THE BRITISH JOURNAL
OF
OPHTHALMOLOGY
APRIL, 1931

COMMUNICATIONS

DARK-ADAPTATION AND THE PERIPHERAL COLOUR SENSATIONS OF NORMAL SUBJECTS

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Introduction

THOMAS YOUNG, in 1800, appears to have made the first careful observations on the sensitivity of the peripheral retina. In his own words: " The visual axis being fixed in any direction, I can at the same time see a luminous object placed laterally at a considerable distance from it; but in various directions the angle is very different. Upwards it extends to 50 degrees, inwards to 60, downwards to 70, and outwards to 90 degrees. These internal limits of the field of view nearly correspond with the external limit formed by the different parts of the face, when the eye is directed forwards and somewhat downwards, which is its most natural position." It is clear that Thomas Young was fully aware of the limitation of the field of vision by the features. If precautions are taken it can be shown that the field of vision has the form of an ellipse with its long axis horizontal and with the blind-spot in its centre (Basil Lang).

A few years later Troxler (1804) found that when coloured papers are moved towards the periphery, certain colours are recognisable at a greater angle than others. Purkinje (1825) confirmed and extended the observations and since that date over 100 papers have been published dealing with peripheral vision. The chief reason for this abundance of papers is that the results of the work appear to contradict the Young-Helmholtz theory of colour vision whilst they favour, on the other hand, the Hering theory. In the consideration of the results their relation to the duplicity theory of v. Kries should be borne in mind. The attitude of the adherents of the Young-Helmholtz theory to the duplicity theory has never been very clearly defined and this aspect of the subject has not been given the attention it deserves. The aim of this thesis is to present some evidence which may help to bridge the gap. Although the results add but one more paper to an already overcrowded literature, they may be useful in that they emphasise the necessity of controlling certain factors in work on the peripheral retina.

Historical

Purkinje (1825) described the changes in hue when a coloured stimulus is moved in from the periphery. All coloured objects appear grey or black when their images fall on the extreme peripheral retina and pass through regular transitions of colour tones as their images approach the fovea. It is probable that Purkinje used coloured papers but he defined neither their area, the amount of light falling on them nor their background. The experiments have been repeated by many workers and their results mostly confirm those of Purkinje.

The results vary slightly with the type of stimulus colour used, and most of the recent work has been done with either spectral colours or filters, it being impossible to get even approximately pure colours with the use of coloured papers. The hue changes are substantially the same whichever type of stimulus is used and all workers agree, in general, on the following changes in hue when the stimulus is viewed with increasing obliquity.

Red soon becomes orange, then yellow, yellow-brown and finally black (or grey if viewed on a black background). Orange passes through yellow to grey. Yellow becomes more and more desaturated and finally appears grey. Green passes through yellow to grey. Blue becomes desaturated and finally appears grey. Violet passes through blue to black. Purple becomes violet-blue and finally grey. In the extreme periphery colours appear grey or black; in the intermediate zone the long wave-lengths appear yellow and the short wave-lengths blue; in the inner zone the hue passes along the spectrum and finally comes to rest at its true colour. From this it follows that there will probably be a wave-length in the yellow and one in the blue which will not change in hue. There will also probably be a wave-length in the green which passes neither through yellow nor blue to white and will appear green at all points of the retina. Add to this green its complementary purple and we have four colours which should undergo no hue changes when viewed peripherally. These colours were shown to exist by Bull (1881) and Hess (1889) and are known as the invariable colours. Hess gave their wave-lengths as: yellow $574{\cdot}5\mu\mu$, blue $471\mu\mu$, green $495\mu\mu$ and the red-purple complementary to the green.

