THE VISUAL PERCEPTION OF FINE DETAIL

By H. HARTRIDGE, F.R.S.

(*Received* 13 *September* 1945 *to* 18 *July* 1946)

CONTENTS

Preface

Many books have been written on colour vision; not so many on the appreciation of form and shape. Few have dealt exclusively with the perception of fine detail. All the experiments described in this paper have one object in view, namely, to elucidate some of the mechanisms, both nervous and otherwise, by which the image formed on the retina is clarified and improved before it reaches the higher centres of the brain.

Brief reference must now be made to some of the difficulties encountered during the performance of the experiments described in this paper. These were of three kinds: apparatus, research rooms, assistants.

When in 1939 the pre-medical branch of St Bartholomew's Hospital Medical College was evacuated to Cambridge, very little room space could be allocated for research purposes. At the same time the assistants and laboratory attendants were almost wholly occupied in class preparation and had no time to spare to help with research.

In 1942 the Physiology block of the London buildings was gutted by fire and all the author's research equipment, books, journals and reprints were destroyed. The apparatus thus destroyed was almost impossible to replace at that time.

The position, so far as apparatus is concerned, has changed recently for the better, as a special instrument has now been constructed, which has shown itself to be suitable for the tasks for which it was designed. This is described in Part X.

I would like to thank my colleagues; those in the Cambridge laboratories; those evacuated with us from London; and particularly those who belong to Bart's. Without their co-operation and encouragement the experiments described in these pages could never have been done at all.

I. Some problems of visual acuity

Experiment shows that the visual acuity of the eye is of a very high order. The replacement of the lens system of the eye by an achromatic, or even an apochromatic, lens would hardly show any improvement. On the other hand, there is ample evidence that the lens system of the eye is uncorrected for colour. The excellent acuity of the eye has hitherto been difficult to account for.

(1) *The problems of visual acuity by the light-adapted human eye*

A problem which has long awaited solution in connexion with the physiology of vision has been to account in a satisfactory manner for the high acuity of the eye for fine detail.

The resolution of a grating test object, by a microscope, as is well known to manufacturing opticians, requires that instrument to possess lenses of fine performance. These contain as a rule achromatic combinations of carefully figured lenses which have been adjusted in relative position with the utmost precision. The design of the eye appears rudimentary in comparison with such lenses, yet practical tests with grating and other test objects show that this elementary lens system, possessing apparently no chromatic correction of any kind, and certainly no fluorite-like medium which could impart an apochromatic correction, behaves in an almost flawless manner. So good, in fact, is the apparent definition of the foveal image, that if the lens system of the eye could be removed and an apochromatic lens, selected for its good performance, could be substituted, it is doubtful if the possessor of this eye would detect any improvement in his perception of fine detail. What he would certainly notice would be a very serious deterioration at the periphery of his visual fields. His original eye lens gave him an angle of view exceeding a right angle (Hartridge 1919). His new microscopic lens gives him a field of view almost insignificant in comparison. He now knows for the first time what it feels like to have 'tubular vision', that is, the type of vision produced by looking down a narrow tube. But other more subtle differences would soon be noticed. His original eye lens adjusted its focus automatically, and was almost equally good for observing near and distant objects. His new microscopic lens possesses no such valuable features. It has been designed to work at one fixed distance between object and eyepiece only, and a small error in this adjustment produces either over- or under-correction for spherical aberration.

The performance of the eye lens is superior to that of the microscope lens, for the purposes for which it was designed. How is that superiority achieved? How does it come about that the eye lens, quite uncorrected for chromatic aberration, gives the performance of an apochromatic lens? These were the questions to which answers were required when this research began, so far as the lens system of the eye was concerned, but there were other questions, no less important, which concerned the retina. Here is a structure which provides the eye with excellent colour perception. For this purpose it consists of photoreceptors responding to different parts of the spectrum. According to the well-known trichromatic theory of Thomas Young, there were three kinds of receptor; according to

Granit's recent researches (Granit 1943, 1945) on the mammalian retina, there are seven kinds for colour perception. If then red light stimulates only a few of all the receptors present, how can we explain the fact that the visual acuity of the eye for fine detail by red light is of such a high standard as to require every one of the photoreceptors present in the human retina to be red sensitive? This is the situation so far as acuity, when using red light, is concerned, but the same question presents itself with regard to acuity when using yellow, green and blue lights.

One further question concerning the retina requires an answer, namely: Can any evidence be obtained for the existence in the human retina of the seven types of receptor with sharp responses ('modulators'), and the one type of receptor with broad response ('dominator'), which Granit has discovered, as mentioned above, in the retinae of many mammals, by means of his ingenious micro-electrode technique? It was principally in order to answer this question that the micro-stimulation apparatus described in Part X was designed.

(2) *The chromatic aberration of the lens system of the human eye*

The evidence for chromatic aberration in the lens system of the eye is of a very convincing character. In the first place an examination of a frozen antero-posterior section through the eyeball discloses the fact that there is no structure of the correct shape, except the vitreous, to play the part of a negative lens composed of flint glass. Further, the refractive index and dispersion power of this structure resemble those of water, as do those of the cornea and the aqueous humour. In consequence, any neutralization of colour error which it might produce would be very small in extent. Several experimental procedures show that chromatic error is present: vision through a purple colour filter demonstrates that red rays and blue rays cannot be sharply focused at the same time, except when using very small pupils (Tscherning 1904). An opaque screen placed before the eye, so that only marginal rays in one meridian reach the retina, causes white light to be spread into a spectrum. This would not be the case if the eye were achromatic. Lastly there is the evidence of chromatic stereoscopy (Tscherning 1904), namely, the fact that to most subjects red objects in the field of vision appear to advance in front of blue ones (see Part VII, p. 586) In consequence of these and other experiments, the statement that the eye is largely, if not entirely, uncorrected for colour error is well founded.

(3) *Previous hypotheses*

Many hypotheses have been proposed to account for the absence of the effects of chromatic aberration. (*a*) That the eye is in fact corrected for colour. (*b*) That the mean refractive index of the eye media resembles that of water, which has a low value. (*c*) The rays reaching the eye consist of narrow pencils, which suffer only a small refraction. (*d*) There is much scattered light in the retinal image, and this masks the chromatic aberration. Each of these hypotheses will be briefly considered.

(*a*) *The eye is corrected for colour.* This hypothesis, advanced by Euler, caused Dollond to invent the crown-flint achromatic doublet, an example of a false hypothesis leading to a valuable discovery. An examination of a section of the human eye shows that the cornea, the aqueous and the crystalline lens are all equivalent to convex lenses. The vitreous, which is equivalent to a concave lens, has the same refractive indices as water, and would in consequence only correct in part the refraction of the crystalline lens, since the latter has higher refractive indices than water for rays of all wave-lengths.

(*b*) *The eye media have low refractive indices.* It is not the mean refractive index which determines the amount of chromatic aberration, but the dispersive power. The latter, for the eye as a whole, has a value of about 0·0171, which is somewhat less than that of water, and resembles that of a heavy crown or a light flint glass (see § 5, p. 526).

(*c*) *The eye transmits narrow pencils of light.* The pupil varies, in normal vision, between wide limits. Under normal conditions of illumination it averages 3 to 5 mm. diameter. With a posterior nodal distance of 17 mm., these apertures would correspond to ratios of focal length to aperture of 3·4 to 5·7, showing that the light rays entering the eye are far from narrow. Manufactured lenses of these apertures would be useless, for example, for photography, unless corrected for chromatic aberration.

(*d*) *Scattered light obscures the aberration.* Undoubtedly there is some scattered light, but this is relatively small in amount because of the slight differences in refractive index encountered by light during its passage through the eye media. Experiment shows that the fringes produced by a glass prism of small angle are visible. If scattered light does not interfere with the visibility of these fringes, it is difficult to see why it obscures the fringes produced by the chromatic aberration of the eye.

(4) *The optimum focusing point for white light*

One factor which plays an important part in the structure of the fringes for white light produced by chromatic aberration is the ray chosen to form the most sharply focused image. The wave-length of this ray was determined previously by the author, by a method which consisted of illuminating by white light a number of parallel strands of unspun silk. An equal number of strands, alternating in position between the above, were illuminated by nearly monochromatic light, obtained by means of sharp-cut colour filters. When yellow light was used, both sets of strands appeared equally sharp, but the difference in sharpness between yellow, orange and green was not well marked. The micro-stimulation apparatus described in Part X, which can produce very sharply defined point sources of light, was employed for some confirmatory tests, as follows. Two sources were employed: one was a small high-efficiency electric lamp; the other was a monochromatic light source of adjustable wave-length. These were arranged to be on the same horizontal line, about 16 cone units apart. The eye of the observer was screened from stray light, so that the pupil would dilate as widely as possible. Both sources were bright, and were adjusted to appear approximately equal in intensity, so that they formed aberration patterns of considerable size and complexity on the retina. The monochromatic source, having been adjusted in wave-length until the patterns appeared to be identical, was readjusted until a slight difference in pattern was noticeable. Two critical wave-lengths were thus found, one on the long-wave side of the optimum, the other on the short-wave side (see table 1).

TABLE 1. OPTIMUM FOCUS FOR WHITE LIGHT

	long-wave limit		short-wave limit
	5820		5675
	5790		5655
	5795		5645
mean	5802	mean	5658

It was found best to have a spherical lens of 2·0D in front of the observer's eye for the determination of the long-wave limit, but a lens of 0·88D for the short-wave limit. There was no detectable difference in pattern between the two sources, from 5802 to 5658A. The optimum focus for white light is therefore probably near the average between these two limits at, say, 5730A. If a more yellow light source was in use, a longer wave-length ray would probably be used for the focusing point, and vice versa.

(5) *The determination of the chromatic difference of focus of the eye*

Many experimenters, for example Thomas Young and Fraunhofer, have measured the focal lengths of the eye for the long and short wave-length ends of the spectrum. Others have determined them for standard spectral lines: thus Helmholtz found the focal length of the eye to be 20·434 mm. for the C line, and 20·000 mm. for the G line; Wolf found the difference in focal length for the C and G lines to be 0·50 mm.; and for the B and H lines, 0·75 mm.; Einthoven found, for the D and F lines, the difference in focus to be 0·2718 mm. Some have expressed their results in dioptres, others in millimetres. The latter method is valueless unless the posterior focal distance, or the posterior nodal distance, is also given, as has been done by Helmholtz. It should be remembered, however, that the value he adopted for the posterior focal distance, namely, 20·00 mm., gives a value for the posterior nodal distance of 15·00 mm., which is short in comparison with that found by most modern observers, in particular Goldmann & Hagen (1942), who, by means of their X-ray method, obtained 16·81D on ten emmetropes (see § 19, p. 536). Because of these uncertainties, and because the micro-stimulation apparatus presents to the observer a very sharply defined test object of small dimensions and known wave-length, the chromatic difference of focus of the author's left eye has been determined, experimentally, and the results are given in table 2.

TABLE 2. THE REFRACTION OF THE HUMAN EYE

wave-length (A)	refraction (dioptres)	total refraction	posterior nodal distance	refractive index whole eye	refractive index water
6500	1·50	59·27	16·87	1·3313	1·3313
6000	1·25	59·52	16·80	1·3327	1·3327
5500	1·00	59·77	16·73	1·3341	1·3344
5000	0·63	60·14	16·63	1·3362	1·3364
4500	0·13	60·64	16·49	1·3389	1·3392

The first column gives the wave-lengths in Ångström units. In the second column are given the observed results in dioptres. The third, fourth and fifth columns have been calculated on the assumption that the refraction of the eye for the D line is equal to 59·5D, which corresponds to a posterior nodal distance of 16·81 mm., Goldmann & Hagen's value. In the last column are given the refractive indices of water.

If the values for the refractive indices of the eye as a whole, and for water, be compared, it will be seen that there is close agreement between them. Since the total refraction of the author's eye has been determined, for each ray, with an accuracy of 0·06D, the refractive indices have an accuracy of 0·0003, which accounts for the differences in refractive index for the eye and for water. This conclusion, that the indices of refraction for the whole eye and for water are substantially the same, was not expected, because it is usually accepted that the index for the eye is the greater. This may possibly be due to measurements which have been made on the eye media at laboratory temperature and not at body temperature. A rise of temperature would lower both the refractive indices and the dispersive powers.

From the values in table 3, similar values have been calculated for five standard spectral lines.

TABLE 3. THE REFRACTION OF THE HUMAN EYE

standard line	wave-length (A)	total refraction	posterior nodal distance	mean refractive index
C	6563	59·25	16·88	1·3311
D	5893	59·58	16·79	1·3330
E	5270	59·93	16·68	1·3350
F	4861	60·26	16·59	1·3368
G	4308	60·72	16·46	1·3403

The differences in posterior nodal distance are compared with those given by Wolf and Einthoven in table 4. This difference is important, because Wolf's value was used as the basis for calculating the diameters of the aberration disks for lights of different wave-length which were published in a previous communication (Hartridge 1918). From the refractive indices for the standard lines given in the last column of table 3 above, the dispersive power for the eye as a whole can be readily calculated from the formula

$$\frac{\mu F - \mu C}{\mu D - 1} = \frac{0{\cdot}0057}{0{\cdot}3330} = 0{\cdot}0171.$$

It will be recollected that the value for water at 20° C is 0·0180. The difference between the two values may be due in part to the difference of temperature between body temperature (37·5° C) and 20° C.

TABLE 4. CHROMATIC DIFFERENCE OF FOCUS

		mm.
Wolf	C–G	0·50
Author	C–G	0·47
Einthoven	D–F	0·2718
Author	D–F	0·20

(6) *The diameters of the aberration disks*

Wolf's value of 0·5 mm. for the difference of focus of the eye, for the C and G standard lines, was made the basis of the calculations previously made of the diameters of the aberration disks for rays of different wave-length. The diameters have been recalculated, using the values for the posterior nodal distances given in table 3 above. Goldmann & Hagen's values for the axial lengths of the eyes of six emmetropes gave a mean of 23·4 mm. The distance from the anterior surface of the cornea to the edge of the pupil has been assumed to be 3·6 mm. The entrance pupil has been assumed to be 12·5 % larger than the real pupil. The exit pupil has been assumed to be 5 % larger than the real pupil, and 0·1 mm. in front of the latter. So that the distance between the exit pupil and the retina, for yellow rays, is $23{\cdot}4 - 3{\cdot}6 + 0{\cdot}1 = 19{\cdot}9$ mm. The aberration disks, calculated from these data, are found to be 7 % smaller than those calculated previously. Their diameters are given in table 5, for an entrance pupil 4 mm. diameter, the eye being assumed to be focused for yellow rays of 5800 A. As was to be expected, the red, blue-green and blue aberration disks are larger than the orange and yellow-green ones. It will be noticed that the blue disks have nearly three times the diameter of the red ones.

The micro-stimulation apparatus was used to check the values in table 5 in the following manner: a fixed source of 4500 A was provided by the spectro-illuminator, while a movable source of red light of 6100–6700 A, produced by a colour filter, was attached to the slide-rest of the apparatus so that it could be adjusted both vertically and horizontally. One source had, unfortunately, to be produced by a colour filter, because two spectro-illuminators were not available. Owing to the smaller dispersion of red rays than blue rays, and the sharper cut of the colour filters available, it was better for the red source to be produced by a filter, and for the blue one to be produced by the spectro-illuminator, rather than the reverse arrangement.

TABLE 5. THE DIAMETERS OF THE ABERRATION DISKS

wave-length	diameter on the retina		
(A)	mm.	cone units	minutes of arc
6500	0·0216	6·43	4·42
6000	0·0078	2·32	1·59
5500	0·0090	2·67	1·84
5000	0·0304	9·05	6·21
4500	0·0588	17·45	12·00

In front of the eye of the observer were placed two narrow, parallel, vertical slits, the centres of which were 3·3 mm. apart. On looking through the double slit at the two sources, both were seen to be duplicated. The definition was found to be best with a +0·67 D lens in front of the double slit. By adjusting the slide-rest, the left-hand red image was placed vertically below the right-hand blue one. The horizontal distance between the two sources was now measured and was found to equal 7·8 cone units. This corresponds to the distance between the centres of the two aberration images, so that the sum of their widths would correspond to 15·6 cone units. But the double slits were 3·3 mm. apart. If they had been 4 mm. apart, the widths would have corresponded to 18·90 cone units. But the diameters of the red and blue aberration disks are given for a 4 mm. pupil, in table 5, as 6·43 and 17·45 cone units respectively, which together equal 23·88 cone units, which is 5 cone units greater than the experimental result. But it should be pointed out that the red source probably had an effective wave-length of about 6250 A, which would account for half the above difference. The other half is probably explained by the round pupil of the observer's eye, which in consequence exposes greater lengths of the inside edges of the double slits to light than their outside edges. Thus if the inside edges alone had been used, which measurement showed to be 3 mm. apart, the widths of the aberration disks would have corresponded to 20·80 cone units, which is 2·0 cone units closer to the calculated value.

(7) *The image of a point source*

The author has shown that from the wave-lengths, diameters and luminosities of the different aberration disks, it is possible to calculate the intensity and colour of different parts of the aberration image of a point source. The effects of diffraction will increase in importance, the smaller the aperture of the pupil. A pupil of 4 mm. diameter will be considered (see table 6), because, in the case of a pupil of this aperture, the effects of diffraction are small. In the first column are given the distances from the centre of the image in μ. In the second column the distances are given in cone units. In the third and fourth columns are given the relative intensity and the colour at different distances from the centre of the image. It will be seen that the centre of the image is a very bright yellow. The intensity falls sharply away from the centre, but the image remains yellow; more and more white light, however, is being added to it with each increase in distance. In addition to yellow rays, the yellow image is made up by the superposition of orange and yellow-green disks, the white being largely due to the blue and violet disks which extend over nearly the whole image, and, being complementary to yellow, make white light when they are mixed with it. At 12·5μ (3·7 cone units), yellow has greatly diminished and white has largely taken its place. At 18·0μ (5·4 cone units) the long-wave disks have almost finished in the red, but the short-wave ones continue. At 21·5μ (6·4 cone units) onwards the short-wave disks are found alone, and the image gets progressively fainter, to terminate at about 60μ (20 cone units). The yellowish white image, which extends to about 5 cone units from the centre, is relatively of high intensity, because the yellow, orange and yellow-green parts of the spectrum, of which it is composed, are the brightest parts; moreover, the light is concentrated within a relatively small area. The blue and violet fringes, which extend to 20 cone units, are of low intensity, because these parts of the spectrum have a low brightness and the light is spread over a relatively large area. This description was checked by means of a telescope with an unachromatized objective, and later by means of a microscope which was being used to examine the magnified image of an unachromatized substage condenser of about the same focal length as the lens system of the eye.

TABLE 6. BRIGHT POINT ON A DARK BACKGROUND

distance from centre (μ)	distance in cone units	relative intensity	colour
0	0	∞	yellow
1·8	0·5	34·0	yellow
3·6	1·1	13·0	yellow
5·4	1·6	5·3	yellow
7·2	2·1	2·3	yellow
8·9	2·7	1·0	yellowish white
10·7	3·2	0·4	greenish white
12·5	3·7	0·2	greenish white
14·3	4·3	0·1	greenish white
16·1	4·8	—	bluish white
18·0	5·4	—	purple
19·5	5·8	—	purple
21·5	6·4	—	blue
25·0	7·5	—	blue

(8) *The image of a linear source*

Calculation showed that there are several differences between the image of a point source and that of a linear source. (1) The intensity does not fall away so sharply from the centre (see table 7, which gives the values for a 4 mm. pupil). (2) A greater amount of white light is present in the central parts of the image, which is due to overlap between yellow and blue disks; this is greater at the centre of the image than elsewhere, because of the superposition, on to one another, of the aberration disks due to the blue and violet rays.

In other respects the images of point and linear sources resemble one another.

From the distribution of light and colour in the image of a linear source of infinite narrowness, it was found that that of a line 7·5μ wide could be derived. Here again there was a further increase in the amount of white light present in the yellow centre of the image.

TABLE 7. BRIGHT LINE ON A DARK BACKGROUND

distance from centre (μ)	distance in cone units	relative intensity	colour
0	0	∞	yellow
1·8	0·5	40·0	yellowish white
3·6	1·1	15·0	cream
5·4	1·6	8·0	cream
7·2	2·1	4·5	cream
8·9	2·7	2·0	white
10·7	3·2	0·8	white
12·5	3·7	0·5	white
14·3	4·3	0·2	greenish white
16·1	4·8	0·1	bluish white
18·0	5·4	—	purple
19·5	5·8	—	purple
21·5	6·4	—	blue
25·0	7·5	—	blue

(9) *The image of an extended source*

The extended source differs from the point and line sources in an important respect, namely, that its image is largely composed of white light, and that colour fringes are only found near its margins. The dimensions of these fringes are given for a 4 mm. pupil in table 8. It will be seen from the table that each of the fringes for a 4 mm. pupil is about 10μ (3 cone units) wide. It should be pointed out, however, that only the parts near the edge are strongly coloured, and that as the distance from the edge increases the yellow fringe becomes progressively whiter and the blue fringe progressively blacker, until the yellow fringe merges imperceptibly with the white interior of the image, and the blue fringe merges similarly with the black background.

TABLE 8. EDGE OF A BRIGHT AREA ON A DARK BACKGROUND

	distance from edge (μ)	distance in cone units	relative intensity	colour
outside edge (blue)	10	3·0	—	black
	9	2·7	0·2	deep violet
	8	2·4	0·4	deep violet
	7	2·1	1·1	dark blue
	6	1·8	2·3	dark blue
	5	1·5	3·9	dark blue
	4	1·2	6·2	blue
	3	0·9	9·6	blue
	2	0·6	13·9	blue
	1	0·3	28	white
edge	0	0·0	50	yellow
inside edge (yellow)	1	0·3	72	yellow
	2	0·6	86·1	yellow
	3	0·9	90·4	yellow
	4	1·2	93·8	pale yellow
	5	1·5	96·1	pale yellow
	6	1·8	97·7	pale yellow
	7	2·1	98·9	cream
	8	2·4	99·6	cream
	9	2·7	99·8	cream
white	10	3·0	100	white

(10) *The images of black points and lines on bright backgrounds*

The light intensity and colour at different parts of the image of other types of source were examined: for example, a black dot and a black line, both narrow and wide, on bright backgrounds, and grating-test objects.

The image of a black dot on a bright background may be derived from that of a bright point source on a black background, because the former is the negative of the latter in the photographic sense, as shown in table 9. Whereas the image of a point source on a black background consists of a bright yellow centre surrounded by a dark blue-violet fringe, the image of a black point on a bright background consists of a blue centre surrounded by a very pale pinkish yellow fringe.

Similar differences are to be observed in the cases of black lines of various widths on bright backgrounds.

TABLE 9. BLACK POINT ON A BRIGHT BACKGROUND

distance from centre (μ)	distance in cone units	relative intensity	colour
0	0	0	blue
1·8	0·5	66	blue
3·6	1·1	87	pale blue
5·4	1·6	94·7	pale blue
7·2	2·1	97·7	bluish white
8·9	2·7	99·0	bluish white
10·7	3·2	99·6	very pale pink
12·5	3·7	99·8	very pale pink
14·3	4·3	99·9	very pale cream
16·1	4·8	—	very pale cream
18·0	5·4	—	white
19·5	5·8	—	white
21·5	6·4	—	white
25·0	7·5	—	white

(11) *The images of black-white grating objects*

The fringes of grating objects vary in intensity and colour with alterations both of pupil diameter and of the widths of the bars of which the grating is composed. A grating with very wide bars will produce an image which consists of alternate white and black areas. Only the margins of these areas are occupied by fringes, the widths of which depend on the diameter of the pupil. Thus the description, starting in the centre of the image of a bright bar, would be: white, narrow yellow fringe, narrow blue fringe—black—narrow blue fringe, narrow yellow fringe—white—narrow yellow fringe, etc.

If the black and white bars of this grating be reduced progressively in width, the blue fringes approach one another as the black area between them gets narrower, until they meet. If the black and white bars be equal in width, the yellow fringes also approach and touch at about the same time that the blue ones do. Obviously the precise width of bar, at which contact of the fringes takes place, depends on the width of the fringes themselves, and one factor of importance is pupil diameter. In table 10 are given the pupil diameters and widths of the geometrical images of the bars on the retina, at which contact of the fringes is observed to take place. When the widths of the bars are less than those given in this table, overlap of the two blue fringes occurs with one another, and similarly with the yellow fringes. When the values are half, or less, those given in the above table, overlap is extensive, and the fringes become modified accordingly in both intensity and colour. (See table 11, where the pupil is 4 mm. diameter, and the grating bars 10μ wide on the retina.) In all the above cases direct observation of the fringes produced by an unachromatized lens, both by white light and by coloured lights, particularly monochromatic lights, assists in understanding the processes which are involved.

TABLE 10. WIDTHS OF BARS OF GRATING

pupil diameter (mm.)	width of image of bar (μ)	cone units	minutes of arc
8	10	3	2·1
6	13	4	2·7
4	20	6	4·1
3	26	8	5·5
2	40	12	8·2
1	80	24	16·5

TABLE 11. GRATING OF BRIGHT AND DARK BARS

		intensity	colour
centre of white bar	0	92	cream
	2	85	yellow
	4	72	yellow
edges of bars	5	50	pale grey
	6	28	blue
	8	15	blue
centre of black bar	10	8	dark blue

(12) *A description of fringe structure*

It will have been observed how greatly the fringes produced by chromatic aberration differ in intensity and spectral composition, with alteration in the shape of the object, an image of which is being produced on the retina. In spite of this, there are properties which are consistently present.

(*a*) Where the object is white on a black background, or vice versa, the fringes always occur in pairs which are complementary in colour to one another.

(*b*) The fringes are never quite in contact. The intervening neutral space is well marked in the cases of points and lines both white and black. In all other cases it is not well marked.

(*c*) The fringes vary in width with the aperture of the pupil, except where the image of the object on the retina is so narrow that the fringes belonging to opposite sides are overlapping one another, as we have seen is the case with a grating of narrow bars.

(*d*) The fringes are usually of about the same width as one another.

(*e*) The fringes are usually yellow and blue, when the normal focus is used, but they may be of other complementary pairs of colours when for any reason different foci are used.

(13) *The hypothesis of the resolving power of the eye*

Evidence has been produced in the previous sections that the eye suffers from chromatic aberration. But when the eye is used in normal vision the existence of this aberration would not be suspected from its performance, for test objects, used at the limit of resolution, fail to disclose its presence.

Many years ago the author considered the problem of the resolving power of the eye (Hartridge 1918). Formulae were produced for calculating the intensity of light in the aberration disks caused by lights of different colour. From these the distribution of light in the retinal image as a whole could be determined.

All relevant factors known at that time were taken into account. From the formulae for this aberration, together with that for diffraction, the distribution of light in the foveal image was calculated for a number of different types of test object. From the values thus obtained, a hypothesis was advanced in order to account for the resolving power of the human eye. This hypothesis, which fits in an entirely satisfactory manner the data available, may be stated as follows: 'Resolution in every case depends on the recognition by the observer of small differences in light intensity, for rays of different colour, incident on the individual foveal cones (Hartridge 1922*a*). Under average conditions at the limit of resolution, the difference in light intensity between one foveal cone and its immediate neighbours was calculated to be between 5 and 20 %. Hecht and his co-workers have shown (Hecht & Mintz 1939) that under the very best conditions this difference may be reduced to 1 % or even less. But this in no way invalidates the hypothesis itself, which does not depend on any one difference in light intensity rather than another. The crux of the hypothesis is that there is a difference in light intensity which is recognized by the observer.

(14) *The examination of a lens uncorrected for chromatic aberration*

For some preliminary tests a telescope with an unachromatized object glass was employed, but this was replaced by a microscope which was used to magnify the aerial images of external objects produced by an Abbé substage condenser. As is well known, the latter is a lens system of wide aperture, the central zones of which are practically free from spherical aberration, but which suffers from chromatic aberration, because it consists of a combination of simple convex crown glass lenses. A condenser was selected which had a focal length nearly the same as that of a normal human eye. The microscope, which magnified about 50 diameters, was fitted with a Leitz step micrometer eyepiece, so that measurements could be made of the dimensions of the fringes produced by chromatic aberration (Hartridge 1941). Measurements of the fringe widths were made with the iris diaphragm of the condenser set at different apertures. This led to the conclusion that in the case of the eye there must be some factor tending to reduce, or even to eliminate altogether, the coloured fringes, and that one of these factors might be the retinal direction effect of Stiles & Crawford (1933).

(15) *The anomalous transmission of light by the pupil*

As is well known, Stiles & Crawford demonstrated that rays passing through the periphery of the pupil have a much smaller stimulating effect on the retina than rays which have passed through its centre (Stiles & Crawford 1933). To a small extent this inefficiency of peripheral rays may be due to losses at the marginal zones of the refracting media. The greater part, on the contrary, whatever its cause may be, must be produced by the retina itself. This reduction in the stimulating effect of the marginal rays reduces the apparent intensity of the light which falls on the retina, it also reduces the effects of chromatic aberration but increases those of diffraction. Calculations showed that, on the whole, there is a net gain in the sharpness of the retinal image.

(16) *The neutralization of chromatic aberration by diffraction at small apertures*

Measurements of the sizes of the chromatic fringes, at different lens apertures, showed that there was a lack of correspondence between them; thus a halving of the aperture caused the widths of the fringes to be more than halved. As the iris diaphragm of the condenser was slowly closed, a point was reached at which the fringes were found to have disappeared entirely. This experiment was repeated with lenses of different focal length, with the same result. Further, when the diameter of the aperture at which the fringes disappeared was plotted against the focal length, a simple mathematical relationship was found to exist between them. Calculations and experiments followed which showed that a form of correction of chromatic aberration, by means of diffraction, was occurring at small apertures. It is well known that the sizes of the chromatic fringes are reduced, but that the sizes of the diffraction patterns are correspondingly increased, as the aperture of a lens is reduced. Moreover, the diffraction pattern is larger for rays of long wave-length than for short, whereas the reverse is the case for most of the fringes due to chromatic aberration. In consequence, as the aperture is reduced in diameter, a point is reached at which the one compensates for the other. This was the phenomenon which had been observed. The aperture at which the most complete compensation took place was called 'the neutralizing aperture'. Calculation showed that light transmission improved as the focal length of the lens system was reduced, so that the neutralizing aperture was more useful with a microscope than with a telescope, and thus is useful for a lens of short focal length such as the eye (see table 12).

TABLE 12. CALCULATED NEUTRALIZING APERTURES FOR CROWN-GLASS LENSES

focal length (cm.)	neutralizing aperture (cm.)	$\frac{\text{aperture} \times 100}{\text{focal length}}$	light transmission
400	1·650	0·41	0·2
100	0·825	0·83	0·7
40	0·522	1·31	1·7
10	0·261	2·61	6·8
4	0·165	4·13	16·9
1	0·083	8·26	68·2
0·4	0·052	13·05	169·0
0·1	0·026	26·10	682·0

As a further test a microscope objective of about 15 mm. focal length, consisting of two simple plano-convex crown-glass lenses, was constructed. Used at the neutralizing aperture it was found that the definition of this objective was quite good. In cases where there is ample light, and high resolving power is not required, such simple objectives might well find a useful application in optical instruments, because of their cheapness.

(17) *The elimination of colours from test objects of small size*

With the Stiles & Crawford effect reducing chromatic aberration at large apertures, and diffraction neutralizing it at small ones, the absence of colour at medium apertures was still left to be accounted for. The following experiment indicated the nature of the problem.

Two similar grating test objects were prepared, consisting of alternate black and white bars. One was examined by ordinary vision, the image of the other produced by the Abbé condenser, mentioned above, was examined through the microscope, the magnification being such that to the observer the two gratings, that seen direct and that seen through the microscope, had about the same dimensions. By the use of an artificial pupil the aperture of the eye was also made the same in both cases. Observation showed that chromatic aberration was absent from the image seen direct by the eye, whereas it was present in the image seen through the microscope. Various modifications did not reduce this difference. The conclusion was obvious: that there is some factor which operates in the case of the eye, which does not do so in the case of the microscope. This conclusion was confirmed by the following experiment: a grating consisting of parallel black and white bars would be expected to appear yellow and blue to the eye, because of its chromatic aberration; we have just seen that it does not do so. It was found further that a grating consisting of parallel blue and yellow bars does not appear coloured either, but looks black and white. Here, then, was clear evidence for the presence of some factor in the eye which has the effect of eliminating colours such as these. Not only can it remove the subjective colours produced by chromatic aberration, but objective colours as well.

A number of trials with test objects of different colour showed that the above phenomenon was not by any means an isolated one, but that as the retinal image is reduced in diameter two changes in colour vision occur: the first is the replacement of full colour vision by reduced colour vision; the second is the replacement of the latter by colourless foveal vision (see § 22).

(18) *The reduced colour vision which occurs at small visual angles*

König (1897) was the first to point out that persons with normal colour vision find that they have abnormal vision when objects subtending small visual angles are being examined. He found, under the above conditions, that all parts of the spectrum could be matched by mixtures of two spectral colours only, red and blue. He claimed that this type of vision resembles most closely that met with in blue-blind, or tritanopic, individuals. Many years later, Willmer (1943) arrived at a similar conclusion. Both König and Willmer thought that the phenomenon is limited to the centre of the fovea. The author (Hartridge 1945*a*) found that this idea was incorrect, for the same visual changes can be shown to occur not only at the fovea, but at the parafovea as well. It was also noticed that there are local differences in colour perception at various parts of the retina, and that these differ according to the observer who is undertaking the tests. It was clear that there were individual differences, but in one respect all were alike, namely, that reduced colour vision occurs for test objects subtending small angles at the eye, not only at the fovea centralis, but in the more peripheral parts of the retina as well.

The author investigated this problem further (Hartridge 1945*b*), considering such factors as peripheral vision, light intensity, shape of test object, and eye movements; he also considered the possible mechanisms by which full colour vision became converted into reduced colour vision. These, and more recent tests, will be briefly described in Parts II to VI of this paper.

Willmer & Wright (1945) have recently confirmed König's experiments and conclusions. They used fields of 20, 15 and 12 min. of arc. Monochromatic colours corresponding to 6500 and 4600 A were found to match all the intermediate parts of the spectrum, when mixed together in suitable proportions. Parts of the spectrum below 4600 A could also be matched. At 5780 A, that is, in the yellow, there was a neutral point. They found that there was a second neutral point in the violet at 4100 A.

(19) *The posterior nodal distance of the human eye*

An examination of the literature shows that there is some uncertainty as to the dimensions of the images of material objects which are formed on the retina, since these depend on the posterior nodal distance of the lens system of the eye. Tscherning (1904), who calculated the optical constants of the eye from measurements on Sanson's images, which are reflected from the surfaces of the eye media, suggested the value 17·13 mm. Helmholtz (1909), who used a similar method, proposed 7·32 mm. as the distance between the posterior nodal point and the anterior surface of the cornea, and 24 mm. as the distance between the fovea and the same surface; from which it can be seen that the posterior nodal distance is 16·68 mm. Gullstrand's suggestion was 17·05 mm. Hardy & Perrins (1932) give as an example '0·25 mm. on the retina subtends at the centre of the exit pupil an angle of 0·70 degree. The corresponding angle in the object space, computed from Lagrange's law, is 0·87 degree.' Calculating from the latter, the distance between the retina and the intersecting point of the light rays is found to be 16·45 mm. Recently, Goldmann & Hagen (1942), using an ingenious method employing two parallel X-ray beams, have measured this distance for a number of living human subjects. They made measurements on ten emmetropes, one hypermetrope and seven myopes. The posterior nodal distance for the emmetropes varied from 15·38 to 17·67 mm., the mean being 16·81 mm. The values quoted above are summarized in table 13.

TABLE 13. POSTERIOR NODAL DISTANCES

Tscherning (1904)	17·13
Helmholtz (1909)	16·68
Gullstrand	17·05
Hardy & Perrins (1932)	16·45
Goldmann & Hagen (1942)	16·81
mean	16·82

(20) *Cone diameter and cone 'inter-centre distance'*

As stated in the previous section, there is uncertainty with regard to the value that should be adopted for the posterior nodal distance. There is even more difference of opinion with regard to the diameters of the foveal cones, and to the distance between the centre of one cone and those of its immediate neighbours. Values varying between 5·4 (Kölliker) and 1·0μ (Polyak) have been given by different observers for the diameter of a foveal cone. These and some other estimates are given in table 14.

TABLE 14. THE DIAMETERS OF THE FOVEAL CONES

	μ		μ		μ
Kölliker	5·4–4·5	Merkel	3·0	Kühnt	2·5–2·0
Koster	4·4	Max Schultze	2·8	Rochon-Duvigneaud	2·5–2·0
Wilcker	3·5–3·1	Greeff	2·5	Polyak	1·0–1·5
Dimmer	3·5–3·0	Wadsworth	2·5		

It is not justifiable, in the author's opinion, to average the above values for the following reasons. It is not definitely known that all the above observers made their measurements on human material, at the exact centre of the fovea. It is likely that many of them measured material embedded in paraffin wax, and did not subsequently correct their results for the shrinkage caused by dehydration. Lastly, the differences between the estimates are far too large for an average to have much significance. If one excludes the results of Kölliker and Koster on the one hand, and of Polyak on the other, because of their differences from the rest, the average is 2·73μ. If they are included, the average is 2·95μ. Until further work has been done in which shrinkage has been adequately allowed for, it does not seem justifiable to adopt a value much below 2·70μ. Østerberg (1935) found the number of cones per sq.mm. of fovea to be 147,000, so that each cone in transverse section would have an average diameter of 2·94μ. Some would be larger and some smaller than this, with corresponding differences in 'the cone inter-centre distance', that is, the distance between the centre of one cone and those of its immediate neighbours.

(21) *The cone unit*

It has been seen in previous sections that there is some uncertainty with regard both to the posterior nodal distance of the human eye and to 'the cone inter-centre distance', the result being that the lateral displacement which an object in the visual field would have to undergo, in order for its image to move from the centre of one cone to the centre of the next one to it, can only be a matter for conjecture. In the absence of precise data, the displacements have been calculated for various posterior nodal distances and for various cone inter-centre distances. These are given in table 15, the displacements being in mm. for an object 10 m. away from the observer.

TABLE 15. DISPLACEMENT, IN MM., AT 10 METRES

cone inter-centre distance	posterior nodal distances			
	16 mm.	16·5 mm.	17 mm.	17·5 mm.
2·75	1·718	1·667	1·619	1·571
3·00	1·875	1·815	1·765	1·715
3·25	2·050	1·970	1·910	1·857
3·50	2·185	2·120	2·060	2·000
3·75	2·342	2·270	2·200	2·141

It will be seen that the values for the displacement of an object situated 10 m. from an observer vary from 1·571 to 2·342 mm. In the absence of exact data the value has been assumed to be 2 mm. for the purposes of these researches. Now, 2 mm. at a distance of 10 m. subtends, at the observer's eye, an angle of 41·236 sec. of arc. This is called 'a cone unit'. The term has been adopted for convenience. An observer with good sight, who has six/fourths vision on Snellen's notation, can correctly read test type the black lines of which are 1 cone unit in width. The conversion table (table 16) may be found useful.

(22) *Reduced colour vision and colourless foveal vision*

It has been found that certain losses of colour take place with reduction of visual angle, which are described in Parts II, III and IV. These losses cause normal colour vision to be replaced first by a reduced form of colour vision which superficially resembles a somewhat rare type of colour blindness, called 'blue-blindness' or 'tritanopia'; with a further reduc-

TABLE 16. CONE UNIT CONVERSION TABLE

cone units	seconds of arc	minutes of arc	displacements at the retina* (μ)	displacements at 10 m. (mm.)	visual acuity
1	41·236	0·687	3·36	2	1·456
2	82·472	1·375	6·7	4	0·728
5	206·180	3·436	16·8	10	0·292
10	—	6·873	33·6	20	0·146
20	—	13·745	67·2	40	0·073
50	—	34·363	168·1	100	0·029
100	—	68·727	336·2	200	0·015

* Assuming a posterior nodal distance of 16·81 mm.

tion in visual angle, these losses cause complete loss of colour vision which somewhat resembles total colour blindness; for example, that seen at the periphery of a normal retina.

Normal colour vision is sometimes referred to as 'trichromatic vision', because the trichromatic theory of Thomas Young has for many years been considered adequately to account for it. It has been recognized, however, that the matching by a normal-sighted observer of the whole visible spectrum by mixtures of any three monochromatic rays cannot be carried out without the use of some negative values. It may be possible to avoid these by mixing four or more monochromatic rays together.

Recently, Granit's micro-electrode experiments on animals have given a stimulus to the idea that human vision may be 'polychromatic'. While this uncertainty exists it would appear better to avoid the terms 'trichromatic' or 'polychromatic', and to use instead such a non-committal term as 'full colour vision'.

Referring now to the first type of vision, caused by a reduction of visual angle, it might be alluded to as 'dichromatic vision'. But in this case also uncertainty exists as to the precise type of vision which is present (see § 69, p. 567). For this reason it would appear better to use the term 'reduced colour vision'.

Finally, with further reduction of visual angle, vision becomes colourless, and this might be referred to as 'monochromatic'. This term is, however, sometimes used to designate twilight vision, and confusion might therefore arise if this were employed. It would consequently appear better to adopt the term 'colourless foveal vision'.

To summarize, for the reasons stated, the terms which will be used in this paper are 'full colour vision', 'reduced colour vision', and 'colourless foveal vision', for the types of vision found on altering the visual angle.

II. THE COLOUR LOSSES SUFFERED BY YELLOW AND BLUE

When the visual angle subtended at the eye by a yellow test object is greatly reduced, it is found to lose its colour and to be replaced by white. This change is so complete that the substitution of the yellow test object by a white one causes no noticeable difference. Experiment shows that important factors in determining the visual angle are the intensity of the light and the area of the test object. Unimportant factors are the shape of the test object and the brightness of the background. The change in colour is still found to occur when, instead of falling on the exact centre of the fovea, the image of the test object is caused to fall on some part of the parafovea.

Under similar conditions a blue test object is found to be replaced by dark grey or black. In this case also, the area of the test object, and the light intensity, play important parts; so also, in this case, does the brightness of the background.

(23) *The changes of colour*

Before experiments were started it was necessary to devise suitable tests for determining whether the retina of the observer was in a state of full colour vision, as witnessed when coloured surfaces subtending large angles at the eye are under examination, or of reduced colour vision, when the coloured surfaces are subtending small ones. One test, founded on the work of König, would have been to ascertain by trial whether all parts of the visible spectrum could be matched by suitable mixtures of monochromatic red and blue rays. This test could not be applied in this case, because the production of the matching fields requires a spectrometer of special design, and this was not available. The alternatives were to use colour filters or coloured cardboard. Neither of these can produce light which is monochromatic, such as that which emerges from a well-constructed spectrometer. On the other hand, it was the primary object of this research, not so much to elucidate quantitatively the properties of the retina, as to find out the conditions under which the coloured fringes produced by chromatic aberration are suppressed. Now calculations and experiments previously published by the author (1918) had shown that these fringes are far from being monochromatic. The sharply focused yellow rays, for example, have, superimposed on them, rays from all other parts of the spectrum, including the blue and violet. Consequently, if strictly monochromatic yellow light had been employed in this research, the experiments would have been done under entirely different conditions from those which are met with in normal vision. It seemed justifiable, therefore, to use as test objects either colour filters or coloured cardboard. The choice between these is not important. Both depend on the use of dyes for removing those parts of the spectrum which are not required, thus permitting the rest to stimulate the retina.

The colour changes which occur when monochromatic patches of light, produced by a spectrometer, which subtend large angles at the eye, are caused to subtend small ones, are shown in table 17.

TABLE 17. THE EFFECTS OF REDUCING VISUAL ANGLES

wave-length (A)	large angles	small angles
6500	red	no change
6000	orange	pale orange
5780	yellow	white or very pale grey
5600	yellow-green	very pale blue-green
5400	green	pale blue-green
4800	blue-green	no change
4300	blue	grey-blue
4100	violet	neutral tint

Except for red (6500 A) and blue-green (4800 A), which undergo no observable change, any of the colours could have been employed for testing the replacement of one type of vision by the other. Two changes seemed to be particularly noticeable: that undergone by yellow, which becomes white or pale grey; and that undergone by violet, which becomes neutral tint. When colour filters and coloured cardboard were tested, it was found that the colour changes which they suffered, owing to reduction of visual angle, were substantially the same as those for monochromatic colours given above (in table 17). This fact, coupled with the knowledge that, as mentioned above, the fringes produced by chromatic aberration are not themselves composed of monochromatic rays, justified their use in these experiments.

It should be emphasized that there is nothing critical with regard to these experiments. The size of the pupil, the intensity of illumination of the test object, and its depth of tint, as will be shown in the sections which follow, all affect the visual angle at which full colour vision is replaced by reduced colour vision, and vice versa (see § 22). For this reason the experiments always consisted of comparisons in which, so far as possible, only one variable was changed at a time.

The yellow test, which was used most frequently for the experiments, consisted of thin white cardboard, such as is used for visiting cards, which had been given, as uniformly as possible, three coats of a saturated solution of pure picric acid in 10 % alcohol in water. The result was a bright lemon-yellow colour. A large sheet of card was prepared at a time, which was then cut up, as required, by means of a guillotine. Neighbouring pieces of card were used for the tests, because these were found to match most closely in tint. Other colours were also used: red, orange, green, blue, violet and crimson. Cardboard was employed, coated three times, using Waterman coloured inks. There was no particular advantage in these dyes: any others of a similar colour could have been used instead.

Unfortunately, it is not possible to determine accurately the Munsell numbers of these colours, because they are brighter and more saturated than the Munsell colours. The nearest Munsell number is given below for the colours most frequently used.

red	5·0R/5/12	blue-green	2·5B/5/6
yellow	10·0Y/8/6	blue	7·5PB/5/14
green	2·5G/7/8	crimson	2·5RP/8/4

Nearly all the earlier work was done with these coloured test papers, because no other method was available at the time. Since then, all crucial results have been checked, using monochromatic light and the micro-stimulator apparatus described in Part X.

