by it. One lamp was kept constantly on the field and then by varying the number of lamps on the tube, from 5 for the first set of readings to 1 on the fifth set, an attempt was made to see whether the ratio had any effect on the readings. Graphs 15 to 19 show the results which were recorded. The various graphs are not the same , though they have the same shape. Still, no regular variation was found, as was hoped, in varying the ratio from 5:1 to 1:1 on tube and field respectively. The effect remains the same whatever the ratio of illumination, though it gets considerably weaker as the ratio approaches 1. This was noticed by Blair in his work, that is the greatest effect was found when the difference of light on the tube and field was greatest.

As was mentioned at the beginning of the thesis the darkening effect is noticed when the tube is





brighter than the field, since the periphery is receiving more light than it would normally. When the tube is opaque to light, that is darker than the field a bright spot is seen. This is due to the fact that the periphery is receiving less light than usual, and it's inhibitory effect on the eye is smaller. If the tube could be illuminated so that the periphery received exactly as much light as did the fovea and macula, then vision would be normal and there would be no difference whether we looked through the tube or not. It seems that instead of there being two different phenomena, we merely have two different phases of the same thing. Starting, with the periphery of the eye getting more light than usual (by means of a well lighted tube) a dark spot is seen. As the light on the tube is gradually diminished the spot becomes lighter and lighter. When the two parts of the eye are getting the same amount of light (the eye without the tube) there is no spot seen at all. Further, as the periphery of the eye receives less and less light, the central portions of the eye receiving the same amount aswhen normal, (the opaque tube) the spot becomes brighter.

With the apparatus that was available for use in measuring the relative intensity of light on the tube and field, this generalization was all that we could derive on the effect of relative illumination. With some accurate system of measurement of the ill-umination, and a careful study of the subject, there may be some regular deviation from the normal found. This, however, will have to be left for future investigators.

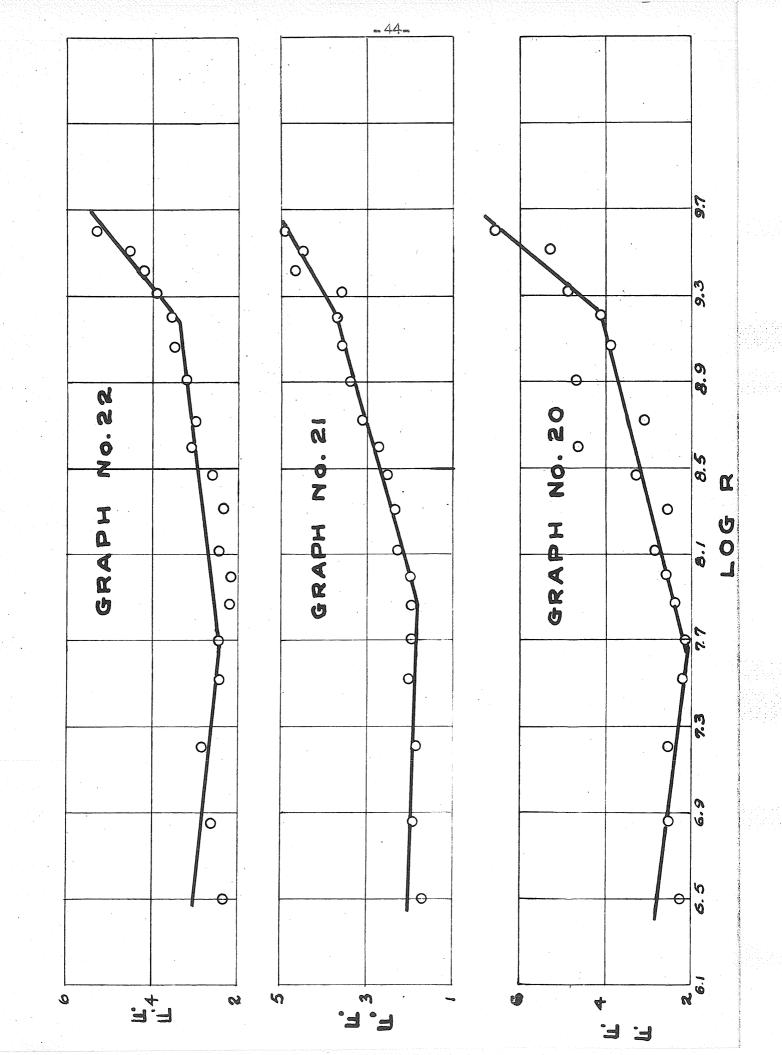
THE EFFECT WITH COMPLEMENTARY COLOURS.