In text-books on the subject there is often to be found a diagram giving the exact position on the peripheral retina at which red, green, blue and yellow can be recognised. It is important to remember that these diagrams were obtained from invariable colours. It is a waste of time to map out a colour field unless this precaution is taken, otherwise the phenomena of peripheral hue changes described above will be obtained. In the usual statement of the phenomena, red and green are described as losing their colour simultaneously and yellow and blue also simultaneously but farther out in the peripheral retina. This statement also needs qualification since it is obviously absurd to compare the field of vision for a bright red with that of a dull green. It is necessary that the colours should have the same " white-valency," that is, that their luminosities measured by heterochromatic photometry should be the same. Provided complementary colours of the same brightness are used, the fields of vision for red and green are coincident. The fields of vision for yellow and blue also coincide with one another, but they are more extensive. At the extreme periphery of the retina there is a zone where all objects are seen in shades of grey (Hess 1889, Hegg 1892). The importance of this phenomenon to the Hering theory of colour vision will be considered later. Guillery (1896) measured the smallest coloured areas which could be recognised by the peripheral retina. His results confirm those of Hess by an entirely different method.

Dreher (1911) investigated peripheral colour sensations in a different way. He used two monochromatic spectral patches, one seen by the fovea and the other seen by the peripheral retina. The wave-length of the peripheral patch was varied so as to appear of the same hue as that of the fovea. No very definite conclusions were reached except that a yellow appears redder when seen peripherally than when seen by the fovea. From this author's results it is clear that a subject will call a much wider stretch of the spectrum yellow when viewed by the periphery. No worker appears to have measured the just noticeable difference of hue in different parts of the spectrum for the peripheral retina.

The experimental difficulties of investigation in the peripheral retina are very great and it cannot be said that they have been very adequately controlled in work up to the present. Considerable attention has been paid in the past to those factors which are known to influence the colour fields. This work is important since it is possible that some of the phenomena of peripheral colour vision have their origin in causes other than the differential sensitivity of the retina to colour.

The peripheral colour fields are enlarged in an orderly manner by an increase in the brightness of the retinal image (Abney 1913 p. 203) and provided it is bright enough, colours can be recognised by the extreme peripheral retina (Landolt,1873). The brightness of the retinal image is regulated by the pupillary diameter and the angle which the incident light makes with the plane of aperture of the pupil. It is of importance to prove, therefore, that the differential sensitivity of the retina to colour is due to neither of these physiological conditions (Landolt, 1874). Ferree and Rand (1916) controlled both these factors by passing their test-lights in a narrow pencil through the centre of the pupil and they showed that the phenomena of peripheral colour vision still held.

The general effect of increasing the size of the coloured test-object is the same as that of an increase in the illumination (Charpentier, 1877, Abney, 1913). Abney found that for all colours the average diminution in field on cutting down the intensity by one quarter was 7·5 degrees, whilst an increase in the area of the test-patch by one quarter led to an increase of five degrees. The optical system of the eye suffers from the defect of chromatic aberration, the result of which will be that the area of retina illuminated will vary according to the colour of the stimulus. It will be noticed that the increase in the field of vision which would be brought about by this cause is very nearly compensated for by the diminution in the brightness of the retinal image, therefore fields of vision should be largely independent of chromatic aberration. Albini (1887) has claimed, however, that with a suitable correction for the chromatic aberration due to each colour and for the error of refraction of each part of the retina used, all colour fields are co-extensive. This worker also claims that lack of practice in everyday life is a factor to be taken into account in the consideration of the poor colour discriminations of the peripheral retina. Subsequent workers do not appear to have confirmed Albini's observations.

From the physiological point of view there is another factor of great importance in certain types of colour-vision experiment, namely the presence within the eye of coloured pigments other than those concerned directly with perception. The influence of macular pigmentation on colour matches at the fovea is too well known to need elaboration (Maxwell, 1860). The distribution of the pigment in the region of the fovea is very variable in different subjects. Its extent is usually determined by subjective experiment and it is not unusual to find unmistakable signs of its presence

10 degrees from the fovea, but beyond this, experimentation is difficult and complicated by the colour phenomena of the peripheral retina. Brücke (1851) has shown that the colour sensations of the retina can also be modified by the presence of haemoglobin within the eye. Although very little attention has been paid to this observation, it will be shown later that it may have a bearing on peripheral colour sensations.