(24) *The description of a typical experiment*

Since no special room, with controlled lighting, was available, the experiments had to be done in an ordinary practical classroom. This occupied nearly the whole of the first floor of the laboratory, and had windows on both sides. The part used for the tests was a long, unbroken length of floor, parallel with, and about 2 m. away from, the north-east outside wall. The tests were done in daylight, with a light-adapted eye (see § 26). Daylight is notably variable, both in intensity and quality, but it will be shown, in § 27, that small variations in light intensity do not play an important part in determining the visual angle at which the colour change from yellow to white, or vice versa, takes place. The test object, attached to the required background, was mounted vertically on one end-wall of the laboratory. About 20 cm. from it was placed a small piece of white card, to aid the observer in his judgements as to the completeness of the colour change from yellow to white (see § 25). If, as the observer varied his distance from the test object, he preserved fixation all the time, it was found that the distance required for yellow to become white was several metres greater than that for the reverse change. Thus the visual mechanism responsible for the changes of colour behaves as if it suffered from 'backlash'. It was found that this phenomenon, which made accurate observation difficult, could be largely eliminated by interrupting the observations by quick glances to either side. It seemed to be immaterial whether two eyes were used or only one.

Two precautions had to be taken during the observations: one was to exclude coloured stimuli, other than the object under test, from the field of vision, for it was found that other coloured objects, particularly yellow ones, tended to decrease the size of the visual angle at which the colour change from yellow to white took place; the other precaution was to use a large background for the test object.

(25) *The completeness of the colour change*

The question arises: when, with decrease of visual angle, a yellow test object appears to have become white, how complete is the colour change? This question was answered by performing the following experiment.

A strip of white cardboard, part of which was tinted yellow, was mounted behind an aperture in a black background, so that white or yellow could be presented to the observer in turn. It was found that when, with reduction of visual angle, yellow had apparently changed to white, the yellow could be replaced by white—by moving the strip of cardboard—without the observer noticing any change in the appearance.

This test proved conclusively that when yellow looks white, it has in fact assumed the appearance of white. This would not be the case unless full colour vision had been replaced by reduced colour vision.

(26) *Light and dark adaptation*

Light adaptation was carried out by looking at the sky for several minutes; dark adaptation, by screening the eyes completely from light. It was appreciated that complete light and dark adaptation would not be achieved by such means. At the same time, if adaptation had been a factor of importance in determining the substitution of reduced colour vision for full colour vision, the tests which were undertaken should have disclosed the fact; such was not the case, however. It is possible that the eye quickly readapts to the level of illumination used for the tests, thus abolishing any effect that adaptation might otherwise have had. In spite of these negative results, time was always allowed, during the experiments described in this paper, for the observer's eyes to adapt themselves completely to the intensity of illumination of the test objects.

(27) *The effect of light intensity*

Preliminary experiments using an artificial pupil of 1·5 mm. diameter showed that light intensity affects the visual angle at which yellow is replaced by white. It was found that a tenfold increase in the intensity of illumination of the test object had the effect of doubling, approximately, the visual angle at which the change of yellow to white took place.

Table 18. The effect of illumination

foot-candles	distance (m.)	cone units	minutes of arc
1	1·7	17·7	12·159
12	3	10	6·873
100	8	3·75	2·575
3000	18	1·67	1·148

The yellow test object, which was square, with 6 mm. sides, was placed on a black background. The values in columns 3 and 4 are for the width and height of the test object when the colour change was seen to take place.

The effect of illumination is seen to be an important one. For this reason experiments were done only at times when the daylight was constant in value.

(28) *The effect of pupil diameter*

The effects of alterations in the diameter of the pupil may be studied under two different conditions: (*a*) where the change in aperture modifies the intensity of light falling on the retina, and (*b*) where the effect of change in aperture is compensated by an increase or decrease in the illumination of the test object, so that the light falling on the retina remains constant in intensity. Both these conditions were investigated.

In table 19 are given the results obtained with a yellow test object, 6 mm. square, on a black background, when the intensity of illumination of the test object was kept constant, and consequently the light on the retina varied with the square of the diameter of the pupil.

TABLE 19. THE EFFECT OF PUPIL DIAMETER, THE INTENSITY ON THE RETINA BEING VARIED

pupil diameter	pupil transmission	distance (m.)	cone units	minutes of arc
5·7	32·5	15·0	2·00	1·38
4·8	23·0	10·5	2·86	1·97
4·0	16·0	9·1	3·30	2·28
3·2	10·2	8·6	3·49	2·40
2·4	5·8	7·5	4·00	2·75
1·6	2·6	6·2	4·84	3·33
1·0	1·0	5·0	6·00	4·13

If the second, fourth and fifth columns be examined, it will be noticed that an increase in the amount of light falling on the retina decreases the visual angle at which the colour change occurs. Further, it will be noticed that there is approximately a twofold decrease in the latter for a tenfold increase in the light intensity falling on the retina. But this was the conclusion arrived at in the previous section, as the result of altering the illumination of the test object, the pupil diameter being constant, which suggests that change of pupil diameter affects the colour change solely because of the alteration in the illumination of the retina which it produces. This conclusion may be investigated by experiments done under condition (*b*) above, in which variations were made both in the diameter of the pupil and in the illumination of the test object, in such a way that the amount of light falling on the retina was kept constant. As before, a yellow square, with 6 mm. sides, on a black background was used. A Stubbs gauge provided artificial pupils of the required sizes, while the apparent intensity of illumination of the test object was altered by placing Ilford neutral-tint filters of suitable density between the test object and the observer's eye. Table 20 shows the results obtained.

TABLE 20. EFFECT OF SIZE OF PUPIL, INTENSITY ON RETINA BEING CONSTANT

intensity of test object	pupil diameter	pupil transmission	distance (m.)	cone units	minutes of arc
100	1·00	1	1·38	21·7	14·9
33·3	1·83	3·3	1·35	22·2	15·2
10	3·16	10	1·33	22·6	15·5
3·33	5·79	33·3	1·30	23·1	15·9

Columns 4, 5 and 6 of the table show that when the intensity of light reaching the retina from the test object is constant, that the visual angle at which the test object changes colour is also approximately constant and is independent of the diameter of the pupil. It should be noted that no correction was introduced for the Stiles & Crawford effect, which would reduce somewhat the light transmitted by the larger pupils, and would, therefore, be expected to reduce somewhat the distances at which the colour change occurs. It is possible that this factor accounts for the small variations in visual angle shown in columns 5 and 6.

(29) *The effect of shape of test object*

The test object in all the previous experiments has consisted of a yellow square. The question arises as to the precise attribute of the test object which determines the colour change. Possible factors might be: (*a*) the area of retina stimulated; (*b*) the length of contour bounding this stimulated area; (*c*) the perimeter of the geometrical image on the retina. To test these points four yellow test objects were used, all having the same superficial area: (1) a square, 12 × 12 mm.; (2) a rectangle, 6 × 24 mm.; (3) a hollow square, 24 × 24 mm. outside, with sides 1·6 mm. wide; (4) nine small squares, 4 × 4 mm., one placed in the centre, eight placed in a circle with 10 cm. radius. The data of these test objects, and the results given by them, are summarized in table 21. All the test objects were on black backgrounds, and were viewed under the same conditions.

TABLE 21. THE EFFECT OF SHAPE OF TEST OBJECT

test object	square	oblong	hollow square	star
area (sq.mm.)	144	144	144	144
length of contour (mm.)	48	128	179·2	144
perimeter (mm.)	48	128	96	628
distance (m.)	24·9	26·7	23·4	21·5
mean width (cone units)	4·81	5·34	4·68	4·30
mean visual angle minutes of arc	7·00	7·77	6·80	6·26

It will be seen from this table that if area is kept constant, then the distance, the mean area in cone units, and the mean visual angle also remain constant within experimental error, in spite of large variations in both length of contour and perimeter. Area appears to be a factor of importance, whereas the others do not. This is confirmed by the observations described in the next section.

(30) *The effect of area of test object*

It was found by experiment that an alteration in the area of a yellow test object on a black background affects the distance at which the transition from yellow to white takes place (table 22).

TABLE 22. THE EFFECT OF AREA OF TEST OBJECT

	area (sq. mm.)		
observer	36	144	576
J.L.D'S.	6·1	11·8	19·3
G.W.J.	8·0	10·1	20·3
H.H.	9·3	17·7	30·0
E.C.T.	10·7	17·7	25·3
J.E.T.	13·5	18·8	23·3
mean	9·9	15·2	23·6

There are individual differences between observers, but the evidence is conclusive on this point. As the area of the test object is varied, so alterations in the visual angle occur as shown in table 23.

TABLE 23. EFFECT OF AREA OF TEST OBJECT

area (sq.mm.)	distance (m.)	cone units	minutes of arc
36	9·9	3·03	2·08
144	15·2	3·95	2·72
576	23·6	5·08	3·50

It was expected that an increase in area, according to the inverse square law, would have been accompanied by a corresponding increase in distance, so that the visual angle would have remained constant. But, as seen in the third and fourth columns of table 23, such is not the case. The cause of this discrepancy may be change in size of the background, which undergoes an alteration, with change of distance between test object and observer. But another possible factor is scattered light, due to dust particles in suspension in the air between the test object and the observer. Such scattered light is usually blue in colour, and this, if present, would tend to alter the colour of the test object towards white, because yellow and blue are complementary colours. This would tend to shorten the distance at which the change of colour due to the eye takes place. But further, the greater the distance between test object and observer, the more effective this factor would be. The possible effect of this factor was tested by taking two test objects, one 8 mm. square, the other 201 mm. square, which were mounted on the same black background. Two mirrors cut from the same sheet, one small and one large, were placed so that the reflected images of the two test objects had the same apparent size and were seen side by side by the observer, so that their tints could be compared. When this was done, it was found that the more distant square appeared to have the less saturated tint. Since the illumination, the actual tints, and the apparent dimensions of the test objects to the eye were the same, the only variation of importance was the light path, which differed in the two cases by about 24 m. The conclusion that it was diffused light which was responsible for the difference in tint in the above experiment was supported by a further test, in which a cloud of tobacco smoke was formed in the light path of the larger test object. When this was done the distant test object was seen to turn white for a short time, while the smoke lasted.

Diffused light appears to be one factor, but there may be other factors, which cause small deviations from the inverse square law.

(31) *Conditioning factors*

When in the immediate neighbourhood of a yellow test object is placed a second yellow conditioning object, it is found that the latter alters the visual angle at which change of colour of the test object takes place. The test object was 6 mm. square. The conditioning object was a rectangle, 100 × 25 mm., which was mounted with its long axis vertical. This was placed at different positions to the left side of the test object, when the results shown in table 24 were obtained.

It will be seen that as the distance between the two yellow objects is reduced, the less does the visual angle become at which the test object appears to be white. The explanation of this phenomenon appears to be that the two objects, when both are near one another in the visual field, behave as if they formed part of a single test object, the visual angle of which has to be greatly reduced before its retinal image reaches the size required for it to become white. The closer the objects the more they behave as one single object, and vice versa.

TABLE 24. THE EFFECT OF A CONDITIONING OBJECT

distance apart of objects (mm.)	distance (m.)	cone units	minutes of arc
∞	8·8	3·40	2·34
200	12·5	2·40	1·65
100	18·5	1·62	1·11
50	23·0	1·31	0·90
5	38·0	1·27	0·87

(32) *The effect of depth of tint*

When test objects of the same dimensions but of different shades of yellow were tried, it was found, as was expected, that the paler the tint the larger the visual angle at which the change to white took place (table 25). This effect of paleness of tint in causing an increase in the visual angle at which loss of colour occurs is important from the point of view of the correction of the chromatic aberration of the eye, because the yellow fringe produced by this aberration is largely diluted with white light (see Part V).

TABLE 25

colour of test object	distance (m.)	cone units	minutes of arc
pale yellow	12·5	2·40	1·65
daffodil yellow	18·0	1·67	1·15
chrome yellow	27·0	1·11	0·76

(33) *The effect of brightness of background*

In all the experiments described in the previous sections of this chapter the test object has been a yellow one, produced in nearly all cases by coating white cardboard three times with a saturated solution of picric acid in 10% alcohol in water. In all, or nearly all, the tests, the background has consisted of black paper which reflected perhaps as much as 5 % of the light incident on it. In this section the effect of using backgrounds having other reflexion factors will be considered (table 26). The dead black background was obtained by lining a box with black paper. An opening was made in the lid of the box, and in the centre of this the test object was suspended by means of fine black silk thread.

TABLE 26. THE EFFECT OF BACKGROUND BRIGHTNESS ON YELLOW

background	distance (m.)	cone units	minutes of arc
white	10·0	3·00	2·06
grey	10·3	2·92	2·00
black	10·6	2·83	1·94
dead black	10·3	2·92	2·00

The visual angles in the above tests are all within experimental error, so that the conclusion in the case of a yellow test object is that background brightness has a negligible effect on the visual angle at which loss of colour occurs.

(34) *The effect of colour of test object*

At the beginning of this part a summary has been given of the principal changes which coloured objects undergo when, instead of being viewed at large angles, they are viewed at small ones. Of the spectral colours, yellow changes to white, or to very pale grey; blue to dark grey or black; while green becomes pale blue-green. Further, of the non-spectral colours, purple becomes brown, mauve becomes red-brown, and crimson changes to red-orange.

Tests were performed in order to ascertain whether there was any essential difference between the mechanism of these colour changes. The effects of intensity, pupil diameter, area, etc., were repeated with each of these colours, and no essential differences in behaviour were observed, except in two respects, namely, background brightness and area of test object. These will now be considered.

(35) *The effect of background brightness in the case of blue*

It has been shown in § 33 that the visual angle at which yellow changes to white is nearly independent of background brightness. Such is not the case with blue, as the values given in table 27 show.

TABLE 27. THE EFFECT OF BACKGROUND BRIGHTNESS ON BLUE

background	distance (m.)	cone units	minutes of arc
white	7·5	4·00	2·75
grey	8·8	3·41	2·34
black	28·0	1·07	0·73
dead black	33·0	0·91	0·63

It is obvious that background brightness has a very big effect on the visual angle at which blue suffers loss of colour. This point will be referred to again when considering the possible mechanisms of these colour changes in Part VI.

(36) *The effect of area in the case of blue*

It will be remembered that when yellow test objects, of the same shape and colour but of different area, were tested, it was found that they did not comply exactly with the inverse square law. Two explanations were offered for this lack of agreement: (*a*) alterations in the visual angle subtended by the background on which the test objects were mounted, which varied with the distance between the background and the observer; (*b*) light scattered by particles suspended in the air between the test object and the observer.

TABLE 28. THE EFFECT OF AREA

test object mm. square	distance (m.)	cone units	minutes of arc
6	3·5	8·6	5·9
12	10·2	5·9	4·0
24	27·0	4·5	3·1

Table 28 shows that in the case of blue test objects of different area, on a white background, a similar lack of exact agreement is to be observed.

It will be seen, in the case of blue test objects, that the visual angle at which loss of colour occurs, decreases with increase in the dimensions of the test object; but it will be remembered that the opposite was found for yellow test objects (see § 30, p. 543). In this case also the same explanations may be advanced, namely, change in the visual angle of the background, and the effects of scattered light. Scattered light usually has a blue colour, and may be expected therefore to extend the distance, and consequently to decrease the visual angle, at which a blue test object loses its colour, as is found to be the case.

(37) *Tests of parafoveal vision*

All the tests described in previous sections have been done with central vision, that is, with the observer performing accurate fixation. It was important, for two reasons, to ascertain whether similar observations could be performed when using peripheral vision. The first reason is a practical one, for it would obviously be valueless to advance the hypothesis that the fringes caused by chromatic aberration are eliminated by the losses of colour described in this part, if the latter were limited to the fixation region of the fovea. The second reason is a theoretical one, for tests of the parafovea should confirm or refute the hypothesis of König and Willmer, that these colour changes are limited to the foveal centre.

The yellow test object, 6 mm. square, was mounted on a black background. A small blue-green fixation mark was placed in position, according to requirement, 4, 8, 12 and 16 cm. away from the test object. The observer was instructed to fix either the test object itself or the fixation mark. Table 29 shows the results obtained:

TABLE 29. TESTS USING PARAFOVEAL VISION

fixation (cm. away)	distance (m.)	cone units	minutes of arc
on the test object	9·0	3·33	2·29
4	9·5	3·16	2·17
8	16·0	1·88	1·29
12	24·0	1·25	0·86
16	21·0	1·25	0·86

In the case of the above observer it will be seen that the same kind of change occurs to the yellow test object, but that the visual angle is reduced at 12 and 16 cm., to nearly one-third its value for central vision. Three other subjects were examined, who gave the results summarized in table 30. It will be observed that one observer, G.N.J., finds that the change of yellow to white occurs at reduced visual angles as fixation moves away from the foveal centre, as was the case for the observer H.H., whose results are given in table 29. The second observer, J.L.D'S., finds the change to occur at visual angles which first become less and then become greater again. The third observer, E.C.T., finds little change. These differences in visual angle for any one observer, and the individual differences in the visual angles, are probably due either to local variations in spectral sensitivity of the photoreceptors of the fovea or parafovea, or to variations in their distribution.

TABLE 30. TESTS USING PARAFOVEAL VISION

fixation (cm. away)	G.N.J. cone units	J.L.D'S. cone units	E.C.T. cone units
on the test object	3·75	1·33	1·62
4	3·00	1·20	1·67
8	2·50	0·97	1·88
12	2·31	1·50	1·88
16	2·31	1·50	1·88

Evidence will be given in Part IX that the photoreceptors of different colours are arranged in a random manner, and that this causes clusters of one kind to occur. It seems likely that this chance distribution accounts for the local variations recorded in tables 29 and 30.

This test was now repeated, using a blue test object, and the same conclusion arrived at, namely, that there are individual differences among observers, but that all of them agree that blue loses its colour at the parafovea, just as it does at the foveal centre.

The values recorded in tables 29 and 30 are shown plotted in figure 1.

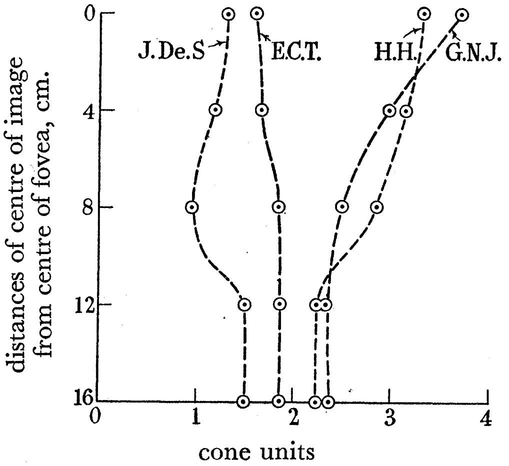

FIGURE 1. The visual angles, in cone units, are shown at which a yellow test object lost colour and appeared to be white. The tests were performed by four light-adapted observers, who had normal colour vision. Tests were done at five points of the retina by each observer.

III. THE COLOUR LOSSES SUFFERED BY YELLOW-BLUE PAIRS

The colour losses suffered by yellow and by blue test objects take place more readily, that is, at larger visual angles, when the yellow and blue pairs are in close juxtaposition.

(38) *The effect of colour of background*

Early in these experiments it was observed that a yellow test object, placed on a blue background, changes to white when it subtends a larger visual angle at the eye than is the case when it is placed on a black background. A similar difference was noticed when a blue test object was placed on a yellow instead of on a white background (table 31). In each case the test object was 6 mm. square. The third, fourth and fifth columns show respectively the distances and the visual angles, in cone units and in minutes of arc, at which yellow became white, or blue became black. These tests showed, in the case of both blue and yellow, that colour elimination occurs at a greater visual angle when coloured backgrounds are used than when colourless ones are in use.

TABLE 31. THE EFFECT OF COLOURS OF BACKGROUND

colour of test object	colour of background	distance (m.)	cone units	minutes of arc
yellow	black	15·0	2·00	1·38
yellow	blue	8·3	3·62	2·48
blue	white	5·3	5·65	3·89
blue	yellow	2·6	11·55	7·99

(39) *The effects of coloured surrounds*

The above experiment was repeated with the coloured background reduced in size, so that it took the form of a narrow border immediately surrounding the test object. The test object and its surround were mounted on either black or white backgrounds, as shown in tables 32 and 33.

Table 32. The effect of coloured surrounds

square object	surround	background	distance (m.)	cone units
yellow	none	black	6·4	9·38
yellow	blue	black	3·6	16·70
blue	none	white	5·2	11·60
blue	yellow	white	2·3	38·40

Table 33. The effect of coloured surrounds

oblong object	surround	background	distance (m.)	cone units
yellow	none	black	18·5	3·24
yellow	blue	black	6·5	9·23
blue	none	white	7·3	8·22
blue	yellow	white	3·4	17·70

The square test object had 12 mm. sides; the oblong one was 30 × 12 mm.

An examination of these tables shows that in all cases the effect of the surround was to increase the visual angle at which the yellow or blue test object lost colour, to become white or black respectively.

The effect of separating the yellow test object, 12 mm. square, from its blue surround, was investigated, with the results shown in table 34.

Table 34. The effect of separation

separation (mm.)	distance (m.)	cone units	minutes of arc
0	6·5	9·23	6·33
5	8·5	7·06	4·85
10	13·0	4·61	3·16
20	16·0	3·75	2·57
no surround	18·0	3·33	2·28

It is clear from these tests that a surround is most effective, in increasing the visual angle at which the colour change takes place, when it is touching the test object; and that increasing the distance separating them reduces its effectiveness.

(40) *The effects of yellow and blue pairs*

The above tests suggested the idea that if a pair of test objects, one blue and one yellow, be placed side by side, they would both be found to lose colour at a greater visual angle than when examined singly. The objects selected for this test were rectangular strips, 100 × 5 mm. These were examined either singly, or mounted side by side with their long axes parallel, on white backgrounds (table 35).

Table 35. The effect of proximity

test object	distance (m.)	cone units	minutes of arc
yellow only	37·0	0·68	0·47
blue only	28·5	0·88	0·61
both together	7·5	3·34	2·29

These tests confirmed the previous ones, in showing that proximity of yellow to blue causes loss of colour at a larger visual angle than would be the case with single test objects alone. The conditions favouring increase of visual angle have been studied in various ways, and the following experiments may be quoted.

On a black background was mounted a yellow test object, 6 mm. square. This was found to become colourless at a distance of 7·6 m. A yellow rectangle, 100 × 5 mm., with its long axis vertical, was now mounted 5 cm. to one side of the test object. Both objects were now found to remain yellow at the longest distance available in the laboratory, namely, 37 m. Close alongside the yellow rectangle, and on the side remote from the yellow square, was mounted a blue rectangle of the same dimensions as the former. The yellow test object was now found to lose colour at substantially the same distance as it had when viewed by itself, namely, 7·6 m. Thus the addition, in the visual field, of the blue-yellow pair of rectangles, had no observable effect on the visual angle at which the yellow square became colourless. The addition of further blue-yellow pairs of rectangles confirmed the above conclusion.

In other experiments, various separations between the blue and yellow rectangles were tried. One of these was performed as follows:

Three yellow rectangles, 100 × 5 mm., were mounted 100 mm. apart, with their long axes vertical, on a white background. They were found to remain yellow at the longest distance available in the laboratory, namely, 37 m. The experiment was continued by mounting three blue rectangles midway between them, so that the colours alternated. All six rectangles were found to become colourless at 23 m. The blue rectangles were now moved close to the yellow ones, so as to produce three pairs, when the position for loss of colour was found to be 8·3 m. This experiment emphasizes the fact that for loss of colour at the maximum visual angle, the blue-yellow pairs of rectangles should be as close together as possible.

(41) *The yellow-blue grating test object*

In the yellow-blue grating test object, the effect of proximity is made as great as possible by mounting rectangles of these colours in close apposition, so that the colours alternate. In one grating prepared in this manner there were eleven yellow and ten blue rectangles, each 100 × 6 mm.

With this test object many of the experiments described in Part II were repeated, that is, the effects of intensity of illumination, diameter of pupil, and similar factors were investigated. Some of these tests will now be described.

In table 36 are shown the results of tests in which results given by gratings composed of yellow and black lines, and blue and white lines, were contrasted with those given by blue and yellow lines. The lines composing the tests were 6 mm. wide. The visual angle in cone units and minutes of arc of the line width, at the eye of the observer, are given in the last two columns. The results confirm the conclusion already arrived at, namely, that the close association of yellow and blue increases the visual angle at which loss of colour occurs.

TABLE 36. GRATING TEST OBJECTS COMPARED

test object	distance (m.)	cone units	minutes of arc
yellow and black	51·0	0·59	0·40
blue and white	17·7	1·70	1·17
yellow and blue	10·6	2·83	1·94

(42) *The effect of angle with the horizontal*

In all the tests so far described, the coloured bars of the gratings have been vertical. The effects of other positions will now be described.

TABLE 37. THE EFFECT OF ANGLE WITH THE HORIZONTAL

line direction	distance (m.)	cone units	minutes of arc
vertical	8·3	3·62	2·50
down to left	9·4	3·19	2·19
horizontal	8·7	3·45	2·36
down to right	7·5	4·00	2·74

The results shown in table 37 were given by a grating of yellow and blue lines, 6 mm. wide. The differences shown are just outside the experimental error, so that there seems to be some factor causing colour to be eliminated at a somewhat greater visual angle when the lines slope down to the right than when they slope down to the left. It is possible that this difference is associated with the fact that in the observer's left eye, which was used for the above tests, the optical axis meets the retina at a point below and to the left of the fixation points for the different coloured rays. This point will be referred to again in Part VII.

Another curious effect was noticed while the above tests were in progress, namely, that with oblique lines the image broke down to produce spurious images much more readily than was the case either with horizontal or vertical lines. This fact also will be referred to again later (see Part XII).

(43) *The effect of light intensity*

It will be recollected that in previous tests an increase in light intensity had the effect of decreasing the visual angle at which loss of colour occurred. A tenfold increase in intensity was found to halve approximately the visual angle. The same relationship was found to hold in the case of a yellow-blue grating, as table 38 shows.

TABLE 38. THE EFFECT OF LIGHT INTENSITY

relative intensity	distance (m.)	cone units	minutes of arc
1000	10·6	2·83	1·94
100	5·7	5·26	3·61
10	3·0	10·00	6·87
1	1·6	18·80	12·90

The differences in intensity were produced by Ilford neutral-tint filters.

(44) *The effect of pupil diameter*

As pointed out in Part II, the effect of a change in the aperture of the pupil may be investigated under two different conditions: (*a*) where the intensity of light on the retina varies with the square of the diameter of the pupil; (*b*) where the intensity of light on the retina is kept constant by a suitable alteration in the brightness of the test object (tables 39 and 40).

When, owing to an alteration in pupil diameter, the retinal illumination is altered, there is a corresponding change in the visual angle at which loss of colour occurs. When, on the contrary, by the use of a suitable neutral-tint filter, the retinal intensity is kept constant, then the visual angle also remains constant within experimental error.

Table 39. Retinal illumination varying

pupil diameter (mm.)	intensity ratio	distance (m.)	cone units	minutes of arc
1	1	7·3	4·11	2·82
3·14	10	13·5	2·22	1·45

Table 40. Retinal illumination constant

pupil diameter (mm.)	intensity ratio	filter transmission	distance (m.)	cone units
1	1	100	7·5	4·00
3·14	10	10	7·1	4·23

(45) *The effect of chromatic aberration*

The fact that a change in the diameter of pupil, when retinal illumination is kept constant, has so small an effect, appears to dispose of the hypothesis previously suggested by the author (1944*a*), namely, that chromatic aberration plays a part in arresting the loss of colour in the case of a grating of yellow and blue lines. This may be explained as follows. It was found by experiment that the brightest rays of the spectrum, namely, the yellow and green rays, normally produce sharply focused images on the retina. In consequence of this, rays of longer wave-length come to a focus behind the retina, and rays of shorter wave-length focus in front of it. When a grating consisting of yellow and blue bars is under examination, then, as stated above, the yellow rays focus sharply on the retina, while the rays from the blue bars, having come to a focus in front of the retina, spread out to form diffusion circles on the retina, the diameters of which vary with the aperture of the pupil. They therefore overlap on to areas of the retina occupied by the sharply focused yellow rays. But blue and yellow are complementary in colour and, therefore, this superposition causes the production of white light. Under ideal conditions the whole of the yellow is in this way changed to white, so that white bars appear to be substituted for yellow ones. Now the blue rays, being spread out to form aberration disks, suffer a considerable reduction in brightness, which causes them to approximate to black.

That this hypothesis is unlikely, or at all events does not play the part preliminarily assigned to it, is clearly proved by the tests described above, in which the diameter of the pupil, and, therefore, the diameters of the aberration disks, were altered in the ratio of more than 3 to 1, without an observable effect on the visual angle at which colour loss occurred. This conclusion was confirmed by other experiments, in which the chromatic aberration of the eye was corrected by means of a suitable crown-flint glass combination. When this was in use the loss of colour of the yellow-blue grating appeared to take place at approximately the same visual angle as it did when no correcting lens combination was in use.

(46) *Comparative visual angles*

It is possible that the results given in previous sections do not bring out the essential difference between the loss of colour of a grating composed of alternate yellow and blue bars, and the losses of colour suffered by isolated yellow and blue test objects. The following comparison may help to bring out this point. Keeping the conditions of illumination, pupil diameter, etc., constant, the visual angles were determined at which a grating test object 115 mm. square, a yellow test object 12 mm. square, and a blue test object 12 mm. square, lost colour. The results are given in table 41.

TABLE 41. COMPARATIVE VISUAL ANGLES

test object	distance (m.)	cone units	minutes of arc
grating	10·3	56·30	38·70
yellow square	9·6	6·25	4·29
blue square	13·7	4·38	3·01

It will be observed how very different are the visual angles at which losses of colour occur in a yellow-blue grating and in the single coloured squares on white backgrounds.

IV. THE COLOUR LOSSES SUFFERED BY RED AND BLUE-GREEN

When red or blue-green test objects which subtend very small angles at the eye are observed, it is found that red is replaced by black, and blue-green by white. Both changes are facilitated by the red and blue-green test objects being in close juxtaposition.

(47) *The preparation of the test objects*

Some of the colour changes which test objects undergo, when they are caused to subtend very small angles at the human eye, have been described in Part II. It was found that yellow appears to change to white; blue to change to grey, dark grey, or black; yellow-green to change to pale blue-green; mauve to change to brown; crimson to change to orange. Three colours were found to remain unchanged at this stage: red, orange and blue-green. It will now be shown that if a still greater reduction of visual angle is effected, then these colours also change.

The colour changes in the case of yellow, blue, yellow-green, mauve and crimson test objects occur at visual angles of 1 to 10 min. of arc. In consequence, in order to see these changes, test objects of moderate size (6 to 24 mm. square) are viewed at moderate distances (4 to 20 m.). The colour changes to be described in this communication occur as a rule at smaller visual angles; in consequence it has sometimes been found, either that test objects of small size have to be used, or that test objects of average size have to be viewed at inconveniently great distances. In order to avoid these difficulties the micro-stimulation apparatus, which is described in detail in Part X, has been used for some of the determinations.

The test objects were prepared by applying suitable aniline dyes, in aqueous solution, to white paper. In all recent experiments Waterman's inks have been used. The nearest Munsell number to these colours will be found in § 23, p. 540. The final result is quite different from that of applying a pigment, since in that case there are white spaces between the pigment particles. It more closely resembles that obtained by viewing white paper through a colour filter prepared from the same dye. In this case, however, there are reflexions of light from the glass-air surfaces to be contended with.

The colour changes to be described do not occur abruptly, but gradually, with change of visual angle; in consequence, a high degree of accuracy is unobtainable. It is for this reason that the results have been given to two significant figures only.

(48) *The effect of size of test object*

It was shown in Part II that size was an important factor in determining the distance at which yellow or blue test objects were apparently replaced by white or dark grey ones respectively. The same statement is true of red and blue-green ones, as table 42 shows. In the first column are shown the sizes of the square test objects; in the second, the distances in metres at which red test objects lost all colour, or appeared dark grey or black; in the third, the distances at which the blue-green test objects lost all colour, or appeared pale grey or white. In all these cases the test objects were placed on white backgrounds. It will be noticed that whereas blue-green resembles yellow in approximating to white, red resembles blue in approximating to dark grey or black.

TABLE 42. THE EFFECT OF SIZE

size of squares (mm.)	distances for red test objects (m.)	distances for blue-green test objects (m.)
4	9	8
8	15	15
16	28	34

With regard to the values for the red or the blue-green test objects shown in columns 2 or 3 of table 42, it will be seen that the distances at which the test objects become colourless are nearly proportional to their linear dimensions. Any deviations from this rule are probably due to experimental error. In this respect red and blue-green test objects differ from yellow or blue ones, since the latter were not found to conform to this rule exactly (see § 30, p. 543 and § 36, p. 546).

(49) *The effect of light intensity*

Three light intensities were tested, using 8 mm. test objects on white backgrounds, with the results shown in table 43. It will be seen that reducing the intensity of illumination of the red test object has the effect of reducing the distance at which it loses its red colour. In the case of the blue-green test object there is, however, no significant change. The cause of this difference in the behaviour of red and blue-green test objects is not known. This difference will be referred to again in Part VI.

TABLE 43. THE EFFECT OF LIGHT INTENSITY

intensities in f.c.	distances for red test objects (m.)	distances for blue-green test objects (m.)
about 3000	16	15
about 100	11	16
about 4	9	13

(50) *The effect of pupil diameter*

Two sizes of pupil were tested, with the results shown in table 44. It will be seen that a change of pupil diameter affects, to an appreciable extent, the distance at which a red test object becomes dark grey. In the case of a blue-green test object, the pupil size appears to have little or no effect. Now a change in pupil diameter will affect both the intensity of illumination of retina, and the structure of the retinal image, since a decrease in the pupil size will decrease the dimensions of the aberration disks produced by chromatic aberration, but will also increase the dimensions of the pattern produced by diffraction of light at the pupil aperture. It seems likely that of these alterations the change of light intensity is the more important. This idea is in keeping with the experimental results which show a change in the distance at which red loses its colour, but no change in that for the blue-green, as was found to be the case with a change of illumination.

TABLE 44. RETINAL ILLUMINATION VARIED

pupil diameter (mm.)	distance for a red test object (m.)	distance for a blue-green test object (m.)
3·6	15	16
1·6	12	15·5

A further test was carried out by changing the diameter of the pupil, and at the same time compensating, by means of Ilford neutral-tint filters, for the alteration in the intensity of the retinal image which would otherwise have been produced. The results obtained in this manner with a 12 mm. square red test object on a white background are shown in table 45. It will be seen that the visual angle, in cone units, at which loss of colour took place was now approximately the same, within experimental error.

TABLE 45. RETINAL ILLUMINATION CONSTANT

pupil diameter (mm.)	relative intensity	filter transmission	distance (m.)	cone units
1·0	1	1000	41	1·47
3·14	10	10	46	1·31

(51) *The effect of shape of test object*

In the case of yellow or blue test objects it was found that shape had no observable effect on the distance at which colour is lost, provided that the total area of the test object was kept constant. The same was found to be the case with red and blue-green test objects (table 46). The distances given in column 2 are substantially the same as one another, showing that test objects of the same area, but different shape, lose their colour at the same, or approximately the same, distance from the observer; a similar statement can be made about blue-green test objects.

TABLE 46. THE EFFECT OF SHAPE

shape of test objects	distance for red test objects (m.)	distance for blue-green test objects (m.)
square	25	27
cross-shaped	24	25
hollow square	26	25

(52) *The effect of proximity of the same colour*

The proximity of an object of the same colour as that of a red or blue-green test object was found to have a very marked effect on the distance at which the latter becomes colourless, as is shown in table 47. In each case the test object was 8 mm. square on a white background. The object, when present, was a rectangle of the same colour as the test object, measuring 16 × 8 mm. This was placed symmetrically in respect of the test object, the distance separating them being given in table 47. It will be seen, in every case, that the proximity of the coloured object has a marked effect in increasing the distance at which the test object becomes colourless. It will be recollected that a similar effect was obtained in the case of both yellow and blue test objects (see § 31, p. 544).

TABLE 47. THE EFFECT OF DISTANCE

conditions of test object	distance for red test objects (m.)	distance for blue-green test objects (m.)
no near object	12	13
object 4 cm. away	24	25
object 1 cm. away	over 40	over 50

(53) *The effect of proximity of the complementary colour*

It was shown in the previous section that proximity of an object of the same colour increases the distance at which a test object becomes colourless. It will now be shown that the opposite occurs when the object and test object are complementary in colour—a red object being close to a blue-green test object, and vice versa (table 48). The test object was 8 mm. square on a white background. The object, when present, measured 16 × 8 mm. In every case the effect of proximity was to decrease the distance at which the test object lost its colour. It will be remembered that a similar result was obtained with blue and yellow test objects (see Part III).

TABLE 48. THE EFFECT OF PROXIMITY

conditions of test object	distance for red test objects (m.)	distance for blue-green test objects (m.)
no near object	14	16
object 1 cm. away	10	10
object touching	6	7

(54) *Results with grating test objects*

Three grating test objects were prepared, one with red and white parallel lines, one with blue-green and white parallel lines, and one with red and blue-green parallel lines. The dimensions of the gratings, and of the lines which comprised them, were the same in each case. All the lines were 4 mm. wide. The colours of the lines were such that when red and blue-green ones were superimposed, e.g. by means of a double-image calcite glass prism, the appearance to the eye was neutral grey. The distances were now determined at which each of the gratings became colourless, with the results shown in table 49. The close proximity of red lines with blue-green ones, which, owing to the strong contrast between these colours, might be expected to increase the distance required for them to become colourless, has in fact the opposite effect. In the case of the red and white, and blue-green and white gratings, the reproduction of the distances of 300 and 350 m., respectively, was effected by means of the micro-stimulating apparatus described in Part X. It should be pointed out that neither the red and white lines, nor the blue-green and white lines, could be resolved into lines by the eye at the distances stated; all that could be seen in either case was a coloured rectangle, which became colourless at the distances mentioned.

TABLE 49. GRATING TEST OBJECTS COMPARED

type of grating	distances (m.)
red and white lines	about 300
blue-green and white lines	about 350
red and blue-green lines	23

(55) *The effect of using peripheral vision*

It has been seen above that when the angle which a red test object subtends at the eye is reduced sufficiently, the test object loses its colour and becomes dark grey, or black. If the test object is blue-green, it becomes pale grey or white. Both changes might be due to the existence, at the precise centre of the fovea, of a minute colour-blind spot, so that, when the image of a coloured test object falls on this alone, it would appear black, white, or some shade of grey; but when the image is larger, so that part of it at least falls on the retina, with a normal colour response, then the true colour of the test object would be appreciated by the observer.

On the contrary, the changes undergone by the red and blue-green test objects might be due to a nervous mechanism which comes into operation when either of these test objects subtends the requisite angle at the eye, that is, forms an image of the required area on the retina. If the former hypothesis were correct, the colour change should be strictly limited to the exact centre of the fovea. If, on the other hand, the hypothesis of a nervous mechanism is correct, it would be expected that this would be found to operate, not at the foveal centre alone, but at other parts of the fovea as well. The choice between these two rival hypotheses can be made by testing parafoveal vision to see if there, also, red and blue-green test objects lose their colour when their dimensions are reduced.

On making some observations with the more peripheral parts of the retina, it was found that within the area of the fovea it was possible to observe what was taking place, but that outside this area the definition was too poor for this to be done adequately. In column 1 of table 50 are shown the positions of the fixation point of the observer's eye, relative to that of the test object. The left eye was alone used, and fixation was performed horizontally, and to the left, so that the retinal image was on the opposite side of the foveal centre to the blind spot. The results obtained showed, conclusively, that both test objects suffer the same loss of colour in the parafovea as they do at the foveal centre. The hypothesis of a nervous mechanism is therefore substantiated, and that of a central scotoma for colour refuted. It will be shown in Part VI that a similar conclusion is reached with regard to yellow and blue test objects. An examination of the figures in columns 2 and 3 of the table shows that when the red test object falls peripherally, the distance decreases at which loss of colour takes place, that is, the visual angle increases. It will be recollected that the same result was obtained in the case of a yellow object (see § 37, p. 547). In the case of blue-green,

TABLE 50. THE EFFECT OF PERIPHERAL VISION

position of fixation (cm. from centre)	distance of red test objects (m.)	distance of blue-green test objects (m.)
exact centre	31	33
10	25	38
20	14	41
30	8	46

on the contrary, the distance increases at which loss of colour occurs, that is, the visual angle decreases. As pointed out previously, in § 37, these local differences may be associated with variations in the distribution of photoreceptors of different colour response.

(56) *The effect of background brightness*

In all the experiments so far described, the background has been a white one. In this section the effects of replacing this by a black background will be given. An examination of table 51, which gives the distances between test object and observer at which the test objects lost their colour, shows that the effect of substituting a black background for a white one has a greater effect in the case of a red test object, 6 mm. square, than it has on a blue-green one of the same size. It will be recollected that in the case of yellow and blue there was a similar difference (see Part III, p. 548).

TABLE 51. THE EFFECT OF BACKGROUND BRIGHTNESS

background	red test object (m.)	blue-green test object (m.)
white	19	23
black	50	35

The position so far as these four colours are concerned may be summarized as follows. The colours yellow or blue-green lose their colour at distances which are affected but little by background brightness. On the contrary, the colours red and blue, corresponding to the ends of the spectrum, are more affected in this respect. A detailed examination of the other spectral colours is proposed at a future date.

V. THE CHROMATIC ABERRATION OF THE EYE AND ITS CORRECTION

Since the eye is uncorrected for chromatic dispersion, yellow and blue fringes must be produced by the lens system of the eye at the edges of objects. These fringes are not observed, however, when the eye is used in normal vision, because, as explained in Parts II and III, yellow is replaced by white, and blue by dark grey or black. A detailed study of chromatic aberration shows that there should be traces of secondary colours—red and blue-green; these are dealt with, as is explained in Part IV, by red being replaced by black and blue-green by white.

(57) *The elimination of colour from artificial fringes*

It has been shown in Part II that colour changes occur as the visual angle of certain coloured test objects are reduced. Thus yellow suffers loss of colour and becomes white, while blue becomes black. It has also been shown, in Part III, that where yellow and blue test objects are in close contact, particularly favourable circumstances exist for these losses of colour to take place.

The matter was investigated further by producing drawings in colour of several test objects, as they would appear when their images were produced by a lens uncorrected for chromatic aberration. The colours used were naphthol yellow, naphthol green and methylene blue. The matching of the colours of the fringes was not found to be so difficult as the gradations of light intensity. The following results were obtained:

(*a*) Yellow dot, 10 mm. diameter, on a blue ground, 30 mm. diameter, appeared to be a white dot on a black background at 5·4 m. distance from the observer. At this distance the visual angle for the dot was 9·2 cone units, and that for the blue ground 27·6 cone units.

(*b*) Yellow strip, 10 mm. wide, between two blue strips of the same width; this appeared white on black at 7·5 m.; the width of each strip equals 6·7 cone units.

(*c*) One yellow and one blue strip, both 10 mm. wide, separating white and black rectangles; these appeared white and black at 11 m.; the width of each strip equals 4·5 cone units.

(*d*) A grating of blue and yellow bars, all 10 mm. wide; this appeared black and white at 8·7 m.; the width of each bar equals 5·7 cone units.

In table 52 the experimental results just given are compared with the calculated widths of the fringes, for a 4 mm. pupil, given in tables 6 to 8 above. It will be seen that in every case the experimental value is greater than the calculated value, that is, the colours of somewhat larger fringes than those actually produced by chromatic aberration would be eliminated.

TABLE 52. THE CORRECTION OF CHROMATIC ABERRATION

test object	experimental width (cone units)	calculated width (cone units)
point source:		
yellow dot	9·2	4·8
blue surround	27·6	15
linear source:		
yellow line	6·7	4·2
blue fringe	6·7	3·2
extended source:		
yellow fringe	4·5	3
blue fringe	4·5	3

(58) *The elimination of colour from real fringes*

The method used in the preceding section was altered, so as to use the real fringes produced by lenses known to be suffering from chromatic aberration, instead of diagrams of fringes. One experiment was performed as follows.

Four uncorrected biconvex crown-glass lenses were taken, two of 20 D and two of 18 D. The two former were mounted about 10 cm. apart, with the two latter midway between them, so that together they formed an erecting lens system having no magnification.

Evidence will be produced in the next section that, at ordinary intensities of illumination, the process of colour loss experienced by yellow and blue is well able to deal with the fringes produced by chromatic aberration, but that as the light intensity increases, the margin between what is available and what is wanted grows less. For this reason the experiments which are now to be described were performed in the best light available. This was done by directing the lens system at the narrow metal bars of a window, in such a direction that they were seen as sharp black lines against the sky. On looking through the centre of the lens system at these bars, and carefully adjusting the focus, it was found that the centre of the field could be rendered almost completely free from colour. Since all the components in this lens system consisted of unachromatized convex lenses, each of which brings the blue rays to a shorter focus than the red rays, the result would be that, even if the eye were chromatically corrected, blue rays which have passed through this lens system would come to a focus closer to the cornea than would the red rays, consequently colour fringes would be visible, unless there were some process for eliminating them.

When the above experiment was repeated with lenses of half the power, there was no difficulty in completely eliminating all colour from images at the centre of the field.

This experiment was tried in two other ways. The image of distant objects formed by an unachromatized triplet lens of 60D, that is, about the same focal length as the eye, was examined by a well-corrected magnifying lens of approximately the same focal length; only very faint colours due to chromatic aberration were present. On doubling the power of the magnifying lens, strong colours were evident.

The same unachromatized triplet was used, at an aperture of 7 mm., to produce a greatly enlarged image of the filaments of an electric lamp. When the observer was close to the screen, chromatic fringes were seen to be present. When, however, the observer was at the same distance from the screen as the projecting lens, fringes were not observed.

These experiments support the view that there is a mechanism, associated with vision, which eliminates the colour fringes that are normally produced by the lens system of the eye. In addition, there is a surplus colour-correcting effect which can be utilized for reducing the colour aberration in such lens systems as spectacle lenses, magnifying glasses and eyepieces. Tests with an unachromatized magnifying glass of 20 mm. focal length failed to disclose any colours due to chromatic aberration.

(59) *The colour fringes of objects at different light intensities*

Under the conditions of the experiments described in previous sections, it will be remembered that the effects of light intensity were tested, keeping the diameter of the pupil constant, and that the effects of varying the diameter of the pupil were studied under two different sets of conditions: (*a*) where the illumination on the retina was allowed to vary, and (*b*) where it was kept constant, by using compensating neutral-tint filters. Now, under the conditions of normal vision, the above circumstances would hardly ever be met with; for example, an increase of light intensity will usually bring about a corresponding decrease in pupil diameter, thus tending to maintain the retinal illumination at a more constant value. Such simultaneous variations of intensity and pupil may introduce unexpected effects with regard to the visual angle at which colour losses take place. An experiment to test this point was performed with the results shown in table 53.