As we have mentioned before, black and white bear the same relationship to each other in some respects as do the complementary toned colours. The next step in the investigation was to see whether or not the same effect could be obtained with complementary colours, and if so to what extent this held, and what effect different pairs of complementary colours would have on the results.

Pure spectral colours would have been the ideal thing to use in this case, and in fact an attempt was made to set up a form of apparatus whereby the light from a spectroscope of special design that was available could be used to give the effect. It was

Blue light on the disk, and yellow light on field and tube.

log R	graph 20 F.F.	graph 21 F.F.	graph 22 F.F.
1.598	6.52	4.88	5.26
T.515	5.26	4.44	4, 49
I.423	4.82	4.65	4.16
Ī.321	4.87	3.54	3.84
I.205	4.10	3.67	3.50
T.071	. 3.81	3.57	3. 44
2.912	4.65	3.33	3.17
2.719	3.07	3.03	2.94
2.603	4.59	2.70	3.03
2.469	3.22	2.50	2.56
2.311	2.50	2.35	2.3 8
2.117	2.81	2.24	2.40
2.001	2.50	1.94	2.17
3.867	2.35	1.92	2.17
3.709	2.08	1.90	2.43
3.515	2.15	2.00	2.38
3.210	2.50	1.84	2.85
4 .862	2.50	1.90	2.63
4.503	2.25	1.72	2.31



found, however, that a number of well nigh insurmountable difficulties arose in manipulation, which
would have taken too long to overcome, and it was
decided to try the effect using coloured papers for
obtaining the complementary pairs of colours.

Coloured papers were sought which would give as close as possible transmitted lights which were complementary in colour. This was achieved by means of a stereoscope, which enabled the two colours to be overlapped on the retina, and which gave a white colour, tinged alternately with one or the other colour. The first pair of colours obtained was blue and yellow. The tube and field were covered with yellow paper and the disk of the epicotister was covered with blue which was fairly dark. When this was tried it was found that at the critical frequency the blue colour disappeared giving place to a most intense black, which was however, slightly tinged at times with purple. A set of disks to fit over the end of the tube was prepared, with central hole sizes the same as those used in the black and white part of the work. Three sets of readings were taken which gave graphs ##20, 21 and 22. These graphs follow the same form exactly as the ones previous, the first one being not quite as good as the second and third, since it took a little more manipulation to keep the end point in sight with colours than it did with black and white.

Next a red green combination was obtained which was not as near to a complementary pair as the blue and yellow. A darkening effect was obtained with this but not definite enough to take readings.

The reverse system of colouring of the blue and yellow was then tried. That is the disk was covered with yellow paper and the field and tube with blue paper. There was a slight darkening, but under no conditions could a real black be obtained. The intensities of tube and field were varied in the attempt but still no real dark spot was obtained. No readings were therefore taken.

A speed was found, higher than the critical frequency at which the yellow color of the disk dasappeared entirely, and the blue field was seen without any trace of flicker. An attempt was made to find the same effect with the colors as originally placed, blue on disk and yellow on tube and field. It was unsuccessful. No attempt can be made to explain this phenomenon.

THEORIES OF COLOUR VISION.

On page 3 of this thesis, it was mentioned that due to the fact that a great many men had worked in the field of colour vision, and because the act of seeing was a physiological one, and necessitated the use of the brain, a great number of different theories of colour vision had arisen.

Two theories in particular stand out in the history of the subject, and they form the basis of most of the other theories that have been originated since, so that we shall briefly outline the views that they give.

THE YOUNG-HELMHOLTZ THEORY.

All sensations of colour can be produced by three colour stimuli in certain definite proportions. Thomas Young in 1801, first advanced the view that to each of these stimuli there corresponded a fundamental sensation. Since it could not for an instant be considered that each point of the retina was capable of responding to all the different wave lengths of light which might fall upon it, Young stated that in his opinion, if each point was cap-

able of conceiving three different colour sensations, this would be sufficient to give the sensation in the brain of any of the different colours including white. When light of any colour falls upon the retina, all the sensations are affected, but the colour which we actually see depends on the excess of the excitation of one or two of the nerve filmes over the other one or two. Young considered that the simplest conception of the mechanism was that there were three kinds of nerve fibres one most easily excited by the red, the second by the yellow and the third by the blue. These colours had their wave lengths in the ratio 8:7:6. However. some subsequent work of Wollaston's, caused him to change his selection of the colours to red, green and violet, and subsequent research proved he was right. When yellow light (which lies bewieen red and green in the spectrum), falls upon the retina, both the red and green nerve fibres are equally stimulated, while the violet is stimulated to a very much lesser degree. This gives to the brain the sensation of yellow, and similarly for the other colours.