Theoretical

The chief arguments against the Young-Helmholtz theory of colour vision are supplied by the changes in colour sensation in the peripheral retina. According to this theory the coloured retinal image excites three mechanisms which, for the sake of illustration, can be assumed to be three types of cone, each type responding to different wave-lengths. The character of the sensation depends on the extent to which these three cones are stimulated and this depends on the wave-length composition of the stimulating light.

According to this theory the sensation, yellow, results from approximately equal stimulation of the red and green receptor cones. When, however, a red light is viewed more and more peripherally, it looks first orange and then yellow. This phenomenon could be explained by assuming that the " green " cones and the " red " cones are being stimulated unequally, the retina having become partially red-blind. This was Helmholtz' (p. 373) explanation, but it is unlikely because a green light viewed peripherally also looks yellow.

If the peripheral retina were red-blind and if white results from equal stimulation of a red, a green and a blue receiving cone, then a white object should appear blue-green peripherally (Berry, 1920). The fact that such a phenomenon does not occur, indicates that if the peripheral retina has become partially blind to red it must also have become equally blind to the complementary colour, namely blue-green. To explain the result in terms of the theory, therefore, one must say that the peripheral retina loses sensitivity to colour in such a way that complementary colours are equally affected. This is precisely the result obtained by Hess in his investigation on colour fields and it may also be explained by Hering's theory.

" Hering regards the whole series of our visual sensations as made up of six primary sensations: but the most novel and fundamental feature of his theory is the arrangement of these six sensations in three pairs, the two members of each pair being antagonistic in nature to each other, and depending on physiological processes of an opposite kind. Each of the three pairs of sensations depends on the action of a special substance, the three substances being called black-white, red-green, yellow-blue. In most kinds of stimulation of the retina all three substances are set in action, and the character of the sensation is determined by the relative amount of action of each." (Rivers, 1900). The red and the green of the red-green substance are complementary, and the diminution of colour sensitivity in the near peripheral retina is explained as a partial or complete absence of this substance. If this is the true explanation then white will still appear white when viewed indirectly.

It has been shown by Landolt (1873) and v. Kries (1897) that vision in the peripheral retina is to be regarded as central vision diminished in sensitivity and that this also applies to the extreme periphery. v. Kries determined the peripheral luminosity values of various spectral lights and compared them with the corresponding values for night vision in the region of the fovea. Provided the eye is light-adapted the luminosity curve in the extreme periphery has its maximum at 608$\mu\mu$ and this roughly corresponds with the maximum for day vision at the fovea. This phenomenon is not to be explained by either of the rival colour vision theories in their original form. Both these theories consider that the peripheral retina of the normal eye shows the same conditions as are found in colour blindness. The Young-Helmholtz theory explained the achromatic vision of the extreme peripheral retina of the normal eye by assuming that in this region all the colour perceiving cones are absent and vision is served by the rods or the organs of night vision. The Hering school assumed that only the black-white substance is present, namely the receptor for night-vision. If either of these were the right explanation, then the peripheral luminosity curve would be the same as that for night vision and also the same as that for the condition of total colour blindness. In view of the work of v. Kries neither of these can be the right explanation.

In order to make the results harmonise with the Young-Helmholtz theory certain assumptions are necessary and the hypothesis of Fick (1890) offers a fairly good explanation. Fick assumed that the colour sensation curves become flatter as the periphery of the retina is approached, the change first affecting the green and red curves, which ultimately coincide. If the three-colour sensitivity of the cones depended on their containing an outer shell of three different coloured pigments, a dilution of these pigments would lead to a flattening of the curves. Another way of expressing the result in terms of broadcast reception would be to say that the colour receptors become less sharply tuned. This will have the effect of making hue perception in the peripheral retina blunter since a change in wave-length will not produce so great a change in the response of the colour receptor as it would at the fovea. According to the hypothesis, the peripheral retina would be less selective than the fovea. In addition those colours containing inherent white at the fovea (Abney, 1913), would contain more of this inherent white in the periphery. Abney (p. 201) did in fact find that a yellow, wave-length $589\mu\mu$, has a larger field of vision than a yellow made by mixing green, $527\mu\mu$ and red, which produced an identical match with the spectral yellow at the fovea. Unfortunately this observation could also be explained by the greater scotopic (achromatic) value of the mixed light.