TABLE 53. THE EFFECT OF LIGHT INTENSITY

light intensity (f.c.)	pupil diameter (mm.)	distance (m.)	cone units
3000	1·9	20·5	1·5
100	2·1	16·0	1·9
12	2·2	11·0	2·7
1	3·2	8·3	3·6
0·05	4·5	6·8	4·4

These tests were performed with a yellow test object, 6 mm. square, but similar tests were performed with a test object consisting of alternate blue and yellow lines. The conclusion arrived at was the same with both these test objects, namely, that as light intensity decreases, and the diameter of the pupil correspondingly increases, there is an increase in the visual angle at which colour losses occur, that is a larger amount of chromatic aberration can be corrected as the light intensity is reduced. Table 54 summarises the position.

TABLE 54. CHROMATIC CORRECTION AVAILABLE AT VARIOUS LIGHT INTENSITIES

light intensity (f.c.)	surplus chromatic correction
1000	very little
100	twice
10	four times
1	eight times

Thus at 10 f.c. there is sufficient surplus correction to deal with the chromatic aberration of a crown glass lens, e.g. a magnifying glass, of four times the refraction of the eye, that is $4 \times 60D = 240D$.

(60) *The effects of the age of the observer*

It is usual to find that the diameter of the pupil, and its reaction to light, decrease as the age of an individual increases. The tests described in the previous section were performed by a subject 59 years old; if they had been done by a younger subject a different result might have been obtained, because the diameter of the pupil at various light intensities might have been different. In such a subject the pupil at high intensities might have been smaller, and at low intensities it might have been larger. If this had been the case it might have had the effect of making the visual angle at which loss of colour occurred somewhat larger at high intensities of illumination, and somewhat smaller at low ones. Some tests were performed by a young observer, 18 years old, and it was found that the visual angle, measured in cone units, altered hardly at all with changes in the light intensity on the test object.

(61) *The colour fringes of objects at different distances*

When the eye is being used in normal vision, the objects looked at are seldom at the same distance from the observer. If they are at different distances, then rays of one wave-length will form the sharply focused images on the retina in the case of one object, and rays of a different wave-length will form them in the case of another object, thus producing variations in the spectral composition and colours of the fringes, as table 55 shows. Thus if the yellow rays are sharply focused for a given object, more distant objects will cause the sharp focusing of rays of longer wave-length, e.g. orange, and nearer objects will cause the sharp focusing of rays of shorter wave-length, e.g. green or blue-green. But coloured fringes are not often seen, except sometimes by uncorrected myopes, in whom the focused fringes may be blue-green, or even blue; or by uncorrected hypermetropes, in whom the focused fringes may be orange or even red. The absence of fringes of orange, red, green and blue-green from normal vision is due, in the opinion of the author, to the secondary losses of

TABLE 55. THE EFFECT OF THE FOCAL POINT

focused ray	colour of focused fringe	colour of unfocused fringe
6200	orange	greenish blue
5800	yellow	blue
5400	yellow-green	violet
5000	green	purple
4600	blue-green	red

colour which occur, at small visual angles, to red and blue-green, as has been described in Part IV. These losses of colour, when all of them have taken place, leave vision monochromatic, so that the eye behaves as if it were as fully corrected for colour as an apochromatic lens. Not only has the removal of yellow and blue, the primary spectrum colours, changed human vision into the equivalent of an achromatic lens, but the further elimination of red and blue-green, the so-called secondary spectrum colours, has perfected the colour correction. It is because of this double process of colour elimination that the retinal image is so free from colour in normal vision.

(62) *The effects of colour of object and of background*

In the previous sections of this Part, the fringes which have been considered have been those produced with white objects on black backgrounds, or vice versa. In this section coloured objects and coloured backgrounds will be considered. The subject is a complicated one, because for a complete description it would be necessary to consider objects of all colours, tints and shades, placed in turn on backgrounds of all these colour differences.

If, for some special case, information is required about the fringes of a particular object on a particular background, the simplest procedure is to examine the fringes in question, using a telescope with an unachromatized objective. When this is done for red, orange, green, blue-green and blue objects, on either white or black backgrounds, it is found, in practically all cases, that it is difficult to observe colour fringes at all. This appears to be due to these colours behaving as monochromatic objects would have done. In the case of yellow on black, feeble orange and green fringes are visible, instead of the strong yellow and blue ones which are visible when white on black is under examination.

When objects having mixed colours, namely, violet, purple, mauve and crimson, are examined on black or white backgrounds, a condition of focal instability is met with, and either the red or the blue component is focused, but not both simultaneously. Suppose red to be sharply focused, then the out-of-focus blue rays form aberration disks which extend, as a single well-marked fringe, beyond the sharp boundary of the red image. When blue rays are sharply focused, then the converse is found to occur. When a piece of cobalt blue, or violet, glass is placed in front of the eye, there is a reduction of light intensity, which causes dilatation of the pupil, thus increasing the diameter of all aberration disks. This accentuates the coloured fringes, as described above.

When a red object lies on a blue background, or vice versa, and red rays are being sharply focused, then its edge is occupied by a purple fringe, caused by the unfocused blue aberration disks overlapping with the sharply focused red image. When the blue component is focused the converse occurs. If these components had been complementary in colour to one another—for example, yellow and blue—both fringes would have lost colour, as has been shown in Part III. But they are not complementary thus explaining the success of the cobalt blue glass test, in disclosing the existence of the chromatic difference of focus of the human eye.

(63) *The effects of pupils of abnormal shape*

Three shapes of pupil have been used under experimental conditions, in order to examine their effects on the fringes produced by chromatic aberration: (*a*) the eccentric pupil, (*b*) the annular pupil, and (*c*) the double-aperture pupil.

(*a*) The eccentric pupil is produced by obstructing one side of the pupillary aperture by an opaque stop. Its use often causes fringes to become visible. When the test is repeated with a telescope with an unachromatized objective, it is observed that the normal yellow and blue fringes are replaced by larger orange-red and blue-green ones.

(*b*) An annular pupil is produced by obstructing the central rays by means of a central stop, which allows the peripheral rays to pass on to the retina. The use of such a stop is usually accompanied by an increase in the diameter of the pupil, thus increasing the diameter of all the aberration disks, and therefore the diameter of the fringes.

(*c*) A double-aperture pupil is produced by placing a narrow black rod in front of the pupil in such a way that rays are permitted to reach the retina through two unobstructed parts on either side of the rod. Here again the pupil usually dilates, causing the fringes which are parallel with the rod to be larger than normal. The fringes at right angles to the rod are often narrower than usual; this depends on the widths of the fringes, which in their turn depend on the sizes and shapes of the two apertures which are in use.

(64) *The sharp localization of the colour changes*

A description has been given, in previous sections of this Part, of the fringes produced by chromatic aberration. In previous Parts experimental evidence has been given that colours, similar to those that are present in these fringes, become colourless as they approach the sizes of fringes. The losses of colour, whatever their cause, do some harm in that they prevent the correct appreciation of the colours of small objects, but at the same time they do incalculable good, in that they prevent the scenes presented to our eyes in everyday life from being spoiled by the fringes of chromatic aberration. It would be worth while to sacrifice the appreciation of the tints of small objects, in order to achieve such a purpose. It would not be worth while, if it were found that the appreciation of the tints of large surfaces had to be sacrificed at the same time.

The question to be considered in this section may be stated as follows: Does the process responsible for eliminating chromatic fringes, which depends on the elimination of the colours of small objects, bring about similar changes in large ones?

Many experiments have been done in order to ascertain the localization of the colour losses; the first experiment was carried out as follows.

The observer stood at a fixed distance of 10 m. from a black screen, to the centre of which had been attached a small white fixation mark. One eye was used, and the position of its blind spot on the black screen was ascertained. Another part of the black screen was selected, and an area 4 cm. square was marked out on it with a sharp black pencil, so as to produce shiny marks. Various coloured objects, 4 cm. square, were then placed over the selected area, in turn, in order to prove the existence of normal colour vision in that area. When this test had been completed, a small yellow test object, 1 cm. square, was taken, and placed methodically in the sixteen positions required to cover entirely the selected area. In each one of these positions the yellow test object was found to appear white, showing that, under the conditions of the test, reduced colour vision was present everywhere in this area.

In the second experiment the test object, consisting of a grating of alternate narrow yellow and blue lines as described in Part III, was placed at such a distance from the observer that it appeared to him to consist of black and white lines. An assistant then placed in contact with the test object a large yellow rectangle, with the result that normal colour vision spread from the rectangle over the test object, causing the white lines to return to their original yellow colour, thus indicating the recurrence of reduced colour vision. So far the result was no different from those described previously in this section. But now a difference was observed, for on increasing the distance between the test object and the observer by a few metres, the lines became black and white once more. The retina was consequently in two different conditions, since it was exhibiting normal colour vision where the image of the yellow rectangle was situated, and reduced colour vision where the image of the grating test object was falling; thus showing conclusively that different parts of the retina may be in different conditions at the same time, so far as colour vision is concerned.

This conclusion helps to elucidate the conditions when the eye is being used in everyday life. Objects possessing fine detail, such as the printed pages of a book, may be in close association with larger objects not possessing fine detail—such as coloured illustrations, which require a high degree of colour perception for their full appreciation. The fine details which would be seriously marred by chromatic aberration have the advantage of reduced colour vision, which largely, if not entirely, eliminates the coloured fringes produced by that aberration, and restores the details to their original appearance. On the other hand, the large masses of colour, and of light and shade, which would not be so seriously marred by chromatic aberration, have the advantage of normal colour vision, which enables their true colour to be appreciated.

For the third experiment, the printed page of a book was modified as follows. The page was divided into six strips, and each was tinted by a pale shade of colour—pink, yellow, green, blue-green, blue and mauve. The page was then viewed by ordinary vision, when no colours due to the fringes produced by chromatic aberration were noticeable, yet the pale tints between the letters were clearly visible. In this case reduced colour vision is in the closest possible association with normal colour vision, yet neither is apparently disturbed by the other.

(65) *The effects of eye movements*

During the experiments described in the previous section, movements of the eyes were not checked, and no attempt was made to keep the gaze fixed on any given part of the test pattern. The experiments were now repeated, making intentional eye movements with the object of testing whether it was possible to detect momentarily indications that colour vision was normal, where it would have been better for it to have been reduced, and vice versa. But no such instances could be detected; the changes from normal to reduced, and back again, appear to take place as quickly as the movements of the eyes themselves. This matter of the rapidity of the change from one type of vision to the other will be referred to again in the next Part.

(66) *The phenomenon of irradiation*

The fact has long been known that, as a rule, white objects on black backgrounds look larger to an observer than do black objects of the same size on white backgrounds. This increase in the apparent size of a white object is called 'irradiation'. Several explanations of it have been advanced: (*a*) that it is due to diffraction and aberration, which cause white to encroach on black; (*b*) that it is due to light from directly illuminated retinal receptors spreading sideways on to those in the neighbourhood, which are not directly illuminated; (*c*) that it is due to the effects of nerve conduction which, either during chemical transmission, or during the performance of some physical process, spreads to other nerve fibres which are close to or are touching nerve fibres, or synapses, which are directly connected to stimulated photoreceptors; (*d*) that it takes place, because of similar processes, in the brain.

All these explanations are feasible, but there is a further possibility. It was seen, in § 7 above, that the distance from the centre of the image of a bright point source, of negligible dimensions, to the edge of the yellow area at the centre of the image is 2·7 cone units: that is, the yellow area has a diameter of 5·4 cone units. This area is surrounded by a white, or nearly white, ring which has a diameter of 9·6 cone units. The former, since it is at a small visual angle in respect of the eye of the observer, and is surrounded by a blue halo on all sides, loses colour and becomes white, with the result that the whole centre of the image, 9·6 cone units in diameter, is now white. It is impossible to state with any degree of precision where the boundary of this image will appear to be to the eye of the observer; all we know for certain is that the blue halo is replaced by dark grey or black, and that the white area which lies inside it has much larger dimensions than the geometrical image of the point source on the retina.

If the same reasoning be applied to the case of a bright line source, a similar state of affairs is met with, for the yellow centre, 4·2 cone units wide, is flanked on both sides by a white line. When therefore the yellow centre is replaced by white, it blends with the white lines on either side of it to produce an area 9·6 cone units in width (see § 8).

In the case of an extended object (§ 9), the area occupied by yellow and white extends beyond the boundary of the geometrical image of the object. The same extension occurs in the case of the white bars of a grating object (see § 11).

In every one of these cases, yellow, which becomes white, and the white already present in the image together encroach on areas which according to geometrical optics should be occupied by black; moreover, the spreading is greater in the case of a bright point, or bright line source, than it is in the case of an extended white object, or the white bars of a black-white grating.

There are two other cases to be considered, namely, a black spot and a black line, both on bright backgrounds. In both cases a condition is met with which may be called 'negative irradiation', because, whereas in normal irradiation white spreads on to the territory normally occupied by black, in both these cases the converse takes place, and black, or grey, spreads on to the territory normally occupied by white.

In the case of the black point, the blue centre of the image is 4·2 cone units wide, while in the latter its width is 4·9 cone units. In both cases, the visual angle being small, and the blue areas being surrounded by yellow haloes, blue is replaced by grey or black. But the width of this neutral area is larger than the geometrical images of the objects themselves, so that in this case it is black or grey which has encroached on white.

To sum up: not only may white objects on dark backgrounds appear to be larger than they really are, because of chromatic aberration, but small black objects on bright backgrounds may appear to be larger also for the same reason.

VI. THE ANTICHROMATIC RESPONSES

Of the various hypotheses advanced to explain the colour changes described in Parts II, III and IV, only one fits in with the observed facts, namely, that there is a neurological mechanism situated somewhere on the nerve path between the photoreceptors of the retina, and the brain; this consists of four separate parts, one for blue, one for yellow, one for red, and one for blue-green: these are responsible for bringing about the colour changes, and are therefore responsible for eliminating the fringes produced by the chromatic aberration of the lens system of the eye. For this reason they have been called the 'antichromatic responses'.

(67) *The colour changes which follow a reduction of visual angle*

An account has been given in previous Parts of the loss of colour suffered by yellow, blue, red and blue-green, when the visual angle which they subtend at the eye is reduced sufficiently. In the previous Part the employment of these colour changes, for the elimination of the fringes produced by chromatic aberration, is described. In this Part it is proposed to consider the nature of these changes, and the possible mechanisms by means of which they are brought about.

Briefly, the colour changes are as follows.

If four test objects of the same size—red, yellow, green, or blue—be placed on separate white grounds, and be viewed in turn, as they are gradually reduced in visual angle, it will be found that the first one to change is the blue, which is replaced by dark grey or black. The next to change is the yellow, which is replaced by white. At about the same visual angle, green is replaced by blue-green; so that there is at this stage a form of dichromatism with primary colours, which are apparently red-orange and greenish blue. With a further decrease in visual angle, these colours also begin to change, until finally the red has been replaced by dark grey, or black, and the blue-green by pale grey, or white. Thus at the final stage there is colourless vision, all the spectral colours appearing to be various shades of grey; very pale shades in the cases of yellow and green; very dark shades, or even black, in the cases of red, blue and violet.

(68) *The colour changes which follow a reduction of light intensity*

It was found by Abney and Festing that as the spectral colours are reduced in brightness the first colour to change is blue, which is replaced by dark grey or black. The next colour to change is yellow, which is replaced by white. At this intensity level, 0·0025 f.c., there is a form of dichromatism, orange-red being one primary and blue-green the other. At a still lower light intensity the blue-green and red parts of the spectrum undergo changes, the former being replaced by pale grey, while the latter becomes dark grey or black. Thus vision has now become colourless. It will be seen that the changes undergone by the different colours, and the order in which these changes occur, when the intensity is reduced, are practically identical with those which take place when brightness is kept constant but visual angle is reduced. These similarities suggest that the processes underlying both phenomena are the same. This conclusion is supported by the following observations: at 0·001 f.c., a large yellow square, at a visual angle of 100 cone units (about one degree of arc), appeared to be colourless, while a blue square at the same visual angle was seen to be dark grey; red was very dark brown; while green and blue-green were shades of grey-blue-green. At 0·0001 f.c., red appeared black; other colours, including the greens, were seen as shades of grey. Central vision had thus become colourless, even at this large visual angle. There seems to be little doubt that there would be reduced colour vision, or even colourless vision, at even larger visual angles, with a further reduction in light intensity. Thus for every light intensity, from direct sunlight to the lower limit of cone vision, there appears to be one corresponding visual angle at which reduced colour vision occurs, and another corresponding visual angle at which foveal vision becomes colourless.

Many years ago it was found by the author (1915) that a light, very nearly colourless to the eye, could be produced by removing from ordinary white light the whole of the violet and blue, together with part of the blue-green and some of the extreme red of the spectrum, by means of suitable dyes, the light thus produced being pale yellow in colour. But the yellowness of this light could be reduced considerably by partly absorbing the yellow rays. Non-colour-sensitive photographic emulsions could be exposed to this light with very little fogging, and in consequence it was used for illumination in the dark room. Many colours could be seen by it in their natural hues, but others were considerably altered. Red, orange, green, blue-green, and pale shades of these colours, appeared normal; so did the same colours mixed with black. Yellow was extremely pale; blue was dark blue-grey; mauve was red-brown; and crimson was replaced by orange. At the time, these facts seemed extremely puzzling. Now, however, that the details of the reduced colour vision which the retina assumes under conditions of small visual angle, or of feeble illumination, are known, the properties of this light are much more easily understood.

(69) *The varieties of dichromatism*

There are many varieties of dichromatism, which, however, are divisible into two main categories: (1) complementary dichromatism, in which the two primary colours are complementary to one another and thus produce white when suitably mixed; and (2) non-complementary dichromatism, in which the two primary colours are not complementary to one another, and so do not produce white when mixed in any proportion.

The first type of dichromatism can readily be witnessed by a normal-sighted observer, by looking through a colour filter which transmits two parts of the spectrum complementary to one another, as shown in table 56. The second type of dichromatism can also be witnessed by a normal-sighted observer, by using a suitable colour filter, which transmits two parts of the spectrum which are not complementary to one another, as shown in table 57. The primary colours shown in this table do not produce white when mixed together, but always produce a colour. Further examples of this latter form of dichromatism

TABLE 56. COMPLEMENTARY DICHROMATISM

first primary	second primary
red	blue-green
orange	greenish blue
yellow	blue
greenish yellow	violet

TABLE 57. NON-COMPLEMENTARY DICHROMATISM

first primary	second primary
red	green
red	blue
green	blue

are: (*a*) the vision produced temporarily by the drug santonin, and (*b*) the vision produced when the eye media are seriously discoloured, usually yellow.

In the case of both varieties of dichromatism there are further subdivisions; those of the non-complementary kind need not concern us here, but those of the complementary kind are: that the parts of the spectrum unoccupied by the primary colours are (*a*) all white, (*b*) all black, (*c*) some white, some black. To take an example: suppose the primaries to be red and blue-green, then there are four possible subdivisions, as shown in table 58.

TABLE 58. THE FOUR TYPES OF RED AND BLUE-GREEN DICHROMATISM

type	yellow part of spectrum	blue part of spectrum
(*a*)	white	white
(*b*)	black	black
(*c*) (i)	white	black
(*c*) (ii)	black	white

(70) *The nature of 'reduced colour vision'*

König stated that, at small visual angles, all the spectral colours could be matched by suitable mixtures of two monochromatic rays. Many years later Willmer (1943) made the same statement. Willmer & Wright (July 1945), on repeating König's observations, found that red rays of 6500 A, and indigo-blue rays of 4600 A, were suitable for matching all parts of the spectrum, including the violet. They found, moreover, two neutral points, one at 5780 A and a second at 4100 A, thus confirming the conclusions previously reached by the author, that yellow and blue are both replaced by neutral colours (Hartridge, March 1945*a*). The author's statement was, 'that yellow loses colour and becomes white, and that blue loses colour and becomes dark grey or black'.

The monochromatic rays used by Willmer & Wright are not complementary to one another. Table 59 gives the wave-length of the colours they used, and for comparison are shown the primary colours found by Helmholtz and by Sinden.

TABLE 59. COMPLEMENTARY COLOURS

observers		long wave-length	short wave-length	ratios
Willmer & Wright	reduced visual angle	6500	4600	1·42
Helmholtz		6500	4920	1·32
Helmholtz		5640	4600	1·22
Sinden		6500	4960	1·31
Sinden		5835	4600	1·27
Tonn	reduced illumination	6680	5473	1·22

It will be seen that the colours of Willmer & Wright are further apart in the spectrum than the normal complementaries. Since in some respects, as pointed out in § 68 (of this Part), a reduction in visual angle resembles a reduction in light intensity, it is pertinent to inquire what are the complementary colours at low intensities of illumination. Tonn found that the complementary to red was a yellow-green of 5473 A, their ratio being about 1·22, so that they were even closer together in wave-length than normal red—blue-green complementaries. So far as reduced vision is concerned, it would seem that there are three possibilities:

(1) That the complementary colours, at reduced visual angles, are farther apart than at ordinary visual angles.

(2) That the usual complementary colours would match all parts of the spectrum at reduced visual angles, just as effectively as those employed by Willmer & Wright.

(3) That reduced colour vision is not dichromatic, but tetrachromatic, with four primary colours, at 6500, 5800, 5000 and 4600A approximately. If that were the case, the colour triangle representing normal vision would now have become truncated, to form a four-sided figure with one of the above primary colours at each corner, and white at the centre. Further research will be required before this point is completely clarified.

(71) *Reduced colour vision and the polychromatic hypothesis*

A suggestion of four primary colours would be at variance with the three-colour theory of Thomas Young, but would not be similarly at variance with the Wundt-Granit polychromatic hypothesis. For, as is well known, the latter, using his micro-electrode technique on the retinae of many animals, found that in addition to 'dominators' with a broad spectral response curve, there are at least seven 'modulators' distributed through the spectrum, so that with full colour vision there are seven or more primary sensations. It should therefore be possible to have, by reduction, the type of vision suggested above, consisting of four primary sensations. Further evidence in favour of the polychromatic hypothesis will be given in Part XI.

Returning now to the consideration of reduced vision, the conclusion is that it is nearly, if not quite, of the complementary variety. There may be one pair of complementary colours, or two pairs. If the latter, they might be (red and blue-green) and (orange and indigo blue). Lastly, with regard to the type of complementary dichromatism which is present, it is clearly of type (*c*) (i), on the classification shown in table 58, p. 568, because yellow is replaced by white, while blue is replaced by dark grey or black.

(72) *The change from 'reduced colour vision' to 'colourless foveal vision'*

If a red test object, 16 mm. square on a white background, be examined at decreasing visual angles, it will be found that the first change is one of diminished saturation: the red colour is gradually replaced by pink. This change begins when the test object is at a visual angle of about 10 cone units, and reaches its maximum at about 5 cone units. As the distance is increased beyond this point, a different phenomenon is observed, for the test object begins to acquire a brownish tint, which gets progressively darker until at about 1 cone unit it passes through chocolate and fuchsin to dark grey or black. With a further increase in distance the grey gets gradually paler, until at very great distances the test object is no longer visible. Now it would seem evident that the first change, from red to pink, and the third change, from dark grey through pale grey to invisibility, are due to one and the same factor, namely, the gradual encroachment, owing to irradiation caused by aberrations and diffraction, of the image of the white background on to territory occupied by the image of the test object. If this is correct, it is not unlikely that this same process is taking place during, and is modifying, the appearances of the second phase, namely, the replacement of pink by dark grey or black. It is tempting to suppose, in the absence of the encroachment of the white background, that the observer would see the gradual replacement of red by black. An attempt was made to prevent this encroachment, by placing a narrow black border round the outside of the test object, that is, between it and the white background. This attempt was partially successful, for the loss of colour of the red test object appeared to be reduced to a considerable extent. In the case of the blue-green test object the three separate phases, that were noticed with the red test object, were not observed, for as the retinal image was reduced in size the colour became more and more dilute until it had been replaced by a pale shade of grey. On further decreasing its size, the test object disappeared altogether. Now these changes might occur owing to the encroachment of the image of the white background on to the territory of the image of the test object, or to some other factor. Some evidence in favour of the latter conclusion has been obtained in the following manner. A blue-green test object, 16 mm. square on a white background, was examined while the visual angle was progressively decreased. At first there was little change of saturation, but when the visual angle was reduced to less than 3 cone units, a much more rapid change appeared to be taking place, and the blue-green colour was rapidly replaced by a patch of grey. This phase of rapid change appeared to be due to some other factor than the encroachment of the white background, for the effect of placing a black border between the test object and the background did not appear to reduce the rate of colour loss appreciably.

The evidence reviewed in this section appears to support the view that in the case of a blue-green test object there is some active process which causes the disappearance of colour, with the result that blue-green becomes pale grey or white. In the case of a red test object on a white background there is again evidence of an active process, but irradiation also appears to play a part in the loss of colour which is observed.

(73) *The rival hypotheses for the changes in colour vision*

Having determined, so far as present evidence permits, the nature of the colour changes which take place with reduction of visual angle, it is now proposed to consider the possible mechanisms by which these changes are brought about. These are: a form of colour blindness affecting the centre of the fovea (Willmer); a phenomenon resembling contrast; light scattered by fine dust particles in the path of the rays between the test object and the observer, a process resembling irradiation; the replacement of cone vision by rod vision; the loss of light intensity suffered by objects with reduction of visual angle; a neurological mechanism.

Each of these hypotheses will now be considered in turn.

(74) *The hypothesis of a colour-blind foveal centre*

Willmer's hypothesis states that the centre of the fovea is occupied by an area which is permanently colour-defective owing to the absence of blue receptors. Since this area is small, subtending an angle of about 1° at the posterior nodal point of the eye, the image of any object used to test this hypothesis must be sharply defined, and eye movements must be guarded against, since these might cause the image to fall momentarily on normal retina, and thus might enable the observer to diagnose correctly the true colour of the test object.

If this hypothesis were correct, the following effects would be expected:

(1) that blue seen by the foveal centre would have a different appearance when it is seen by the parafovea;

(2) that blue, purple, mauve or crimson would alter in appearance when moved from the parafovea to the foveal centre, or vice versa;

(3) that visual acuity when using blue light would be definitely inferior to that for other colours.

It will be shown in the pages which follow that none of these statements is true.

A comparison of blue by central and by peripheral vision. The loss of intensity of blue, which would be expected on Willmer's hypothesis, was sought for by comparing the appearance of a blue test object when it fell on the central area of one eye, and on a peripheral area of the other eye. Details of the method used are as follows. The observer was at a fixed distance of 10 m. from a large black background; to this was attached a blue test object, 4 cm. square, in the centre of which was a small white fixation mark. A second white fixation mark was placed at a distance of 16 cm. from the first. The first fixation mark was looked at steadily by one eye, while the other eye looked at the second fixation mark. By means of a weak glass prism of variable angle, obtained by decentring a convex lens of +5D in relationship with a concave lens of −5D in front of one eye, the two fixation marks were caused to coincide, in the field of vision, to give a single binocular image. The fields of the two eyes were now similar, except that to one eye the blue test object appeared at the foveal centre, while to the other eye it appeared at the periphery of the fovea, outside the rod-free area. Now, as stated by Willmer, the area devoid of blue receptors subtends an angle of 0·9° approximately, at the posterior nodal point of the eye. When an observer, situated at 10 m., fixates a mark, then the boundary of this blue-defective area coincides with a circle 8 cm. radius, with the fixation mark at its centre. In the above experiment, therefore, the image of the blue test object falls well within this circle in the case of one eye, but well outside it in the case of the other. According to Willmer, there should be in consequence an obvious difference of appearance between the two images, for the one on the fovea should appear darker, and of a different colour, probably more green, than the one on the periphery. No such differences could be observed, however, in any of the tests which were done, using first one eye and then the other for foveal observation, and varying the parts of the periphery on which the comparison image was caused to fall. It will be observed that the two images were separated by an interval, and therefore were not seen under ideal conditions for an exact comparison to be made, since it is usual in colorimetry to place the images as close to one another as possible. This could not be done in the present case without running the risk of causing one image to leave the area which, according to Willmer, is blue-defective, or of causing the other image to enter it. In spite of this, any marked difference, such as would be expected on Willmer's theory, should have been readily observable. But as mentioned above, no such differences were found.

A comparison of brightness and colour by central and by peripheral vision. If Willmer's hypothesis of the absence of blue receptors from the foveal centre is correct, one would expect a blue test object to undergo an obvious change of brightness, or colour, or both, when its image is moved from a position on the retina where the blue receptors are present, to one where they are absent. Similarly, when this is done with a purple, mauve or crimson test object, one would expect a detectable change of colour towards red. This experiment was done in several ways.

Method 1. Two similar blue test objects on a black ground were presented simultaneously to one of the observer's eyes. The test objects were 4 cm. square, were 10 m. from the observer, and their centres were 16 cm. apart. One test object was fixed accurately so that its image fell wholly on the central area which, according to Willmer, is devoid of blue receptors. The image of the other fell outside this area, that is, on normal retina. The two images were compared.

Method 2. Only one test object was used, and it was examined monocularly. The observer maintained fixation on a mark attached to a black background, while the experimenter moved the test object so that its image fell first outside the supposed blue-blind area, and then inside it. This was done a number of times in different positions in respect of the fovea. The object of this test was to see if any sudden change in appearance could be detected as the image moved from a peripheral part of the retina, with normal trichromatic vision, across the boundary on to the central area which, according to Willmer, is deficient in blue receptors.

Neither of these methods disclosed any differences in the appearance of blue, such as would be expected on Willmer's hypothesis.

The tests were now repeated, using test objects of other colours, particularly purple, mauve and crimson, but again no evidence of any colour change was detected.

It will be shown in Parts IX and XI that when very small test objects are used, colour differences are to be found when different parts of the fovea are stimulated.

Visual acuity using blue light. Experiments will be described in Part VIII, in which the visual acuity of the eye was determined using red, green, blue and white lights. It was found that acuity for blue was equal to that by other lights, within the experimental error of the method. But it would be very unlikely that this would be the case if the foveal centre were blue-blind, because this part of the retina is known to have the highest acuity, and that a departure from this point invariably causes a serious fall in the ability to observe fine detail.

The position so far as Willmer's hypothesis is concerned may be summarized as follows: If the fovea is indeed colour-blind, it would be expected that one or more of the above tests would have disclosed the fact; but it has been shown that they do not do so.

(75) *The contrast hypothesis*

It is well known that simultaneous contrast is a phenomenon which occurs chiefly at the contours which separate one surface from another. If then the colour losses described in Parts II, III and IV were due to a phenomenon resembling contrast, it would be expected that the following conditions would favour colour loss:

(1) The splitting up of a test object into several small parts.

(2) Increasing the length of contour separating the test object from its background.

(3) Placing colour near the edges, instead of near the centre, of a test object.

That subdivision of a test object, or increasing the length of contour, has no effect on the visual angle at which loss of colour occurs has been proved already by experiment (table 21, p. 543).

That colour near the centre of a test object is affected by loss of colour, just as is colour near the edge, was tested by preparing two test objects of the same dimensions, the centre of one and the edges of the other being tinted yellow with picric acid solution, in such a way that the coloured and colourless areas were equal in both objects. When these were placed on black backgrounds, they were found to lose colour at approximately the same visual angle.

No experimental evidence has therefore been found to support this hypothesis.

(76) *The diffused light hypothesis*

The scattering of light by fine airborne particles has been previously referred to (see § 30, p. 543). The question presents itself: To what extent does this phenomenon play a part in producing the colour losses now under consideration? One method of testing this point would be to interpose a long, evacuated tube between the test object and the eye of the observer, for this should eliminate the airborne particles. A glass tube, about 2 m. long, was connected to a vacuum pump, and the method tested. It was not found to be very satisfactory, because of reflexions at the glass-air surfaces. But, so far as could be seen, no alteration in colour loss was to be observed.

An alternative method was tested, namely, by using very small test objects, to reduce correspondingly the distance between test object and observer. With test objects about 1 mm. square, this distance was reduced to less than 1 m. But it was found that the losses of colour took place as before, without any apparent modification. In these tests the effects of scattered light were not eliminated entirely, but, if they played an important part, it is felt that some noticeable change would have been produced by the reduction of distance.

Two other possible effects of scattered light, which might have a modifying influence, were also investigated, namely, light spreading from the background on to the test object, owing to irradiation in the eye of the observer, and light scattered during transmission by the eye media. (Another form of irradiation will be considered in the next section.) The first possibility was investigated by mounting the test object in front of a dead-black background, which was produced by lining a large wooden box with black paper. The second was investigated by causing the observer to look down a long black tube, which completely screened the eye from all light except that coming from the test object and its background. Neither of these methods appeared to modify at all the losses of colour.

(77) *The irradiation hypothesis*

According to this hypothesis, the progressive losses of colour are caused by the encroachment of the background on to the test object, and vice versa, due to retinal irradiation or to some allied phenomenon. If this hypothesis were correct, it would be expected that test colours on a white background would lose colour, in the order of their own brightness, namely, yellow, green, orange, blue-green, red, blue and, lastly, violet. But the order found by experiment is: violet, blue, yellow, green, blue-green, red and orange. If a black background were in use, the order, according to this hypothesis, should be: violet, blue, red, blue-green, orange, green and, lastly, yellow. But, according to experiment, the order is: yellow, green, blue-green, violet, blue, red and orange. Thus with neither background is the order found, by experiment, the same as that required by the hypothesis.

On reduction of visual angle, certain colours are found to suffer an alteration of tint; thus yellow-green and green alter to pale blue-greens, while mauves, purples and crimson alter to shades of red and orange. The hypothesis is unable to offer any explanation of these colour variations.

When, with reduction of visual angle, a yellow test object has become white, the placing of a second test object of the same colour, shape and size, near the first, in the visual field, causes it to revert to yellow. The same test may be repeated with other colours. The hypothesis can offer no explanation of this experimental result.

Alternate yellow and black strips, and alternate blue and white strips, both retain their colours at smaller visual angles than do alternate yellow and blue strips of the same width and length. The hypothesis is unable to offer any explanation of this fact.

In several other ways this hypothesis fails to account for observed facts, and must therefore be abandoned.

(78) *The rod vision hypothesis*

It is well known that rod vision replaces cone vision at low intensities of illumination; according to this hypothesis this replacement is responsible for the losses of colour which are observed with reduction of visual angle. Four facts are at variance with this view:

(1) The fovea, which was exclusively used in these experiments, is usually accepted to be devoid of rods.

(2) Except for the experiments performed at low intensities of illumination, the observer's eye was fully light-adapted, which would automatically exclude the use of rod vision.

(3) This hypothesis offers no explanation of the changes of colour that are observed in the following cases: yellow-green to pale blue-green; green to blue-green; purple to brown; mauve to red-brown; crimson to orange.

(4) Wright found that the luminosity curve at a visual angle of 20 min. of arc was of substantially the same shape as that for ordinary large visual angles, except for a slight inflexion at 5800 A. If rod vision had, to an appreciable extent, replaced cone vision, it would be expected that the luminosity curve would have been noticeably shifted towards shorter wave-lengths, see figure 4, p. 652.

(5) Rod vision is usually associated with very poor acuity for detail. In these experiments normal detail perception was met with.

The conclusion is that this hypothesis is not supported by evidence.

(79) *The light-intensity hypothesis*

According to this hypothesis, the loss of colour is directly due to the decrease in light intensity reaching the retina from the object, as the visual angle is reduced. If such were the case we might expect loss of colour to take place first with colours of low-reflexion factor, as the visual angle is reduced. The order of colour loss would therefore be: blue, red, blue-green and yellow. But experiment shows that the order is: blue, yellow, blue-green and red. Yellow is definitely out of place. The order of disappearance of red and blue-green is variable.

One further point: it would be very difficult, on this hypothesis, to account for the changes in colour undergone by green, purple, mauve and crimson.

(80) *The neurological hypothesis*

If this nervous process conforms with others of a similar kind, there should be a stimulus and an end-organ on which it acts. From the end-organ, nerves should conduct impulses, via one or more synaptic relays, to the place where the response operates. The response should be of a specific nature of facilitation or inhibition.

In order to simplify the sections which follow, it is proposed to give a brief description of the responses, so far as they are known at present.

Evidence has been found for four nervous mechanisms: for red, for yellow, for blue-green and for blue. These usually act independently, but may act together. They operate locally in all parts of the fovea and parafovea. In normal vision they operate with extreme speed, but under experimental conditions they may be made to act slowly. Unlike electric switches, which in some ways they resemble, they can be partly 'on' and partly 'off'. These four mechanisms, and the alterations which each brings about, will now be described.

The 'red' mechanism controls the connexion between the long-wave receptors (*L.R.*) and the cranial centre for long-wave colour vision (*L.C.*). The 'blue-green' mechanism controls the connexion between the medium-wave receptors (*M.R.*) and the cranial centre for long-wave colours (*M.C.*). By means of these two mechanisms acting together, colourless vision is replaced by reduced colour vision.

The 'yellow' mechanism controls the connexion between the medium-wave receptors (*M.R.*) and the cranial centre for short-wave colour vision (*S.C.*).

The 'blue' mechanism controls the connexion between the short-wave receptors (*S.R.*) and the cranial centre for short-wave colour vision (*S.C.*).

According to the above scheme, there are five nervous connexions between photoreceptors and cranial centres:

(C. 1) The connexion between the long-wave receptors (*L.R.*) and their cranial centre (*L.C.*), which is controlled by the 'red' mechanism.

(C. 2) The connexion between the medium-wave receptors (*M.R.*) and the cranial centre for the long waves (*L.C.*), which is controlled by the 'blue-green' mechanism.

(C. 3) The connexion between the medium-wave receptors (*M.R.*) and their cranial centre (*M.C.*), which is always in operation.

(C. 4) The connexion between the medium-wave receptors (*M.R.*) and the cranial centre for the short waves (*S.C.*), which is controlled by the 'yellow' mechanism.

(C. 5) The connexion between the short-wave receptors (*S.R.*) and their cranial centre (*S.C.*), which is controlled by the 'blue' mechanism.

If the mechanisms acted singly, their effects would be as shown in table 60.

TABLE 60. MECHANISMS ACTING SINGLY

mechanism	C. 1 *L.R.* to *L.C.*	C. 2 *M.R.* to *L.C.*	C. 3 *M.R.* to *M.C.*	C. 4 *M.R.* to *S.C.*	C. 5 *S.R.* to *S.C.*
none	N	C	C	C	N
red	C	—	—	—	—
blue-green	—	N	—	—	—
yellow	—	—	—	N	—
blue	—	—	—	—	C

C = connexion; N = no connexion.

When these mechanisms act in sequence, their effects on vision are as summarized in table 61.

TABLE 61. MECHANISMS ACTING IN USUAL SEQUENCE

	C. 1 *L.R.* to *L.C.*	C. 2 *M.R.* to *L.C.*	C. 3 *M.R.* to *M.C.*	C. 4 *M.R.* to *S.C.*	C. 5 *S.R.* to *S.C.*
colourless foveal vision	N	C	C	C	N
'red' mechanism	C	C	C	C	N
'blue-green' mechanism	C	N	C	C	N
reduced colour vision at this stage					
'yellow' mechanism	C	N	C	N	N
'blue' mechanism	C	N	C	N	C
full colour vision at this stage					

It will be observed that the 'red' and 'blue-green' mechanisms, acting together, change colourless foveal vision to reduced (so-called 'dichromatic') colour vision. The 'yellow' and 'blue' mechanisms together alter the latter to full colour vision (see § 160, p. 663).

(81) *The evidence for four nervous mechanisms*

The supposition that there are four separate mechanisms rests on the following facts:

(1) The different colours lose colour at different visual angles; red and blue-green at small angles; yellow and blue at larger ones.

(2) The visual angles at which yellow, green and blue-green lose colour is practically independent of background brightness, whereas the visual angles at which violet, blue, red and orange lose colour are affected by alterations of background brightness.

(3) Five colours have been found to undergo alterations in tint: yellow-green, green, purple, mauve and crimson. The two former lose yellow and thus become shades of pale blue-greens. The three latter lose blue and thus become shades of red and orange. It would be impossible to account for these changes in colour if yellow and blue-green lost colour together, owing to the action of the same mechanism; or if blue, orange and red similarly lost colour owing to the action of the same mechanism.

(4) One colour, namely, green, differs from the rest in being but little affected by light intensity so far as loss of colour with reduction in visual angle is concerned.

It is on these grounds that four different mechanisms have been held to be present. The differences in the four mechanisms are summarized in table 62.

TABLE 62. DATA OF RESPONSE MECHANISMS

mechanism	visual angle	change of light intensity	change of back-ground brightness	spectral region affected	connexion or non-connexion
red	small	effective	effective	red end	C
blue-green	small	nil	nil	red end	N
yellow	large	effective	nil	blue end	N
blue	large	effective	effective	blue end	C

In the last column is given the effect of the mechanism on the nerve paths connecting photoreceptors and cranial centres for colour vision.

(82) *The resting condition*

It will have been observed that the assumption has been made that the four mechanisms are adjusted for the production of colourless vision, when the fovea is not being stimulated. But that when a stimulus falls on the latter, the mechanisms bring about either reduced or full colour vision, according to the visual angle, the intensity of the stimulus, and the colour of the stimulus.

Some evidence on this point is as follows. If by means of an iris diaphragm, or a Stubbs gauge, the visual angle of a coloured stimulus be progressively increased, then it is first seen as grey. As the visual angle is increased its colour begins to be seen. This suggests that the resting condition of the mechanisms is to produce colourless vision. The following experiment appears to support this conclusion. A small yellow test object was attached near the edge of a black disk of cardboard which was mounted on a turn-table which could be rotated by hand. The test object was at such a distance from the observer that when stationary it appeared to him to be white. The turn-table was now rotated about 1 rev./sec. and in consequence the image of the test object was spread into an arc by the persistence of vision. Observation showed that this image was yellow; but on stopping the rotation, it became white once more. The explanation seemed to be that when stationary the yellow test object subtends so small an angle that it is changed to white; but, on the other hand, when it is rotating and its image is spread out by the persistence of vision, thus causing its image to be at a sufficiently large visual angle for it to appear in its normal colour.

When the light was good a further point was noticed, on some but not on all occasions, namely, that the leading edge of the yellow arc appeared to be white. This could not be seen by everyone. If correct, this observation suggests that the resting condition of the retina is in adjustment for reduced colour vision, but that it rapidly changes over to full colour vision when large coloured areas are being looked at. Further evidence in support of this conclusion will be given later (see §§ 84 and 85).

(83) *The normal sequence of the four mechanisms*

Evidence has been produced in § 80 that, of the four separate mechanisms, two, namely, the blue and the yellow, are responsible for the first change, and that two, namely, the red and the blue-green, are jointly responsible for the second change. The question arises: Do these two members of each pair of mechanisms act together or separately? In order to obtain an answer to this question, the following experiments were performed.

Using white and mauve test objects, the sequence of events was determined, as illumination was increased from zero to full daylight, the eye being kept so far as possible light-adapted all the time, and the fovea alone being used for observation. These two precautions were taken in order to avoid effects due to rod vision. It had been anticipated, in view of Abney's statement: 'White light becomes greenish blue as it diminishes in intensity': that the white test object would appear as he suggests, with reduced illumination. However, it did not seem to do so; for the white test object appeared to have a faint brown colour, while the purple test object looked red-brown. The illumination was now gradually increased until it reached full daylight; during this change both test objects slowly regained their normal appearance. This discrepancy between the opinion of Abney and that of the author clearly called for further experimental tests.

The following arrangement was finally adopted. A shallow box was lined with black paper. On to the bottom of the box was dropped a disk of white cardboard. The lid of the box was replaced by another disk, cut from the same sheet of cardboard as the first disk; and in the centre of this was cut a hole roughly 1 cm. diameter. The inner disk was viewed through the square hole in the outer disk. The box was placed in the open air, on a day when the sky was overcast, about 0·5 m. from the observer. The illumination falling on the inside disk was varied by sliding the outside one so as to admit more or less daylight. In this manner adjustment could readily be made from black to white. This arrangement has two advantages: the eye remains light-adapted, and comparison can be made between the outer disk, which receives full daylight, and the inside disk, the lighting of which is reduced.

The results obtained were quite definite, for the inside disk looked brownish in colour, in comparison with the outside one. The brownness was not due to transmission of light through the outside disk, because placing sheets of black paper or tinfoil behind this disk did not cause any observable alteration in the result.

It seems clear from these experiments that, of the two mechanisms—the 'yellow' and the 'blue'—the former comes first into operation. As light increases in intensity from zero, the sequence of events appears to be as follows: first there is colourless foveal vision, due to the stimulation of the green receptors and their connexion with all the visual centres. This is followed by reduced colour vision, probably with primary colours of orange-red and blue-green. At greater intensities the yellow and yellow-green colours are added by the 'yellow' mechanism coming into operation, thus causing white to appear brownish in colour. At higher illuminations still, the 'blue' mechanism operates, causing the short-wave colours to be seen in their proper hues, thus restoring white to its normal appearance. In this manner full colour vision comes into being.

The above description is in agreement both with the experiments on increasing the visual angle, described in this paper, and with the graph published by Abney as the result of investigations on the photochromatic interval. For this shows that at first the spectrum is colourless. Then, as intensity is increased, reduced colour vision appears, with orange-red and blue-green components. At a somewhat higher intensity, yellow is added; and lastly, the blue and violet receive recognition.

(84) *The effects of brief exposure*

In order to obtain further evidence with regard to the resting state of the retina, the following experiments were performed.

The eye, having been kept in the dark for some minutes, was allowed, by means of a shutter, to view momentarily a small yellow test object on a black background. It was seen to be yellow. The test object was now placed on a white background, with the same result. A blue test object was now placed on the white background and viewed by short exposure, the result being blue. These results seemed to prove that the eye, in each of these cases, was in the condition of full-colour vision.

The experiment was now varied, by reducing the visual angle of the test objects, so that the yellow one appeared white, and the blue one black, by prolonged examination. They were then re-examined by brief exposure, and were seen to be white and black respectively, the conclusion being the precise opposite of the one arrived at above. Now, it is clear that the experiment must be in some way at fault for it to give contradictory results. The explanation would appear to be found in the persistence of vision, which may be described as follows: in the case of both large and small objects, their images appear to continue for a time after they have been removed either by means of a shutter, or by closing the eyes.

This continuation is called 'the persistence of vision'. To this phenomenon the success of the cinema is largely due. In consequence, the responses operate in the same way as they would have done when using ordinary continuous observation.