When any of red, green or violet light was incident on the eye, that nerve fibre, was of course excited to a much greater degree than the others

and gave the sensation of that colour. Young's theory was not accepted till Helmholtz and Maxwell used it to explain some of their work, and the three great names behind the theory were enough to get it accepted by the great majority of the physiologists of the day. It has therefore been known as the Young-Helmholtz theory. The theory is really independent of the mechanism and has been stated by Maxwell as follows:

"We are capable of feeling three different colour sensations. Light of different kinds excites the these sensations in different proportions, and it is by the different combinations of these primary sensations that all the varieties of visible colour are produced.

Young's theory had the great fault that it could not explain the cause of successive induction, and this led Hering to put forth his theory.

HERING'S THEORY.

Hering supposed that there are three hypothetical visual substances in the retina. A redegreen substance, a yelloweblue substance, and a black-white substance (the third pair being a later addition to his theory). He considered that red, yellow and white were inherently bright, and

1. Houston, Vis. & Col. Vis. pg. 185

that green, blue and black were inherently dark. He supposed that these substances were subject to anabolic changes (assimilation) and katabolic changes (dissimilation). When the red-green substance undergoes an anabolic change we see green, and when it undergoes a katabolic change we see red. Similarly with yellow and blue and black and white - an anabolic change giving the inherently dark color, a katabolic change giving the inherently bright one.

Hering's black is not the ordinary blackness due to the absence of light, but a deeper black - a positive sensation - which occurs only as the result of simultaneous or successive contrast.

Thus if we look at a bright white object, the black after image which we see after closing the eyes is what Hering calls "black".

There are two main objections to Hering's theory. First he asks us to suppose too much. No substance like his red-green or yeklow-blue has ever been found in the anatomical investigation of the retina. Secondly he has to introduce a brightness and darkness to get true colour matches, as he cannot account for unsaturated colours.

Allen has overcome the difficulties of the Young-Helmholtz theory and Hering's theory by his introduction of reflex action in the nerve fibres, these same nerve fibres at the same time giving a better mechanism than Hering's imaginary visual substances, for we know that these nerve fibres do exist. He believes the changes which Hering supposes are anabolic or katabolic photochemical changes to be photoelectric changes in the nerve fibres.

OTHER THEORIES.

V.Kries put forth the "duplicity theory" as it is called, in which he maintains that light adapted vision (photoptic) and dark adapted vision (scotoptic) are due to the cones and rods respectively, and to these only.

Mrs.Ladd-Franklin, Edridge-Green and others have formulated other theories which are modifications of Young-Helmholtz and Hering.

Burch, Houston and others have attempted to explain colour vision on the idea that there is in the retina a system of natural resonators, either

one or three (Houston and Burch respectively), and that these suffer forced vibration under the action of different wave lengths of light.

DISCUSSION.

The black spot which is seen seems to be a blacker color than the ordinary everyday black and is likely the result of simultaneous contrast enhanced by the flicker phenomenon. Emerson and Martin consider the rods to be the organs chiefly concerned in the reflex actions producing enhancement of vision, Hering's idea of inherent brightness and darkness may explain the difficulty that was encountered in getting the black spot with the yellowon the disk and the blue on the field and tube.

V.Kries theory puts forth the idea that there is some difference in the mechanism of the macular and peripheral areas. The three parts of the retina have long been distinguished anatomically, the fovea by it's shape, the maculaand periphery by the difference in color. Also measurements have been made on the areas of these parts. This is, however, a method of differentiating functionally between

^{1.} The Photometric. Match. Field -11 Roy. Soc. Pr. Vol, 108 1925.

the three parts of the eye, as well as determining the areas that these portions occupy in the retina. The break points are very clearly defined and we feel that the method is very conclusive in bringing out the results, and rather more than fairly accurate, dealing with the eye and it's changeable condition from day to day.

In the writer's opinion, it would be instructive and interesting for this investigation to
be carried out some time in the future, using
pure spectral colours instead of coloured papers,
as a "white" effect is a mass effect, since the
electric filament is giving off light of all
wavelengths jumbled together, and a clearer
cleaner result might be obtained with spectral
colors, pure, rather than approximately so.