If true, another interesting consequence of this hypothesis would be that the total stimulation value of a uniformly bright retinal image would be higher in the periphery than at the fovea; subjectively white light would be brighter. The reason for this would be that the coloured shell of the cones would be more dilute in the periphery and the physical intensity of the light transmitted to the light-sensitive layer would be greater. No one appears to have undertaken the difficult task of putting this point to the direct test. It is known, however, that the critical frequency of flicker value is higher in the periphery than at the fovea for day vision. This fact cannot be explained by assuming that the rods are the elements responsible for the perception of flicker in the periphery (Lythgoe and Tansley, 1929 *a*).

The Young-Helmholtz theory is concerned only with the cones, the colour sensitive receptors of day vision. Adherents of the theory usually look on the rods as being pre-eminently the organs of night vision, capable of giving rise to only one type of colour sensation, that of bluish-white.

The fovea contains cones only: the peripheral retina has very few cones and many rods. According to the Helmholtzian view the sensations of the peripheral retina should be a mixture of colour sensations from the cones and a colourless sensation from the rods. Since the rods have very considerable powers of dark adaptation, the light threshold sensitivity rising about one thousand times during half an hour's stay in the dark, the resultant sensation and the peripheral luminosity curves are very profoundly modified by dark-adaptation of the eye (Hering, 1895, Tschermak, 1900). It is generally agreed that the character of the surrounds considerably modifies the colour sensations from the peripheral retina (Aubert, 1857), but some workers have denied that the background has any influence (Woinow, 1870; Krükow, 1874). Ferree and Rand (1920) have paid considerable attention to this point and always use a surround having the same brightness as the test-patch. It is often assumed that the influence of the surrounds is due to some type of simultaneous contrast. Another possibility should, however, be taken into account, namely, that the effects may be due to the local condition of adaptation of the retina in the region of the test-patch. By surrounding the test-patch with black the rods might become dark-adapted and more sensitive and in this way dilute the colour by a colourless sensation.

In the consideration of the relation of the Young-Helmholtz theory to the duplicity theory, there is one outstanding point of great interest and that is the contribution of the rods to visual sensations at high illuminations (v. Kries, 1894, 1896). It is possible that the whole of their visual purple content becomes bleached, so becoming insensitive and playing no part in the peripheral luminosity values (v. Kries, 1897; Parsons, 1924, p. 215). Another explanation is that they have become "saturated," an increase in stimulus causing no increase in sensation. A third view is that the rods are the receptors for blue. Although there is no evidence for this suggestion it is attractive from some points of view, since it is not in keeping with our conceptions to think of a structure lying idle in the body as the rods would do if they were functionless at high illuminations.

Parsons (1927) has examined in great detail the histological evidence bearing on the duplicity theory. There is overwhelming subjective evidence of a dual mechanism of vision and superficially this seems to bear some relation to the relative distribution of rods and cones. There are, however, some very serious difficulties in the way of accepting the histological side of the theory, amongst which can be mentioned (1) the lack of uniformity in the shape of the rods and cones amongst different animals; (2) the rod-like shape of the "cones" in the human fovea; and (3) the paucity of cones in the human peripheral retina. Parsons is of the opinion that the number of peripheral cones is quite inadequate to explain colour vision in the periphery, the most serious objection being that the periphery has exactly the same characters as the fovea but to a less degree. Their photopic luminosity and colour mixing curves are the same and the peripheral curves show none of the characteristics of rod vision. To account for this Parsons advances the attractive suggestion "that under high intensities of excitation in normal man, the 'dyscritic' (night) mechanism is capable of giving the same chromatic responses as the cones, or essentially epicritic mechanism." (p. 177). If this view be adopted it is necessary to examine closely the evidence derived from dark-adaptation. During the course of dark-adaptation the dyscritic mechanism becomes increasingly sensitive. How is this accomplished? What is the fate of the epicritic mechanism after prolonged dark-adaptation and what is the fate of the dyscritic mechanism at high general levels of illumination? According to Parsons the responses of the peripheral retina become almost entirely epicritic at high illuminations in the light-adapted eye, whilst the presence of dyscritic mechanism cannot be detected. During the course of dark-adaptation the responses of the peripheral retina become more and more of the dyscritic type and one would expect the epicritic mechanism to have become less sensitive. Instead of enquiring into the fate of the rods and cones at high and low illuminations respectively, if we follow Parsons we must continue the enquiry in terms of the dyscritic and epicritic mechanisms, both of which are served by the peripheral rods. The chief question to be answered is whether the responses of the peripheral rods become epicritic at the expense of the dyscritic mechanism and *vice versa.*