(85) *The time relations of the 'yellow' mechanism*

Several attempts were made to determine the time taken for the response to occur, but all of these failed, because it appeared to be instantaneous. For example, on suddenly substituting a small yellow test object for a larger one, the small test object appeared to become white immediately the substitution had taken place. Success was obtained, however, by using the following method.

Five small square openings, arranged in the form of a cross, were cut in a piece of black card. Behind the centre opening was fixed a yellow test object. Behind the other openings was arranged a sliding shutter which had two positions; in one position the openings disclosed white areas, whereas in the other position the openings disclosed yellow ones.

It has been shown previously (see § 24) that white does not affect this antichromatic response, whereas, on the contrary, yellow affects it strongly. On placing the observer at a suitable distance from the apparatus and moving the shutter, the test object is seen to change colour, being yellow when the yellow areas are disclosed to view, and changing to white when the yellow areas are replaced by the white ones. If the distance between the apparatus and the observer be reduced, and the test object in consequence made larger, there is an increase in the time required for the antichromatic response to take place. This is shown in table 63. The times were taken with an ordinary stop-watch.

TABLE 63. THE TIME RELATIONS OF THE YELLOW MECHANISM

distance in m.	time in sec.
3·0	change incomplete
3·5	12·1
4·0	6·4
4·5	3·6
5·0	2·0
5·5	0·8
6·0	very fast

Under experimental conditions it is possible to control the responses in such a way that they cause vision to change slowly either from trichromatic to monochromatic vision, to change in the reverse direction, or to remain poised at some stage in between the two. Under normal conditions of vision, on the contrary, they must operate with extreme rapidity, as fast in fact as sight itself.

If a grating test object be prepared, consisting of alternate parallel strips, 1 cm. wide, of plain yellow paper and newsprint, and if this be examined at a distance of about 2 m., the yellow strips appear a uniform yellow and the newsprint appears sharp and free from colour. Moving the gaze rapidly from point to point does not noticeably alter the conditions. Now, the recognition of yellow requires full trichromatic vision, whereas the elimination of colour from the print requires monochromatic vision. The change from one type of vision to the other takes place so rapidly that both types of vision retain their normal properties. In everyday life the same changes must be taking place all the time when we shift our gaze. Observation from a moving object, such as a train or motor car, must test the mechanism in a very crucial manner; but, so far as can be observed, it does not fail at any time, see p. 563.

(86) *The position of the response centres in the visual pathway*

Burch (1900) showed that the phenomena of simultaneous colour contrast occurred separately in respect of each eye. Having confirmed that grey on a red background would become coloured blue-green, that on a blue background it would appear yellow, and that on a purple background it would appear apple green, he used a simple stereoscope to present grey on a red background to one eye, and grey on a blue background to the other. The backgrounds combined to produce a purple, but the greys were not both apple green in consequence; on the contrary, they were different, being blue-green to one eye and yellow to the other, as was the case with monocular vision. Burch concluded, correctly, that each eye has its own centre for simultaneous colour contrast, and that these are situated at a point between the retinae and the centre in which binocular fusion of colours occurs.

The centres for the mechanisms of the antichromatic responses might therefore occupy one of three possible positions on the visual pathway:

(*a*) between the retina and its centre for simultaneous contrast;

(*b*) between the two simultaneous colour contrast centres and the centre for binocular colour fusion;

(*c*) above the latter.

If (*a*) is the case, it would be expected that actual colours would be affected by the antichromatic responses, but that the colours produced by simultaneous colour contrast would not.

If the centre, or centres, for the responses lay between the centres for contrast, but below those for binocular fusion, it would be anticipated that real colours and contrast colours would both be affected. On the other hand, the responses would act independently in the two eyes, just as Burch found the contrast centres to do.

Lastly, if the centre for the responses is above that for binocular fusion, both real and contrast colours will be affected by them, and the two eyes will act together, so far as the responses themselves are concerned. Table 64 summarizes the above point.

TABLE 64. PLAN OF VISUAL PATHWAYS

left retina		right retina
(*a*)		(*a*)
left contrast centre		right contrast centre
(*b*)		(*b*)
	binocular fusion centre	
	(*c*)	
	visual perception (in the brain)	

If at (*a*) real colours only are affected, and each eye is separately affected;

(*b*) real and contrast colours are affected, and each eye is separately affected;

(*c*) real and contrast colours are affected, and the two eyes are affected together.

The two crucial experiments to decide these points were performed as follows:

The first experiment. A neutral grey test object was placed on a bright blue background so that colour contrast would cause the test object to change colour to yellow. When this was seen to have occurred, the distance between the test object and the observer was increased, thus reducing the visual angle subtended by the test object. The test object was then seen to change from yellow to white, showing that a contrast colour was affected in the same way as a real colour.

The second experiment. A small yellow test object, placed on a black background, was viewed at such a distance that it changed from yellow to white. Near it, on the same background, was placed a larger yellow conditioning object, whereupon the small test object was seen to have reverted to yellow. The experiment was now varied by using a simple prism stereoscope: the test object, on its background, was viewed by one eye, while the larger yellow object, on its own black background, was viewed by the other eye. Suitable adjustments were made so that the test object and the larger object were seen to lie close together, side by side, in the binocular visual field. But the small test object remained white, apparently quite unaffected by the proximity of the larger yellow object.

Thus the two eyes must act independently. Since both real and contrast colours are affected, and since the responses in one eye are unaffected by conditions in the other, it is concluded that the response centres are situated at (*b*), that is, between the contrast centres and the binocular fusion centre.

(87) *The spectral composition of the stimuli*

It has been shown, in previous Parts, that certain factors, e.g. visual angle and light intensity, play an important part in determining whether there shall be full colour vision, reduced colour vision, or colourless foveal vision. Another factor of importance was found to be the proximity to the object under test of a second object of the same, or of a closely similar, colour. The following results, for a yellow test object on a black background, may be quoted, the distance being measured at which loss of colour took place.

TABLE 65. DIFFERENT CONDITIONING COLOURS

colour of additional object	distance (m.)
(no object)	3·5
red	3·5
orange	8·4
yellow	13·5
green	10·2
blue-green	8·5
blue	4·1
violet	3·7

Whereas red, blue and violet hardly affect the distance at which yellow suffers loss of colour, orange, yellow, green and blue-green do affect it.

Using the micro-stimulation apparatus described in Part X, the above test was repeated, using a monochromatic source as the additional object. Before beginning the determinations, the intensity and visual angle of the test source were adjusted until it was colourless.

It was found that if the monochromatic source was red, blue-green, blue or violet, then the yellow test source remained colourless. But that if the monochromatic source was orange, yellow or yellow-green, then the yellow source was seen in its true colour. The tests were performed by determining the long and the short wave-lengths at which the transition from yellow to colourless, and vice versa, took place. The results obtained are given in table 66. Series A and B were separated by an interval of about 3 hr. The end-points are not sharp, and the means of the two series differ somewhat. Both series agree, however, on the following points: the part of the spectrum above 6100 A in wave-length, that is, the whole of the red region, is without effect; the parts of the spectrum below 5600 A in wave-length, that is, the green, blue-green, blue and violet, are without effect. An attempt to determine the most effective wave-length in producing the colour change showed that it was 5850 A approximately. One curious effect was noticed while doing these tests: when the wave-length was 5700 A the test light was seen to be definitely more yellow than the monochromatic light, which by contrast appeared to be nearly white.

Table 66. Spectral response limits for yellow

	long wave-length		short wave-length	
	A	B	A	B
	5960	6145	5645	5655
	5985	6140	5665	5665
	6030	6085	5650	5670
	5935	6030	5690	5560
	6045	6060	5660	5540
mean	5991	6088	5662	5618
	6040		5635	

So far as the 'yellow' mechanism is concerned, the following conclusion appears to be justified: that the effective parts of the spectrum are the orange, yellow and yellow-green, with a maximum at, or near, 5850 A, and limits at 6088 and 5618 A. The values correspond, as well as can be expected, with Granit's data for the yellow modulator, which has a maximum sensitivity at 5800 A.

On the basis of Young's theory, according to which yellow is a mixture of red and green, both the latter should prove effective in the case of the 'yellow' mechanism. But it has been seen above that this is not the case.

It was now attempted to make similar determinations on the 'red', 'blue-green' and 'blue' mechanisms. The 'red' mechanism was affected by rays from about 6450 to 5880 A, the maximum being at, or near to, 6200 A. One unexpected effect was noticed: the spectrum became visible at 6800 A; as the wave-length was shortened it became brighter, and in doing so it appeared to have a depressing effect on the luminosity of the red test source. This continued until about 6550 A, when the maximum depression of the test source occurred. At 6450 A, enhancement of the luminosity of the test source began, and it continued until 5880 A, as stated above. With regard to the 'blue-green' mechanism, the longest wave-length at which enhancement took place was 5450 A. The maximum sensitivity was at about 5200 A. It was not possible to determine the short wave-length limit, because this was clearly being reduced in intensity by the action of the 'blue' mechanism, which, at the visual angle in use, terminated the spectrum at 4950 A. The 'blue' mechanism, for the same reason, could not be investigated at all by this technique.

The situation, so far as the four mechanisms of the antichromatic responses are concerned, may be summarized as follows: of the four mechanisms, the 'yellow' has proved the easiest to investigate. The receptors which bring it into operation appear to have a relatively sharp spectral sensitivity curve; this property will be referred to in Part XI, when considering the evidence in favour of the Wundt-Granit hypothesis.

In table 67 are summarized the data of the spectral regions which act as stimuli for the four mechanisms, so far as they are known at present.

TABLE 67. SPECTRAL RESPONSE LIMITS

	long-wave limit	maximum sensitivity	short-wave limit
red	6450	6200	5880
yellow	6088	5850	5618
blue-green	5450	5200	—
blue	—	—	—

(88) *Simultaneous contrast and the antichromatic responses*

In previous sections, the emphasis has been placed on the changes in colour brought about by the antichromatic responses. In this section it is proposed to deal shortly with their effects on intensity. When white is substituted for yellow, there is not only a change in tint but a gain in intensity as well. On the contrary, when blue is replaced by dark grey or black there is a fall in intensity. Now these changes of brightness have long been recognized, and are usually described as the effects of simultaneous contrast (or spatial induction) (Parsons 1915). The idea is suggested either that the antichromatic responses and simultaneous contrast are allied phenomena, or that the effects which have been described by previous workers as being due to simultaneous contrast, should now be ascribed to the antichromatic responses.

(89) *The advantages of retaining blue-green for vision instead of red*

When the yellow and blue fringes have been eliminated, there are left the secondary colours, the red-orange and blue-green. These also produce fringes, because they are not both brought to the same focus. Thus, if the red rays were sharply in focus, the blue-green ones would form out-of-focus fringes, and vice versa. Now, it is not necessary to eliminate both red rays and blue-green ones at the same time, in order to remove the fringes; it is sufficient to remove one of them. Suppose a choice could be made: which would be preferable, to remove the red rays and employ the blue-green ones, or vice versa?

The blue-green rays have three advantages over the red ones: their intensity is greater; their shorter wave-length gives them greater resolving power; lastly, they approximate more closely in wave-length to the rays used in twilight vision, and therefore may be focused at the same time as the latter. For these reasons it would be preferable to suppress the red rays rather than the blue-green ones. It has been seen above that it is the red rays which are suppressed in the case of the human eye.

This important matter may be considered in a somewhat different way. White light may be thought of as consisting of three groups of rays: long wave, medium wave and short wave. The medium rays of high intensity, namely, yellow, green and blue-green, are those which form sharply focused images on the retina. The long and the short rays, red and blue, are of low intensity and they form unfocused images on the retina, which in consequence tend to spoil definition. By means of two nervous mechanisms these rays are intercepted, so that their perception is prevented. At the same time two other mechanisms link the green retinal receptors, which are viewing the sharply focused images, with the brain centres for red and blue. In consequence, not only is loss of light avoided, but also the greenish tint which would otherwise be present is removed from vision, and hence white objects are seen as white.

(90) *The coloured lights used for signalling purposes*

There is an important difference between the conditions of the experiments described here, in which daylight was used for illuminating not only the test object but the laboratory in which it was situated, and those of appreciating the colours of signals seen at night against an unilluminated, or a partially illuminated, background. There is a further difference, namely, that during these tests the eye was kept in a fully light-adapted state, whereas at night it would be partially, if not completely, dark-adapted.

Two factors are found, both in these experiments and in the recognition of coloured signals at night, namely, that coloured test objects to be identified subtend small visual angles at the eye, and that colour photoreceptors—that is cones—are used for making the judgement.

On comparing the results of these tests, and the recommendations made by Holmes on the use of coloured signals, there is good agreement as to the colours which are easily recognized and those which are not easily recognized under these two different sets of conditions.

Holmes concluded that colours which are easily identified are red and green. But the latter should not be used if blue is employed at the same time. If blue is selected in preference to green, it should be bright and fully saturated. Yellow or white form possible third colours, but should never be used together in the same signalling system.

The micro-stimulation apparatus was used to imitate a signal light as seen at a great distance. For these tests, other light sources were excluded from the laboratory, and the observer's eyes were allowed to become dark-adapted. Two series of tests were performed: (*a*) with monochromatic lights, (*b*) with colour filters. The results with monochromatic lights are given in table 68. Those with colour filters in table 69.

TABLE 68. THE RESPONSES OF A NORMAL SUBJECT

A units	10 cone units	1·0 cone unit	0·5 cone unit	0·2 cone unit
7800	red	—	—	—
7600	red	—	—	—
7400	red	faint brown	faint brown	—
7200	red	amber	dark brown	faint brown
7000	red	dark red	red-brown	faint brown
6800	red	dark red	dark red	dark brown
6600	red	red	red	brown
6400	orange-red	red	orange-red	orange-brown
6200	orange	orange	orange	pale orange
6000	orange	pale orange	pale orange	pale orange
5800	yellow	white	white	white
5600	yellow-green	pale green	pale blue-green	pale blue-green
5400	green	blue-green	blue-green	grey-blue-green
5200	green	blue-green	dark blue-green	grey
5000	blue-green	dark blue-green	dark blue-green	very dark grey
4800	blue-green	dark blue-green	dark blue-green	—
4600	blue	faint blue-green	dark grey	—
4400	indigo	faint blue-green	—	—
4200	violet	dark grey	—	—
4000	violet	—	—	—

The results of these tests confirm what has previously been stated (see § 23, p. 539), with regard to the changes which colours undergo with reduction of visual angle. So far as signal lights are concerned, current practice requires no modification.

TABLE 69. THE RESPONSES OF A NORMAL SUBJECT

colour	10 cone units	1 cone unit	0·2 cone unit
red	red	brown	—
orange	orange	orange	faint brown
yellow	yellow	white	white
yellow-green	yellow-green	pale blue-green	white
green	green	pale blue-green	grey
blue-green	blue-green	blue-green	grey
blue	blue	—	—
violet	violet	—	—

(91) *A subject with defective responses*

During the examination of a suspected case of colour-blindness, the subject was tested with objects at small visual angles. The illumination was daylight, and the retina was fully light-adapted. All the test objects were 12 mm. square. Tests were done on both white and black backgrounds; there was no substantial difference in the results, and only the former are reported here (table 70).

TABLE 70. A SUBJECT WITH DEFECTIVE RESPONSES

colour of test object	30 cone units	12 cone units	6 cone units	2·5 cone units
red	red	red	brown	grey
orange	orange	light red	yellow	brown
yellow	yellow	yellow	white	white
yellow-green	yellow-green	light green	greenish grey	light blue
green	green	blue-green	blue-green	blue
blue-green	blue-green	blue-green	blue	blue
blue	blue	blue	blue	blue
violet	violet	violet	blue	blue
purple	purple	violet	blue	blue

On examining the results given by the subject, it will be seen that no mistakes at all are made in colour recognition at a visual angle of 30 cone units. At 12 cone units, the reports might have been those of a person with normal colour vision. At 6 cone units, blue still retains its colour, while red and orange have largely lost their colour; both these effects are unusual. With normal-sighted persons, blue would have been replaced by black, while red and orange would have been unchanged. The replacement of yellow by white is, of course, quite normal. At 2·5 cone units, colours have become largely monochromatic, except for blue, which continues to retain its colour in a very unusual manner. The fact that this observer is normal-sighted at large visual angles suggests that his photoreceptors are normal, and that therefore he is not at all colour-defective in the ordinary sense. Like normal-sighted persons, his colour vision deteriorates with decrease in visual angle, but in an unusual way. The changes observed could be accounted for by supposing the subject to possess abnormal red and blue response mechanisms: a 'red' mechanism which changes at too large a visual angle, and a 'blue' mechanism which changes at an angle which is too small. It is not easy to explain these deviations from the normal in any other way.

VII. THE CHROMATIC DIFFERENCE OF MAGNIFICATION

As light passes through the eye media it suffers prismatic, as well as lenticular, dispersion. The former is responsible for chromatic difference of magnification. Two methods have been employed for measuring its amount; and a method is described of correcting it. After such a correction has been applied, there is a small but quite noticeable improvement in visual acuity.

(92) *The dispersion of the eye media*

It is well known that light rays suffer two different kinds of dispersion as they are penetrating, and are refracted by, the media of the eye, namely, lenticular dispersion and prismatic dispersion. The former causes the chromatic difference of focus which has been considered in Part V. The latter causes chromatic difference of magnification, which is to be considered now.

The correction of the chromatic difference of focus of the eye has been attempted by Helmholtz, Javal and other more recent experimenters, with surprisingly little improvement in visual acuity. The correction of chromatic difference of magnification may not be found to have a more beneficial effect. There was a further object in view in measuring and correcting this aberration. It was proposed, by means of the micro-stimulation apparatus described in Part X, to attempt to produce on the retina, points of light so sharp that they would stimulate effectively no more than one foveal cone. For such an attempt to succeed, it would be necessary to study, and if possible to correct, all disturbances of the wave fronts which are converging on to the chosen retinal point. When a monochromatic light source is in use, the correction of chromatic difference of magnification is superfluous; but when the light is not monochromatic, for example, ordinary white light, the correction of this aberration would appear to be important, for in its absence a spectrum, and not a point of light, would be formed on the retina. The production of this spectrum may be explained as follows. If the rays of light which reach the retina traverse each of the surfaces of the eye media, normal to those surfaces, then they will suffer neither refraction nor dispersion, and all of them, irrespective of wave-length, will arrive at the same point of the retina. But the centres of the curves of the surfaces of the eye media do not all lie on the same straight line, neither does the line which most closely intersects these points—the 'optical axis'—meet the retina at the fovea in most normal human subjects. In the majority of the latter the fovea is on the temporal side of the 'axial point', the point at which the optical axis meets the retina. Not only does the distance between the fovea and the axial point vary in different human subjects, but the fovea may be at a higher or lower horizontal level than the axial point; when that is the case, the spectrum produced by chromatic difference of magnification will be at a corresponding angle with the horizontal. This matter will be referred to again later.

(93) *The angle alpha*

The fixation axis, that is, the line passing from the posterior nodal point to the centre of the fovea, makes an angle with the optical axis which is called 'the angle alpha'. Tscherning determined the value of this angle by means of a special telescope fitted with a double-image prism, by observing the reflexions which took place at the surfaces bounding the three principal eye media: (*a*) the anterior surface of the cornea, (*b*) the anterior surface of the crystalline lens, and (*c*) the posterior surface of the crystalline lens. When the gaze of the subject under test was so directed that the reflected images appeared to be in line, as seen through the telescope, then the angle between the long axis of the telescope and the line of fixation was carefully measured. This is the angle alpha.

At the same time that the angle alpha is determined as described above, the precise direction of the gaze is also noted, that is, the angle which the fixation axis makes with the horizontal.

These two angles, the angle alpha and the angle of fixation, enable us to determine the exact position of the axial point in respect of the fixation point, as they would appear projected into the field of vision in front of the observer. In order to calculate their positions on the retina, it would be necessary to know also the posterior nodal distance of the observer; failing that, the use of cone units is indicated.

(94) *The eccentric position of the pupil*

There are two different ways of considering the effects of the angle alpha on the course of rays of different wave-length through the eye: (*a*) Einthoven's basis: the eccentric position of the pupil in respect of the fixation axis; (*b*) the author's basis: the dispersion of rays at the surface of the cornea.

According to Einthoven, the eccentricity of the fovea in respect of the axial point causes the ray, which passes from that structure to the posterior nodal point, to continue from the anterior nodal point eccentrically through the pupil. Suppose the distance from the centre of the fovea to the axial point to be 1 mm., the distance from the retina to the posterior nodal point to be 16·8 mm., the distance between the nodal points to be 0·3 mm., and, lastly, the distance from the anterior nodal point to the plane of the iris to be 2·7 mm., then the eccentricity of the fixation axis at the plane of the iris will be $2{\cdot}7/17{\cdot}1 = 0{\cdot}016$ mm. If the focal points for the ends of the spectrum be 0·6 mm. apart (see § 6, p. 527), their eccentricity will be $0{\cdot}016 \times 0{\cdot}6/19{\cdot}7 = 0{\cdot}0049$ mm. For the C and F lines, for which the focal points differ in position by 0·29, the value for the eccentricity of the pupil would be 0·0025.

(95) *The dispersion of rays at the cornea*

From a knowledge of the angle alpha, and of the mean refractive index and the dispersion of the eye media, it is possible to calculate, for any two spectral rays, the angle which they will make with one another during their passage through the eye to come to a focus on the retina. Suppose, for example, that the two spectral rays are the C and F standard lines, and that the mean optical constants of the eye media are the same as those of water at 20° C, then the refractive indices are as given in table 71:

TABLE 71. THE REFRACTIVE INDICES OF WATER AT 20° C

r	1·3308	*F*	1·3371
C	1·3311	*G*	1·3406
D	1·3330	*v*	1·3428
E	1·3352		

Assuming, as before, that the distance between the foveal centre and the axial point is 1 mm., then the distances between the points at which rays corresponding to the C and F lines strike the retina are given by the formula $(R^{\mathrm{F}} - R^{\mathrm{C}})/R^{\mathrm{D}}$, where R^{F}, R^{C} and R^{D} are the refractive indices for the F, C and D lines respectively given in the table above. Then the distances between the points $=(1\cdot3371-1\cdot331\,\mathrm{D})/1\cdot3330=0\cdot0045$ mm. If, instead of taking the C and F lines, we take the *r* and *v* lines, near the ends of the spectrum, the above formula gives 0·0090 mm., which is about double that given by Einthoven's basis.

Gullstrand, who calculated the distance between the focusing points of the rays corresponding to the ends of the spectrum, gave the value of 0·03 mm. at a distance of 1 mm. from the axial point. It is not known how this value was obtained. These different values are compared in table 72. In every case 1 mm. on the retina is held to be equal to 297 cone units, the value obtained from Goldmann & Hagen's measurement of the posterior nodal distance, namely, 16·81 mm.

TABLE 72. THE DISPERSION OF THE EYE MEDIA

		dispersion			
		C to *F*		*r* to *v*	
angle alpha	author	mm.	cone units	mm.	cone units
1 mm. on retina 3·4 degrees 204 minutes of arc 297 cone units	Gullstrand	0·016	4·77	0·030	8·94
	Einthoven	0·0025	0·75	0·0049	1·46
	Hartridge	0·0045	1·46	0·0090	2·68

(96) *The measurement of the dispersion*

An attempt was made to put this matter to a practical test, using the micro-stimulation apparatus described in Part X. Two sources were used, a red and a blue. The former consisted of an electric light and colour filter; the latter was provided by a Hilger constant deviation spectro-illuminator. Unfortunately, two such instruments were not available. Owing to the chromatic difference of focus of the eye, it was not possible to focus simultaneously these two sources of different wave-length on the retina. By choosing a suitable correcting lens, a compromise was found at which both sources appeared to be about equally sharp.

The two sources were adjusted so that they appeared to be vertically in line with one another to the observer looking directly through the instrument. For this to be the case, the red source had to be to the left of the blue one. This point will be understood after reference to § 103 which follows.

The gaze was now directed a few centimetres, first to the right and then to the left, and the alinement of the sources carefully examined. It was found that no relative movement could be detected with certainty, because definition deteriorated as soon as the image left the foveal centre. It might be anticipated that the definition would actually improve as the image of the source was caused to approach the optic axis of the eye, but no such improvement could be detected. It is proposed to investigate this matter later.

In spite of the poor definition away from the point of fixation, the conclusion reached is that, while dispersion undoubtedly exists at the foveal centre, it undergoes little alteration at points a short distance from that centre.

(97) *Chromatic difference of magnification*

It has been seen that short spectra are produced by white light on the retina, instead of superimposed images, owing to dispersion in the eye media. No spectra are to be found at the axial point, but the farther the image is formed from this point, the longer do the spectra become. The long axes of these spectra always go through the fixation point, and their short wave-length ends are always nearer to this point than their long wave-length ends. These spectra are responsible for chromatic difference of magnification. The use of this term will be more clearly understood if it be supposed that the object in the visual field of the observer is a circular one, and that his gaze is fixed at its centre. The rays from every part of the circle will be deviated during transmission through the eye media, the blue rays suffering more deviation than the red rays. In consequence, the blue circle will appear to be smaller than the red one, while the green circle will lie between them.

The actual value of chromatic difference of focus at any point of the retina depends on the distance of that point from the axial point and the magnitude of the dispersion suffered by the light rays during their passage through the eye media. In practice, for an object of finite size, the value is found to be a percentage of its linear dimensions. The value of the percentage depends on wave-length of the rays which are forming the images of the objects. In table 73 are given the percentages at different wave-lengths, calculated on the bases adopted by Gullstrand, Einthoven and the author. Thus, according to the latter, the chromatic difference of magnification for rays corresponding to the ends of the spectrum probably has a value of about 0·5 %. It is stated by Tscherning that the angle alpha has, in most subjects, a value of 5 to 7°. If Goldmann & Hagen's value for the posterior nodal distance, of 16·81 mm. is adopted, this is found to correspond to a distance between the foveal centre and the axial point of between 1·5 and 2·1 mm., assuming the author's value for the chromatic difference of magnification to be correct.

TABLE 73. CHROMATIC DIFFERENCE OF MAGNIFICATION

	6500 to 4000 A %	6000 to 4500 A %
Gullstrand	3·00	1·60
Einthoven	0·49	0·25
Hartridge	0·90	0·45

(98) *Chromatic stereoscopy*

If in one or both eyes of an observer there is dispersion of the spectral colours, the phenomenon called 'chromatic stereoscopy' may show itself. Two necessary conditions for this to occur are that the observer should have good visual acuity, and stereoscopic vision. But further, if the rays of long wave-length are caused to fall on corresponding retinal points, those of short wave-length must not do so, and vice versa. With regard to the latter, chromatic stereoscopy will be met with if (*a*) the retinal images produced by long wave-length colours are to the nasal side of those produced by short wave-length colours, in both eyes; (*b*) as in (*a*) but to the temporal side, in both eyes; (*c*) they are more to the nasal side in one eye than they are to the temporal side in the other eye. Thus, if they are moved to the nasal side in one eye and to the temporal side in the other eye, by equal amounts, no stereoscopy due to this cause will show itself.

Chromatic stereoscopy, caused as described above, is of two kinds, positive and negative. It is positive when the observer sees a blue object, which is at the same distance from him, and is on the same black background, as a red object, appear as if it were at a greater distance. It is negative when the blue object appears to lie in front of the red. These differences in apparent position may be explained as follows. In ordinary stereoscopic vision a near object produces images on the retina, which are to the temporal side of the images of distant objects to the left eye, and are also to the temporal side to the right eye. If, then, the points on the retina occupied by those images be connected by lines to the posterior nodal points, and if those lines be continued from the anterior nodal points, the lines corresponding to near objects will meet at points which are closer to the eyes than are the lines corresponding to distant points. Applying this test to chromatic stereoscopy, if lines drawn through retinal points on which blue rays fall meet behind those drawn through points on which red rays fall, there is positive chromatic stereoscopy. If, on the contrary, they meet in front, there is negative chromatic stereoscopy. But if they meet in the same place, then this phenomenon is not present.

(99) *The effect of the decentration of the pupils*

The positions which the pupils occupy in respect of the visual axes of the two eyes play an important part in determining the amount of chromatic stereoscopy. This may be proved by the following tests. On screening the nasal halves of both pupils, a production of positive stereoscopy is found by most observers by blue appearing to be more distant than red; on screening the temporal halves, the opposite is found to be the case. The explanation is as follows. On screening part of a pupil, the light rays which are limited to the other half, suffer refraction by the eye media towards the screened side. In consequence, since blue rays are more refracted than red rays, these will meet the retina at a point which is on the screen side of the point occupied by the red rays. Thus if the screen is on the nasal side in both eyes, the blue image will be situated on the nasal side of the red one on both retinae. In consequence, lines through the nodal points from the blue retinal images will meet behind lines through the nodal points from the red retinal images.

To summarize: screening the nasal halves of both pupils normally causes positive chromatic stereoscopy, while screening the temporal halves causes the negative variety.

(100) *The effect of colour on chromatic stereoscopy*

An explanation of the stereoscopy of coloured objects on black backgrounds, which has been given in the previous section, also applies to coloured objects on white backgrounds, with suitable modifications. On black backgrounds the order of the colours is red, orange, yellow, green, etc., as in the spectrum. On white backgrounds the order is quite different, namely, blue-green, greenish blue, blue, purple, red, orange and yellow. Thus an observer who had positive colour stereoscopy would see blue-green in front of red, and both in front of yellow. The explanation of this change in order will be readily understood by taking an example: if to red on a black background be added blue-green in suitable equal amounts, then red becomes white, and black becomes blue-green.

TABLE 74. CHROMATIC STEREOSCOPY

background	nearer	farther
red	black	white
orange	black	white
yellow	black	white
green	white	black
blue-green	white	black
blue	white	black

It will now be seen why white appears to be nearer than black, when both are situated on a blue-green background. This and other pairs of black and white objects on coloured grounds are given in table 74. In the author's opinion, the stereoscopic effect is more striking in the case of red and blue-green backgrounds than it is with the other backgrounds mentioned.

(101) *The effects of chromatic difference of magnification on vision*

Two visual phenomena are affected: (*a*) stereoscopic vision, and (*b*) acuity for fine detail. With regard to the former, subjects in whom there is positive chromatic stereoscopy owing to the optical axes being to the nasal side of the visual axes in one or both eyes—and, according to Tscherning, this is usually the case—see what artists refer to as advancing and retiring colours: warm colours, such as red, orange and brown, advance, while the cold colours, blue-green, blue and violet, retire. These facts skilfully used may be very effective in paintings. The value of this form of stereoscopy lies in the fact that it operates for objects of all sizes and for objects at all distances from the observer. Normal stereoscopic vision—increasingly effective the nearer the object to the observer—fails at great distances, owing to the smallness of the range base provided by the interocular distance. Not so chromatic stereoscopy, which therefore becomes relatively more valuable the farther the objects are away. There is, however, this important distinction, that normal stereoscopic vision operates independently of colour, and therefore for black and white objects, while colour stereoscopy—as its name implies—is valueless for colourless objects. (*b*) Its effects on visual acuity are due to the displacement of the aberration disks of different wave-length, relative to one another. At the optical axis the disks will be superposed so that their centres coincide. Away from the optical axis their centres will be displaced sideways, short wave-length disks being nearer the axial point than long wave-length ones. As the distance from the axial point increases, a stage is reached at which the relative displacement of the disks has attained such a value that the disks do not overlap at all. The retinal image now has the shape of a figure '8', one loop being caused by long wave-length colours and the other loop by short wave-length colours, the medium wave-length colours occurring at the junction of the two loops. The point at which overlap of the disks ceases depends on the aperture of the pupil; the smaller the pupil, the nearer to the optical axis does overlap cease.

Calculation shows that the side-shift of the disks has an important effect on the distribution of light in the retinal image. If the image at the axial point be taken as standard, there is an improvement of definition of 20 to 30 % in the images produced a little way away from this point. When, however, the critical point is reached, at which overlap ceases, there is a sudden deterioration of definition down to half, or even less than half, that found at the axial point.

This matter will be referred to again in § 105, p. 595.

(102) *The stereoscopic method of measuring dispersion*

Two methods have been devised by the author for determining the amount of chromatic dispersion at the foveal centre: (*a*) by chromatic stereoscopy, (*b*) by direct measurement. The first method has two disadvantages, namely, that the two eyes have to be measured simultaneously, and it has to be assumed that they have the same chromatic dispersion, and that the method only gives a measure of the dispersion in horizontal axes, and gives no information about the dispersion in vertical axes. The second method has neither of these disadvantages, but requires the use of special apparatus.

The first method was performed as follows. Some red and some blue patterns were placed near to one another on a black background, and were examined by daylight at a distance of about 4 m. from the observer. Two biconvex crown-glass lenses of 0·88 D focal length were placed one before each eye, care being taken to look through the centres of the lenses. The result was that the observer saw the blue patterns apparently farther away than the red ones, therefore positive chromatic stereoscopy was present. The two lenses were then decentred by equal amounts in a temporal direction—that is, away from one another—until the stereoscopic effect had all disappeared. The precise amount of decentration required to cause this disappearance was difficult to determine, but it appeared to be between 15 and 20 mm. Assuming the exact amount to be 17·5 mm., and the correction required by both eyes to be the same, then the dispersion produced by the eye media is equal in value, but opposite in sign, to that produced by a decentred lens of 0·88 D. Now the refractive indices of this lens, for rays of different wave-length, were not known. Suppose they were those of a typical crown-glass given in table 75. Then the dispersion for a refraction of 17·5 mm. would be equal to

$$17{\cdot}5 \times (RF - RC)/RD = 17{\cdot}5 \times 0{\cdot}0085/1{\cdot}5170 = 0{\cdot}0982 \text{ mm.}$$

This is, then, the amount of the dispersion at a distance of 1/0·88 = 1·136 m. At a distance of 4 m. the dispersion would be 0·0982 × 4/1·136 = 0·346 mm. This corresponds to 0·85 cone unit, and is for the C and G lines. For the *r* and *v* lines near the ends of the spectrum, it would be about double the above, namely, 1·70 cone units. Thus the lateral dispersion at the fovea is not as large as 2 cone units, yet it is sufficient to produce well-marked chromatic stereoscopy.

TABLE 75. THE REFRACTIVE INDICES OF CROWN-GLASS

standard lines	wave-length (A)	refractive indices
C	6563	1·5145
D	5893	1·5170
F	4861	1·5230

(103) *The triple-source method of measuring dispersion*

At first a single red source, but later two red sources, were attached to the slide rest of the micro-stimulation apparatus described in Part X, so that they could be adjusted either horizontally or vertically in position. At the same time a stationary source of short wave-length monochromatic light was produced by a Hilger constant deviation spectro-illuminator.

The two red sources—which were electric lamps fitted with colour filters—were vertically in line with one another, with the short wave-length source about midway between them. It would have been far better for all three sources to have been monochromatic, but this was impossible owing to lack of suitable apparatus.

Reduced images of these sources being presented, by means of the micro-stimulation apparatus, to the eye of the observer, the red sources were adjusted in position by rotating the screw of the slide rest until all three sources appeared to be vertically in line with one another. The positions of the sources on the plotting board of the apparatus were now recorded, and the adjustment repeated. The results of five settings are given in table 76. The settings are difficult to make, and are not very consistent, but this is explained by the small amount of dispersion which is being measured, namely, less than 1 cone unit. The dispersion of water is 0·0035, for rays of the same wave-length as those used in the above experiment. That for the C and F lines is 0·0060.

TABLE 76. THE MEASUREMENT OF THE DISPERSION OF THE EYE

	cone units displacement	
red: about 6250A	0·40	(red source to left
	0·60	of green source
and	0·60	in visual field)
	0·45	
green: 5400A	0·35	
	Mean 0·48	

If the dispersion at the fovea be increased in the ratios of the dispersions for water just given, the value for the C and F lines obtained is approximately 0·82, and for the *r* and *v* lines 1·65 cone units. These values compare favourably with those obtained by the method of chromatic stereoscopy described in the previous section, namely, 0·85 and 1·70 cone units, respectively.

Later, the method described in this section was repeated, using wave-lengths as near as possible to those of the C and F lines, when a value of 0·81 was obtained.

The method was now used for determining the vertical dispersion at the fovea. It was found in this case that the red sources had to be 0·7 cone unit below the green source, in order that the three sources should appear to the observer to be horizontally in line.

The total dispersion at the fovea for 6250A and 5400A is therefore equal to two components, red being 0·5 cone unit to the left of and 0·7 cone unit below the green. This gives a total dispersion of 0·86 cone unit at an angle with the horizontal of about 54°. For the C and F lines the total dispersion would be about 1·5 cone units, and for the *r* and *v* about 3·0 cone units.

In order that red and blue images should be superposed at the fovea, a red would have to be placed below and to the left of a blue one by the amounts just stated. When a white light source is in use, its image on the fovea will consist of a spectrum sloping upwards and to the right, at an angle with the horizontal of 54°, the length of the spectrum being about 3 cone units and its short wave-length end being at the top. But the long axis of this spectrum passes through the axial point, and its blue end is nearer to that point than its red end, in consequence the foveal centre must be below and to the left of the axial point. This conclusion agrees with that of Tscherning.

From the length of the spectrum at the fovea, some idea can be gained of the distance of the fixation point from the axial point. Thus, suppose the author's estimate for the amount of dispersion given in § 6 to be correct, a length of spectrum of 3 cone units would be produced by refraction of about 270 cone units. This would correspond to a distance from fixation point to axial point of 0·9 mm., and an angle alpha of about 3°. On Einthoven's basis this angle would be about half, and on Gullstrand's basis it would be about double, the above value.

(104) *The correction of chromatic dispersion*

It is well known that a prism may be used to re-form white light out of a spectrum, in the same way that it may be used to produce a spectrum from white light. This principle can be applied for the correction of the chromatic aberration of the eye. Since, in most subjects, the spectra produced on the fovea resemble those which would be produced by a weak prism with its base towards the nose, so in most subjects the spectra may be caused to recombine to form white light; that is, the dispersion may be corrected, by placing in front of the eye a weak prism with its base away from the nose. A subject who requires a lens to correct his refraction may find that decentring that lens corrects the dispersion at the same time. If he possesses positive chromatic stereoscopy, a convex lens would have to be decentred away from the nose, while a concave lens would have to be decentred towards the nose. If, on the other hand, he has negative chromatic stereoscopy, the decentration should be the reverse of that just given. For emmetropic, or near emmetropic, vision, requiring no lens, or a very weak one, the required prism effect may be obtained by placing a concave lens of suitable power, say 2D, carefully centred, in front of the eye, and then placing in position as well a decentred convex lens of the same power. Such decentred lenses provide prisms of small angle, which are sometimes difficult to obtain.

The prism, or the decentred lens, required to correct a given case, can be ascertained in two ways: by determining the correction by trial and error; or by calculating the correction which is required, from previous measurements of the dispersion. Both methods have been tested by the author.

The trial-and-error method consists in placing prisms or decentred lenses in front of the eye, in turn, until the one is found which gives the best correction. Two test objects were employed: one was composed of a brilliant purple cross; the other, of a red cross with a blue centre. The first test consisted in finding a prism or lens which would cause the red and blue images to be symmetrical to one another; the second test, in finding a correction which would cause the blue centre to appear to be central with the arms of the red cross. On the whole, the second method was found to be the better.

The calculation method was performed as follows. A convex crown-glass lens of 1·25D was first decentred 15 mm. to right, and then to left; in each case the observer, looking through this decentred lens into the micro-stimulation apparatus, adjusted the red and blue-green sources to be in line, as he had done previously. When the lens was decentred to the right, the red sources had to be adjusted to a position to the right of the blue-green one, and vice versa, as shown in table 77.

TABLE 77. THE MEASUREMENT OF THE DISPERSION OF A CROWN-GLASS LENS

	lens decentred 15 mm. to right red source to right of blue-green by (cone units)	lens decentred 15 mm. to left red source to left of blue-green by (cone units)
	1·40	0·40
	1·45	0·40
	1·45	0·65
	1·40	0·25
	1·45	0·45
mean	1·43	0·43

The total displacement of the sources was $1{\cdot}43+0{\cdot}43=1{\cdot}86$ cone units, for a total decentration of 30 mm.

It has been shown in the previous section, that the dispersion of the eye was 0·48 cone unit horizontally, and 0·70 cone unit vertically. The decentration required to correct these dispersions was found to be $30\times 0{\cdot}48/1{\cdot}86=7{\cdot}8$ mm. horizontally, and

$$30\times 0{\cdot}70/1{\cdot}86=11{\cdot}3 \text{ mm.}$$

vertically. This decentred lens was adopted as standard when using the micro-stimulator described in Part X.

(105) *The effects on vision of correcting the chromatic dispersion*

Without any spectacles, there was a just noticeable difference in colour at the edges, on either side of a black bar seen against a sky background. This colour difference disappeared on correcting the chromatic dispersion of the eye by means of two lenses of 2D, one convex and the other concave, suitably decentred.

The effects on visual acuity, using test-type, were just noticeable. Without correction of the dispersion, all the characters excepting two ('*H*' and '*N*'), of the 5 m. line of Hay's test type could be read at 10 m.; but none of the 4 m. line. With correction of the dispersion, all the 5 m. line could be read correctly, and half the 4 m. line. The letters in the latter line were at a visual angle of 2·75 cone units. If the correction was reversed, colour fringes became very obvious; there seemed to be a curious kind of astigmatism present, and there was difficulty in reading any of the characters in the 5 m. line, at a distance of 10 m.

The chromatic dispersion in the author's eye appears to be about half that in the average eye. If, then, an average eye, with otherwise good acuity, were corrected for chromatic dispersion, it would be expected that a material improvement of vision would result. This correction has been used for all work with the micro-stimulation apparatus described in Part X, where good acuity was required. Correction was particularly important during the investigation of the colour properties of the foveal receptors, described in Part XI, because the lateral displacement, in respect of one another, of rays of different wave-length, might cause one particular point of the retina to appear to possess receptors of several different kinds, whereas another point nearby, for the same reason, might appear to be devoid altogether of photoreceptors.

VIII. THE ACUITY OF THE EYE, USING LIGHTS OF DIFFERENT COLOUR

The visual acuity for fine detail is found to vary but little, when lights of different colour are used. In every case acuity is so high that it can only be accounted for by supposing that the retinal receptors, for each of the colours that was used, are as close together as possible. These observations led to the advancement of the cluster hypothesis, which is described in the following Part.

(106) *The results obtained by previous observers*

Measurements of visual acuity have been made, for many years, in order to determine the resolving power of the lens system of the human eye. The results of such measurements have also been compared with those to be expected from the diameters of the foveal receptors. So far as is known, they have not been used in an attempt to elucidate the precise arrangement of the receptors in the fovea.

Many previous workers have determined the visual acuity of the human eye for lights of different colour. One of the earliest was König (1903). He used an artificial source of white light, and red, green and blue filters, in order to produce the coloured lights, but he did not adjust the intensities of these lights so that they appeared of equal brightness to the eye. He obtained about equal acuities for white, red and green lights, but reduced acuity, of about one-half, for blue light.

Roaf (1930) also used colour filters and an artificial white light source. He measured the visual angle required in order to identify letters of different sizes. He did not determine directly the relative intensities of his coloured lights, but he measured instead the intensity at which each became extinct. From the values he gives, it may be inferred that the blue light was less bright than the other lights. The results he obtained for the acuity of the eye resemble those of König, namely, about equal values for red and green; somewhat better acuity for white; but reduced acuity, between one-half and one-quarter, for blue.

Shlaer, Smith & Chase (1942) used Wratten colour filters and an artificial white light source. They used two different test objects: Landolt's broken C, and a grating. The images of these test objects were altered in visual angle by a telephoto lens of variable focal length (Shlaer 1937). These observers did not equalize the intensities of the coloured lights, nor did they measure their relative intensities. They state, however, that in all probability the light intensity was so great that it did not limit acuity. The results they obtained with both test objects differed from those of both Roaf and König. With the grating, they found a gradual rise in acuity as the wave-length of the light was made shorter. This rise continued as far as the green; for blue and violet there was a slight fall. With the C test object, they obtained substantially the same acuity for white, red, yellow and blue lights. Thus in the case of neither test was there the marked fall in acuity for blue light found by the other two observers mentioned above.

(107) *The accuracy of measurements of visual acuity*

Those familiar with the technique of measuring visual acuity know how difficult it is to obtain a sharp end-point in such determinations. As the angle subtended by the test object at the observer's eye is made smaller, it becomes increasingly difficult for him to make correct estimates. Fixation has to be made with greater precision, and the eye has to be more accurately focused. In addition, the times required for judgements become more and more prolonged. The result is that fatigue may cause mistakes to be made long before the visual limit is approached. Further, when the limit is nearly reached, mistakes usually do not increase in a regular manner with decrease in the visual angle of the test object. These facts make the precise determination of visual acuity difficult. In order to decrease fatigue, and in consequence to increase accuracy, the following method may sometimes be adopted.

In the case of a letter of the alphabet, or a character similar to it, its diagonal is measured to the nearest millimetre. The observer now places himself at a distance from the test object equal to one thousand times the diagonal. Thus, if the diagonal of the test letter be 19 mm., he places himself 19 m. away from the test object. His observations are now recorded, and if found to be accurate the distance is doubled, and so on. If, on the contrary, they are found to be inaccurate, then the distance is halved. Having in this way found the critical region in which his estimates become incorrect, this region is explored by successively subdividing it. It is often found that this method saves time and reduces fatigue. In the case of the broken C test, four thousand times the size of the gap gives a suitable distance for the first observations. But even with this technique the end-point is far from sharp.

In table 78 are shown the number of correct estimates, out of a total of ten, at each distance, obtained by the author, using blue light and Landolt's broken C test. At distances less than 16 m., the observer's estimates were usually correct. At distances greater than 30 m. correct estimates were made occasionally. An explanation of this will be given later.