The Objects of the Experiments

The experiments to be described were designed with a view to finding the fate of day (cone or epicritic) vision during dark-adaptation and they were a continuation of some work on the changes in the critical frequency of flicker during the course of dark-adaptation (Lythgoe and Tansley, 1929, *a*). Several subjects took part in these experiments, readings being taken at many points on the retina. Since some of the results were difficult to explain, it was decided to make a parallel investigation on peripheral colour sensations. The points at issue were: (1) the differences in colour sensations between the light and dark adapted eye, and (2) the relative behaviour of the different subjects.

The conclusions drawn from the experiments on the critical frequency of flicker were that the highest perceptible rate of alternation of black and white increases during the course of dark-adaptation for the rods and decreases for the cones. The evidence advanced for these conclusions was as follows: There was a progressive fall in the critical frequency of flicker (1) at the fovea whatever the illumination of the flickering test-patch, and (2) with a red test-patch at all points on the retina. There was a progressive rise in critical frequency (1) when a faintly illuminated test-patch was viewed peripherally. (2) This phenomenon was more pronounced as the periphery of the retina was approached. The duration of the rise was about 45 minutes and was therefore comparable with the time occupied in the establishment of night vision as measured by the light threshold. At high illuminations of the test-patch the critical frequency measured by the periphery fell whilst at intermediate illuminations there was a quick fall followed by a long drawn-out rise.

There seemed no doubt that the rise in critical frequency due to the rods should be correlated with their increased sensitivity during dark-adaptation. A fall in critical frequency should therefore be associated with decreased sensitivity. If this argument were applied to the cones it would indicate that they become less sensitive during dark-adaptation. A certain amount of evidence was collected to show that this is not improbable. Another factor, the swamping effect of the rods, probably modifies and might wholly account for the fall in critical frequency readings due to the cones. In the dark the sensation due to an illuminated area of the retina would be derived both from the cones and from the rods. Since the sensitivity of the rods increases so vigorously during dark-adaptation the resultant sensation would become more and more due to the rods during the stay in the dark. Applying this reasoning to the perception of a flickering test-patch, one could imagine conditions where the cones could, by themselves, appreciate the flickering whilst the rods' contribution to the resultant sensation would be a bright non-flickering sensation of light. During the course of dark-adaptation this non-flickering sensation might become sufficiently intense to swamp and to mask completely the flickering sensation from the cones. Since, however, the critical frequency at the fovea and with a red light at all points on the retina, both fall during dark-adaptation, it is highly improbable that the masking effect is sufficient in itself to explain all the phenomena. The final conclusion was that the cones become less sensitive during dark-adaptation.

The perception of a coloured stimulus by the peripheral retina might be influenced by these factors. The coloured stimulus in the light-adapted eye would stimulate the cones and give rise to a sensation of colour. In the dark-adapted eye this colour sensation would be diluted by a colourless sensation from the rods and in addition the sensation from the cones would become less intense if they became less sensitive.

In the experiments which are to be described an attempt has been made to compare the sensations evoked by coloured stimuli in the light and dark-adapted eyes. The main points which have been kept in mind are the desaturation of the colour and difficulties in colour recognition.