TABLE 78. VISUAL ACUITY MEASUREMENTS

distance (m.)	series 1	series 2	series 3	average
16	10	10	9	9·7
18	7	7	8	7·3
20	7	8	7	7·3
22	5	6	6	5·7
24	7	5	4	5·3
26	5	3	4	4·0
28	2	4	1	2·3
30	3	1	1	1·7

The gradual failure of vision makes the numerical evaluation of acuity somewhat difficult. The shortest distance at which mistakes are made might be one possible criterion; another might be the distance at which mistakes reach a maximum; while a third might be the distance at which an equal number of correct, and incorrect, answers are given. Two factors render the precise location of all these distances somewhat uncertain: (*a*) the effects of 'chance'; (*b*) the effects of inattention, or of fatigue. With regard to the former, since there are only eight positions of the gap of the test object, there is always a one-in-eight chance of giving a correct answer when it would not otherwise be made. In consequence, the results, particularly of low scores, are better than they ought to be. With regard to the latter, the observer, no matter how careful he may be, may make from time to time, inaccurate judgements which are not due to failure of acuity. These inaccuracies tend to spoil the scores, particularly at high acuities. To some extent these two sources of error tend to counteract each other. This is more likely to occur if the number of tests is large. It is for this reason that a large number of tests has been made during the course of this research. But even then accuracy is not of a high order, as is shown by taking separate means for the three series of tests shown in table 78 above. The means were found to be: 5·0, 4·9 and 4·4. These differ by nearly 14 %. It is likely that the means of other series would differ at least as much.

Inaccuracies such as these are inherent in visual acuity measurements. In the opinion of the author they can be minimized in only one way, namely, by performing large numbers of tests. It was noticed that Shlaer, Smith & Chase made only four, or sometimes eight, determinations for each colour and pupil diameter. Instead of using a test object of fixed size, and varying its visual angle by altering the distance between it and the observer, as is usually done, Shlaer, Smith & Chase looked at an image of their test object, which was altered in visual angle by a telephoto lens of variable focal length. They used this optical device in order to avoid alterations in the focal distance of the eye, which by changing the posterior nodal distance, might alter the scale of the retinal image. Thus, halving the distance between the observer and the test object would be expected to double the linear dimensions of the retinal image of the latter. But they contend that this would not be the case if the posterior nodal distance of the eye changed at the same time. These views are correct; so also is their method of eliminating the possible errors due to this change. There is, however, a possible objection to the use of lenses, namely, that they introduce scattered light because of multiple reflexions from their surfaces. In consequence, it is better, if it can be done, for the observer to look directly at the test object rather than at an aerial image of it.

There is another method, which has been used by the author, of eliminating variations in the posterior nodal distance of the eye, which will be described in the next section.

Variations in the visual angle of the image of the test object were effected by Shlaer, Smith & Chase by moving the carriage on which the test object was mounted. This was done by turning a knob which was limited to a rotation in one direction only, namely, that which increased the visual angle of the test object. The reason why this was done did not appear to be given in the two communications quoted, but it may have appeared elsewhere.

(108) *The effect of variations of the posterior nodal distance*

It was shown by Helmholtz (1909), Tscherning (1904) and others, that the nodal points of the crystalline lens are closer to the retina than are those of the cornea. Consequently, as the refracting power of the crystalline lens is increased during accommodation for near objects, the nodal points of the eye as a whole move in a posterior direction towards the retina, thus decreasing the posterior nodal distance of the whole eye, and so reducing the scale of the images of external objects which are formed on the retina. The decrease in size is not large, being about 1·6 % for every dioptre of accommodation. If, then, an object 1 cm. long be placed at a distance of 1 m. from the anterior nodal point of the eye, and if another object 0·5 cm. long be placed at a distance of 0·5 m. from the same point, then the images formed of these objects on the retina will differ by 1·6 %, because 1 dioptre of accommodation is required to change the focus of the eye from the more distant to the nearer object. This fact may be stated in another way: the image of a given object on the retina increases in linear dimensions by 101·6 %, when its distance from the anterior nodal point of the eye is halved. The effect of doubling the size of the test object by using some other distances is shown in table 79.

TABLE 79. ERROR PRODUCED BY DOUBLING THE SIZE OF AN OBJECT

smaller distance	1 m.	4 m.	16 m.
larger distance	2 m.	8 m.	32 m.
change of focus	0·5D	0·125D	0·031D
error in size	0·8 %	0·2 %	0·05 %

It will be seen from table 79 that, provided the distance between the observer and the test object is not less than 2 m., the error due to a doubling of the size of the test object does not exceed 1 %. In the author's experiments, the distances at which tests were made were not less than 16 m., so that no error was likely to have been produced by this effect.

(109) *The use of colour filters and correcting lenses*

Since suitable commercial filters were not available, four filters were prepared by the technique previously described.

As sunlight was used for the acuity tests, this source was also used during the adjustment of the colour filters. The filters, which were made as sharp-cut as possible, had the transmissions shown in table 80.

TABLE 80. TRANSMISSIONS OF COLOUR FILTERS

density	red		green		blue	
0·5	to	6070	5780	5330	4950	to
1·0	end	6030	5830	5240	5070	end
2·0	of	5950	6020	5090	5240	of
3·0	spectrum	5730	6370	4800	5450	spectrum

The red and green filters when superposed transmitted the orange, their combined densities being about 3·0. When the green and blue filters were similarly superposed, they transmitted a band in the blue-green, with an equivalent density of about 4·0. If the red and blue filters were superposed, a very faint violet light was transmitted, the density being about 8·0. Thus the three filters overlapped one another very slightly.

Their general transmissions were tested with daylight, using a Megatron photo-cell and galvanometer, with the results shown in table 81. Thus the general transmissions of the three filters were nearly alike to the photo-cell; they were also nearly alike to the eye. The amount of light transmitted by the filters proved to be less than was at first thought to be the case, namely, about 8 % of the total light in each case.

TABLE 81. GENERAL TRANSMISSIONS OF FILTERS

red filter alone	green filter alone	blue filter alone	neutral filter (1·0 density)
5·2	4·9	5·2	6·0

When in use, these filters were placed in front of the observer's eye so that not only the test object, but the whole of its surroundings, were appropriately coloured. The observer was slightly hypermetropic, requiring +0·5 D spheres R. and L. for correction in white light. For the coloured lights, other correcting lenses had to be used because of the chromatic aberration of the eye. The effects of this aberration have been variously estimated by different workers; thus Thomas Young estimated it at 1·3 D; Fraunhofer found 1·5 to 3·0 D; while Helmholtz gives the value 1·8 D (see Tscherning 1904). The corrections which were required, were ascertained in the following way.

With each colour filter the minimum power of lens and the maximum power of lens which would give distinct vision was ascertained by trial and error (see table 82).

TABLE 82. THE CORRECTING LENSES EMPLOYED

colour	minimum	maximum	lens used
white	+0·38	+1·00	+0·63
red	+0·63	+1·25	+0·88
green	+0·38	+1·00	+0·63
blue	−0·25	+0·33	—

In addition to the lenses and the colour filters, an artificial pupil, 2 mm. diameter, was placed in front of the eye of the observer. The test object consisted of Landolt's broken C, which had been drawn on white card in black ink. This was given an octagonal outline, so as to facilitate placing the gap in the C in one of eight positions. The gap measured 4 mm. square. During the tests, light adaptation was carefully preserved, and the colour filters frequently changed in order to avoid fatigue.

(110) *The geometrical hypothesis of visual acuity*

Two hypotheses have been held, at different times, to account for the acuity of the human eye:

(*a*) the geometrical hypothesis;

(*b*) the diffraction-threshold hypothesis.

For perception to take place, according to the first hypothesis, the geometrical image of an object formed on the retina must not have a fineness of detail which exceeds the diameter of the retinal receptors. For perception to take place according to the second hypothesis, the diffraction pattern of an object formed on the retina must not exhibit differences of intensity which are below the threshold of difference perception of the retinal receptors.

The early workers on visual acuity assumed that the retinal image was produced according to the rules of geometrical optics. This assumption was apparently justified by the fact that the visual limits found for the test objects, which were employed at that time, fitted in with the hypothesis that between two stimulated retinal receptors there was a third receptor which did not receive stimulation. Thus the angular separation of two neighbouring stars, which just permitted them to be appreciated as two by the unaided eye, was very nearly equal to the angular separation of two photoreceptors which have an intervening receptor between them. In the case of Landolt's broken C test, the same reasoning applied when the C itself was white on a black background. When, on the contrary, the C was black and it lay on a white background, the opposite reasoning seemed to apply, namely, that the images of the ends of the C, on either side of the break, protected the photoreceptors from stimulation; but that between these two, there was a third which was stimulated by the light which was coming through the break.

When the resolution of letters and other characters in the form of test type came under consideration, the same apparently satisfactory result was obtained on the geometrical basis; and it was because of this that the recognized standard of acuity, namely, 1 min. of arc, became universally accepted (see p. 604).

At that time, the retinal receptors were thought to have a mean diameter of about 4μ, and the posterior nodal distance was considered by Helmholtz to be 15·5 mm. For the image of one point-source to fall on receptor A, and for the image of another point-source to fall on receptor C, leaving receptor B—which lay between A and C—in an unstimulated condition, it would be necessary for the sources to subtend at the eye about 1 min. of arc; and this was the angle found by most experimenters. Thus theory and practice appeared to be in satisfactory agreement.

(111) *The diffraction-threshold hypothesis*

The geometrical hypothesis outlined in the last section lasted for perhaps half a century, when difficulties in accepting it began to show themselves. Thus it was found by Bryan & Baker (1912) that the space separating two lines could be bisected with an accuracy exceeding the diameter of a photoreceptor. Measurements of the acuity of stereoscopic vision by Crawley (1905) and others, also gave values of so precise a character that the different parts of a receptor would have to act separately in order to account for them. Moreover, it was found by the author that a black line could be seen when its geometrical image on the fovea was less than one-tenth the diameter of a receptor (Hartridge 1922*a*). Lastly, observations and calculations on the chromatic aberration of the lens system of the human eye convinced the author that this factor alone necessitated the abandonment of the geometrical theory. When diffraction was taken into consideration as well, the position of this theory became even worse, because it became clear that the retinal image consists of a diffraction-aberration pattern, which is entirely different from the sharp images produced on the basis of geometry, and entirely different also from the apparently sharp impressions received by the visual centres of the brain. Thus two problems had to be solved: (*a*) to explain how it comes about that these diffraction-aberration patterns are compatible with the high acuity of the eye for test objects of every kind; and (*b*) to explain why it is that neither these diffraction patterns nor the coloured fringes which should accompany them, because of the chromatic aberration of the eye (Hartridge 1918), are observable when the eye is used in normal vision.

While seeking for a solution to these two problems, a large number of calculations were performed by the author, on the distribution of light in the retinal image, for pupils of different size, taking both diffraction and chromatic aberration into consideration. It was found that in every case perception could be accounted for, if it could be assumed that small differences of light intensity were perceived by neighbouring receptors. From the evidence then available it appeared to be likely that the perception of an intensity difference, of perhaps 10 %, would account for the different acuity values of the eye, in a satisfactory manner.

At that time, the importance of the area surrounding the test object was not known. It was not until Lythgoe (1932) proved the necessity of having an extensive background of the same brightness as the test object that the effect of this in raising acuity was appreciated. When this background is provided by the experimenter, greater acuities than before are found for nearly, if not quite, all types of test object (Hecht & Mintz 1939). It was at once clear that this would necessitate a revision of the 10 % difference of intensity proposed by the author, and the adoption of some lower figure. It is important that this point should be fully appreciated, for as these revised acuities are reported as the result of further research, the idea seems to be prevalent that they refute the author's theory (Hartridge 1922*a*). Such is not the case, however; the value of the least perceptible intensity difference may need revision from time to time, but the theory itself will remain unchallenged until some one proves that resolution is in fact taking place when there are no differences of light intensity to be perceived by the fovea.

(112) *The limits to visual acuity*

Four factors are now known to determine acuity in the case of the human eye. Two of these concern the lens system, and two concern the retinal receptors; they are:

(*a*) diffraction at the pupil;
(*b*) the aberrations;
(*c*) the fineness of the retinal mosaic;
(*d*) the ability to detect differences of brightness.

Diffraction and the aberrations are to some extent interconnected, because diffraction causes deterioration particularly at small pupils, whereas the aberrations cause deterioration particularly at large ones. In consequence, between these two limits there is an optimum at which definition reaches its highest value. Factors (*c*) and (*d*) are not obviously interconnected. In the case of a grating test object, for example, resolution might fail for two different reasons: either because its bars were painted in shades of grey which were too nearly alike; or because the bars were so close together that the whole of the width of two neighbouring bars, one black and one white, fell on every one of the retinal receptors, so that the latter were all stimulated alike. In any given case it is usually possible to find out which of these factors is limiting resolution, in the following way:

If it is caused by diffraction, the acuity should be improved by an increase in the diameter of the pupil, or by the use of light of shorter wave-length.

If it is caused by aberrations, the acuity should be improved by replacing white light by monochromatic light, thus removing chromatic difference of focus. Chromatic difference of magnification can also be corrected (see § 104).

If it is caused by the retinal mosaic, it would be expected that the acuity would be made worse by the use of monochromatic light instead of ordinary light, because, according to the accepted theories, the former stimulates fewer receptors than the latter, and in consequence makes the retinal mosaic appear to be coarser. On the other hand, an increase in light intensity may improve the acuity if the intensity is low at first; this may possibly be due to an increase in the number of receptors which are responding, thus making the retinal mosaic act as if it were finer.

If it is caused by the difference of brightness threshold, acuity may be improved by making the bright parts of the test object brighter and its dark parts darker. Further, an increase in light intensity may improve the acuity.

These points of differential diagnosis, which must be used with discretion, are summarized in table 83.

TABLE 83. ALTERNATIVE HYPOTHESES

factor	pupil larger	brighter light	green light*	blue light*
diffraction	better	—	—	better
aberrations	worse	—	better	better
mosaic	—	better†	worse	worse
threshold	—	better	—	—

* Instead of white light. † If illumination is poor at first.

(113) *Shlaer's visual acuity hypothesis*

As the result of experiments, using the apparatus referred to in § 106, Shlaer advanced the following hypothesis: 'The limiting factor in the resolution of the eye for the grating is the diameter of the pupil when it is less than 2·3 mm. and the size of the central cones when the pupil is larger than that.' The results put forward by Shlaer in support of this hypothesis, which were obtained with a 2 mm. pupil, are given in columns 1 and 2 of table 84.

TABLE 84. TESTS WITH GRATING

wave-length (A)	acuity found	acuity calculated
6700	1·80	1·80
6250	1·82	1·93
6050	2·00	1·99
5750	2·08	2·10
5350	2·14	2·26
4900	2·12	2·46
4500	2·08	2·68

Since the pupil diameter employed is less than 2·35 mm., the visual acuity, according to Shlaer, should progressively increase with decrease of wave-length, as pointed out in the previous section. In column 3 of table 84, the acuities have been calculated on this basis, making the acuity for 6700 A the same as the experimental value. A comparison of columns 2 and 3 shows that there is good agreement at the longer wave-lengths, but that after 5750 A the acuity found by experiment stays almost level, while the calculated acuity continues to improve. This difference appears to the author to indicate that a limit has been reached in the experimental acuity, at about 2·1, due to some other cause—most probably due to the retinal mosaic—so that even at a pupil diameter of 2 mm. the limiting factor does not appear to be diffraction by the pupil as Shlaer supposed.

The results obtained by Shlaer and his co-workers in the case of Landolt's 'broken C' test, also appear to refute Shlaer's hypothesis which was advanced in the case of a grating test object, but which should also apply to the Landolt test, because it is in effect a grating consisting of only three bars.

If the pupil diameter was in fact the limiting factor, then acuity should increase with increase in pupil diameter, as well as with the use of shorter wave-length light. That neither of these expectations from Shlaer's hypothesis is found in practice, is shown by their results which are given in table 85. In this case also, since the experimental results are independent of pupil diameter and of the colour of the light, some limit other than diffraction of the pupil seems to be involved. To the author it appears in this case also to be the fineness of the retinal mosaic.

TABLE 85. TESTS WITH 'BROKEN C'

	E.L.S.	A.M.C.	
red	2·56	2·77	2 mm. pupil
yellow	—	2·76	2 mm. pupil
blue	2·54	2·79	2 mm. pupil
red	2·51	2·73	3 mm. pupil
yellow	—	—	3 mm. pupil
blue	2·48	2·79	3 mm. pupil

(114) *The author's experimental results*

The author used two different varieties of test object during these experiments: (*a*) selected characters, and (*b*) Landolt's 'broken C' test. The characters, which were A, Λ, Q, O, R, P, E, and ⊏, were white on a black background. The results obtained are given in table 86.

The results for the Landolt's 'broken C' test, which was black on a white background, are given in table 87.

TABLE 86. TESTS WITH SELECTED CHARACTERS

colour of light	relative intensity	visual acuity	cone units
white	12	2·2	0·66
red	1	1·8	0·81
green	1	2·1	0·69
blue	1	1·7	0·86

TABLE 87. TESTS WITH 'BROKEN C'

colour of light	relative intensity	no. of tests	visual acuity	cone units
white	12	180	1·89	0·77
red	1	160	1·63	0·89
green	1	180	1·86	0·78
blue	1	240	1·72	0·85

Both series were done in sunlight, by the same observer, using an artificial pupil of 2 mm., and a lens of suitable power in order to focus the test objects sharply, with whichever light was in use. The usual convention has been adopted, namely, that the visual acuity is unity when the widths of the lines of which the characters are composed, subtend an angle at the eye of 1 min. of arc. In the case of Landolt's 'broken C', it is the gap in the C which subtends this angle at the eye of the observer. Thus, in both cases, a visual acuity of 1·7 would indicate that the visual angle was 0·59 min. of arc. It will be observed, with both kinds of test object, that the acuity when using blue light, instead of giving better results than with green light, actually gave somewhat worse. It will be remembered that both König and Roaf obtained a similar result. So that in these cases also, acuity does not appear to be dependent on diffraction at the pupil, but on some other factor. It seemed unlikely that this factor would be chromatic aberration, because if it were, a coloured light should give a better result than a white one, and such is not found to be the case. Neither does the difference threshold for light intensity seem a likely factor, because in this case the fact that the white light was twelve times as bright as any of the coloured lights would have caused the visual acuity for white light to be substantially better than that for the colours, and this was not found to be the case.

The most likely factor appeared to be the retinal mosaic. But if this were the case, it would be expected that the result with white light would be markedly superior to that given by any coloured light, because, as has been pointed out above, white light stimulates all the foveal receptors, while coloured light stimulates only a few. But the author did not find this, because the acuity he obtained by coloured lights, particularly by green light, was substantially equal to that obtained by white light. Other observers, except Roaf,

TABLE 88. RELATIVE ACUITIES

observer	white	green
König	1·50	1·50
Roaf	1·50	1·00
Shlaer: grating	2·10	2·14
Hartridge: C test	1·89	1·86
Hartridge: letters	2·20	2·10

have obtained a similar result, as shown in table 88, in which the visual acuity found for white light is compared with that for green.

In the author's case, the differences between the acuities for white and green are within the experimental errors of the methods used.

(115) *The alternative hypotheses*

The main conclusions arrived at in previous sections of this Part may be stated as follows:

(*a*) On the diffraction hypothesis, it would be expected that visual acuity would be highest when blue light is being employed for illuminating the test object.

(*b*) On the aberration hypothesis, it would be expected that any coloured light would be superior to white light.

(*c*) On the retinal mosaic hypothesis, white light would be expected to give better results than coloured light, because it stimulates more receptors.

(*d*) On the difference threshold hypothesis, white light would be expected to give the best results, because in these experiments it had the highest intensity.

Experiment, on the other hand, showed none of the differences mentioned above.

This is well seen in the values shown in table 89, in which all acuity results are multiplied by a suitable factor so as to bring those for white light to unity in each case.

TABLE 89. RELATIVE ACUITIES BY LIGHTS OF DIFFERENT COLOUR

observer	test object	white	red	green	blue
Shlaer *et al.*	grating	1	0·91	1·02	1·00
,,	Landolt's C	1	1·00	—	1·00
Hartridge	letters	1	0·82	0·96	0·77
,,	Landolt's C	1	0·84	1·00	0·90
	means	1	0·89	0·99	0·92

If the mean values for white light and for the three coloured lights be compared, it will be seen that those for white and for green are practically identical, while those for red and blue lights are only some 10 % lower. So small are the differences that it is questionable whether they are not all within the experimental error which, as pointed out in § 3, is unavoidably large in this kind of work. Not only, therefore, are the results for the four lights almost alike, but they are obtainable in different directions on the retina. Take the grating, for example: it can be resolved in four different directions, i.e. with lines vertical, horizontal, sloping down to the right and sloping down to the left. With the C test it is the same, whatever its position, with the gap in one of eight positions, it is resolvable. This means that at the fixation point of the retina there must be sense organs capable of responding adequately, not only to the different positions of these test objects when illuminated by white light, but by coloured light as well.

There are only two inferences possible: either that the receptors at the centre of the fixation area are different from the receptors elsewhere in the retina, in that they are able to respond to light of all colours; or that the receptors are normal, each one responding to light of one colour only, but that by their arrangement they are able to provide the acuity which is found by experiment. But this acuity, as many previous observers have pointed out, is of the same order of fineness as the diameters of the tips of the receptors themselves.

In consequence, resolution is pictured as taking place when three neighbouring receptors, at least, co-operate with one another. In the days when a geometrical image of external objects was supposed to fall on the retina, the criterion of resolution was that while the first receptor and the third receptor, of such a linear triplet, received adequate stimulation, receptor number two, lying between the two others, did not. If this reasoning were to be applied to the acuity measurements made with the C test, the result would be as shown in table 90.

TABLE 90. THE GEOMETRICAL IMAGE ON THE RETINA

observer	visual acuity	geometrical size on retina (mm.)
Shlaer	2·55	0·00186
Chase	2·78	0·00170
Hartridge	1·89	0·00250
	mean, say	0·00200

The values in the last column were calculated on the assumption that the posterior nodal distance of the human eye is equal to 16·81 mm. This value is based on the measurements of the eyes of 10 emmetropes, by an X-ray method, by Goldmann & Hagen. Adopting this figure for purposes of calculation, and also taking the mean size of the geometrical image of the gap in the C test, given at the foot of table 90 above, namely, 2·0μ, it is possible to determine roughly the relative intensity of light falling on the various receptors. If the full intensity falling on the receptors, where no part of the image of the C falls, be made unity, then that of the receptors on which part of the C falls will be about one-third; and the intensity falling on the receptor on which the gap in the C falls, will be about two-thirds. These differences in illumination are quite large, probably far larger than they would ever be in practice.

This intensity difference, whatever its precise value may be, appears to be substantially the same for white and for coloured lights, in the case of the C test.

Similar reasoning applies to the grating test used by Shlaer and his co-workers, and to the characters of a more complicated pattern employed by the author.

The final conclusion, therefore, appears to be that the acuity values found by experiment are at variance with expectations based on all four hypotheses mentioned above; but that the hypothesis which most closely accounts for them is the one which is based on the dimensions of the retinal mosaic. If it be assumed that the fineness of structure be the same for all colours as it is for white light, then the similarity in the experimental values is adequately accounted for. With regard to the latter, there are two alternatives: either (*a*) the foveal receptors have specialized properties, enabling them to respond equally well to white light and to coloured light; or (*b*) that the foveal receptors of similar spectral response, are collected into small groups or clusters, as explained in detail in the next section.

(116) *The arrangement of receptors at the fovea*

For many years there have been two rival hypotheses concerning the functioning of the foveal receptors: the single-receptor theory and the triple-receptor theory. According to the former, all retinal receptors are capable of responding to light of every colour. According to the latter theory, the retinal receptors belong to one of three groups: those responding to red light, those responding to green light and those responding to blue light.

Recently, two other hypotheses have been advanced: the polychromatic hypothesis of Granit (1943) and the cluster hypothesis (Hartridge 1944*b*). According to the former, there are not three groups of receptors as postulated by the triple-receptor plan; still less, one kind of receptor, as demanded by the single-receptor plan; but on the contrary many groups, each group responding to light of a particular band of frequencies. Granit's present idea is that one group of receptors, called 'dominators', is stimulated by white light, while other groups, called 'modulators', are stimulated by light at and near the following wave-lengths: 6000, 5800, 5400, 5200, 5000, 4600 and 4300A. These different varieties of receptor were discovered in the retinae of many animals, by the use of an elegant micro-electrode technique; but they have not, so far, been shown to be present in the retina of man.

The cluster hypothesis does not run counter to any of the above hypotheses; it merely adds what appears to be an essential detail to either the triple-receptor plan, or the poly-receptor plan of Granit. The cluster hypothesis is unnecessary if the single-receptor plan proves to be acceptable. It is not proposed to consider, in this section, all the pros and cons of these rival views, but to deal with one aspect alone, namely, the results presented in this Part, on the acuity of the eye for lights of different colour.

It has been shown in previous sections that the eye has the same, or nearly the same, high acuity for white, red, green and blue lights. Further, Shlaer, Smith & Chase have shown, with a grating test object, that the same statement was true for lights of practically all colours. It has been shown, moreover, that the same, or nearly the same, acuity is found, whatever the direction taken either by the lines of the grating or of the gap in the C. But our own everyday experiences show us that these conclusions are not limited to the particular test objects used during these experiments, since they apply to letters, to numbers and to objects of all kinds, and of various shapes and sizes.

How are we to explain this high acuity for lights of all colours? This is difficult enough on the triple-receptor plan, but almost impossible on the poly-receptor plan of Granit. Clearly, the hypothesis which most easily fits in with the observed facts is the single-receptor plan. For, according to this, no matter what the colour of the light may be, every receptor is capable of responding. Nevertheless, there are grave difficulties in the way of the acceptance of this plan, into which it is not proposed to enter in detail here; but it is, for example, contrary to the results of Granit's experiments. It seems most unlikely that man's retina is fundamentally different in design from that of other mammals.

According to the cluster hypothesis, either by accident or by some factor acting during growth, receptors of a given variety tend to collect together. Thus at one point of the retina there may be a cluster of Granit's 'dominators'; at another, there may be a group of green-sensitive receptors; while at a third point there may be some blue-sensitive ones. According to the cluster hypothesis, this uneven distribution is made use of in the following manner.

Suppose that the C test object is to be resolved, when illuminated by means of red light; then the test object is fixed, that is, the image of a part, possibly even of an important part, is caused by suitable adjustment of the external eye muscles to coincide with the red fixation point. Evidence will be given in the next Part that there are several fixation points (see § 148, p. 644).This evidence has been confirmed by the employment of the micro-stimulation apparatus. With the latter it has been shown that there are separate fixation points, differing slightly in position, for red, orange, yellow, yellow-green, green, blue-green, blue and violet. According to the cluster hypothesis, each one of these is the centre, or nucleus, of a small group of receptors of the same, or similar, response. Thus the red fixation point is near the middle of a red fixation area, which contains red receptors and orange receptors, and possibly even some yellow receptors, since the spectral width of the response curves of the latter will probably enable them to respond, to some extent at all events, to red light rays, particularly since such rays, when produced by natural objects or by pigments and dyes, are far from being monochromatic.

Thus a red object, when it has been fixed by the observer, produces an image on the red fixation areas of his eyes, and since the receptors in these areas all respond, a high acuity for detail is the result. In the case of a yellow object, the images fall on the yellow fixation areas of the two eyes, and so on for objects of all colours. It is in this manner that the cluster hypothesis offers an explanation of the high acuity for all coloured lights.

In the case of white light, it may be that a special fixation area is used, composed of receptors of all possible varieties. Alternatively, the green fixation area may be used, because in normal vision it is the green rays which form sharply focused images, while the red and blue rays spread to form aberration disks, owing to the chromatic aberration of the eye, and are subsequently eliminated, on their way to the brain, by the antichromatic responses, described earlier in this paper.

IX. Cluster formation by the cones of the fovea

If the retinal receptors responding to different colours have a chance distribution in the retina, it would be expected that they would be found in small groups, or clusters: at one place a cluster of red receptors, at another place a cluster of green receptors, and so on. A number of experiments have been performed, in order to ascertain the positions of clusters of different kinds in the fovea of the author's left eye. As the result, a plan has been made of the foveal area.

(117) *The cluster hypothesis and colour vision*

Reference has been made in the last Part to the cluster hypothesis of the retina (see § 116, p. 606). According to this scheme the arrangement of the photo-receptors in the retina, near the fixation point, and probably elsewhere as well, is such that those of similar property are collected together into little groups. Thus at one spot there might be a collection of receptors responding most strongly to red rays, while at another spot there might be a group of blue responding receptors, and so on. This aggregation of the sense organs into groups, or clusters, might be intentional or accidental. If intentional, there would have to be some mechanism, of an at present unknown character, which would operate during the embryological development of the retina. If accidental, it would have to be accounted for by the laws of chance. That chance can produce clusters of objects of similar property is shown by an examination of the Lumière starch-grain screen used for colour photography. This screen is prepared by mixing together red grains, green grains and violet grains, in roughly equal quantities. They are then spread, one grain thick, on a glass plate, and behind this is placed the light-sensitive emulsion. Such a screen, examined by a low-power microscope, shows the clusters formed by the grains extremely well.

It was shown in the previous Part that measurements of the acuity of the human eye by lights of different colour disclose almost equally good results whatever the colour of the light may be. This can be accounted for in a satisfactory manner by the cluster hypothesis (see § 118). Another visual phenomenon which can be adequately explained on the cluster hypothesis is the retinal direction effect of Stiles & Crawford. This will be dealt with in § 123. It is also proposed to describe other phenomena which appear to substantiate this view. Before doing so, however, it will be necessary to consider in greater detail than has been done so far, the arrangement of the elements in a cluster, and the disposition of the clusters in relation to one another. It should also be pointed out that the cluster hypothesis in no way provides an explanation of colour vision. Thus it does not attempt to stand as a rival to such well-known theories as the trichromatic theory of Thomas Young. What it does attempt, is to supplement those theories by adding an essential detail which enables them to account for certain facts of vision which alone they would be unable to do. There might be, for example, a trichromatic-cluster hypothesis, or a polychromatic-cluster hypothesis; the latter being obtained by combining the experimental results of Granit with the view that the sensory elements discovered by him in the mammalian retina are collected together into clusters.

(118) *Examples of cluster formation*

The hypothesis that the formation of clusters is due to chance, and that the Lumière screen is a typical example of such cluster formation, clearly requires further examination before it can be accepted, and conclusions from it applied to the retina. Such an examination might be done practically, or mathematically, or both. Some practical tests were carried out as follows: about 1 oz. of the fine granular cereal 'semolina', was divided roughly into three equal parts. One part was dyed red, another part green and the third part violet. These were mixed together as thoroughly as possible, and then dropped in a thick layer on a flat surface. Examination of the upper free surface disclosed the presence of numerous clusters, some red, some green and some violet. But in addition to the clusters of the primary colours it was observed that there were clusters of the secondary colours, yellow, blue-green and purple, which were produced by groups of red and green grains, green and violet grains, and violet and red grains, respectively. When viewed at a distance the whole surface of the mixture of grains appeared to be mottled just as a Lumière screen does. One curious fact was noticed, however, namely that the scale of the clusters was different in the two cases. In the Lumière screen the clusters of any given colour, for example red, were 0·5 mm. apart, and the starch grains on the average 0·01 mm. diameter, so that the distance from the centre of one red cluster to the centre of the next was equal to about 50 grain diameters. In the case of the semolina, on the other hand, the centre of one red cluster to the centre of the next measured about 10 mm. and the granules had a diameter of roughly 0·6 mm.; so that the clusters were separated by only 17 grain diameters. Another point noticed was that the clusters in the Lumière screen appeared to be larger than those in the case of the semolina. It is not very easy to determine the precise limits of a given cluster, nevertheless, the above differences appeared to be too large to be due to errors of observation. The following tentative explanations were suggested in order to account for the differences referred to above; variations in grain size, population size and perfection of mixing. Of these three, population size seemed as if it might lead to the required result. The populations in the case both of the Lumière screen and the semolina are quite large, but probably not of the same size. The effect of quite a small population was therefore tested. Of 201 pieces of paper, 67 were marked 'R', 67 'G' and 67 'B'. They were then mixed, and picked out at random one at a time. A diagram was marked out into small circles, and these were coloured red, green or blue, according to the indication given by the pieces of paper. The completed diagram contained between 900 and 1000 coloured circles for which the pieces of paper had to be mixed, and picked out, nearly five times. When this diagram was examined for clusters none appeared to be present, for the circles of any one colour seemed to form short lines of various shapes and lengths, which were fairly uniformly distributed throughout the diagram.

The conclusion suggested by the above experiment is that for cluster formation to occur a population much more numerous than a few hundred is required. This conclusion was tested in another way, namely, by taking a small sample from the mixed grains of semolina. When this sample was thoroughly mixed and spread on a flat surface the clusters seemed definitely less evident than before. Whether this is a true effect, or an artefact, remains to be proved, but so far as the retina is concerned a justifiable conclusion appears to be that cluster formation ought to take place because the rod and cone populations are both large; roughly thirty million cones, and about three times that number of rods. At the centre of the fovea there is stated to be a small rod-free area, elsewhere the two populations are mixed, the rods predominating more and more as the periphery is reached.

The position, so far as the fovea is concerned may, perhaps, be summarized as follows: it seems likely that conditions there are such that cluster formation may occur. As explained elsewhere, this provides an adequate basis for the high acuity of the human eye for lights of different colour. It also helps to account for the retinal direction effect of Stiles & Crawford (see § 123). A warning must be given, however, that factors of an unknown kind may be present which may either facilitate, or inhibit, the process of cluster formation. What is wanted is independent evidence that such clusters do in fact exist in the retina. Suppose such evidence to be forthcoming, then a further question would arise, namely, why is it that these clusters do not disclose their presence in normal vision? This point will be considered in Part XII.

(119) *Some experimental evidence for cluster formation*

Before experiments were started, in order to search for evidence of cluster formation, it was anticipated that there would be difficulties in the way owing to the action of the process of repair which will be described in Part XII. This anticipation proved to be fully justified for a number of experiments, several gave no result. A single bright flash of light sometimes gives an appearance of a fine mosaic of coloured points. The application of pressure to the front of the eyeballs sometimes produces a somewhat similar effect. Occasionally, the examination of a distant source through mist, suggests the same appearance. But it was found on subsequent detailed examination that the effects produced were too variable to be brought forward as evidence. A different line of approach was therefore looked for. When a small test object is at the limit of visibility mistakes are frequently made in its identity. Thus R may be mistaken for P, and E for F. If such a test object be placed not at the extreme limit of visibility, but near to it, the precise nature of the object should be detectable with light of a particular colour when its image falls entirely on a cluster of cones which are sensitive to that light, but should not be detectable when its image falls entirely outside such a cluster. Such an experiment as this clearly depends very largely for its success on the observer being able to direct his gaze at points near the test object, and on his ability to keep it there. Evidence that this can be done is given in Part XI. The experiment was carried out in the following manner: the test letter was drawn in white on a black background, and was placed at such a distance from the observer that its image on the retina had a diameter equal to 5 cone units. Fixation marks had been drawn at various distances from it so as to assist the observer in keeping his gaze still. The test object was viewed monocularly with diffuse sunlight; a red filter, a correcting lens and an artificial pupil of 2 mm. were also used. When the mark 10 cone units from the centre of the test letter was fixed by the observer, details of the test letter were found to be hard to decipher. When the fixation mark 5 cone units from the centre of the test letter was used instead, the definition of that part of the letter nearest to the fixation mark was definitely improved. When the gaze was fixed at the centre of the test letter the details of the whole of it became clearly visible, but the actual part at which the gaze was directed was seen to be better than the rest. Similar tests were carried out using the green and the blue filters. The results obtained were not noticeably different from those described above for the red filter.

Another test was performed on somewhat similar lines; using the correcting lens, artificial pupil, and the three colour filters in turn, the distance at which a printed page could be read correctly was measured. Keeping this distance, the observer tried, as he slowly ran his eye along one line, to read the one above or the one below it. It was found that a few words, of two or of three letters, were legible, but that the majority were not. The centres of the lines of type were 5 cone units apart. The conclusion from these experiments is that there is at, or very near to, the centre of fixation for any colour, a very small area of retina possessing the highest resolving power for fine detail in that colour. This maximum acuity area has a diameter roughly equal to from 4 to 8 cone units, that is, it contains probably not fewer than 10, nor more than 40 cones. The defining power of this area is such that every, or nearly every, cone must be able to function by monochromatic light. Two points should be noted, however; first, that the precise limit of the area is difficult to define, which specializes in providing acuity for one colour, and contains only one variety of cone; and secondly, that the evidence provided by these experiments, in no way excludes the probable presence in such an area, of a few cones of different function from the ones which occupy the greater part of it. Thus an area occupied largely by red-sensitive cones, may also contain a few green and a few blue ones.

One further experiment may be considered in this section. A series of rough sine-wave curves of various wave-lengths and amplitudes were drawn, and these were used in turn as test objects with the results shown in table 91. In the first and third columns are given in μ the wave-length and amplitude of the image produced on the retina. The second and fourth columns give the same factors in terms of the probable diameter of a foveal cone assumed to equal $3{\cdot}6\mu$. As a result of a number of tests it appears that wave-lengths longer than $3{\cdot}6\mu$, that is 1 cone unit, are resolved provided their amplitude is more than $3{\cdot}6\mu$. If, on the other hand, their wave-length is much shorter than this, then they cease to be resolved, as would be the case with gratings of similar fineness. Further, if their amplitude is made much smaller than 3·6μ then in this case also they are not resolved but are found to be mistaken for straight lines. These effects may be explained on orthodox views of cone function. The point of interest here is an effect observed during these tests, particularly with the curve having an image on the retina with a wave-length and amplitude of 7·2μ. The drawing of this curve consisted of seven complete waves. When the centre of this curve was fixed by the observer, who, as before, used a correcting lens and an artificial pupil, he noticed that the part near the fixation mark had a normal appearance but that the ends seemed to wriggle as if they were living flagellae. The use of a red, green or blue filter did not seem to alter the appearance materially. The explanation of this effect which most closely fits the facts is that at the centre of fixation, where there is a cluster, small fortuitous eye movements do not materially affect the appearance of the curve since its image only moves off one set of cones to fall on another set substantially like them. The ends of the curve, on the other hand, fall outside this cluster, on parts of the retina where the cone population, responding to the particular coloured light in use, is relatively sparse. Here the image falls on only a few cones, and in consequence repair has to take place before the image as a whole is presented to consciousness. Now repair may take place in many different ways, producing as many different final images. If certain cones are stimulated the final image after repair may have one appearance; but if, owing to movement of the retinal image, other cones are stimulated the final image after repair may have a different appearance. Thus the apparent undulations of the ends of the curve are due to differences in the final images which are presented in turn to consciousness.

TABLE 91. THE VISIBILITY OF SINE-WAVE CURVES

length of image on retina		amplitude of image on retina		resolved by the eye
(μ)	(cone diameters)	(μ)	(cone diameters)	
1·8	0·5	3·6	1·0	no
1·8	0·5	7·2	2·0	no
3·6	1·0	3·6	1·0	yes
3·6	1·0	1·8	0·5	no
7·2	2·0	1·8	0·5	no

The evidence obtained from these experiments may be summarized as follows: there appears to be at or near the fixation spot of the human fovea a small cluster of cones, all of similar colour response, the cluster having in consequence a very high acuity. This forms what may be called 'the maximum acuity area' for that colour. Each maximum acuity area appears to have a diameter which is not less than four nor much more than eight times that of a foveal cone. If such an area had a spherical form it would contain not less than 10 nor much more than 40 cones. Outside this area of maximum acuity there is a surrounding zone, 'the medium acuity zone', in which the cone population in question is less dense. In consequence, the acuity of this zone is not so high as that found in the area of maximum acuity.

The medium acuity zone has an outside diameter roughly three times that of the maximum acuity area, that is, its diameter is from twelve to twenty-four times the mean diameter of a foveal cone.

(120) *The position of clusters at the fixation point*

The essential feature that clusters of different colour response occupy different positions was investigated. Test objects consisting of tiny disks of coloured paper 3 mm. diameter were mounted on black backgrounds. The first test comprised one red and one green disk, their centres being about 3 mm. apart. This test, like the C test used in a previous research, could be placed in eight different positions, so that the red disk could be situated above, below, to the right, to the left or in one of the four intermediate positions in respect of the green one. The second test similarly comprised one red and one blue disk, while the third test comprised one green and one blue. With each of these tests the technique employed was as follows: at a distance of 3 to 4 m. to begin by fixing one of the disks, for example the green, then to fix the other disk, for example the blue, and to estimate the amount of eye movement required to fix first one and then the other. At first an assistant watched the eye which the observer was using in order to determine the amount of movement which was taking place, but this procedure proved to be unnecessary for the observer was found to be able to do this for himself. Each position of the test object was tried in turn in order to determine which one required the smallest amount of movement. Suppose, for example, that this occurred when the blue was below, and to the right, of the green, then this was held to indicate that the image of the blue disk was falling on a part of the retina which was closer than any other part to the fixation point for blue. Each eye was tested with the three test objects, with the following results. In the case of the observer's left eye, with red and green disks, the red fixation point was found to be down, and to the left of the green fixation point; with the red and blue disks, the blue fixation point was found on the right of that for red; with the blue and green disks, the green fixation point was found to be up, and to the left of the blue one. Similar tests with the right eye gave results in substantial agreement with the above, but with less certainty, because the definition of this eye is not so good as the other.

The conclusion from these experiments is that the fixation points for the different colours occupy different positions on the retina, as should be the case in accordance with the cluster hypothesis. The three fixation points appear to lie at the corners of an imaginary right-angled triangle with the right angle forming the apex. The green fixation point corresponds to the apex, the red one corresponds to the left-hand end of the base, while the blue one corresponds to its right-hand end. Leaving out of account the fact that the green fixation point lies above the other two, the order of the points, travelling in a horizontal line in a nasal direction are: red, green and blue, in the case of the left eye. In the case of the right eye they are in the reverse order, namely, blue, green and red. This reversal makes it impossible for the order in both eyes to be due either to the decentred lens which was used in these experiments, or to uncorrected chromatic difference of magnification. In order to confirm this conclusion, so far as the lens was concerned, a few tests were done without any lens. The order of the fixation points was still found to be the same, although their displacements relative to one another were different, and the experimental results less clear.

The relative position of the fixation points described above was investigated, using the micro-stimulation apparatus, an account of which will be found in Part X. Use was made of a small scotoma for red rays, which was found near the fixation area of the author's left fovea. The red fixation area found in the above experiment, contains both the red and orange fixation points. The green fixation area, which was above, and to the right, of the red one, was found to contain the fixation points for yellow, yellow-green, green and blue-green. The blue fixation area, which was below, and to the left, of the green one, contains the violet fixation point, the blue one being at the line of junction of this area with part of the high acuity area for green. Thus the positions of all three fixation areas described above has been confirmed (see § 148, p. 644).

(121) *Retinal astigmatism*

Many workers on the subject of visual acuity have remarked on some of the curious inconsistencies shown by their observers who, apparently without reason, find certain test objects difficult, while others are found to be easy. These irregularities are particularly noticed when letters are used as tests. Thus Tscherning (1904) writes: 'It is certain, indeed, that some of the letters are more easily read than others of the same size', and 'the legibility of a letter is, indeed, a very complex affair, which is far from depending altogether on the size of the intervals separating the different lines.' Hartridge & Owen (1922) found the same thing, and recommended the use of 9 letters only, which had about the same difficulty factor. Some of the mistakes seem to be due to small amounts of astigmatism, which, however, appeared to be difficult to remove by correcting lenses.

Shlaer (1937) is the first, or among the first, to claim that the retina may be responsible rather than either the lens system of the eye, or the visual centres of the brain. He called the phenomenon 'retinal astigmatism'. This name seems to be a very apt one. He wrote as follows: 'Another difficulty is the pronounced retinal astigmatism found in every eye thus far examined. It is possible to rotate a just resolved test field so slowly that the observer can follow the direction of rotation, and yet have the field become unresolvable at certain angles' (see p. 171 of the same communication). 'Thus, for example, in one run for E.L.S. on 10 June 1936, at a log I value of $-1{\cdot}057$ photons, the values for the log visual acuity were $-0{\cdot}529$ for the angle 45° to the right and $-0{\cdot}725$ for 45° to the left, a difference of about 0·2 logarithmic unit. At about 0·7 logarithmic unit higher in intensity the values were $-0{\cdot}173$ for 45° to the right and $-0{\cdot}058$ for 45° to the left, a difference about half as large, and in the opposite direction. Finally at a log I value of 0·118, no astigmatism could be detected.' On p. 170 of the same communication Shlaer wrote: 'An attempt to supply a fixation point by pasting a small circular black paper dot on the field lens was only partially successful in overcoming this difficulty [of the stripes of the grating appearing suddenly and without warning] since the resolution does not occur at the fixation point. This is unlike the C which can be fixated and resolved at the point of fixation.'

I have, myself, often used the grating test object, and I can confirm, from personal experience, everything that Shlaer has stated on this point. The explanation of these retinal astigmatic effects, and their variation with change of light intensity, appears to be as follows. At low intensities of illumination a part of the retina towards the periphery of the macula is used for the perception of detail. At such a spot the rods probably predominate over the cones. As light intensity is increased, a part of the retina nearer the fovea is utilized. Soon the intensity is such that the fovea itself is employed for the acutest perception.

Finally, at high intensities the fixation spot at the foveal centre is used. In accordance with the cluster hypothesis, every one of these spots, whether in the periphery, in the parafovea, in the fovea or at the fixation point itself, is occupied by a cluster of appropriate composition. When red light is in use, it is a cluster largely composed of red receptors that is employed for vision. When blue light is in use, it is a blue cluster which is selected. Similarly for green light. When white light illuminates the test object it is a yellow-green cluster which is selected because the rays of this hue have a higher visual luminosity than have the red and blue rays, and because the yellow-green rays, being more sharply focused than the rest, play in consequence, a more prominent part in the perception of fine detail. Now these different clusters, employed with lights of different spectral composition and different intensity, not only differ in position in the retina, but differ in shape as well. An examination of the Lumière screen discloses the fact that no two clusters are precisely the same either in size, shape or make-up. Some are almost spherical, some are elliptical, some are spiral and so on. Like pebbles they vary one from another, and no two are exactly alike. Any cluster which has greater dimensions in one direction than it has in another will give greater acuity in the longer direction; that is, it will show retinal astigmatism. The better acuity will be parallel to the longer dimension of the cluster. When a different cluster is in use, the pattern of the retinal astigmatism will be different. When the cluster is spherical, there will be no retinal astigmatism at all. With the C test, and bright sunlight, the author has greater acuity with green light when the broken ends of the C lie either in a horizontal or in a vertical direction, than is the case when they lie obliquely, either 45° to the right, or 45° to the left. The conclusion is that the cluster in use has good vertical and horizontal components, but poor oblique ones. Thus it may be L-shaped, T-shaped, or +-shaped, according to the precise arrangements of its two components. The conclusion from all these examples is that the cluster hypothesis accounts in a satisfactory manner for the interesting and intricate phenomenon of retinal astigmatism.

(122) *The process of fixation*

Evidence has been given in the previous sections that fixation can be performed by several different groups, or clusters, of cones lying near one another at the centre of the fovea. That more than one cone group can perform this important function is shown by the results of eclipse- or after-image-blindness, and by a number of pathological conditions of vision. Some of these will be dealt with in this section.

Eclipse-blindness is a condition frequently met with by ophthalmologists following an eclipse of the sun. A similar condition is met with after any very intense source of light has been looked at without proper precautions. Examination of the patient usually shows the existence of a scotoma which occupies part of the fovea. This scotoma may be temporary or permanent. Careful questioning of the affected person obtains in most cases the following description: the scotoma is like a coiled snake; the coils approach one another but do not overlap; they are curiously beaded, as if the sun's image produced a small circular blind spot at a point of the retina, and then moved to a neighbouring part of the retina to produce another blind spot; and so on from point to point until a considerable area of retina is affected. This production of a number of separate punctate scotomata was difficult to account for. The cluster hypothesis does, however, offer a feasible explanation, namely, that the sun's image is first caused to fall centrally on a cluster at the fixation spot. When, owing to the intensity of the illumination, this has become affected by a scotoma, the sun's image disappears. The eyes are now rotated by their muscles until another cluster, close to the previous one, receives the image and performs fixation on it. This then suffers the fate of the first cluster, and the process is repeated until exposure to the sun's rays ceases.

A scotoma of the same, or nearly the same, variety may be produced under experimental conditions by looking for a few seconds at a naked carbon arc light, so that the image of the source falls as precisely as possible on the fixation point. The result is a small punctate central scotoma which gradually fades as recovery takes place. Now, if, during the persistence of the scotoma, the observer looks at a test object with the affected eye he clearly sees the scotoma lying close to the test object. If, under these conditions, his acuity be measured it will be found to be a fraction only of his normal acuity, but that vision is quite good enough for normal purposes. According to the cluster hypothesis, what has taken place is that the cluster of cones, usually employed for fixation because of their high acuity, having been temporarily put out of action by the arc light, a neighbouring cluster, not so acute as the first, has taken on the function of fixation.

This argument raises an interesting point, namely, the nature of the attribute which causes the selection of a particular retinal area to act as the fixation point. It would not be unreasonable to expect that this point would lie on the optic axis of the lens system of the eye because the definition here would probably be higher than it is elsewhere. But such an expectation is contrary to the facts. The fixation point is usually situated to the temporal side of the axial point, but varies greatly in position in different people. Tscherning (1904) put the matter as follows: 'Calling the imaginary line which joins the posterior nodal point with the fixation point "the fixation axis" then this line makes with the optic axis the angle alpha which varies usually from 4 to 7° horizontally, and from 2 to 3° vertically' (see Part VII). From these angles we can readily calculate the displacement of the fixation point from the axial point. On the assumption, made previously, that the posterior nodal distance of the eye is 16·81 mm., the fixation point is found to be from 1·13 to 1·99 mm. outwards, and from 0·56 to 0·85 mm. downwards from the axial point. It is clear then that the statement made above is correct, namely, that the fixation point varies in position in different subjects. This raises the question as to the cause of one particular point being selected for purposes of fixation rather than another point. There is little doubt that there is a marked fall in acuity as soon as the fixation point is left, but there is no justification for the supposition that this is due to deterioration in the definition of the image on the retina. If such a failure in the retinal image did in fact occur, as one passed away from the fixation point, then one would expect to find, perhaps, a deterioration as one moved in a direction away from the axial point, but a corresponding improvement as one passed away from the fixation point but towards the axial point. Such, however, is not found to be the case, in all directions there is deterioration; showing that this supposition is incorrect. Since the lens system of the eye is not responsible for the breakdown in acuity, we must seek for the cause elsewhere, for example, in the retina, or in some other part of the organ of vision. It appears to the author that both the choice of a particular fixation point, and the deterioration which occurs when it is departed from, can be accounted for on the cluster hypothesis as follows: cluster formation occurs everywhere all over the retina. In some places these clusters are arranged in a particularly favourable manner. Some of these favourable points occur in situations towards the periphery of the retina where their good qualities cannot be made use of because the retinal image is too poor in definition. Others, however, occur where the definition is good. If one of the latter is found at, or near, the centre of the fovea, which owing to developmental factors is usually on the temporal side of the blind spot, then specially favourable conditions will be met with because the cones in the fovea are more tightly packed than those found elsewhere. Such a favoured spot as this will be ideal as a fixation point, and will be selected for this important function as the result of experience. When, however, this superlative spot is put temporarily out of action, or is destroyed for example by disease, some other spot, not so good as the previous one, but still better than the average, is selected to take over the function of fixation.

(123) *The retinal direction effect*

When Stiles & Crawford first described the retinal direction effect which they had discovered, various possible explanations were discussed. An attractive explanation was that every foveal cone still retains the ancestral property which it shared with its homologue, the omatidium of insects, namely, of being much more strongly stimulated by the ray which coincides with its long axis than by any other ray. The insect type of eye depends largely for its success on this strong directional effect. It seemed not unreasonable to assume that the Stiles & Crawford effect has a similar causation. Take a mammalian eye and replace its retina by the omatidia of an insect eye, moulding the latter so that each omatidium points at the opening of the pupil, and there are the necessary conditions for the production of an artificial retinal direction effect. Stiles (1939), continuing this work, determined the magnitude of the direction effect using red, yellow, green and blue lights. He measured the amount by which a beam of light, which is passing through the periphery of the pupil, has to be increased in intensity in order that it shall match a beam that has passed through the centre of the pupil. With each coloured light a different direction effect was obtained as shown in table 92.

TABLE 92. THE RETINAL DIRECTION EFFECT (STILES & CRAWFORD)

	3 mm.	2 mm.	1 mm.	0	1 mm.	2 mm.	3 mm.
red	4·8	2·7	1·5	1·0	0·9	1·1	1·6
yellow	3·8	2·3	1·4	1·0	0·9	1·0	1·4
green	4·7	2·6	1·4	1·0	0·9	1·1	1·7
blue	5·2	3·2	1·5	1·0	0·9	1·1	1·8

The first three columns refer to the nasal side of the pupil; the last three columns to the temporal side. The largest directional effect is shown on the nasal side at 3 mm. Blue rays require the largest increase, red and green rays a moderate increase, while yellow rays require the least. Thus yellow light does not behave as if it were a mixture of red and green light. This point will be referred to again in Part XI.

Since the directional effects for the colours are different, the conclusion is that the receptors for these colours point at somewhat different parts of the pupil. But this attractive idea meets with difficulties, for if the receptors for these different colours all lie intermingled and closely paired side by side, all interstices being filled up, how does it come about that the red cones all seem to be pointing in one direction, the green cones in another direction, the blue cones in a third direction, and lastly, the yellow cones, if such there be, in a fourth direction? Alternatively, if in fact, by some curious arrangement, the cones of different response do point in different directions, why is evidence of this entirely lacking when sections of the mammalian retina are examined microscopically? To neither of these questions was there a suitable answer, nor was a satisfactory explanation of the retinal direction effect forthcoming. But the cluster hypothesis offers such an explanation. Stiles & Crawford found their effect by comparing the visual luminosities of two narrow beams of light, one of which had passed through the centre of the pupil, while the other passed through some other part which could be chosen at will. Now D'Silva & Turton (1947) have shown that when colorimetric comparisons of brightness or colour are being made, a small, and possibly a very small, part of the retina is actually being used for the purpose. Thus it is quite likely that the clusters of red-sensitive cones near the fixation point, which are used when high pattern acuity is required, are also used for purposes of colorimetric comparisons when red light is in use. Support for this view is obtained from the recollection that, in both form acuity and comparison acuity, it is the perception of a small difference of light intensity on which both really depend. But similar reasoning applies to the green- and the blue-sensitive cones. Now whole clusters might well point in slightly different directions, in fact it would be an extraordinary thing if they did not. We have then, in the cluster hypothesis, a feasible explanation of this retinal direction effect.

(124) *The colours of an intermittent point source*

A small intermittent point source of light was fixed by one eye, and was given small irregular jerking movements. The result was that colour changes, sometimes pink and sometimes pale blue-green, were observed. For the experiment to succeed, the source must be of the correct brightness, it must flash every 1 or 2 sec., and its movements must subtend at the eye from 1 to 10 min. of arc. It was unusual for the colours to be seen without much careful adjustment and prolonged observation. These experiments have shown that four conditions have to be satisfied for the changes in colour to be perceived by the eye. The source must subtend a very small angle at the eye, it must be of a certain brightness, it must undergo small movements, and lastly, it must be intermittent. If any one of these conditions be not satisfied the experiment is found to fail. Any hypothesis which is advanced to account for the colours must also account for all four of these conditions. This the cluster hypothesis is found to do. As is well known, the image of a point source produced on the retina consists of a diffraction pattern. When the source is bright its image stimulates a considerable area of retina. As the source is decreased in brightness the area which it stimulates becomes smaller and smaller. As it is further reduced in brightness the size of its image may be so much reduced that the whole of it can fall inside the limits of a single cluster or even on a single cone. Now only two varieties of clusters respond in the case of very small objects, owing to the action of the antichromatic response: those responding to red light and those responding to blue-green. As pointed out in § 119, every red cluster contains a few green elements, and vice versa. Thus even when the image of a point source falls entirely inside the boundary of a cluster it does not stimulate red cones only, or green cones only, but many red cones and a few green cones, or the reverse. Also there will always be some stray light falling on odd cones outside the cluster. In consequence, the colour of a point source will never be a pure red, or a pure blue-green, but always dilute shades of these colours: namely, pink and pale blue-green. If, however, the point source be insufficiently bright, even when its image does fall entirely on a single cluster, the colour produced by that cluster maynot be perceived because vision is colourless, since the intensity is below the threshold for the perception of colour as Abney (1895) has shown. The cluster hypothesis thus accounts for four of the observed facts: (1) why a point source must be used; (2) why its intensity must lie between certain limits; (3) why colours are seen so rarely; and (4) why only pale colours are seen. We have still to account, on the cluster hypothesis, for the necessity for the source of light to be intermittent, and for it to be moving. Movements are necessary in order to prevent fixation of the source by the eye, because the source, consisting as it does of white light, would comprise green rays which are sharply focused, and red and blue rays which are not. Further, the green rays have the greater luminosity, the result being that a green cluster is selected for fixation. By moving the source this fixation by a green cluster is prevented. If a continuous source of white light be moved so that its image is continually changing its position on the retina, then even if, by chance, that image falls on the centre of a cluster, for example, a red cluster, the colour, which would normally be produced by that cluster, will not be seen, because repair of the image occurs, as will be explained in Part XII (see § 162, p. 665).

If, on the contrary, the point source is an intermittent one, the process of repair is interrupted, and in consequence, when the image does chance to fall on a cluster the colour produced by the stimulation of that cluster reaches consciousness. Thus we see that the cluster hypothesis is able to account for all the facts that have been mentioned in this section.

The above experiment with an intermittent light source, was performed with a focus type, 3 V electric bulb, the brightness of which was controlled by means of a resistance. The bulb had to be reduced from full brightness by being underrun—from 1·5 to 2 V appeared to be most suitable.

Two other examples of colours produced by intermittent sources have recently been observed, in which no physical explanation appeared to be available: sunlight reflected from water which was being ruffled by the wind, and light reflected from small particles in a non-skid surface. These examples will be referred to again in Part XI.

(125) *The arrangement of the foveal receptors*

Evidence has been produced in § 120 that each primary colour has a fixation point peculiar to itself, and that to some extent the positions of these points relative to one another can be determined. In § 121, as a result of examining the phenomenon of retinal astigmatism, the suggestion was advanced that in the author's left retina the fixation point for green rays was T-shaped, L-shaped or +-shaped. It is proposed, in this section, to endeavour to ascertain in greater detail the arrangement of the photoreceptors of different colour response at, or near, the fixation point.

Before describing the method, and the results which have been obtained, it should be emphasized that the technique described in this section, and in § 120 above, is in its infancy. It may be that the use of improved methods will necessitate some revision in the conclusions to be presented here.

The test object employed consisted of two tiny disks of coloured paper, one green and one grey, mounted on a black background with their centres 3 mm. apart. As before, the background had an octagonal shape so that it could be stood in one of eight positions. This test was placed about 4 m. away from the observer's light-adapted eye. In front of the latter was placed a lens of 0·88 D and this was decentred so as to correct the chromatic difference of magnification at the fixation point, as explained in § 120. The observer carefully fixed the green disk, but noted the colour of the grey one, with the results shown in table 93.

TABLE 93. THE APPARENT COLOURS OF A TEST DISK AT DIFFERENT POSITIONS IN RESPECT OF THE GREEN FIXATION POINT

position	apparent colour	photoreceptors stimulated
above	grey	blue
above and left	pink	red
left	pale blue-green	green
below and left	pink	red
below	pale blue-green	green
below and right	grey	blue
right	pale blue-green	green
above and right	pink	red

We see, from table 93, that the grey disk varies in colour according to its position, and that the colours seen are pink and a pale blue-green similar to that seen when a green test object subtends a small angle at the eye. This suggests the idea that the perception of green is due to the stimulation of green receptors, but that the tint observed has been modified by the antichromatic response. If such is indeed the case, is it not possible that when grey is perceived it is due to the stimulation of blue receptors, but that in this case also the tint observed has been modified by the antichromatic response? In order to elucidate this point similar tests to the above were performed using two disks, one green and one blue, fixation as before being on the green, but the colour of the blue one being recorded. The results obtained are substantially the same as those shown in table 93, the blue disk appearing grey when above the green, or when below, and to the right of it, just as the grey one had done. This confirms the view that the antichromatic response is modifying the colour of the blue test object by the substitution of grey as has been described previously.

An attempt will be made to link together the pieces of evidence which have so far been obtained, to see if a provisional plan can be worked out for the positions of photo-receptors of different colour response at or near the green fixation point. To this problem there are probably a number of solutions; one possible one is given in table 94.

The plan given in table 94 fits in with the three pieces of evidence which are at present available: that given in this section; that given by retinal astigmatism, namely that the green fixation point has well-marked vertical, and horizontal components associated with it; and that given in § 120, namely, that the red fixation point is down, and to the left from the green fixation point; that the blue one is to the right of the red one; and lastly, that the blue one is down, and to the right of the green one. On the assumption that table 94 gives a rough indication of the positions of these colour-sensitive areas, the question arises as to the scale of the plan. The test objects used in this section, and in § 120, consisted of coloured disks roughly 3 mm. diameter. These were viewed by the observer at a distance of 3 to 4 m. They therefore subtended at the eye an angle of about 160 sec. of arc, that is that their images on the retina, according to the rules of geometrical optics, had diameters a little over three times that of the average diameter of the foveal cones. The effect of decreasing the diameters of the test disks was tried, but the results appeared to be less clear than before; increasing them on the other hand, until the diameters of their retinal images were 5 cone units, appeared to improve the brightness of the colours. It was assumed that this was due to the images of the test objects falling more exactly on the clusters of different colour response than they had done previously. On increasing the sizes of the retinal images of the test objects still further, a less satisfactory result was obtained. When the best result was obtained the test objects stimulated about 25 cones each, and the plan shows nine positions for these objects, so that the whole plan includes about 225 cones. Each side of the plan, therefore, measures 15 cone units. The plan itself is only a crude one, giving rough indications of the arrangements of the cones which it includes. What is wanted now is a study of each separate cone, so that its spectral response curve may be ascertained. When this has been done, information should be obtained of the area surrounding that covered by the plan. At the moment only meagre evidence is available concerning this surrounding area. There is, however, a little information about the T-shaped sensory area for green rays which may be stated briefly as follows. The vertical limb of the T does not extend far in a downward direction as is shown by the experiments described in § 120. It was found there that the area of maximum acuity for green light is not much larger in diameter than 8 cone units. Assuming the point for accurate fixation to be situated at the centre of the plan, then the lower limit of the T is not much more than 4 cone units from that centre, that is that the T-shaped area terminates very close to the lower edge of the plan. With regard to the horizontal arms of the T some indication of their length can be obtained from a consideration of the reading of short words. If various words consisting some of three letters, some of five letters, and some of seven letters, be viewed at such a distance that the separate letters are just legible, and if in each case the middle letter be fixed by the eye, it is found that the words of three letters can be read easily, the words of five letters can be read with some difficulty, while those of seven letters can be read hardly at all. The long axes of the five-letter words were found to subtend at the observer's eye an angle of about 12 min. of arc, so that the length of the image of such a word on the retina would be about 16 cone units. Now this is approximately the length of the horizontal arms of T so that

TABLE 94. PLAN OF CONES AT CENTRE OF FOVEA

red area	blue area	red area
green area	green fixation area	green area
red fixation area	green area	blue fixation area

(This plan is inverted on the retina.)

it seems unlikely on this evidence that they extend far beyond the boundaries of the plan.

This provisional plan of the fixation area of the fovea and the T-shaped sensory region which it contains agrees in a satisfactory manner with the experiments of Vernon (1930) on the movements of the eyes during reading. She confirmed the fact that, instead of moving steadily along a line of print, the eyes perform a series of small jerks, with pauses between the jerks during which the eyes remain stationary. According to the cluster hypothesis these pauses enable fixation to occur, and this is accompanied by the perception of the exact shapes of the letters as their images fall on the horizontal limbs of the area with maximum acuity for green rays. As pointed out previously (§ 6, p. 527) these rays play the major part in vision by white light because the red rays and the blue rays form diffuse unfocused images owing to the chromatic aberration of the eye.

X. THE MICRO-STIMULATION OF THE HUMAN RETINA

Micro-stimulation consists in applying to the human retina, narrow, accurately focused pencils of light. A special apparatus has been designed for this purpose, which is composed essentially of a microscope used in reverse. The objects to be presented to the observer's eye are placed so that light from them passes in at the eyepiece of the microscope via a right-angled prism. The rays then emerge from the objective, to reach the observer's eye after reflexion in a plain mirror. The optical constants of the micro-stimulator which is being used at present, are such that each centimetre on the stage of the micro-stimulator corresponds to 1 cone unit, that is, to the probable diameter of an average foveal cone.

(126) *Micro-electrode and micro-stimulation methods contrasted*

Test objects have long been employed in order to ascertain the presence of visual abnormality. Of recent years they have been used to determine the properties of the lens system of the human eye and also those of the retinal receptors, both when used for day, and for twilight vision. In §§ 114 and 116 they have been used for ascertaining the special properties of small areas of the fovea which surround the fixation point. In this research an attempt is made to find out the individual responses of the retinal receptors. A special apparatus has been designed for this purpose which has been called a retinal micro-stimulator. This has already proved useful in other pieces of research.

In recent experiments on animals using his micro-electrode technique, Granit (1943 and 1945) has shown that it is possible to ascertain, with considerable precision, the physical properties of the different receptors which are present in the retina. His method consists in stimulating the retina by lights of known wave-length, and observing the frequency of the nerve impulses which travel from the retina up single fibres of the optic nerve. He finds that there are present in most animals both dominators, with a broad spectral response, and modulators, each of which has a response limited to a narrow region in a particular part of the spectrum. So far his method has not been applied to man, and it is not easy to see how this could be done without risk; for the optic nerve and its connexions are normally out of reach of electrodes, even micro ones, without the subject of the experiment first undergoing a serious operation. It is possible that a patient being operated on for some other purpose, e.g. for the removal of a neoplasm, might submit himself to the application of Granit's method. This is always a possibility which should be kept in mind.

But in the meantime it seems to be desirable to ascertain if similar information cannot be obtained in the case of man, in some other way. Since it is impossible by the use of Granit's technique to detect what is taking place in a very limited part of an observer's retina as the result of general stimulation, it is proposed, instead, in this research, to investigate the possibility of stimulating a very limited part of the observer's retina, by a narrow pencil of light, placing dependence on his ability to describe with sufficient accuracy what the results of that stimulation are. The use of this method appears to be fully justified, because the eye of the observer does not undergo surgical interference of any kind. During the experiments the observer is asked to state whether a given light source increases or decreases in brightness, or alters in colour. These are questions with which he is familiar, and to which he should be able to return a correct answer. From his answers and the readings of the scales of the apparatus, are inferred the physical properties of the retinal receptors, which are receiving stimulation.

The two methods, that used by Granit, and that to be described in this communication, may be contrasted as follows: in both methods the eyes are stimulated by monochromatic lights of chosen wave-length. In Granit's method the light is applied generally to the retina, the cornea, crystalline lens, etc., having been removed. In the author's method the light is applied to the retina, as locally as possible, in a sharply focused narrow beam, the lens system of the eye playing its usual role. In Granit's method the response is detected electrically by the use of a micro-electrode applied to a single optic nerve fibre. In the author's method the response is detected and assessed by the observer's visual centres. The apparatus used is as follows. Both Granit and the author employ a spectro-illuminator for obtaining the monochromatic light which is used to stimulate the retina. Granit uses in addition a balanced valve-amplifier of high gain and a loudspeaker, in order to ascertain the degree of stimulation of the optic nerve fibre with which the micro-electrode is in contact. The author, on the other hand, uses a micro-stimulator for applying an extremely small point source of spectral light to a known part of the observer's retina. Granit's method requires that the eye should remain quite still in order that the micro-electrode may stay in contact with the required fibre of the optic nerve. The author's method also requires the eye to remain still, for even slight eye movements will displace the beam of light on the retina.

(127) *The purposes of the method*

Ever since the time of Hering, there have been rival theories of vision. Hering's theory (1874) itself receives little support to-day, but several other rival views have taken its place. Some of these are:

(1) That every retinal cone resembles every other cone by responding to all the parts of the spectrum. This is one of the basic principles of Edridge-Green's theory of vision.

(2) That the retinal cones form three groups, one principally sensitive to red light, another principally sensitive to green light, and a third principally sensitive to blue light. This is the basis of Thomas Young's theory of colour vision.

(3) That there are a number of different groups of retinal cone responding individually to different parts of the spectrum. This theory which was advanced by Wundt, has been recently substantiated, for the retinae of many animals, by the micro-electrode technique of Granit.

(4) That the retinal receptors, whatever their responses may be, are not distributed in the retina in a uniform pattern, but are collected into groups or clusters. Some evidence for the cluster hypothesis has been described in Part IX.

The object of this communication is to describe the apparatus which has been designed for the elucidation of the responses of the retinal receptors to lights of different colour, in order to determine which of the three rival views mentioned above is correct, and to ascertain if additional evidence for cluster formation can be obtained.

(128) *The correction of aberrations*

In order to micro-stimulate the retina it is necessary that the most perfect image of external objects be produced on the observer's retina by the lens system of the eye. In the first place, it is required to correct in the most exact way possible, not only such errors of refraction as hypermetropia, myopia and astigmatism, but also such intrinsic errors as chromatic difference of magnification and spherical aberration. The correction of the refractive errors is a comparatively simple process. The correction of the intrinsic errors, mentioned above, is far more difficult. So far as the author is aware no one has succeeded in eliminating, by means of external lenses, both chromatic difference of focus and chromatic difference of magnification at the same time. Ordinary achromatizing lenses which correct effectively chromatic difference of focus, introduce as a rule chromatic difference of magnification of their own. Moreover this alters in amount with any lateral displacements of the optical axis of the eye in relationship with the optical axis of the correcting lens. Such lateral movements must be allowed to take place. Because of these difficulties the method adopted, for the experiments to be described in this communication, avoids so far as is possible the need for correcting the chromatic difference of focus of the eye, by using monochromatic, or nearly monochromatic, beams of light. With regard to chromatic difference of magnification, however, correction is not difficult. It was found that it could be eliminated for all practical purposes, by decentring the convex lens which was placed before the observer's eye in order to correct his refractive errors. In the case of an observer who does not need such a lens, a weak crown-glass prism, of suitable power, would be required with its base probably on the temporal side of the optic axis (see §104, p. 594).

Spherical aberration does not form an important error when small pupils are being used, but it becomes increasingly important as the pupil is dilated. For these reasons the use of an artificial pupil is indicated. Here again, however, difficulties present themselves because it is very difficult to prevent relative movements between the optical axis of the observer's eye and the artificial pupil. The dental-impression method can be used for keeping the observer's head in a constant position, but this does not ensure that the optic axis of the eye will be fixed in relationship with an artificial pupil unless the observer is always looking at one fixation point. Such is not the case in the present research, since it is often necessary for the observer's gaze to follow a moving test object. If movements of the eye occur relative to a fixed artificial pupil, then, as Einthoven (1885) pointed out, variations must also occur in the chromatic difference of magnification of the eye, thus making a correction of this latter error uncertain. For these reasons it seemed best to avoid the use of an artificial pupil altogether and to take steps to prevent the natural pupil of the eye from exceeding

4 mm. This result was achieved by preserving light adaptation and by performing the experiments in a room lit by ordinary daylight of adjustable intensity.

Diffraction, being a property of light, cannot be eliminated from normal vision. The size of the diffraction pattern, however, as is well known, varies inversely with the size of the pupil, as shown in table 95. For this research it would obviously be advantageous to make the diffraction pattern as small as possible, so that a 4 mm. pupil would be better than a 3 mm. one, and a 5 mm. pupil would be better than either. There is, however, the risk of introducing peripheral aberrations when large pupils are being employed. For this reason it was decided to use a pupil as near as possible 4 mm. diameter. For reasons stated above, the natural pupil is superior to an artificial one. The method adopted therefore, was to adjust the curtains in the laboratory so as to admit more or less daylight until the pupil had been adjusted to approximately this diameter.

TABLE 95. DIAMETER OF FIRST DARK RING OF DIFFRACTION PATTERN AT DIFFERENT PUPIL DIAMETERS

		pupil diameters		
colour of light	wave-length (A)	3 mm.	4 mm.	5 mm.
red	7000	0·0094	0·0070	0·0056
yellow	6000	0·0080	0·0060	0·0048
green	5000	0·0067	0·0050	0·0040
blue	4000	0·0053	0·0040	0·0032

Reference to table 95 will show that with a 4 mm. pupil even green light produced a diffraction pattern substantially larger in diameter than that of a foveal cone. Nevertheless, when the centre of the diffraction pattern falls on the centre of a cone, calculation shows that owing to the shape of the pattern the greater part of the light falls on this cone, and only a little light on the cones which surround it. Thus if with green light of 5600 A the central cone receives light equal in intensity to 100, then the ring of cones immediately surrounding it receives light having an intensity of less than 10. The ring of cones which surround this inner ring receives light equal in intensity to less than 2 and so on. It is possible that the use of a Zernike (Linfoot 1945) quarter-wave disk would materially improve the concentration of light on the central cone. The idea of using such a disk at some future date is being kept in mind.

(129) *The effect of intensity of illumination*

As soon as stimulation of the retina began, with the apparatus described above, it was found that not only did the precision of focusing play an important part in determining the apparent size of the image, but also the intensity of illumination. In fact the sharpest image was obtained if both focus and intensity were adjusted at the same time. The following observations were made with the fixation lamp at its brightest, its image being examined critically with the reducing apparatus. With a lens of 1 D before the observer's eye, the image of the fixation source as seen in the apparatus appeared to consist of a disk of finite size with a bright sharp edge. With a lens of 1·25 D the image was smaller, but several narrow bright streaks were seen to proceed from it for a short distance. With a lens of 1·5 D the image was still smaller but the streaks longer and more obvious. If with this lens in use the source was diminished in brightness, then it was found that the streaks became shorter and narrower until finally they disappeared altogether. At the same time it was noticed that the image itself became sharper and smaller. This was the adjustment that was always aimed at, namely, that which produced the sharpest possible image. As mentioned in the next section this image at its sharpest has an apparent diameter little larger than that of a foveal cone. This adjustment for minimum size of image appears to be the crux of the situation, so far as concerns the attempt to stimulate, and thus ascertain the properties of, single foveal cones.

(130) *The distribution of light on the foveal receptors*

As mentioned above (§§ 19 and 20), there is considerable ambiguity both in the average diameter of human foveal cones and in the posterior nodal distance of the lens system of the eye. Allowing for shrinkage, a tentative estimate of the distance from the centre of one cone to the centre of the one next it is about 0·00336 mm.

The above calculations were checked in the following manner: two green lines, 2 mm. wide, were mounted parallel to one another on a black background with their centres 12 mm. apart. They were now placed in bright sunlight and examined at various distances until one was found at which the black space between the lines appeared to be equal in width to the images of the lines themselves. When this was the case the apparent width of either of the bright lines, which is partly due to diffraction and aberrations, was equal to half the distance between their centres, i.e. 6 mm. The distance between test object and observer was found on successive trials to be 19, 20, 19, 20, 21, mean = 20·2 m. At this distance the width of a cone would correspond to about 4 mm. (see § 21, p. 537). The apparent width of the bright lines was, therefore, about 1·5 times the width of a cone, assumed in the previous section. Now part of the apparent width of the bright lines was due to their actual width, viz. 2 mm. If the lines could be made infinitely narrow their apparent width would probably be less than in fact it is. In other words the apparent width of the images of the bright lines on the retina would be little larger than the diameter of a foveal receptor. This confirms the calculations referred to at the beginning of this section and shows that the effective definition of the retinal image is quite good, justifying an attempt to stimulate single receptors, or small groups of receptors by means of a controlled narrow beam of light.

The above experiment has been repeated using silver-paper lines 1 mm. wide on a black background. The centres of these lines were also 12 mm. apart. It was found that for the images of these lines to be half the width of the distance between their centres, the observer had to be about 24 m. from the test object. At this distance the width of a cone corresponds to roughly 4·8 mm. so that the apparent widths of the bright lines (6 mm.) is equal to 1·25 cone units. This confirms the idea that with infinitely narrow bright lines as test objects the apparent widths would be little greater than 1 cone unit. For this reason in the apparatus to be described in §§ 131, 136 and 140, the sources were kept as small as possible, corresponding usually from one-fifth to one-tenth, of a cone unit.

(131) *The micro-stimulation apparatus*

There are several ways of producing a small but accurate image on the retina. The advantages and disadvantages of these methods will be briefly considered.

(1) Test object of moderate size situated at a considerable distance. A skilled assistant to manipulate the test object is essential.

(2) Test object of moderate size reflected in a mirror. This method requires half the distance of method (1) and the observer can manipulate the test object for himself. The mirror must be of the highest optical accuracy.

(3) Very small test object situated at a moderate distance. This method requires an accurate distance control of the test object by means of levers, screws or Bowden cables.

(4) Test object of moderate size, reduced by means of an optical device, the apparatus being so arranged that the observer can easily manipulate the test object for himself.

Of the four methods the last was selected for the purposes of this research.

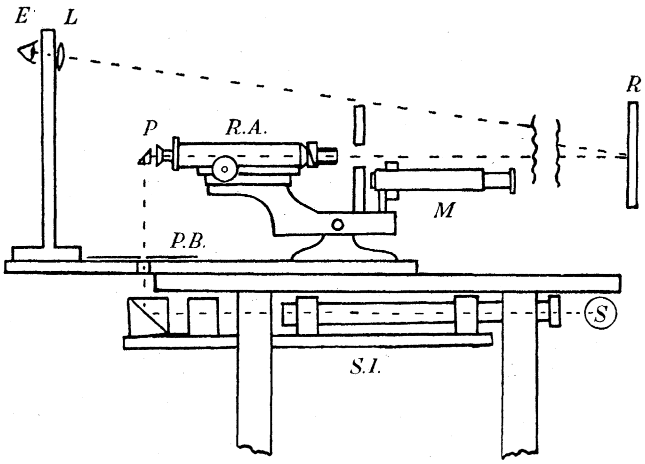

FIGURE 2. Diagram of apparatus. *E*, the eye of the observer; *L*, the correcting lens; *R*, the plane reflector; *M*, microscope for observing image when required; *R.A.*, reducing apparatus; *P*, right-angled prism; *P.B.*, plotting-board; *S.I.*, spectro-illuminator; *S*, source of light for spectro-illuminator.

Reference to figure 2 will disclose the arrangement of the apparatus. The observer sits at a table. In front of him, close to his hand is a black plotting-board which is divided by pencil lines into squares which are numbered consecutively. These lines reflect light with sufficient brightness for them to be readily seen by the experimenter. Below the table is mounted the spectro-illuminator (see § 134). The light from this is projected vertically upwards through an aperture in the plotting-board; but arrangements are also made so that white light, or coloured lights produced by filters, may be used instead. Above the plotting-board is a right-angled prism which directs the rays horizontally through an apparatus for reducing the size of the image (see § 136). The observer looks at the end of this apparatus through the plain mirror shown in the diagram. He is provided with a chin rest so as to assist in keeping the head still. Each eye is tested separately, the necessary correcting lens being placed in front of the eye under test.

It will be noticed that the light suffers two reflexions on its way from the plotting-board to the eye of the observer. Its first reflexion is at a right-angled prism. Its second reflexion is at a plane mirror. This arrangement has the following advantages. The plotting-board being horizontal, test objects placed on it remain in position; the line of sight is horizontal; and a movement of a test object on the plotting-board is seen as a corresponding movement of its image appears in the mirror; thus if the test object is moved downwards, and to the left, its image is seen to move downwards and to the left also. All these points add to the convenience of the apparatus.

A lathe slide-rest was fitted to the front of the plotting-board, so that precise movements in two directions at right angles could be given to the movable light source. Using the slide-rest, the observer could cause the light source attached to it to move to and fro in horizontal or vertical directions, as required. The gaze being directed at the source, which was controlled by the slide-rest, as seen in the reducing lens system, the image of the fixed source was caused to travel from point to point of the fovea, as might be required. This arrangement was found to perform in an entirely satisfactory manner, without the aid of an assistant. For much of the work described in this and recent communications, no laboratory assistance was available. The making of new apparatus and alterations to existing apparatus had to be carried out by the author.

(132) *The scope of the method*

The apparatus referred to in the previous section can be used for a variety of different purposes.

(1) Ordinary test letters and characters, greatly reduced in size, can be presented to an observer.

(2) Alterations can readily be made in the amount of the reduction, in the intensity of illumination of the test object, and in the spectral composition of the light employed.

(3) Modifications may be made in the test object during observation, since it lies on the table immediately in front of the experimenter.

It is in the latter respect that the apparatus proved to be specially useful for this research. The observer looking in the mirror sees the reduced image of the plotting-board. Through the centre of the latter is projected the test beam of monochromatic light. A beam of white light, or coloured light, produced by colour filters can be used instead if desirable. On one of the squares of the plotting-board is placed the source used for purposes of fixation (see § 133) This is seen by the observer as he looks in the mirror, and he fixes it as accurately as possible. By shifting the fixation source to different positions on the plotting-board the experimenter causes the image of the test source to fall on different parts of his fovea in turn. In this way observations may be made at any part of the fovea which may be required.

This apparatus has proved itself useful for many of the experiments which are described in this paper in

Part IV. The effect of a long distance on colour.
Part V. The ray of optimum focus for white light.
Part V. The chromatic difference of focus of the eye.
Part V. The widths of the chromatic fringes.
Part VI. The spectral response of the four antichromatic mechanisms.
Part VII. Chromatic stereoscopy.
Part VII. Chromatic difference of magnification.
Part VII. Chromatic properties of a lens.

Part VIII. Spectral transmission of colour filters.
Part IX. Visual acuity at the fovea.
Part XI. Nearly all the experiments described in this Part.
Part XII. Many of the experiments described in this Part.

(133) *The process of fixation*

As pointed out above, for purposes of fixation a ray of medium wave-length is indicated, because when the eye is used in normal vision these are the rays which are shown by experiment to form the most sharply focused images on the retina (see § 4, p. 525). Granit using his micro-electrode technique, found that there were two varieties of modulators approximating to the yellow-green, those having a maximum response at 5800 A and those with a maximum response at 5400 A. Of these the former are much the more rare in the retinae of the various mammals which he examined. Assuming that these are also present in the human retina, a wave-length between these two, namely one of 5600 A, would appear to be indicated for purposes of fixation.

As pointed out above, the fixation point consists of a small battery-driven electric lamp. The filament of the lamp is a tightly-wound wire spiral which, viewed from above, measured about 0·7 and 0·2 mm. It will be shown in § 135 that the dimensions of the apparatus are such that 10 mm. on the plotting-board corresponds to 0·00336 mm., i.e. the width of a foveal cone. The filament of the fixation lamp is, therefore, less than one-tenth the diameter of a cone. This small size was used in order to keep the retinal image of this source as small as possible.

The fixation source was controlled in intensity by means of a variable resistance. The purpose of this will be described later.

(134) *The spectro-illuminator*

The spectro-illuminator consisted of a Hilger constant-deviation spectroscope with two collimators mounted at right-angles to one another. Both of these were fitted with slits. On one of these the source of light was focused. Through the other the selected part of the spectrum passed on its way to the rest of the apparatus. The following arrangements were tested:

(1) The image of the exit slit was focused by means of a lens on to the aperture in the plotting-board, the result being that the observer looking in the mirror would see a greatly reduced image of this slit produced by the reducing lens system.

(2) An image of the slit was focused on the prism of the reducing apparatus. It was found that very careful adjustment of the position of this image was required, because otherwise there was a serious loss of light.

(3) The second collimator was omitted and the rays from the flint-glass prism of the spectroscope were reflected by means of a right-angled prism through the aperture in the plotting-board on to the prism of the reducing lens system, suitable lenses being mounted in the plane of this aperture so that a sharp image of the spectrum was projected on to the latter.

Of these methods, the third was found to give the most satisfactory results, so far as ease of adjustment and brilliance of illumination were concerned. With regard to the spectral purity given by this method the facts are as follows: an image of the observer's pupil is in effect projected by the second lens of the reducing apparatus, that is the objective, into its own upper focal plane. With a 4 mm. pupil, a distance between instrument and observer of 1·8 m., and an objective of 40 mm. focal length, the size of this image is approximately 0·10 mm. Now an image of this aperture is projected by the first lens of the reducing apparatus into its own upper focal plane. This lens, the eyepiece, has a focal length of 60 mm. If then the tube length is 160 mm., the Ramsden disk will have a diameter of 0·03 mm. It is this small aperture which selects the part of the spectrum which is to be transmitted to the observer's eye. The spectrum was approximately 30 mm. in length. In consequence, approximately one-thousandth part of the spectrum is transmitted at any one time to the observer's eye. This is approximately equivalent to 3 A for a ray of medium wave-length. For long waves the purity will be less and for short waves the purity will be greater than 3 A. It was considered that this degree of purity was quite sufficiently high for the purpose of these experiments, and in consequence the third method was adopted in setting up the spectro-illuminator. The aperture in the plotting-board through which the monochromatic beam is projected has a diameter of 2 mm., that is, its image on the retina, produced by the apparatus, has a diameter of about one-fifth the diameter of a foveal cone. It was found that the spectral purity of the monochromatic beam could readily be gauged by placing a prism grating in front of the observer's eye. This dispersed the beam into a bright line, the length of which was a measure of the purity of the beam. The wave-length of the beam was read off from the drum of the spectroscope which had been previously calibrated.

(135) *The optimum dimensions of the apparatus*

As pointed out above (§§ 126 and 127), the object of this research was to stimulate if possible a single foveal receptor. It would obviously be necessary in the first instance to form images on the retina of such small dimensions as to be within the limits of one receptor or of a very small group of receptors. Further, it would be advantageous to know approximately what amount of movement of the fixation point must take place in order that the beam of light, used for testing purposes, may be transferred from one receptor to its next-door neighbour.

As pointed out in Part I, we have no precise knowledge of the dimensions of a foveal receptor, neither do we know exactly what is the posterior nodal distance of the human eye. It has been assumed for the purposes of this research that the mean cone diameter is equal to the distance from the centre of one cone to the centre of the next one to it, and that these are equivalent to a distance of 2 mm. at 10 m. distance from the observer, that is to 1 cone unit (see § 21).

It is obvious that the squares on the plotting-board can be made of any dimensions, and that these can be made to subtend any required angle at the eye. A very convenient size for the squares would be 10 mm. because this would enable the fixation mark to be easily adjusted by hand with an accuracy of 1 mm. and, if it proved to be necessary, with an accuracy of 0·1 mm.

If then the dimensions of the apparatus were such that 10 mm. corresponded to 1 cone unit, then a movement on the plotting-board of 1 mm. would move the retinal image a distance equal to 0·1 cone unit; and if necessary a movement of 0·01 cone unit could be effected. Now for 10 mm. to correspond to 1 cone unit, it would be necessary for this length to be viewed at a distance of 50 m.

Suppose that the reduced image of the plotting-board, produced by the reducing lens system, be 1 m. distance from the eye, the reduction required of this lens system would have to be 50 to 1. The required reduction was obtained by using a two-stage lens system; the first lens, the eyepiece, producing a reduced image of the plotting-board, which was then reduced a second time by the second lens, namely, the objective. Further details of this reducing lens system will be given in the next section.

(136) *The design of the reducing lens system*

It was decided that a practical form for the reducing apparatus would be to use an ordinary microscope the reverse way round, by presenting the object to the eyepiece, and by causing the observer to look at the lower end of the objective. It is clear that a reduction of 50 to 1 could be obtained by various combinations of eyepiece and objective. A Zeiss projection eyepiece of 4 diameters magnification was available, and this had a focal length of approximately 60 mm. There was also available a Baker semi-apochromatic objective of about the same focal length. When these were used together they were found to have approximately the correct reducing power. This could be adjusted to precisely the required value by altering either the distance between the plotting-board and the eyepiece, or the distance between objective, the mirror and the observer's eye, or both distances.

The distance between the plotting-board and the eyepiece must obviously not be made too large, for otherwise the observer would not be able to see over the top of the instrument (as shown in figure 2). A height of 30 cm. was found suitable. If the distance between the objective of the reducing lens system and the eye via the mirror was made 1·7 m., the required reduction, was found to be achieved.

Now a microscope has, as a rule, extremely good central definition, but not such good peripheral definition. This might be a disadvantage in this instrument. In the case of high-power microscope objectives, and eyepieces, there is usually considerable curvature in the peripheral parts of the eyepiece field, and the definition of rays passing through the periphery of the objective bears no comparison with that of central rays. In this instrument both objective and eyepiece are of low power and in consequence marginal aberrations are not serious. Tests on this point will be described in the next section. The procedure adopted, however, was such that the rays from the spectro-illuminator passed through the centre of the system where the definition was good, and the rays from the fixation light, which are not so important, pass through a less good part of the lens system.

For different purposes images of different sizes would probably be required. The degree of reduction can be altered at will by the use of objectives of different focal length. In order to facilitate this alteration Zeiss objective changers were used.

During the preliminary tests of the method a reversed telescope was used in place of a reversed microscope. Instead of looking at the aerial image of the test object, which was produced in the lower focal plane of the microscope objective and which was situated some little distance from him, the observer looked directly through the telescope objective at the aerial image, as if he were looking at a distant scene through an aperture in a partition. Each of these methods has its good points, but the following were in favour of the microscope method: changes in the degree of reduction are more readily effected; the eye is less dependent on the corrections of the objective; and the correction of the chromatic difference of magnification of the eye (see § 104) is optically simpler.

In cases where the degree of reduction required is not large, and where the correction of the chromatic difference of magnification of the observer's eye is not wanted, a telescope, or even an opera-glass of suitable power, held in the hand makes a convenient and simple reducing lens system.

(137) *Tests of the reducing lens system*

Tests of a very searching kind should be applied to any apparatus of new design. These are particularly necessary in the case of the instrument described in this communication, because one essential part, the reducing lens system, is being used for a purpose for which it was not originally designed, in fact the rays of light are passing through it in the reverse direction to the normal. Table 96 lists those tested or measured.

TABLE 96. THE TESTS OF THE REDUCING LENS SYSTEM

definition, both central and peripheral
secondary spectrum
diffusion
flatness of field
distortion
flare
uniform illumination
ratio of reduction
diameter of field
dimensions of fixation source
dimensions of test source

For these tests and measurements a microscope fitted with a Leitz step-micrometer was mounted in line with the reducing lens system so that an image, magnified approximately fifty times, was presented to the eye of the observer. Before the definition was examined it was necessary to make certain that the spherical and chromatic aberrations of the reducing lens system had been reduced to a minimum. The former is controlled by 'the tube length', that is the distance between the objective and the eyepiece. The latter is controlled by 'the eyepiece adjustment', that is the distance between the two eyepiece lenses. The tube length was adjusted using the method of testing previously described by the author. The eyepiece was adjusted by trial and error until the margin of the objective field was as free from colour as possible.

The definition was examined, using as test object a sheet of print which had been selected for the clearness of its characters. This was mounted as flat as possible on the plotting-board. Definition was found to be good, for in spite of reduction and remagnification the print would have been easily legible if it had not been transposed from right to left by the prism of the reducing lens system. As was to be expected, there was some falling-off in definition in the extreme periphery. It was anticipated, since apochromatic lenses were not in use, that slight coloured fringes would be in evidence due to the uncorrected secondary spectrum. These were difficult to observe with the print test object, but their presence was disclosed when the fixation source, without a colour filter, was brought into use. The amount of diffusion was determined in the following manner. A brass disk with an aperture measuring 7·05 mm. drilled in it, was placed in the centre of the plotting-board, and a beam of light passed through it into the reducing apparatus. The image of the aperture was measured by the micrometer microscope, and its diameter was found to equal 15·8 scale divisions. A millimetre scale was now placed on the plotting-board and 15·8 scale divisions was found to equal 7·34 mm. The amount of diffusion was, therefore, equal to 7·34 − 7·05 = 0·29 mm. But this diffusion was due to the use of two instruments in series of about the same power, the reducing lens system, and the micrometer microscope. It seems reasonable to suppose that roughly an equal amount of diffusion is produced by both, namely, 0·15 mm. This is negligible in comparison with the dimensions of the test and fixation sources, and of the projected size of a foveal cone (see table 97).

The field was found to be flat, and distortion was not noticeable. There was no sign of flare. The illumination of the field appeared to be uniform. The ratio of reduction of an object placed on the plotting-board was found to be 29·4 to 1. The diameter of the field was 3·66 mm. which corresponds to a circle on the plotting-board of 10·8 cm. Thus 10 mm. on the plotting-board corresponds to 0·34 mm. in the field of the reducing lens system. This viewed by the observer at a distance of 1·7 m. would correspond to 2 mm. viewed at a distance of 10 m., namely, the standard size and distance proposed in § 21. The distance between the centre of one foveal cone and the centre of the next one to it would thus correspond to 10 mm. on the plotting-board as proposed in § 135.