Apparatus

The apparatus was the same as that used in the experiments on the critical frequency of flicker. The subject sat inside a large whitened cube whose sides measured 152 cm. The test-patch was viewed through a square hole cut in the wall of the cube and subtending an angle of one degree at the subject's left eye. The advantages of this arrangement are that the whole of the subject's retina can be uniformly light-adapted by illuminating the walls of the cube and also that the subject can be instantaneously plunged into complete darkness by switching off the light inside the cube.

The subject sat on a stool and rested his chin on a mould of dentist's wax. The mould was supported on a bracket hinged in such a way that horizontal movements of his head were about an axis passing through the observing eye, whose position in the cube therefore remained approximately the same. On the same horizontal plane as the test-patch and the observing eye were fixation points on the wall of the cube making various angles between the test-patch and the eye. If the subject fixated the 30 degree mark, then the retinal image and the fovea subtended an angle of 30 degrees at the nodal point of the eye. Streaks of luminous paint served as fixation marks when the subject was in the dark. Only the horizontal meridian of the left retina was explored and vision of the test-patch by the right eye was prevented by adhesive tape on the side of the nose.

The test-patch outside the cube was of matt-surfaced opal glass and, to the subject, it appeared to fill the opening in the cube completely. A gas-filled lamp run off the mains at a constant voltage was enclosed in a box through a hole in which the lamp illuminated the test-patch. In front of this hole combinations of Wratten colour filters were placed. Details of these filters are given in Table 1. Considerably narrower bands of wave-lengths could have been obtained by the use of a spectroscope, but it was felt that filters were sufficiently accurate for this type of comparison experiment.

TABLE I.

Details of the colours used in the investigation.

Combination of Wratten filters	Resultant colour of filter	Wave-lengths transmitted in $\mu\mu$	Brightness of test-patch in equivalent foot-candles
25 and 34	RED	End of spectrum to 637	0·2
25 and 56	ORANGE	700 to 680 635 to 584	0·5
22 and 57	YELLOW	632 to 552	1·0
15 and 45	GREEN	542 to 514	0·18
4 and 45A	BLUE-GREEN	530 to 473	0·2
34 and 45	BLUE	492 to 442	0·03
36 and 47	VIOLET	480 to end of spectrum	0·003

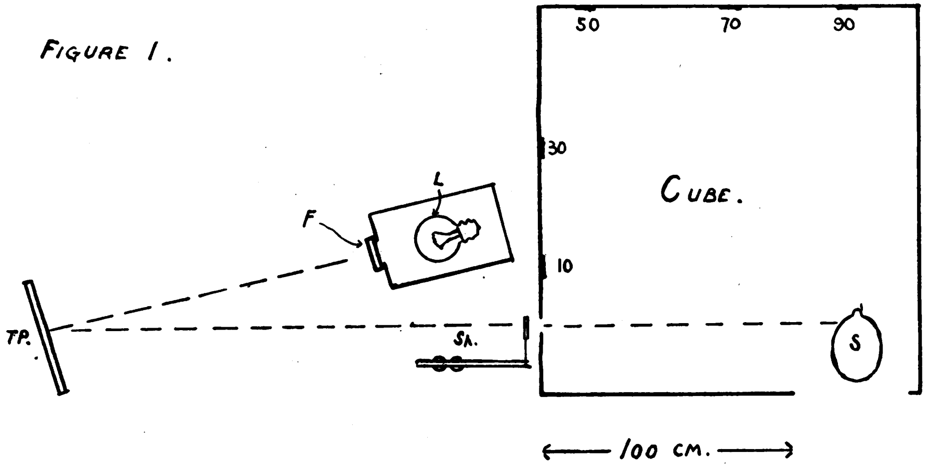
The brightness of the test-patch was determined by the critical frequency of flicker method.

A shutter of white paper was mounted immediately outside the cube. It was activated by a rotating contact allowing observation of the test-patch for 1·2 seconds. When closed the walls of the cube and the aperture had the same apparent brightness. The object of this device was to keep the subject's eye at the same level of adaptation, since a continuous light from the test-patch could in itself interfere with this level.