TABLE 97. DATA OF THE REDUCING LENS SYSTEM

	size on plotting-board (mm.)	size in reduced field (mm.)
cone diameter	10	0·34
fixation source (length)	1·83	0·062
fixation source (width)	0·44	0·015
test source diameter	2·74	0·093
field diameter	108·0	3·66
amount of diffusion	0·15	0·005

The values given in table 97 for the fixation and test sources are the sizes of the images in the field of the reducing lens system. It will be noticed that both are smaller than the projected size of a cone (see § 21).

The conclusion reached, as a result of these tests and measurements, is that the projection lens system is adequate for the purposes of this research.

(138) *The stimulation of single cones*

It is clear that in spite of the efforts which have been made in the design of the apparatus to stimulate one cone and one cone only, this ideal may fail to be achieved. This may be due to two different causes: (1) to the retinal image not having the required definition, (2) to the image falling on more than one cone, owing to the centre of the image not coinciding with the centre of a cone. In either case the effect will be to present to the brain of the observer an impression which is due to a process of summation of the effects of stimulating the several cones. Suppose, for example, on changing the wave-length of the light from the spectro-illuminator that there are found to be three points in the spectrum where a bright effect is produced, with intervening spectral areas where the effect is not so bright. This effect may either be due to the stimulation of a single cone which has three separate maxima of stimulation, or, on the contrary, it may be due to the stimulation of three separate cones each possessing one of these maxima. In the light of Granit's researches, using micro-electrodes, the latter is the more likely, but it is possible that the light stimulus might fall not on a modulator with a sharp spectral response, but on a dominator with a relatively wide one.

If in fact three different cones are receiving stimulation, each possessing a single maximum, then it should be possible to alter the respective heights of these maxima by shifting the image by small amounts on the retina, because this should increase the light on one or both of the other cones. In this way, by shifting the fixation light by small amounts, adjustment could be made until the purest effect was obtained. Thus, having investigated the properties of one cone, by moving the fixation mark, the properties of a neighbouring cone could be similarly investigated. At the same time that spectral analysis discloses the properties of the cones the positions of the fixation light on the plotting-board should give a clue as to the relative positions of these receptors, in respect of one another, in the fovea.

(139) *The interconnexion of the retinal cones*

According to Polyak (1941) more than one retinal receptor may be connected with one and the same fibre of the optic nerve, thus combining in some way the effects produced in these receptors by the incidence of light on them. It is not known whether such interconnexions exist in the human retina, neither is there any precise knowledge of the effects that such interconnexions would produce, but the possibility of such interconnexions should be borne in mind when attempting to stimulate an extremely small retinal area, as is being done in this research. It is, therefore, justifiable to inquire what the effects of such interconnexions might be, if these existed. Suppose, for example, that there were three cones, in close proximity to one another, all connected with the same nerve fibre, and that these cones have the same responses when stimulated by monochromatic light, then it would be anticipated that a single wave-length would be found to produce its maximum effect when it fell on any of them, and no important modification in the result would be produced, if part of the light fell in addition on one of the others. On the other hand, if these three cones had different responses, one, for example, having a maximum in the yellow, another in the green and a third in the blue, then it would be anticipated that a maximum would be discovered by micro-stimulation in the part of the spectrum corresponding to the maximum of the cone on which the greater part of the light was incident. At the same time there would be feebler maxima produced by the neighbouring cones, if any appreciable amount of the light happened to fall on them. But these weak maxima would not seriously interfere with the detection of the strong maximum produced by the cone on which the main part of the light was falling. In other words, the interconnexion of the retinal cones, so that their impulses are conveyed up one optic nerve fibre, should not interfere to a serious extent with the type of observation which it is intended to make in this research.

While it would be idle to deny that potential connexions such as Polyak has described may exist, in fact the evidence for the existence of such connexions appears to be entirely lacking. It has been shown in a previous section (130) that it appears to be possible to stimulate the retina with a point of light so small that almost all of it falls on one foveal cone. When this is done there is no indication that there is any spreading of the image, either due to optical phenomena or to neurological interconnexions. If in fact spreading takes place, its effect must be entirely eliminated by the visual centres of the brain.

(140) *Micro-stimulator design*

During the experiments with the first micro-stimulator, described in earlier sections of this Part, it became evident that two modifications would be desirable: (1) to increase the diameter of the plotting-board, so that a larger area of retina could be stimulated, this being done in such a way that the definition is not sacrificed; and (2) to provide means so that, when necessary, more than one monochromatic beam of light could be used for stimulating the retina, both of these being movable in the visual field, or one being movable and the other remaining stationary.

It has been found that several types of stimulator are possible:

Type 1. Where the plotting-board is close to the eyepiece, and the observer looks at the end of the objective through a mirror. This is the type described in the earlier sections of this Part, and shown in figure 2 on p. 627.

Type 2. Where the distance between the eyepiece and plotting-board is increased by raising the microscope above the eye-level of the observer. As in type (1), he looks at the objective through a mirror, but this deflects the rays downwards into the eye, instead of upwards as in type (1).

Type 3. Where the distance between the plotting-board and eyepiece is increased by the use of a mirror and right-angled prism; thus the rays from the plotting-board first pass vertically upwards to the mirror, which deflects them downwards and forwards towards the right-angled prism. Consequently any distance between plotting-board and eyepiece can be used, according to requirements. In this type the microscope lies below the line of sight of the observer, as was the case with type (1).

There is one important point of detail with regard to this design. Since the light suffers two reflexions on its way into the eyepiece, it must also suffer two reflexions between the object and the eye of the observer, if movements of objects on the plotting-board are to be correlated with their apparent movements in the visual field.

Type 4. In all the previous types the eyepiece of the microscope has been nearer to the observer than the objective. In this type, their positions are reversed and the observer can look directly at the objective. Rays reach the eyepiece by two reflexions. Proceeding vertically upwards from the plotting-board, they are deflected downwards and forwards by a mirror, to be reflected into the eyepiece by means of a silvered right-angled prism.

It will be noticed that in this type, the distance between plotting-board and eyepiece is long, whereas that between the objective and the observer is short. That is precisely the opposite of the arrangement found in types (1) and (2).

Type 5. Resembles type (4) in that the objective is relatively close to the eye of the observer, but there is no plotting-board, a narrow beam of light being directed from the monochromatic illuminator into the reducing lens system, by means of a movable right-angled prism.

Two arrangements are possible: either the prism rotates about a single axis which, for example, causes the tiny ray of coloured light to appear to move horizontally from right to left across the objective field, in which case rotations in other directions are obtainable by means of a rotatable prism placed before the eye of the observer; alternatively, the prism is arranged to rotate on two axes at right angles, in which case the rotatable prism is unnecessary. The above arrangement provides the movable monochromatic source. The other monochromatic source is provided by a second monochromatic illuminator, which is projected, by means of a lens system and right-angled prism, to one side of the visual field.

One advantage of this arrangement is that when one of the monochromatic sources is of long wave-length and the other of short wave-length, so that there is some chromatic difference of focus, this may be to a large extent corrected, by causing the monochromatic ray of shorter wave-length to come to a focus at a point closer to the observer than the ray of longer wave-length. One convenient method of doing this, is to mount the second monochromatic illuminator on the slide-rest of a lathe, so that by rotating the slide-rest's screw threads it can be placed in the required position.

Of these five methods, the last is in a different category to the other four and will not receive detailed consideration in this section. Types (1) and (2) are superior to types (3) and (4), because the latter require the provision of a large silver-surfaced mirror of good optical quality and this was not available.

The formulae relating the optical properties of all these methods, are as follows:

$$\text{(i)}\quad D'\times N=A\times 5000; \qquad \text{(ii)}\quad D''\times A=L\times P;$$
$$\text{(iii)}\quad P=N\times \text{c.u.}; \qquad \text{(iv)}\quad D'\times D''=5000\times L\times \text{c.u.};$$

where D' and D'' are the distances between observer and lens system, and plotting-board and lens system, respectively; A and L are the aperture and focal length of the lens system; P is the diameter of the plotting-board; and c.u. is the projected size of a cone unit on the plotting-board. All the above are in cm. N is the number of cone units in the diameter of the plotting-board, and 5000 is the reciprocal of a cone unit in radians.

Using these formulae the ideal distances and lens systems were calculated, assuming that the required value of N is 50, and that c.u. $=1$ cm., so that $P=50$ cm. (see tables 98 to 103).

TABLE 98. CONSTANTS OF REDUCING LENS SYSTEM

type	A	L	D'	D''
1	1·0	0·8	100	40
2	1·0	1·2	100	60
3	0·5	1·2	50	120
4	1·0	2·4	100	120
5	0·5	1·0	50	10

The lenses available were: a holoscopic 4 mm. focal length, 8 mm. aperture; a Zeiss B 10 mm. focal length, 8 mm. aperture; and a special lens system consisting of two Cooke lenses in combination. Each of these lenses could either be used by itself, or in conjunction with a wide-angled eyepiece, which had the effect of halving the focal length of the objective, leaving the aperture unaltered.

TABLE 99. Type (1)

	A	L	N	P	D'	D''
(*a*)	1·00	0·8	50	50	100	40
(*b*)	0·75	1·5	15	15	250	30
(*c*)	0·80	0·4	60	60	67	30
(*d*)	0·80	1·0	32	32	125	40
(*e*)	1·20	1·2*	40	40	150	40

* With ×2 eyepiece.

(*a*) is the ideal; (*b*) is the arrangement used for the researches described in this Part; (*c*), (*d*) and (*e*) are possible arrangements.

TABLE 100. Type (2)

	A	*L*	*N*	*P*	*D'*	*D''*
(*f*)	1·0	1·2	50	50	100	60
(*g*)	0·8	1·0	40	40	100	50
(*h*)	1·2	1·2*	60	60	100	60

* With × 2 eyepiece.

(*f*) is the ideal; (*g*) and (*h*) are possible arrangements. Of all these, (*h*) is closest to the ideal, but has the disadvantage of requiring an eyepiece. Probably (*g*) is the next best; it falls in only one way, namely, that *N* and *P* are somewhat smaller than the ideal—but probably sufficiently large, being nearly three times those of (*b*).

TABLE 101. Type (3)

	A	*L*	*N*	*P*	*D'*	*D''*
(*i*)	0·5	1·2	50	50	50	120
(*j*)	0·8	1·0	80	80	50	100

(*i*) is the ideal; (*j*) is sufficiently close for practical purposes.

TABLE 102. Type (4)

	A	*L*	*N*	*P*	*D'*	*D''*
(*k*)	1·0	2·4	50	50	100	120
(*l*)	1·2	2·4	60	60	100	120

(*k*) is the ideal; (*l*) is very near to it.

TABLE 103. Type (5)

	A	*L*	*N*	*P*	*D'*	*D''*
(*m*)	0·5	1·0	50	5	50	10
(*n*)	0·8	1·0	80	8	50	10

(*m*) is the ideal, and (*n*) is very close.

Of all the above, probably (*g*), (*h*) and (*n*) are the most suitable for further trial.

XI. THE POLYCHROMATIC THEORY OF HUMAN VISION

Evidence has been slowly accumulating that appears to be at variance with the trichromatic theory of Thomas Young, but is in favour of what the author has called the 'polychromatic theory' of human vision. The latter theory resembles closely one advanced by Wundt (1893); it also agrees with the experimental results on the retinae of many animals, obtained by Granit, using his micro-electrode technique.

The micro-stimulator described in Part X has been used in a search for evidence concerning the photoreceptors of the human fovea. Evidence is slowly increasing, as the result of this work, in favour of the 'polychromatic' theory.

(141) *Historical survey*

When Thomas Young first proposed the three-colour theory it captured the popular imagination because of its simplicity: 'Take three pigments of the purest colour: red, yellow and blue, and by mixing them you will find you can match all known colours.' A few years later, as the result of Wollaston's work on the prismatic spectrum, Young substituted green for yellow and violet for blue. He no longer discussed the mixing of coloured pigments, but of coloured light rays: 'It is certain that the perfect sensations of yellow and of blue are produced by mixtures of red and green and of green and violet light respectively, and there is reason to suspect that those sensations are always compounded of the separate sensations combined; at least, this supposition simplifies the theory of colours: it may, therefore, be adopted with advantage, until it may be found inconsistent with any of the phenomena; and we may consider white light as composed of a mixture of red, green and violet only....' This theory remained unassailed for nearly eighty years, when Hering (1876) advanced his famous rival hypothesis, of 'the six opponent colours': white-black, red-green and yellow-blue. Omitting details and disregarding the fact that white and black were regarded as separate sensations, this hypothesis was the first to advance a claim for four primary colours: red, yellow, green and blue, as opposed to the triad suggested by Thomas Young.

From that moment physiologists took sides: some were in favour of Young's theory, while others preferred Hering's theory. It was not long before a fierce contest began, which was destined to continue for many years; a contest which did much good, for it stimulated research in the field of vision. As a result, alternative theories began to make an appearance, coupled with such famous names as Donders (1881), Ladd-Franklin (1893) and McDougall (1901).

But, meanwhile, in 1893, a theory of a very different character made its first appearance, at the hands of Wundt: 'When the retina is stimulated by a coloured light, two essentially different processes are set into operation; one of these is colourless, while the other is coloured, being in fact a function of the wave-length of the incident light. Thus, there is a sensation corresponding to every part of the spectrum. Not three, or even four, primary colours, but many.' That is to say, what Wundt proposed was a polychromatic theory of vision. Now followed a period in which new theories of colour vision appeared with almost monotonous regularity.

Recently this spate of theories has abated, and workers have turned their attention to research, rather than to invention. During this period the three-colour theory of Thomas Young has played a most vital part; for first there was three-colour printing, then three-colour photography, and lastly technicolour. Not only has Thomas Young's theory played an essential part in the growth of new methods of colour reproduction, but in precise colour measurement as well. Also it provided a most valuable classification for the colour-blind. So that, even if it should prove to be a fact that human vision is not trichromatic, and that Young's theory has had its day, yet the heritage which it will leave behind will continue for many years to come, in practical applications of many kinds, possibly even colour television.

(142) *Colour mixture determinations*

Some years ago the author collected all the evidence available at that time, for and against Young's three-colour theory, because it had been noticed that many observers, using different methods for investigating a wide range of visual phenomena, had found the basis of three primary sensations insufficient to account completely for their experimental results. That evidence, which consisted of notes, reference cards and reprints, was destroyed by fire when incendiary bombs were dropped on the City of London in 1942. The evidence thus having been destroyed, all that remain are recollections of a few experimenters and their more important conclusions.

While it is justifiable to state, in general terms, that the spectral colours can be matched by suitable mixtures of red, green and blue monochromatic lights, in fact the matches thus made are far from perfect, because, in nearly every case, the monochromatic light is noticeably more homogeneous, that is, it contains less white light, than the mixture. This imperfect matching is usually expressed in colour-mixture equations by giving negative values to one of the component colours: to blue, when the yellow and orange parts of the spectrum are being matched; to red, when the blue-green is concerned; to green, for both the blue-violet and the red spectral regions. The magnitude of the negative values in these four parts of the spectrum depend on the wave-length of the rays which have been selected by the experimenter for making his colour mixtures. Thus, when making a match for the yellow or orange, with red and green, the nearer the green ray is to the red ray in wave-length, the smaller does the negative value of the blue ray become. But this selection of a green ray near to the red would have the effect of increasing the distance between the green ray and the blue one, and thus would increase the negative value required in the blue-green part of the spectrum. Thus, the shifting of the green benefits one region at the expense of another. The same statement applies to the shifting of the red and the blue primaries. Experiment shows that it is impossible to select three primaries so that no negative values are required in any part of the spectrum. Abney (1895) took considerable pains to reduce these negative values as far as possible, the wave-lengths he selected being 6500, 5300 and 4600 A. From the matches which were made by ten observers with normal colour vision, using these selected rays, the average negative values for the four spectral regions were about 2 % in the red (7500 A), and in the yellow-green (5500 A); about 14 % in the blue-green (5000 A); and about 4 % in the violet (4000 A). The negative values are not large, except in the case of the blue-green, but all of them are too large to be accounted for as being due to experimental error.

Three explanations of these negative values have been offered: (*a*) that the red, green and blue sensations are purer, that is, more saturated than any spectral colour; (*b*) that the negative values are due to central inhibition; (*c*) that vision is, in fact, polychromatic and that in consequence three primary colours when mixed do not match all the spectral colours (Granit 1945).

With regard to the first explanation, it is thought that the retinal receptors, which are responsible for arousing the three primary sensations, are stimulated to some extent by rays from all parts of the spectrum. Thus, the green receptors not only react to rays near the middle of the spectrum, but also slightly to red rays and blue-violet rays as well. In consequence, a mixture of red rays and green rays, which causes a sensation of yellow light, also causes a sensation of blue at the same time. Since the latter is complementary to yellow, the result is that the yellow appears to be diluted with white. Yellow rays, on the other hand, which stimulate the red and the green receptors, affect the blue receptors hardly at all, so that these rays appear to possess a greater degree of purity than a mixture of red rays and green rays.

Another way of stating these same facts is, 'that the primary sensations are situated at points which lie outside the colour triangle'. It should be pointed out that this hypothesis concerning the three hypothetical sensations has not been proved experimentally.

With regard to the central inhibition hypothesis: Göthlin (1943), having surveyed the work of other observers in the matter of these negative values, advances the hypothesis that they are due to central, that is, cerebral, inhibitions, which of necessity accompany the impulses to the complementary colour. 'Every impulse from the retinal receptors to a colour sensation is necessarily combined with a certain degree of central inhibition of the complementary colour in the same area, the degree of this inhibition being bounded by a certain law.'

Putting on one side a detailed discussion of these rival views, Granit (1945) has pointed out that there is a third, and simpler, alternative, namely, that there are not three kinds of receptor in the human retina, for colour vision, but several—possibly as many as seven. Thus, if seven rays in the spectrum were selected, of suitable wave-length, it is very likely that all parts of the spectrum could be matched, without the need for negative values at all. The wave-lengths of these rays would probably have to be determined by experiment; but if the primaries were 4600, 5200 and 6400 A, suitable secondaries would appear to be 4400, 5000, 5400 and 6600 A.

(143) *Adaptation to coloured lights*

Burch (1900), having concentrated sunlight, which had passed through a colour filter of the required colour, into the eye by means of a lens, examined coloured objects and 'the spectrum'. He formed the opinion, as a result of testing seventy subjects with normal colour vision, that there are four sensations, with transitions shown in table 104.

TABLE 104. TRANSITIONAL WAVE-LENGTHS BETWEEN SENSATIONS (BURCH)

sensation	transition occurs at (A)
red to green	5730
green to blue	5003
blue to violet	4480

Edridge-Green & Marshall (1909), using light of considerably less intensity, paid particular attention to yellow. After looking for some minutes at a powerful sodium flame, they found the yellow of the spectrum to be obliterated and only a faint orange to separate the red and green. With still stronger initial illumination of the eye by sodium light, they saw the red and the green meeting. The red looked somewhat purple and the green somewhat blue-green. They concluded that there must be a yellow sensation, in addition to the others mentioned. This Burch denied: 'I have entirely failed, though I have sought it carefully, to detect any physical evidence of a separate sensation of yellow.' To the author it would appear that this failure was due to the use by Burch of rays which were excessively bright.

(144) *Peripheral colour vision*

Nearly all observers who have examined the colour vision of the periphery of the human retina, have found green to have a relatively small area of response, but yellow to have a large one. Thus Ferree & Rand (1920), who used monochromatic lights of equal energy-content, found that red, blue and yellow have the same area, but that green is narrower. Abney (1895), who also used spectral colours, found the order with moderately intense illumination to be green, red, yellow, blue. With low illumination the order was still the same.

These results point to yellow as being a separate sensation from either green or red, on the grounds that if yellow is compounded of red and green it must cease where either of its constituents ceases. But this is not found to happen. Moreover, Abney found that a red and green mixture which matched the yellow (5892A), in hue and luminosity, had a considerably smaller field than that of the pure yellow itself. Thus again pointing to yellow as a separate sensation.

(145) *The retinal direction effect*

As mentioned previously, Stiles found a different direction effect for yellow from that for red and/or green. Moreover, if the mean values for red and green be compared with those of yellow, it will be seen (table 105) that in no single case is there agreement between them.

TABLE 105. RETINAL DIRECTION EFFECT (STILES & CRAWFORD)

position	side	amount (mm.)	red	green	mean	yellow
fovea:						
light or	nasal	3	4·8	4·7	4·75	3·8
dark	temporal	3	1·6	1·7	1·65	1·4
adapted	nasal	2	2·7	2·6	2·65	2·3
periphery:	nasal	3	3·8	2·8	3·30	2·9
light	temporal	3	3·0	2·6	2·80	3·2
adapted	nasal	2	1·9	1·6	1·75	1·6
periphery:	nasal	3	2·9	1·0	1·95	1·3
dark	temporal	3	2·3	1·0	1·65	1·3
adapted	nasal	2	1·9	1·0	1·45	1·1

Now if the yellow sensation were in fact a mixture of red and green sensations, it would be expected that the direction effect for yellow would have a value which is equal, or nearly equal, to the mean values for red and green; but such is not the case. This suggests that the visual mechanism for yellow is separate from that of both red and green.

(146) *The colour discrimination curve*

On the basis of Young's theory it would be expected that there would be poor colour discrimination at each end of the spectrum, since only one sensation is aroused here. In the green region, discrimination would be expected to be better, because the red- and blue-sensation curves are both approaching the base line. In the yellow region, very good discrimination would be expected, because the red and green curves are intersecting and one curve falls steeply, as the other rises, with change of wave-length. The same reasoning applies to the blue-green region, where in consequence high colour discrimination would be anticipated. When, therefore, colour discrimination is plotted against wave-lengths, a W-shaped curve would be expected, that is, two troughs, one in the blue-green and one in the yellow, separated by a crest in the green.

Laurens & Hamilton (1923), who investigated this matter experimentally, found a more complicated curve than that just described; so also did Pitt & Wright (1934). In the case of the former, there were four troughs instead of only two, separated by three well-marked rounded crests. The troughs were at 4300, 4850, 5800 and 6150A; the crests were at 4550, 5300 and 6050A. The general level of acuity is higher in the yellow-green than it is elsewhere. None of these facts is easy to account for on the three-colour theory. With three crests and four troughs there must be five different receptors distributed throughout the spectrum. But, as Granit has pointed out (1945), additional receptors would probably be required in the green and in the yellow regions of the spectrum, in order to provide the high discrimination which experiment shows to be present there, for the trough in the green is not only deep, but wide; while the yellow trough is even deeper, and it is flanked on the long-wave side by the red trough, with which it is practically continuous.

(147) *The accuracy of fixation*

A consideration of the principles underlying chromatic differences of magnification, shows that fixation is not a simple process. Instead of the rays of different wave-length, which comprise white light, falling together on the same retinal point, they are spread out in the form of a short spectrum, blue rays being to the nasal side of green rays, and red rays being to the temporal side (Tscherning 1904). In different people, the length of this spectrum varies because of alterations in the position of the fixation axis relative to the optical axis. It has been found that the long axis of this spectrum, in some subjects is not horizontal but oblique.

The discovery that there are different fixation points for red, green and blue lights, as published previously and confirmed in the next section, leads to the conclusion that when a white object on a black background is fixed by an observer, each separate colour may take part in the fixation process as it falls on its own particular part of the fovea. But there is another factor to be considered, namely, the antichromatic responses; for when the object which is being fixed is small, these eliminate, or at all events tend to eliminate the red and blue rays, leaving the yellow and green rays alone to take part in the fixation process.

A kindred subject is that of the eye movements. It has been claimed by Adler & Fliegelman (1934), that the eyes, even when performing accurate fixation, are actually undergoing rapid, small oscillatory movements. These may be of the nature of an intention tremor originating in the nervous system, or may be caused by accidental and unavoidable variations of tension in the external eye muscles. It is strange that the existence of these movements is not confirmed either by visual, or by kinaesthetic, sensations. The following experiment substantiates this point. Two white lines on a black background are placed at such a distance from the observer that the distance between their centres is equal to 2 cone units, that is, to twice the average distance between the centres of two neighbouring foveal cones. If the centres of the lines are 4 mm. apart, the distance of the test objects from the observer should be 10 m. (see Part I). At this distance the observer will find that he can fix either line, or the space between them, at will, and there is no evidence that the eyes are performing oscillatory movements. From time to time the gaze does undergo chance shifts. The observer is aware of these, and he takes steps to correct them; they are relatively rare, unless the eyes are tired. Three explanations of the reports of other observers of the oscillatory movements are possible: (1) that the subjects were not normal in this respect; (2) that they were not given a sufficiently small fixation point; (3) that the method used in making the observations was in some way unreliable.

The view that the results of Adler & Fliegelman are for some reason at variance with the facts, is supported by the following observations. There is near the fixation point of the author's left eye, a small blind-spot for red rays, which can be readily identified by microstimulation with light of 6400A. Since it is extremely unlikely that this spot alters its position on the retina, the determination of the position of the fixation point for green rays relative to this spot enables any changes in position of the green fixation point to be easily determined. Thus, if two successive determinations vary, these variations may either be due to experimental error or to a displacement of the fixation point, or both. In table 106 are given five successive determinations of the position of the green fixation spot in cone units (see § 21, p. 537).

TABLE 106. POSITION IN VISUAL FIELD OF FIXATION POINT FOR GREEN (5200 A) RELATIVE TO BLIND-SPOT FOR RED RAYS

	above by (cone units)		to right by (cone units)
	4·60		1·00
	4·65		1·00
	4·70		1·15
	4·60		1·05
	4·70		0·90
mean	4·65	mean	1·05

These determinations were continued the next evening, and between them the following alterations were made in the micro-stimulator: mirror removed and replaced in new position; eye lens rotated to new position; eyepiece rotated; objective rotated; all lenses cleaned and replaced. The results obtained are given in table 107.

TABLE 107. POSITION IN VISUAL FIELD OF FIXATION POINT FOR GREEN (5200 A) RELATIVE TO BLIND-SPOT FOR RED RAYS

	above by (cone units)		to right by (cone units)
	5·5		0·8
	4·9		0·7
	5·0		1·1
	5·4		1·2
	5·2		0·7
	5·5		0·6
	5·4		1·2
	4·8		1·3
mean	5·21	mean	0·95

If the values given in table 107 be compared with those given in table 106, it will be observed that there is more scatter in the second series. This may be due either to disturbance of the instrument or of the eye of the observer. The means of the two sets of readings differ by 0·56 cone unit in a vertical direction, and by 0·1 cone unit in a horizontal direction, that is, in both directions the variation was less than 1 cone unit, and may be due to experimental error. Since the blind-spot for red rays can be assumed to be fixed in position, the fixation point for green rays, if it has moved at all, has moved by less than 1 cone unit, that is, that one and the same foveal cone has been performing fixation during two successive evenings.

So unexpected did this conclusion appear that a third series of determinations has recently been made, with the results shown in table 108.

In between the readings given in table 108 the eye of the observer was subjected to different kinds of disturbance: dark adaptation, light adaptation, internal strabismus, distant vision and near vision. The mean values now obtained do not, however, differ materially from those recorded previously. This indicates that the same foveal receptor was still being used for purposes of fixation with green light as was being used on the two previous occasions reported above.

Yellow light (5800 A) was now substituted for green light, and the results given in table 109 were obtained.

TABLE 108. POSITION IN VISUAL FIELD OF FIXATION POINT FOR GREEN (5200 A) RELATIVE TO BLIND-SPOT FOR RED RAYS

above by (cone units)	to right by (cone units)
5·0	1·4
6·0	1·8
5·2	1·8
4·4	0·3
4·4	1·1
5·7	0·2
4·4	1·7
mean 5·01	mean 1·19

TABLE 109. POSITION IN VISUAL FIELD OF FIXATION POINT FOR YELLOW (5800 A) RELATIVE TO BLIND-SPOT FOR RED RAYS

above by (cone units)	to right by (cone units)
4·3	2·1
3·2	2·3
3·4	2·2
4·3	—
4·2	—
3·9	—
4·3	—
mean 3·9	mean 2·2

On comparing these results with the previous ones, it is clear that a different fixation point is used for yellow rays from that used for green rays. This fact will be referred to in the next section.

(148) *The positions of the fixation points for different colours*

Evidence was produced (in § 120, p. 613) that different fixation points are used for rays of different colour.

In the case of the author's left eye, the red fixation point was found to be below, and to the left of, the green one, whereas the blue fixation point was below, and to the right of, the green one. It should be noted that this description applies to the apparent positions of these points in the visual field, and not to their actual positions in the retina. The method used for determining the relative positions of these fixation points depended on the correct appreciation by the observer of the extent of his own eye movements. It was obvious that a better method of locating these fixation points was provided by the use of the blind-spot for the red rays, which was employed for the investigations described in the previous section. Briefly, the method is as follows: a source of variable but known colour being fixed by the eye of the observer, the position of the blind-spot for red rays is determined by moving the source of red light until it coincides with it. Some results obtained by this method are given in table 110. In the first and second columns are given the colour and the wave-length of the light used for the fixation. In the third column are given the vertical positions, in the visual field, of the fixation points for the different colours, above the blind-spot for red rays. In the fourth column are given the horizontal positions, in the visual field, of the fixation points to right and left of the blind-spot for red rays.

TABLE 110. FIXATION POINTS FOR LIGHTS OF DIFFERENT COLOUR

fixation for	wave-length (A)	vertical direction (cone units)	horizontal direction (cone units)
red	6600	2·1 above	4·4 left
orange	6200	3·9 above	1·5 left
yellow	5800	4·2 above	1·7 right
green	5400	5·7 above	3·0 right
blue-green	5000	6·1 above	4·2 right
indigo blue	4600	4·8 above	5·6 right
blue	4200	2·6 above	7·4 right

If the values given in table 110 be plotted, it will be found that the fixation points for the different colours from red to blue-green fall roughly along a straight line, which slopes down to the left. On the contrary, the fixation points for blue-green, blue, and violet also fall roughly along a straight line, but this slopes down to the right. Thus the positions of the fixation points for red, green, and blue lights, as previously obtained, are confirmed, and the two different methods are found to give almost identically the same results. Another fact of interest is that the fixation points for the colours from red to blue-green are in the same order as the colours of the spectrum, and, therefore, in the same order as the colours produced by chromatic difference of magnification. Moreover, the spectrum produced by the latter slopes downwards to the left, because the fixation axis lies in the visual field below and to the left of the optic axis, so that the slope of the spectrum corresponds roughly with the slope of the fixation points.

Now it might be expected that, with similar slopes and colours in similar order, the positions of the colours would also be similar: red rays falling on the red fixation spot, orange falling on the orange fixation spot, yellow on yellow, green on green, etc. But in fact, the precise opposite is the case, for whereas the fixation spot for red rays is down and to the left of that for green rays, in the visual field, the red rays are situated up and to the right of the green ones, in the visual field, in the spectrum produced by chromatic difference of magnification.

This lack of correspondence is not as important as would appear at first sight, for whereas the fixation points for red rays and blue-green rays, in the case of the author's left eye, differ in position by nearly 10 cone units, the same rays when they fall on the retina differ in position by less than 1 cone unit.

No theoretical reason can at present be given to explain why these fixation points fall along straight lines. On the other hand, there is a definite advantage if they are arranged in the same order as that of the spectrum. This may be made clear by considering the case of green. If a design drawn in this colour be under examination, and a part of it be falling on the fixation area for green rays, then other parts will be falling on retinal areas in the immediate vicinity. Now, areas sensitive to red, orange, blue or violet would be useless for its correct appreciation, because green light would not stimulate them. But the same criticism would not apply to areas sensitive to yellow-green, or blue-green, because both would, to some extent, be stimulated by green rays. Since the same reasoning applies to other colours, the best arrangement of the areas sensitive to different colours, is for these to be in the same order as the colours of the spectrum. This, as shown above, has been found to be the case.

It is very unlikely that the fixation point for any given colour would be situated in the middle of a region devoid of receptors of that colour. It is much more likely that the opposite would be the case, and that the red and orange fixation points would be situated at or near the centre of a red or orange cluster. Similarly one would expect that the yellow, green and blue-green fixation points would be within a green cluster, and that the blue and violet fixation points would be surrounded by a cluster of receptors resembling themselves.

If the provisional plan, previously given, for the positions of the various groups of receptors in the foveal area, be compared with those now put forward for the positions of the fixation points for lights of different colour, it will be observed that these positions are confirmed (see table 94, p. 621). Here, then, is additional support for the cluster hypothesis, an account of which has been previously given.

Thomson (1946) has recently reported small local differences in the sensitiveness of the fovea close to the fixation point for rays of different wave-length. It is stated, in the same communication, that Thomson & Wright (1947) have shown that there is an increase of sensitivity to blue light as the image of a matching field is moved from the centre towards the edge of the central fovea. The latter confirms the results obtained by the author on several observers, using blue, green and yellow lights, namely, that local variations of sensitivity occur (see § 37, p. 547).

Before passing on, there are two other matters which require consideration. The position of the fixation point when an object illuminated by white light is being fixed, and the implication of these experiments with regard to the number of types of retinal receptor present in the human fovea.

In order to obtain information with regard to the fixation point for white light, the same technique was employed as that described above. A point source of white light being fixed, the position of the small blind-spot for red rays was located by means of the movable red source. It was found that this had to be placed in the same position on the plotting-board of the micro-stimulator as was the case when a green light of 5400 A was being fixed.

This gives confirmation to the suggestion made previously, that when fixation is being performed on a white object it is the green rays which are taking the major part in the fixation process, and white as such seems to be taking no part. If then there are receptors with a broad response (Granit's 'dominators') within the fixation area, their presence is not disclosed by this method.

With regard to the number of different types of receptor present in the human fovea, it would be difficult to explain why there are different fixation points for red, orange, yellow, green, blue-green, blue, and violet rays, unless there are also special receptors for all these different colours. This matter will be considered together with other evidence at the end of § 152, p. 652).

(149) *The receptors found in the human fovea*

When, as the result of the interest aroused by Granit's earlier experiments, the author's researches were first started in order to ascertain the properties of the photoreceptors of the human retina, a number of new phenomena in connexion with foveal vision were encountered, which have been described in previous Parts, but little or no progress was made in the primary object of the work. Thus when Snellen's test type was examined using white, red, yellow, green or blue lights, it was found that six/fourths vision was achieved in every case. Not only was there no fall in acuity on replacing white by a coloured light, but the acuity obtained was the highest that is normally met with in the case of an emmetrope. Such a result is explicable only if the image of the test object falls on a retinal area which consists entirely of sense organs which respond to the particular light which is illuminating the test object. Thus the conclusion from the above experiment was that the retinal area used for discrimination consists entirely of red receptors, yellow receptors, green receptors and blue receptors at one and the same time; an impossible conclusion unless all the receptors are alike, in which case, how are colours discriminated? This was the kind of difficulty met with, the evidence appearing to point either to the presence in the human retina of sense receptors having very different characteristics to those found by Granit in the case of other animals, or to the existence of some process, nervous or otherwise, which prevents the colour characteristics of the individual receptors from disclosing themselves.

On the other hand, in two different experiments the presence of receptors of the Granit type had apparently been observed; these were (1) the changes of colour of tiny test disks, blue or grey, placed in different positions in relationship to a green fixation mark, and (2) the changes in colour of a small moving interrupted point source, which have been described in §§ 124 and 125, pp. 618, 619.

With these two apparent successes in view the experiments were persisted with, and the micro-stimulation apparatus designed and constructed. It was clear that if progress were to be made there would have to be very close correlation between the eye and the hand of the observer; provision for this was one of the features of the micro-stimulation apparatus.

During this period, two other examples of colours due apparently to retinal processes were noticed. When sunlight is reflected from the surface of water which is being ruffled by a breeze, and when daylight coming down a passage is reflected by non-skid paving. In both cases colours are not always to be observed. Thus, in the former case, during observation for 1 hr., colours were seen three times for about 1 min. on each occasion. On each of these occasions one eye was being used for purposes of observation. On no occasion were colours seen when both eyes were in use. When the colours were seen they were quite unmistakable, being various shades of red-orange mixed with white, and blue-green mixed with white. As with the examples previously given, on no occasion were blue, yellow, crimson, purple or violet observed. Thus vision appeared to be dichromatic, with the primaries which are usually found under the action of the antichromatic responses.

These observations gave encouragement that in time success would be achieved with the micro-stimulation apparatus. This proved to be justified, for late one afternoon a satisfactory result was obtained. The conditions were as follows: daylight was failing, although it was still possible to read easily in the room. Two orange lights were being used for stimulation; one was produced by the monochromatic illuminator, the other by means of a colour filter placed over the battery-driven light source. The latter was being moved slowly by hand over the surface of the plotting-board. The stationary monochromatic source was fixed, while the movements of the other were observed as its image shifted from point to point over the surface of the retina. Suddenly the moving source was seen to undergo changes in colour, at one point appearing a deep orange-red, at another point appearing colourless. The points of colour were exceedingly small, but quite clear and easily recognizable. The changes of colour were watched for 2 or 3 min., when they disappeared as suddenly as they had appeared. On many occasions after that a similar result was achieved. The experiment was varied in as many ways as possible, and the following conclusions arrived at:

(1) The two sources must not be very different in wave-length, for if they are it is not possible to focus both simultaneously, owing to the chromatic aberration of the eye. Thus if one source is red the other cannot be green, blue or violet, but must be red, orange, or possibly yellow.

(2) The power of the lens used to correct the observer's vision must be adjusted according to the part of the spectrum to which the coloured lights belong.

(3) The intensity of illumination of the two sources must be approximately equal, and neither should be too bright.

(4) The eye should be unfatigued but fully light-adapted.

(5) It is an advantage for both sources to be alike in colour for, when they are, the variations of colour of one of the sources are most readily perceived.

(6) It is a matter of indifference which of the two sources is used for fixation and which for testing, for a monochromatic source appears to be as likely to undergo colour changes as one of the same colour produced by colour filters. Usually it was the test source which changed colour, while the source being fixed by the observer remained unchanged. At times the opposite was observed. Rarely both sources underwent the same change of colour at or about the same time.

The colour changes which were observed are summarized in table 111.

With regard to table 111, it should be noticed that the stimuli are small in size, in consequence the colours seen are modified by the antichromatic responses. Particularly is this the case for blue, which appears a dark blue-green grey. So that where blue is recorded in the table as having been seen, it means that the colour observed could not be distinguished from the spectral blue light when seen under the same conditions.

Sometimes the image of a coloured test source could be located on what appeared to be a black spot surrounded by a faintly-lit halo. These spots have been observed in the cases of red, orange and yellow sources, but not, so far, in those of green or blue ones. The appearance is thought to be due to the incidence of rays on receptors to which they are unresponsive. One spot such as this, which was insensitive to red rays, was used for the experiments described in § 147 above.

The above observations lead to the conclusion that there are, in the human fovea, receptors of several different kinds: for red, orange, green, blue-green and blue. Evidence for the existence of receptors for yellow and for violet were not obtained by this method, owing to the antichromatic responses.

TABLE 111. SUBJECTIVE COLOURS OBSERVED UNDER MICRO-STIMULATION

actual colour of test light	apparent colour of test light
white	red of 6400 A
	orange of 6100 A
	green of 5400 A
	pale blue-green
	blue of 4800 A
	white
red	red
	orange
orange	red
	orange
	very pale orange
yellow	red
	orange
	green
	white
green	green
	very pale green
	white
blue	blue-green
	blue
	grey

(150) *The mechanisms of the antichromatic responses*

The mode of action of the antichromatic responses, by means of which normal colour vision is changed, first to reduced colour vision and then to colourless foveal vision, has been considered in Part VI, on the basis of the three-colour theory of Thomas Young. Now, however, that evidence is accumulating in favour of a polychromatic theory of vision, it seems advisable to reconsider the position of these responses. Suppose, for example, that it were proved ultimately that there are four kinds of colour receptor present in the human retina: red, yellow, blue-green, and blue; then the antichromatic responses might act in the following way: first, blue is replaced by black, by severing the nerve path between the blue receptors and the blue sensation area situated in the brain. At, or nearly at, the same visual angle yellow is replaced by white, by the nerve path for the yellow receptor being similarly severed. Thus leaving the red and the blue-green receptors in operation to produce a form of dichromatic vision. At this stage it would be expected that the luminosity curve for the spectral colours would show two troughs: one in the yellow, the other in the blue. The yellow one, as pointed out in the next section, is, in the author's view, shown in the curves obtained by Wright for a small foveal area. The deficiency in the blue is also shown, but not so clearly.

With a further reduction of visual angle, other changes take place, causing red to be replaced by dark grey or by black, and blue-green to change to pale grey or white. The alteration to the red might be brought about by severing the red nerve path in the same manner as has already been supposed to have occurred to the blue and the yellow. The modification of blue-green to white is obviously of a different nature. One suggestion is that in some way, at present unknown, the blue-green receptors have become altered into dominators. The fact that the latter were found by Granit to have response curves extending over nearly the whole of the visible spectrum, does not prove that when stimulated they would cause a sensation of white to be perceived, but that seems to be a justifiable supposition, for dominators would be expected to give a colourless sensation, just as the rods do in twilight vision. A possible alternative view is that the blue-green receptors give a colourless sensation, not by their conversion into dominators, but by their being linked with the other colour centres in the brain: either the red one only, or more probably the red, yellow and blue. It should not be difficult to decide which of these two alternative schemes is correct, by an examination of the shape of the luminosity curve for colourless foveal vision; for on the first hypothesis it should be of the dominator type, as found by Granit—that is, an exceptionally broad type of response curve should be obtained; on the other hand, if the second hypothesis is correct the response curve should be narrow, resembling that of one of Granit's 'modulators'.

The shape of the luminosity curve for very small foveal areas has been recently investigated by Wright. He finds much the same broad type of curve as that obtained by Granit, for the dominators in different animals, which supports the first hypothesis. This matter will be referred to again in § 153.

(151) *The response curve of the yellow receptor*

The responses throw light on the receptors present in the fovea in two different ways: (*a*) in the rays which are effective in causing one or more of the response mechanisms to come into operation; and (*b*) in the types of vision which are produced under their action. With regard to the former it will be recollected that a certain part of the spectrum was found to be effective in the case of each mechanism. These parts were red, between 6450 and 5880A, for the 'red' mechanism; yellow, between 6088 and 5618A, for the 'yellow' mechanism; green, from 5450 to probably about 5000A, with a maximum at 5200A, for the 'green' mechanism; and probably blue rays, for the 'blue' mechanism.

With reference to the modifications of vision produced by the responses, it will be recollected that first blue and then yellow lose colour, thus producing a form of dichromatism in which red-orange is one primary and greenish blue the other. Since these are not complementary in colour, it was suggested that there might be four primaries: red and its complementary blue-green, 5000A; orange and its complementary greenish blue, 4600A. If the latter is the case, the following receptors are present: red, orange, yellow, blue-green, greenish blue and blue. But we saw above that on the effector side there is evidence for receptors for red, yellow, green (5200A), and blue: that is, the addition of green should be made to the above list.

An attempt was made to determine approximately the shape of the response curve of the receptors used for the 'yellow' mechanism, by testing the effect of altering the intensity of the spectral lights used in the above experiments, by means of Ilford neutral-tint filters. The results shown in table 112 were obtained. These values are plotted as circles in figure 3. There are also plotted the approximate values for the three receptors found by Granit in the retinae of the frog, cat and rat, by means of his micro-electrode method. It will be seen that the general forms of the curves are alike, which suggests that there may be similarity in the shapes of the response curves in the frog, rat, cat and man. This may indicate that the photochemical processes forming the basis of both, are similar.

Measurements unfortunately could not be made at points near the base of the curve, in the case of man, because when the intensity of illumination of the monochromatic light source is high, it becomes difficult to judge the colour of the yellow test source. It is possible, however, to obtain a limiting value for the long-wave foot of the yellow response curve, from a consideration of the results of colour mixture, for it is found that the red part of the spectrum has a uniform tint, although of course it differs in brightness. From about 7000A to the extreme long-wave end of the spectrum, one part matches another part when a suitable alteration of intensity has been effected, and it is not necessary to add any other colour in order to obtain a perfect match. This indicates that the response curve of the yellow receptors cannot extend at all into this part of the spectrum, for if they did, a colour-change would be introduced. This argument does not enable us to state the wave-length at which the response curve reaches the base line, but we can say that it must do so at some shorter wave-length than about 7000A. From this we can infer two things: first, this response curve, which has been called 'yellow', cannot possibly be identical with, or be a modification of, the red response curve—it must be quite separate from it; and secondly, the conclusion previously arrived at is confirmed, namely, that the yellow response curve must be a somewhat narrow one.

Table 112. The responses of the yellow receptors

log of intensity	wave-length (A)	
1	5850	
2	6030	5680
3	6110	5560
4	6240	5390
5	—	—

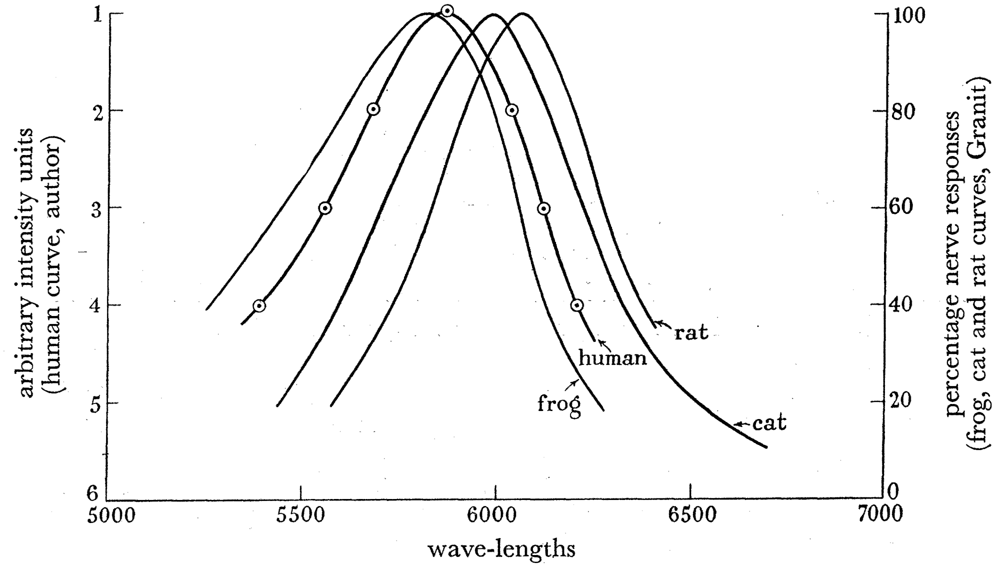

Figure 3. Response curves of four photo-receptors.

There is a second method by means of which the shape of the yellow response curve can be inferred, namely, by comparing the luminosity curve for the spectral colours when a large retinal area is being investigated, with that obtained when the investigation is carried out on only a small one.

Both these curves have been obtained by Wright, by means of his double-prism monochromator.

As the retinal area receiving stimulation is reduced in size, colour vision undergoes an alteration, so that from full colour vision there is reduced colour vision, which resembles a form of dichromatism. The principal changes are that yellow is replaced by white, and blue by dark grey or black. We should, therefore, expect modifications in the luminosity curves in both the yellow and the blue parts of the spectrum. A comparison of the response curves shows that such is indeed the case, for Wright confirmed the conclusion arrived at by Sloan, that there is a kink in the yellow region; and if Wright's two luminosity curves are compared it will be observed that there are also differences in the blue. Thus in figure 4 the luminosity curve for a large foveal area is shown at *A*; for a small foveal area at *B*; and the differences between these curves at different wave-lengths are shown at *C*. It will be observed that the latter consists of two parts: a well-defined part in the yellow, a poorly-defined part in the blue. With regard to the yellow curve, it will be observed that it reaches a maximum value at 5850A, which is identical with the maximum of the luminosity curve for the yellow human receptor found by the method described above. Further, it will be noticed that the general shapes of the curves obtained by the two methods are the same; there are differences in detail, for curve *C* is even narrower and sharper than that arrived at by the previous method; many explanations may be offered for this difference, one point that should be noticed being that the retinal area, stimulated in the author's method, is considerably smaller than that used by Wright when he obtained curve *B*.

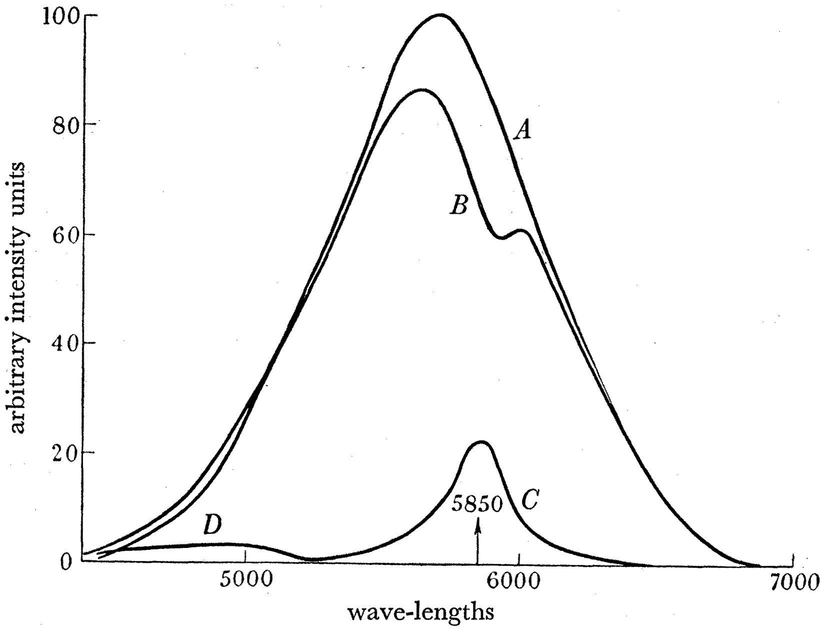

FIGURE 4. Luminosity curves; *A*, for a large foveal area (Wright). *B*, for a small foveal area (Wright). *C*, for yellow receptor (author). *D*, for blue receptor (author).

(152) *The polychromatic theory of human vision*

As mentioned at the beginning of this Part, according to Wundt's theory two different mechanisms are put into operation when light is incident on the retina: (*a*) chromatic, and (*b*) achromatic. The former consists of many sharply-defined receptors, which vary in their relative activity according to the spectral composition of the stimulus which is applied to them. The latter, on the other hand, is the same for all parts of the spectrum, except that a maximum effect is produced by the yellow-green, and that there is a gradual decrease in effect as the red and violet ends of the spectrum are approached. The resemblances between this theory and Granit's discoveries on the mammalian retina are very striking, for whereas Wundt's chromatic mechanism is well represented by Granit's seven 'modulators', his achromatic mechanism finds its counterpart in Granit's 'dominators'.

Now, it appears to the author that strong support for what may be called the Wundt-Granit polychromatic hypothesis is given by the experiments described in § 148 above, namely, the presence of different fixation points in the human fovea for red, orange, yellow, green, blue-green, blue, and violet rays. Further support is provided by the experiments described in § 149, which are summarized in table 111. Since, in a general way, agreement is striking, details must now be considered. As stated above, Granit found seven 'modulators' and one 'dominator'; the maxima of the former correspond to the following wave-lengths in Angstroms:

6000	5800	5400	5200	5000	4600	4400
orange	yellow	yellow-green	green	blue-green	greenish blue	blue

It will be noticed that receptors for red and violet are missing. The evidence in favour of each of these receptors will now be considered.

Red (maximum at about 6500 A). This has a clearly marked fixation point of its own (see § 148, p. 644). This sensation may be produced by micro-stimulation by white, orange, and yellow lights. It has long been recognized as one of the primary colours of human vision. It was found to have a specific direction effect by Stiles & Crawford. It takes part in the antichromatic responses. Its claims for inclusion seem to the author to be as strong as those of any other colour.

Orange (maximum at about 6000 A). This photoreceptor is probably identical with that found by the author, at the fixation point for orange of 6200 A; and the same as those receptors which are found to give an orange sensation when stimulated by white, red or yellow lights. Thus there is some evidence that this receptor has been identified in the human retina.

Yellow (maximum at about 5800 A). A definite fixation point was found for yellow rays, but in no case was a sensation of yellow produced by micro-stimulation with other coloured lights. Even yellow light itself looked white when a narrow ray was caused to fall on the fovea. This substitution has been shown to be due to the antichromatic responses. In favour of the presence of this receptor is the fact that this part of the spectrum has a very high brightness. It is unlikely that this would be the case if there were in fact no receptors present from 6000 or 6200 A on the one side, to 5400 A on the other. Stiles & Crawford found quite a different retinal direction effect with yellow rays than for red, green, and blue rays. Even allowing for experimental error, the magnitude of their effect in the case of yellow was not the mean between that for red and that for green. This lends support to the idea that yellow receptors are also present in the human fovea.

Many workers in the field of colour vision—Hering, Donders, and G. E. Muller—have regarded the claim of yellow to be a primary colour, nearly as strong as those of red, green, and blue. This view is substantiated by the result of experiments on adaptation. The colour discrimination at this part of the spectrum is exceptionally high. It plays an important role in the antichromatic responses, and the shape of its response curve has been determined approximately. Its claims for recognition appear to be very strong indeed.

Yellow-green (maximum at about 5400 A). There is a definite fixation point for a colour of this wave-length, and a green sensation may be produced by micro-stimulation, by both white and yellow lights. A colour of this wave-length, or one close to it, is an essential primary for matching by colour mixture; it has a specific retinal direction effect. The presence of this receptor is supported by very strong evidence, such as peripheral vision, adaptation, colour discrimination and the antichromatic responses. It has long been regarded as a fundamental colour.

Green (maximum at about 5200 A) has a definite fixation point in the fovea. It has the maximum effect on the 'green' mechanism of the antichromatic responses. It has been found by Granit in the retinae of many animals, using the micro-electrode technique. This colour is sometimes seen as a result of micro-stimulation. There seems to be a fair amount of evidence for its presence in the human retina.

Blue-green (maximum at approximately 5000 A). This colour is nearly the complementary to red (actually 4960 A (Sinden 1923)). It was one of the primary colours adopted by Hering. It would eliminate the negative values for red in colour-mixture curves, if adopted as a primary. It has a definite fixation point in the fovea, and it was found by Granit in the eyes of many animals.

Indigo blue, a bluish green (maximum at about 4600 A) is frequently adopted as one of the primaries in colour mixture. It was this wave-length which, when mixed with red (6500 A), was found by Willmer & Wright (1945), to match all spectral colours when viewed at small visual angles. It has a definite fixation point in the fovea. It was found by Granit in the eyes of many animals, and is sometimes seen on micro-stimulation.

Blue (maximum at about 4400 A) is the colour often adopted as the third primary, on the trichromatic theory. It has a definite direction effect. It is well seen by peripheral vision. It has a definite fixation point in the fovea, and has a mechanism of the antichromatic responses for its suppression. Granit found it in the retinae of animals.

TABLE 113. SUMMARY OF EVIDENCE FOR POLYCHROMATIC THEORY

6500	6200 or 6000	5800	5400	5200	5000	4600	4400	4000
red	orange	yellow	yellow-green	green	blue-green	indigo	blue	violet
TY	—	—	*TY*	—	—	—	—	*TY*
H	—	*H*	—	—	*H*	—	*H*	—
CM	—	—	*CM*	—	*CM*	—	*CM*	*CM*
A	—	*A*	*A*	—	—	—	*A*	*A*
PV	—	*PV*	*PV*	—	—	—	*PV*	—
RD	—	*RD*	*RD*	—	—	—	*RD*	—
CD	—	*CD*	—	—	*CD*	—	*CD*	—
F	*F*	*F*	*F*	*F*	*F*	*F*	*F*	—
MS	*MS*	—	—	*MS*	—	*MS*	—	—
—	*ME*	*ME*	*ME*	*ME*	*ME*	*ME*	*ME*	—
R	—	*R*	—	*R*	—	*R*	*R*	—

TY, primary colour advanced by Thomas Young; *H*, primary colour advanced by Hering; *CM*, primary required for colour mixture; *A*, primary required by adaptation experiments; *PV*, primary required by peripheral vision; *RD*, primary according to retinal direction; *CD*, primary according to colour discrimination; *ME*, micro-electrode method on animals; *F*, fixation point in human fovea; *MS*, micro-stimulation of human fovea; *R*, primary required for antichromatic responses.

Violet (maximum at about 4000 A) was adopted by Thomas Young as a primary, in place of blue. Burch suggested its presence as a result of adaptation experiments. Neither Granit nor the author have so far found evidence for it.

The above evidence is summarized in table 113.

In the opinion of the author, in view of the evidence given in table 113, the polychromatic theory seems to be at least as likely as the trichromatic theory of Thomas Young.

(153) *The nature of the retinal dominator*

When Granit investigated the retinae of such animals as frogs and snakes, he found two types of receptor in the light-adapted eye: receptors with a narrow spectral response, which he called 'modulators', and receptors with a broad response, which he called 'dominators'. He observed that the shape of the dominator curve is extremely like, if it is not identical with, the luminosity curve of the human light-adapted eye. Since dominators were not found to be present in the eyes of rats or guinea-pigs, which are stated to be devoid of cones, he concluded that cones are essential elements for the existence of dominators. When, later, he investigated the retinae of cats, these ideas were confirmed; he found, moreover, in these animals that the photopic dominators gave a response with a hump at about 6000 A, very alike in shape to that found by Wright when a small foveal patch, of 20 min. of arc, is investigated in the human eye.

Granit found several other facts concerning dominators. First, that by selected adaptation a dominator can apparently be split into the individual modulators which compose it. Further, that it was possible to synthesize the human photopic luminosity curve, on the basis of three fundamental sensation curves: blue, green and red, the latter being made up of two modulators, MY and MR. With regard to the number of dominators present, Granit stated that about 36 % of the fibres which were isolated by his method in the light-adapted cat's eye, gave the dominator response. Presumably the remaining fibres gave a response of the modulator type, that is, there was evidence that they were connected to receptors with a narrow spectral response.

This idea that the dominator is composite, being built up of several modulators, all connected with the same nerve fibre, agrees with the work of Polyak, who described both rods and cones converging on the same optic nerve fibre. It is not, however, in agreement with the hypothesis advanced by Professor Wundt, who proposed separate receptors for the appreciation of white. The latter did, however, suppose there to be a number of different receptors for colour, such as Granit's work has now established, in the retinae of many mammals.

The question which obviously presents itself is: what evidence is there for the presence of dominators in human vision, and how would the existence of such receptors fit in with the cluster hypothesis, which I have described in Part IX of this paper?

With regard to the precise composition of dominators, since Granit found them to have identical response curves, they must also have identical constituents: thus, according to Granit, one and all must consist of four modulators—two red, one green and one blue; moreover, the latter must have wide curves, as shown in figure 6 of Granit's publication in *Neurophysiology*—not the narrower modulator response curves illustrated in figure 2 of that communication. If by chance the blue modulator was missing from the dominator make-up, it would not seriously affect the shape of the curve; but if either of the red ones, or the green component, were missing, a very misshapen curve would result. From the evidence that the curves are all alike, we may therefore assume, as Granit does, that in fact the composition of all dominators is the same, each consisting of three, or possibly four, modulators. Since 36 % of all nerve fibres give a dominator response, and since, as we have just stated, every one of these must be connected to at least three—and possibly four—receptors, it follows that, on the average, for every six foveal receptors, two act as separate modulators, each being connected with its own nerve fibre; the remaining four are connected together, to link with a single nerve fibre having a dominator response.

Now the acuity for fine detail, given by a dominator, must be inferior to that given by a modulator, because, as has been stated, the dominator consists of four receptors which act together as a single physiological unit; so that dominators, if present in large numbers, will cause serious deterioration in the appreciation of fine detail. But it is well known that the detailed perception of the human eye can only be adequately explained on the hypothesis that each separate receptor is connected to its own nerve fibre; which seems to point to the human fovea containing few, if any, dominators of the type found by Granit in the cat.

The same idea is suggested by the results of experiments in which a small point source of white light was caused to explore in detail a small area near the centre of the fovea. The test source was moved in horizontal lines, each line being approximately 1 cone unit from the last. An area of approximately 20 cone units each way was investigated, that is, about 400 in all. At no point in this area was any evidence obtained for the interconnexion of retinal receptors, as might be indicated by the test source appearing to increase in size, or by it appearing to remain stationary. Therefore, if in fact dominators composed of three or more modulators are present in the retina, either they are excluded from the foveal centre or in some way their presence is masked by some, at present unknown, factor. There is, however, a further possibility, namely, that dominators do not consist of physiological units produced by the linking of two red, one green and one blue modulator; but that they are receptors which, under the action of the antichromatic responses, have been deprived of colour vision, and are giving what has been called in earlier Parts of this paper, 'colourless foveal vision'. This view is substantiated by the experiment described above, in which a small white test source was caused to move over the surface of the fovea. At no point during this experiment was it seen to undergo a change of colour, such as might have been expected if it had fallen on a modulator with a sharp spectral response. Moreover, two such sources adjusted in position so that there was a clear space between their images, apparently equal to the diameter of the images themselves, were found to be separated by a distance equal to little more than 1 cone unit.

It seems clear, therefore, from this experiment, that it is not a few cones of the fovea which are giving a wide 'white' response, but that every cone is doing so; in other words, every cone has become a dominator.

Now this is a very revolutionary idea, for it supposes one and the same receptor to be a dominator at one time and to be a modulator at another; it is a dominator when the light falling on it is feeble in intensity and small in visual angle; it becomes a modulator, capable of differentiating coloured lights, when the area of retina stimulated is larger and the light brighter. It is obvious that much research work will be required before such an idea can be accepted. If indeed it proves to be the case, then apparently, in some way at present unknown, the response curve of the retinal receptors is under some sort of control: at one time these receptors can respond, like Granit's dominators do, almost equally to light of all wave-lengths; at another time, they can act as modulators, responding critically to a certain isolated part of the spectrum. It is possible that this change of behaviour is brought about by mechanisms resembling those of the antichromatic responses.

XII. The repair of the retinal image

A large number of observations made with the aid of the micro-stimulator, show that there are processes of repair taking place in some part of the visual apparatus. Thus the individual properties of the photoreceptors seldom show themselves in normal vision. Nor does the retinal mosaic disclose its presence when, for example, the sharp image of a bright line on a dark background is caused to move slowly, broadside-on, across the surface of the fovea. An investigation of phenomena taking place at the blind-spot, has been found to throw light on some of these processes of repair.

(154) *The properties of the blind-spot*

One of the objects of the research described in this paper, was to obtain information concerning the properties of the photoreceptors of the human fovea. It was hoped that this would be done by causing an extremely narrow ray of white light to move slowly over the surface of the retina. It was anticipated that the ray would appear first one colour and then another, because, on the accepted theories of colour vision, receptors which differed in property would be stimulated in turn. At one moment the ray would fall on a red receptor, and a red sensation would be the result; at another moment it would be a green receptor which responded, and so on. Even if two or three receptors were stimulated at the same time, there would presumably be changes of tint as the ray explored the visual field.

When, in due course, the micro-stimulation apparatus described in Part X, had been constructed, and this experiment was carried out, it met with complete failure, for the ray remained white under all the conditions which were tested.

Alterations in the illumination of the test object, in the adaptation of the eye, in the diameter of the pupil, etc., produced no observable effect, so far as this experiment was concerned. Nor was any success met with when coloured sources were used. It was noticed, however, that such sources became modified in tint, yellow becoming white, yellow-green becoming pale blue-green and blue disappearing entirely, thus producing a kind of dichromatism, with red or orange as one primary, and blue-green or indigo-blue as the other. Sometimes, when the intensity of the light stimulus was low, all colours disappeared, and foveal vision had become colourless. These phenomena were familiar, and it was probable that they were produced under the action of the antichromatic responses.

If, then, a coloured ray can appear to be colourless, when sufficiently small in size, an explanation is offered for a ray of white light remaining colourless, when it is caused to fall in turn on receptors of different spectral response.

During the course of other experiments, it became clear that not only are changes of colour taking place, but also that alterations of shape, intensity and size are occurring, during the perception of objects which subtend small angles at the eye. It is probable that some of these modifications are caused by the aberrations of the lens system of the eye; but others appear to be due either to the retina, to the brain, or to some structure lying on the nervous pathway between the two.

Some of these modifications are of a beneficial nature, making good the defects inseparable from a lens system consisting of refracting surfaces and a retina made up of a mosaic of receptors of finite size. These processes can be very effective in the improvements which they introduce into everyday vision. But they are indiscriminate—they cannot pick and choose; on the whole they do good, but at times they may cause deleterious effects.

To revert to the subject of micro-stimulation by means of a small coloured ray; what were expected were changes of colour, when, for example, a yellow ray fell first on a red receptor and then on a green one; also tiny black spots, or scotomata, were to be looked for when a coloured ray fell on a receptor which was incapable of responding to it—for example, when a yellow ray fell on a blue receptor. But such scotomata were seldom observed, neither so far as could be observed did changes of intensity occur, as a narrow ray of coloured light explored the surface of the fovea. It seemed as if there was some process taking place which filled in the gaps left by the inactive receptors—that is, if there were any of the latter. The same mechanism appeared to be at work when a uniform coloured surface was looked at, or the image of a coloured line was caused to advance, broadside-on, across the retina; for in neither case were scotomata, or even reductions of intensity, observed. But an even more conspicuous example of reconstruction, was found in the case of the papilla of the optic nerve.

When the blind-spot was first discovered by Mariotte, its description caused a great sensation, and Mariotte's statements were questioned even by persons who were blind in one eye. A number of monocular experiments on the blind-spot have been performed by the author, some of which may be briefly described here: a fixation point is placed near the centre of a large black background, which is viewed, at a distance of about 50 cm., by the left eye. A horizontal strip of cardboard, 1·2 cm. wide and 12 cm. long, is now placed on the background, to the left of the fixation mark, in such a position that part of it coincides with the projection of the blind-spot in the visual field. It will be seen that the strip appears to be uninterrupted by the blind-spot. Now move the strip slowly to the left, and suddenly its right-hand end disappears. On reversing its movement, this end reappears as suddenly as it disappeared. Further tests on these lines suggest the following conclusions. When the image of a white object of definite shape, reaches the edge of the blind-spot and overlaps on to it, the latter part is obscured by the blind-spot. When, on the other hand, its image reaches the edges on opposite sides of the blind-spot, it appears to the observer to be continued across the area occupied by the blind-spot. Thus some part of the visual mechanism replaces the missing parts of the image.

On testing with uniform coloured surfaces, it is found that the part of the visual field which corresponds with the blind-spot, is apparently occupied by a sensation of precisely the same colour. The same statement applies to surfaces of various shades of grey. When simple patterns are tested, it is found that they also are reproduced over the blind-spot. Thus, on looking with the left eye at a printed page, the part corresponding to the blind-spot is occupied by lines of print corresponding to those seen by the rest of the retina. When, however, an endeavour is made to read the print, where the blind-spot is situated, it is, of course, found to be impossible to do so.

The movements of objects may be similarly investigated: if the white strip of cardboard on a black background, used in a previous experiment, be moved broadside-on, so that part of its image crosses the region of the blind-spot, it will be noticed that the latter does not apparently cause any interruption in the movement. The same conclusion is reached when objects are watched from a moving vehicle.

These experiments demonstrate that not only can colours, and various neutral tints, be improvised at the blind-spot, so that the gap which it produces in the visual field is made good, but also that movements of objects, both slow and rapid, are imitated as well.

The hypothesis is advanced that these processes of repair which take place at the optic papilla, also take place at the far smaller scotomata produced in the visual field when a coloured light falls on receptors which cannot respond to it.

(155) *The perception of a point test object*

A honeycomb pattern is drawn in black ink on white cardboard. A disk is now cut, the diameter of which is equal to the distances between the parallel lines of this pattern, and it is placed so that it lies entirely inside one of the hexagons. If the disk is now shifted sideways towards a corner of the hexagon, it will be noticed that it begins to encroach on two other hexagons. On the contrary, if it is shifted towards a side of the hexagon on which it lies, at first it will be found to encroach on one, but later on three other hexagons, thus making four in all. When the image of a point which has been falling almost entirely on one retinal sense organ shifts sideways much the same kind of change must occur, and in consequence either two or three additional sense organs must begin to receive stimulation. This should cause not only a change of apparent shape, but an alteration in size as well. It may be objected that the distribution of light in the retinal image corresponds more to a curve, which rises gradually to a summit and then falls away again, rather than to a disk which rises abruptly, stays level for a distance, and then drops abruptly once more. But in spite of this difference it would appear justified to apply the same reasoning. Thus, if the centre of the image of a point be made to correspond with the point where three cones touch, then an equal amount of light will fall on each one of them, and a trefoil shape should, in consequence, be presented to consciousness. On the other hand, when the centre of the image falls on the centre of the line where two cones touch, then both these cones should be equally stimulated, and an oval shape should be perceived in consequence. Using the micro-stimulator, a white source of light of small dimensions was presented to the eye of an observer, and carefully fixed by him. The test object was watched for some minutes but no changes either of size or shape were noticed. The gaze was now intentionally directed slightly upwards, downwards or sideways, but again no changes in the image of the point of light were apparent. The conclusion appears to be that through some process, at present unknown, the patterns produced by stimulating several cones simultaneously by a point of light fail to reach consciousness. Some evidence in favour of this conclusion may be obtained as follows: three white test objects were prepared, a square with 8 mm. sides, an oblong with 6 by 11 mm. sides, and a trefoil having about the same area. Over the plotting-board of the micro-stimulator was placed a piece of black velvet so as to obtain as dark a background as possible. The test objects were placed on this, and they were illuminated by an electric spot-light. They were examined singly and together. It was found that their shapes could not be recognized, in fact, it was difficult to distinguish them apart. Now there can be little doubt that diffraction and the aberrations, both of the apparatus and of the eye, cause the distribution of light on the retina to differ materially from a geometrical image in the case of each one of these test objects. None the less, material differences in the shapes of the images should exist. Yet none were noticed by the observer. The conclusion arrived at previously is confirmed, namely, that not only do the patterns produced by the stimulation of the retinal cones by a point of light fail to reach consciousness, but actual patterns of similar form as well.

Thus, there appears to be some process taking place in the visual pathway which smooths out the irregular shapes of objects when they subtend small angles at the eye. This loss of shape is a disadvantage. But at the same time the process eliminates the spurious shapes which objects, e.g. stars, would undergo owing to the arrangement of the receptors of the retina in the form of a mosaic.

(156) *Tests with two colourless objects*

In the tests described in this section one source was used for purposes of fixation while the other was used for testing purposes, the object being to examine more critically than in the previous section the effects produced when the image of a point source is moved slowly over the surface of the fovea. Both sources were disks of white card about 5 mm. diameter. One was fixed in position, the other was attached to a piece of black wire so that it could be moved by hand in the required direction. The test disk was moved in a rough circle round the fixed disk, careful fixation being preserved all the time on the latter. The size of the circle was such that the two disks could be readily discriminated from one another. The direction of rotation was revised and the speed varied, the intention being to see if a spot could be found at which the test disk appeared to alter in either shape, size or colour. No such place was found, however. The reasons for anticipating that there might be changes of size and shape were given in the previous section.

Another phenomenon was looked for. It is probable that the image of the moving test disk falls on twenty or more cones during one complete circuit. It also seems probable, since the test disk does not change in size or shape during its movements, that one receptor responds until another is ready to function in its place. In other words, twenty or more times during one complete rotation the image should appear to be stationary, as if it were being seen between the teeth of a cog-wheel. This phenomenon was looked for, but no sign of it could be seen, for the rotation of the test disk appeared to be entirely uniform.

To summarize the evidence of this and the previous sections: neither by changes of shape, intensity or velocity of the image, did the retinal receptors disclose their presence.

(157) *The perception of a line test object*

Various experiments have been performed with line test objects, one of these being as follows: on a black background were placed a straight white line, about 1 mm. wide and 110 mm. long, and a small movable white fixation mark. On looking in the microstimulator at the centre of the reduced image of the line, it was seen to extend to either side in a straight and uninterrupted manner. The fixation mark was now placed over the centre of the line, and was carefully fixed. Fixation was now continued, while the observer moved the mark slowly away from the line, in a direction roughly at right-angles to it. The line, as before, continued to appear straight and uninterrupted. Now the movement of the gaze as it followed the fixation mark would cause the image of the line to advance slowly over the surface of the retina. Since the retinal receptors are arranged in an irregular manner, they would be stimulated irregularly by the image of the line as it proceeds over them. Thus, at one point a receptor would begin to respond, then somewhere else another would do the same. At the same time, on the other side of the line, receptors would be ceasing to be stimulated as the image of the line moved away from them. These processes of the commencement of stimulation, and of its cessation, would be taking place all the time that the image of the line moved across the retina, but the observer did not see any indication of either of these events. At no time did the line appear to lose its straightness, or even momentarily to become irregular. There seems to be a process of smoothing going on all along the line, with the object of removing chance irregularities. It is apparently this same process, or one closely related to it, which is responsible for the failure to appreciate the precise shapes which are produced when the image of a point source falls on the retina.

A wavy line was now drawn, 12·5 mm. wide and 160 mm. long. The crests of the waves were 31 mm. apart. The troughs were midway between the crests, and were 5 mm. below a line joining the latter. The opposite sides of the line rose and fell together, so that the width of the line remained constant. When this line was viewed by an observer with good acuity, so that its width was at a visual angle of 2 cone units, the line appeared to be straight. Not only, therefore, are the irregularities due to the retinal mosaic smoothed out, but real irregularities as well.

The process which brings this about appears either to be the same as, or closely related to, the one which operates in the case of a point test object, which has been described in the two previous sections.

(158) *The perception of a grating test object*

If the angle subtended at the eye by the lines of a grating consisting of alternate black and white lines, be gradually reduced, a condition is soon reached at which the sharpness of the lines begins to suffer. The first change consists of the edges of the lines appearing to be nodular, rough and indented. With decrease in visual angle the second stage is reached, at which some of the lines appear to be wavy and sometimes to approach and join one another. At the third stage most of the lines have joined, causing a criss-cross appearance. At the fourth stage the test object consists apparently of irregular diamonds. At the fifth stage there are very faint horizontal lines. At the sixth stage all structure has disappeared. These six stages are not clearly defined, but merge with one another.

The visual angles for the width of the bars, in cone units, at which these stages were reached, in the case of a large grating test object, are given in table 114.

The explanation of the appearances summarized in table 114, appears to be that when the bars begin to compare with the receptors in width, the repair mechanism begins to come into play, and, since more than one interpretation is possible, so the pattern varies. On looking away from the grating, and back again, the original appearance of the grating is restored, only to break down again. On looking at a uniform white surface, after looking at the grating a curious scintillating appearance is seen, moving to and fro at right-angles to the lines of the grating.

TABLE 114. THE APPEARANCES OF THE BARS OF A GRATING

stage	appearance	width of bars (cone units)
1	nodular	3·0
2	wavy	2·0
3	criss-cross	1·7
4	diamonds	1·5
5	fine horizontal lines	1·0
6	uniform	0·8

During these observations, another curious fact was noticed: when the correcting lens in front of the observer's eye, was moved vertically or horizontally, the nodular or wavy appearance also seemed to move across the pattern. When the movement of the lens was parallel with the bars of the grating, the pattern appeared to move in the same direction as the lens; when the movement of the lens was at right-angles to the bars, the pattern appeared to move in the opposite direction to that of the lens. The cause of these movements is not known.

(159) *The perception of small coloured test objects*

Attention has been directed previously to the fact that yellow and blue test objects in close apposition, tend to decolorize one another. This was particularly noticed in the case of a grating consisting of alternate blue and yellow bars, which were replaced by black and white (see § 41, p. 550). But a similar observation was also made in the case of a grating with bars of red and blue-green, which also became black and white.

Some tests were performed with very small test objects, by means of the micro-stimulation apparatus, with the following results. When the colours were complementary, e.g. one red and the other blue-green, or one yellow and the other blue, it was found that both appeared to be colourless. This occurred if the disks were close to one another, but also if they were sufficiently far apart for there to be a clear dark space between their images. On separating them still further, their usual colour gradually returned, but when they were 5 cone units apart some loss of colour was still to be observed. As was to be expected, the disks which lost their colour most readily were the yellow and blue. The effect of using other pairs of colours, not complementary to one another, was tested and some loss of colour was sometimes found. Even white, grey or brown objects produced a little loss of colour, in coloured test objects.

Some tests were now performed using three colours: red, green and blue. For this purpose a large number of little disks of these colours were arranged in a random manner. There were places where one colour—red, green or blue—tended to predominate. In other places two colours tended to occur, to the exclusion of the third colour. In other places, on the contrary, all three coloured disks appeared to be equally represented. The arrangement of disks described above was viewed in the micro-stimulator, with the result that the larger part was seen to be almost entirely colourless. Here and there, however, patches of colour were to be seen, due to the predominance of one or other variety of coloured disk.

There can be little doubt that part of the loss of colour, noted in the above experiment, is due to the spreading of one colour on to its neighbours, owing to the diffraction and aberrations of both the instrument and the observer's eye. This spreading would obviously be reduced in amount by placing the disks farther apart. At the same time, however, there might be some reduction in the effectiveness of the colour-neutralizing process now under investigation. It was decided to test the matter further as follows. A screen was prepared by punching several rows of holes, 4 mm. diameter, in a sheet of black cardboard, alternate rows being staggered. The distance between the centre of one hole and those nearest to it, was 20 mm. All the holes were glazed with colour filters, some red, some green and some blue. In all the rows the order of the colours, from left to right, was: red, green, blue, red, green, etc. Red was the first colour in all the rows with an odd number, while blue was the first colour in all the rows with an even number, and the latter rows began half a row to the right of the former. In consequence of this arrangement, no two neighbouring holes have the same colour. The screen was illuminated from below by means of an optical lantern, its reduced image being examined, as usual, in the micro-stimulation apparatus. It was found that no colours were visible, the whole area occupied by the holes being a grey colour. Variations in the ratio of reduction, which were made by changing the focal length of the objective, had no noticeable effect.

In the above experiments, one fact was observed which will require further experiments for its elucidation. It will be remembered, when a grating consisting of yellow and blue lines was examined at a distance, that the colours neutralized one another, yellow changing to pale grey or white, while blue became dark grey or black, according to tint. The same change occurs with a grating of red and blue-green lines; in this case it is the red lines which change to dark grey or black, and the blue-green lines which become pale grey or white. On the other hand, when a red and a blue-green object are so placed that their retinal images are small and close together, the colours are neutralized but both objects remain visible. The red test object does not become dark grey or black, but appears to have much the same brightness as the blue-green one. The same thing happens in the case of yellow and blue. With the three-colour screen used above, it was also observed that red and blue remained visible as light grey, and were not replaced by black or dark grey dots as would have been the case if they had been on a bright background. The cause of these differences in brightness is not known.

(160) *The perception of uniform white or neutral tint surfaces*

It has been shown in the last section that when two small test objects, complementary in colour, or three small test objects corresponding approximately to the three primary colours, are close together, they mutually decolorize one another. It has also been shown that when a large number of such coloured sources are suitably arranged, a neutral tint is produced. The hypothesis now put forward is that the mechanism, whatever it may be, which causes neutralization of colour in the case of these actual sources, is also able to operate in the case of the colours produced by the stimulation of the photoreceptors of the fovea. Thus, if the neutralizing process can deal with real red, green and blue test objects, when their images fall on red, green and blue receptors, it can also deal with white, or neutral grey, objects when their images fall on red, green and blue receptors. This applies to white or neutral objects both large and small. In the case of extremely small, colourless test objects, so small that their images would fall on single photoreceptors, the antichromatic responses come into play, to produce a colourless impression. So it comes about that white objects of all shapes and sizes, appear white.

Experiments have been described which support the view that these photoreceptors are collected into groups, or clusters, of sense organs of similar, or nearly similar, property. These groupings make the process of colour neutralization somewhat more difficult; but they clearly do not prevent it altogether, or a white object would be seen as though it were mottled. It seems likely that a process of colour adaptation takes place locally. In fact, adaptation as known at present may be nothing more than a demonstration of the presence of this phenomenon.

Evidence has been advanced in Part XI, in support of the polychromatic theory, and in Part IX for clusters of sense organs of similar property. It is possible that as many as seven or eight different kinds of receptors are to be found in the human fovea. If this is confirmed, two questions will require an answer: (1) Is it not very unlikely that clusters will occur when there are present sense organs of so many different kinds? and (2) If, in fact, there are all these different kinds of cluster, will not the mottling which they produce be very troublesome when, for example, a uniform white surface is looked at?

The reply to the first question appears to be as follows: a cluster does not necessarily consist of receptors of only one kind. Thus, if red rays are being perceived, the clusters may consist of all those varieties of receptor which can respond to red rays. These could be red receptors, orange receptors, violet receptors, possibly yellow receptors, and 'dominators' which respond to all rays, if such be present in the human retina. In the perception of green rays, the receptors might be green, yellow-green, blue-green, possibly yellow and indigo blue, and 'dominators'. The inclusion, or exclusion, of a receptor in a cluster would depend on the wave-length of the light and the widths and spectral positions of the response curves.

The answer to the second question is that clusters depend, for their size, their number and their distance apart, on several factors, one of which is the precise widths of the spectral response curves. This may be readily understood by taking an extreme, and very unlikely, case. If the response curves of the receptors were so wide that they responded to the entire spectrum, then all of them would form a single cluster, and this would be so large that it would occupy the whole of the rod-free area of the fovea. When the widths of the response curves are known, it will be possible to calculate the probable sizes of the clusters, and their distribution.

(161) *The perception of uniform coloured surfaces*

According to the three-colour theory of Thomas Young, or its modern counterpart, the polychromatic theory of Wundt and Granit, there are receptors of specific spectral response in the retina. Many who adhere to the former theory are of the opinion that the receptors are not sharp in their responses, but are set into activity by most, if not by all, parts of the spectrum. Particularly is this so in the case of the green receptor. Thus if, by some means, this receptor could be stimulated by itself, a far purer sensation of green would result than any usually seen in normal vision. The red and the blue receptors, on the contrary, have more selectivity. Thus the blue receptor is not stimulated by rays of long wave-length,—for example, the yellow, orange and red. The red receptor, similarly, is not stimulated by rays of short wave-length, except that the violet rays do, to some extent, stimulate this receptor. According to Granit, on the other hand, there are receptors of two kinds: 'dominators', with broad responses; and 'modulators', with very sharp ones. Moreover, there are usually several different kinds of the latter in the retinae of most mammals. Some evidence has been given in Part XI, for as many as eight kinds in the retina of man. Now if there are all these kinds of 'modulators', and if they have sharp response curves, there must be large numbers of receptors either not being stimulated at all, or being only feebly stimulated, when an observer looks at a uniform surface illuminated by means of monochromatic light. But when this is done, the field appears completely uniform, and there are no signs of numerous punctate scotomata such as might be expected from Granit's experiments, and would also be expected on the basis of Young's theory—particularly if red light were used for purposes of illumination. Are these experiments in some way invalid? It would seem that the answer is, 'No', provided that the assumption can be accepted that the scotomata, which would otherwise occur, are eliminated by similar processes to those that are observed to take place at the blind-spot, and which have been described in § 154, p. 657.

(162) *The perception of the colour of intermittent test objects*

Three types of test object were found to suffer changes in colour, when physical explanations appeared to be excluded: (*a*) an intermittent point source of white light; (*b*) sunlight reflected from water which was being ruffled by a breeze; (*c*) daylight reflected from particles in granolithic non-skid stair-treads. The colours seen were always either pale orange-red or pale blue-green, as would be expected because of the antichromatic responses.

An explanation is needed, not of the appearance of colours which presumably are due to the stimulation of receptors with specific colour response, but of the rareness with which colours are perceived. The explanation appears to be as follows. If the source which produces an image on the retina, subtends so small an angle, and is of such feeble illumination that it stimulates only one receptor, then the latter responds with a colourless sensation, because the angle and intensity are such as to cause colourless foveal vision under the action of the antichromatic responses. If, on the other hand, the visual angle and intensity are such as to cause the recognition of colour, then several receptors are stimulated, some of one response, some of another, and the fact that the stimulus is a colourless one is at once recognized. Thus the test object remains white almost all the time. Occasionally, however, the image falls on receptors with the same response, when the colour sensation proper to those receptors is momentarily appreciated.

The reason why it is necessary for the source to be intermittent is probably accounted for as follows. When once the source has been recognized as white, it appears to remain white under conditions where a new source would be judged to be coloured. The mechanism which is responsible for this is probably the same as, or similar to, the one which prevents the perception of scotomata or coloured dots when a uniform surface is being looked at.

(163) *Perception by the peripheral retina*

There is evidence that the fovea plays a part in the perception by the more peripheral parts of the retina. The following experiment supports this view. A sheet of plain white foolscap paper was folded several times longitudinally, and was then spread out in front of the observer, at a distance of about 50 cm., with the folds horizontal. It was lit from in front, so that the folds showed up as changes in brightness. The definition of the folds, both central and peripheral, was carefully noted. Then, while the centre of the sheet of paper was fixed with one eye, a circular disk of white cardboard, 5 cm. diameter, was placed in position so that its centre corresponded approximately with the point of fixation. It was now noticed that perception by the periphery of the retina, of the folds in the paper, had suffered marked deterioration. Under suitable conditions the folds may disappear entirely. The use of coloured disks or disks with patterns, instead of a plain white disk, appeared to make little or no difference to the above observations. Also placing the folds at different angles had little or no effect.

When the above experiment was repeated with a sheet of paper which had been folded irregularly, it was found that the placing of the circular disk into position had little or no effect on the appearance of the folds.

The conclusion drawn from the above tests was that the apparent sharpness of perception by the peripheral retina is improved, sometimes very greatly improved, by the sharpness of the foveal image, but that these beneficial effects do not take place unless the pattern in the visual field is one which repeats itself in an obvious manner. Examples of the latter would be: a row of street lamps, the images of which cross from side to side of the visual field; a brick wall; a number of wires or pipes; or the beams of a roof.

Some tests were performed to see if the apparent definition of a peripheral image could be improved by previously examining that same image by the fovea. Thus, if this were the case, then during reading there should be a streak of good definition left behind in the periphery of the retina, as the fixation point travels across the page to the right. But this is not found to occur. Neither, so far as can be judged, does the close examination of an object by the fovea subsequently improve the definition of its image when it is caused to fall on the periphery.

This improvement of the apparent definition of one part of the visual field, brought about by good definition in another part, in some ways resembles the phenomena occurring at the blind-spot. There are differences, however. Thus at the blind-spot there is no intitial image from which to build up, and the whole sensation has to be improvised, whereas in the case now under consideration there is an initial image, although it may be an ill-defined one.

(164) *The processes of repair*

These processes have been referred to many times during the course of this paper. The antichromatic responses are themselves examples, so also are such well-known phenomena as simultaneous contrast and local dark- and light-adaptation. But in addition, the existence of other processes have been pointed out, such as: (*a*) scotoma elimination, for example at the blind-spot and in the case of uniform coloured surfaces; (*b*) smoothing, for example at the edges of dots, lines and areas; (*c*) improvements of definition in one part of the retina, in consequence of better definition in another part. All these, together with contrast and adaptation, form a complicated series of processes, hard to define and difficult to understand, which must play a highly important part in everyday vision; straightening lines which the retinal mosaic would cause to be irregular; making surfaces uniform, which would otherwise be marred with black dots which would move about with the gaze;

increasing graduations of brightness, which have suffered owing to diffraction and aberrations of the lens system of the eye; filling in the area of the blind-spot; and probably in many other ways benefiting vision. Only one of these processes has been studied in this paper, namely, the antichromatic responses. The other processes mentioned seem to the author to be deserving of closer investigation.

REFERENCES

Abney, W. 1895 *Colour vision.* London: Longmans, Green & Co.

Abney, W. & Festing 1892 *Phil. Trans.* A, **183**, 537.

Adler, F. H. & Fliegelman, M. 1934 *Arch. Ophthal., N.Y.*, N.S. **12**, 475.

Bryan & Baker 1912 *Opt. convention*, p. 252.

Burch, G. J. 1900 *J. Physiol.* **25**, 17*P*.

Crawley 1905 *Opt. convention*, p. 122.

Donders, F. C. 1881 *v. Graefes Arch. Ophthal.* **27**, 1, 155.

D'Silva, J. L. & Turton, E. C. 1947 In course of publication.

Edridge-Green, F. W. & Marshall 1909 *Trans. Ophthal. Soc.* **29**, 211.

Einthoven, W. 1885 *v. Graefes Arch. Ophthal.* **31**, 211.

Ferree, C. E. & Rand, G. 1920 *Amer. J. Ophthal.* **3**, 772.

Goldmann, H. & Hagen, R. 1942 *Ophthalmologica*, **104**, 15.

Göthlin, G. F. 1943 *The fundamental colour sensations in man's colour sense*, p. 70. Stockholm.

Granit, R. 1943 *Nature*, **151**, 11.

Granit, R. 1945 *Nature*, **155**, 711.

Hardy & Perrins 1932 *The Principles of Optics*, p. 189. New York and London: McGraw, Hill.

Hartridge, H. 1915 *J. Physiol.* **50**, 95.

Hartridge, H. 1918 *J. Physiol.* **52**, 175, 222.

Hartridge, H. 1919 *J. Physiol.* **53**, 17*P*.

Hartridge, H. 1922*a* *J. Physiol.* **57**, 52.

Hartridge, H. 1922*b* *J. Roy. Micr. Soc.* 243.

Hartridge, H. 1941 *Refractionist*, **30**, 154.

Hartridge, H. 1944*a* *J. Physiol.* **103**, June.

Hartridge, H. 1944*b* *Nature*, **153**, 775.

Hartridge, H. 1945*a* *Nature*, **155**, 391.

Hartridge, H. 1945*b* *Nature*, **155**, 657.

Hartridge, H. 1947 *J. Ill. Eng. Soc.* In course of publication.

Hartridge, H. & Owen, H. B. 1922 *Brit. J. Ophthal.* December.

Hecht, S. & Mintz, E. U. 1939 *J. Gen. Physiol.* **22**, 593.

Helmholtz, H. 1909 *Physiological Optics*, 3rd ed., p. 145.

Hering, E. 1874 *S.B. Akad. Wiss. Wien*, **69**, 179.

König, A. 1897 *S.B. Akad. Wiss. Wien*, p. 559.

König, A. 1903 *Gesammelte Abhandlungen Physiol. Optic*, p. 353.

Ladd-Franklin, C. 1893 *Z. Psychol. Physiol. Sinnesorg*, **4**, 211; *Mind*, N.S. **2**, 473.

Laurens, H. & Hamilton, W. F. 1923 *Amer. J. Physiol.* **65**, 547.

Linfoot, E. H. 1945 *Nature*, **155**, 76.

Lythgoe, R. J. 1932 *Spec. Rep. Ser. Med. Res. Coun., Lond.*, no. 173.

McDougall, W. 1901 *Mind*, **10**; N.S. **52**, 210, 347.

Østerberg, G. 1935 *Acta Ophthal. Kbh.*, suppl. 6.

Parsons, J. H. 1915 *Colour vision*, p. 289. Camb. Univ. Press.

Pirenne, M. H. 1944 *Nature*, **154**, 741.

Pitt, F. H. G. & Wright, W. D. 1934 *Proc. Phys. Soc.* **46**, 459.

Polyak, S. L. 1941 *The retina*, p. 607. Chicago: Univ. Chicago Press.
Roaf, H. E. 1930 *Proc. Roy. Soc.* B, **106**, 276.
Rochon-Duvigneaud, A. 1906–7 *Arch. Anat. Micr.* **9**, 315.
Shlaer, S. 1937 *J. Gen. Physiol.* **21**, 165.
Shlaer, S., Smith, E. L. & Chase, A. M. 1942 *J. Gen. Physiol.* **25**, 553.
Sinden, R. H. 1923 *Proc. Opt. Soc. Amer.* **7**, 1123.
Stiles, W. S. 1939 *Proc. Roy. Soc.* B, **127**, 64.
Stiles, W. S. & Crawford, B. H. 1933 *Proc. Roy. Soc.* B, **112**, 428.
Thomson, L. C. 1946 *Nature*, **157**, 805.
Thomson, L. C. & Wright, W. D. 1947 *J. Physiol.* **105**, 316.
Tscherning, M. 1904 *Physiological Optics*, pp. 37, 66, 112, 280. Philadelphia: Keystone Press.
Vernon, M. D. 1930 *Spec. Rep. Ser. Med. Res. Coun., Lond.*, no. 148.
Willmer, E. N. 1943 *Nature*, **151**, 213, 632.
Willmer, E. N. 1944 *Nature*, **153**, 774.
Willmer, E. N. & Wright, W. D. 1945 *Nature*, **156**, 119.
Wright, W. D. 1929 *Spec. Rep. Ser. Med. Res. Coun., Lond.*, no. 139.
Wundt, W. 1893 *Grundzüge physiol. Psychol.* **1**, 535.

SUBJECT INDEX

AUTHOR INDEX