Method

After the subject had been five minutes in the dark the light in the cube was switched on, the resultant brightness of the surrounds being then 0·6 equivalent foot-candles. After another five minutes in this light the subject fixated the 90 degree mark and the shutter was opened. After a short rest the subject fixated the 80 degree mark and the exposure of the test-patch was repeated. This procedure was repeated for fixation marks at 70, 60, 50, 40, 30, 20, 10 and 5 degrees and finally the subject looked straight at the test-patch. At each position he described the resultant colour sensation. After all seven colours had been investigated the light in the cube was switched off for three-quarters of an hour in order to bring about dark-adaptation. The investigation was then repeated in the dark using the same method except that a rest of two minutes was given between the exposures of the different colours. The illumination of the test-patch was exactly the same for the light- and dark-adapted series. Long intervals were left between the exposures in the dark, both to preserve the condition of dark-adaptation and also to prevent after-images. These after-images have complicated the results of several workers in the peripheral retina (Hellpach, 1900) and it is stated by Baird (1905) that they result from taking readings too quickly after one another.

Figure 1.



Each of our five subjects repeated the experiment at least twice and usually five times. The subjects had normal vision except for trifling refractive errors.

Results

In experiments dealing with the description of subjective sensations the presentation of results is a difficult problem. At 40 degrees on the peripheral retina, for instance, the subject may on successive days describe the yellow filter as " greenish yellow," " yellowish green," " yellow but greener," " deep yellow," and so on. The remedy lies either in giving the results of all experiments verbatim or in setting down the results of all experiments side by side and then interpreting the answers on some fixed basis, averaging where necessary. The latter plan has been adopted in Fig. 2. The meaning of the symbols used can best be

Fig. 2.

appreciated by the aid of an example. In dark-adaptation blue-green is seen by the extreme peripheral retina as white. The test-patch takes on a bluish hue at about 40 degrees, the actual reading varying from day to day and amongst different subjects. From there on the patch appears progressively greener up to the point where the eye is looking straight at the patch, when it is described as either green or blue-green.

There is a marked difference between the hue changes in passing from the periphery to the fovea according to whether the eye is light- or dark-adapted. In the light it is usually possible to give an approximate value to the position where the test-patch first appears in its true hue, the subsequent changes being small. This cannot be done for the dark-adapted eye and this phenomenon is almost certainly connected with the change over from day to night vision. The sensation from a coloured stimulus under these conditions is made up of an intense achromatic response to which is added the feeble colour sensation from the mechanism of day vision.

When the readings were taken in the dark the changes in hue in passing from the periphery to the fovea were slower. These changes were almost identical with those found by other workers. In the dark-adapted series, for instance, yellow becomes progressively more saturated. Orange first appears yellow, then orange-yellow and then orange. Red first appears yellow, then orange and finally red. In the light-adapted series the intermediate yellow stage did not appear, but it is possible that the transition was too rapid to be detected by the method used. The blue-green, blue and violet first appeared as blue in both light- and dark-adaptation. It will be noticed that there was no decided hue change in the case of the blue and yellow although there was a change in saturation. These two colours had the same wave-length as Hess' invariable colours. The third invariable colour, the green, was found to appear sometimes as blue and sometimes as green especially in dark-adaptation. It is possible that if its wave-length had been a little longer there would have been no hue change.

A superficial examination of the results would indicate that with the same filter, the colour of the test-patch is less easily recognized in the dark than in the light. Although this is interesting empirically, it is not possible to draw any deductions as to the fate of the mechanism for colour perception during dark-adaptation owing to the complication introduced by the achromatic response of night vision.

Green was extremely difficult to recognize by the dark-adapted peripheral retina and in some of our experiments the subjects were quite unable to name the colour until they looked straight at the test-patch. This phenomenon has also been described by Gotch (1912). "In my own case such colour recognition may not occur with the Board of Trade green light until this is focussed on the retina within 1½ to 2 degrees from the centre when the dazzle disappears and the colour becomes quite plain."

At the fovea centralis the phenomena of night vision are absent and this is associated with the absence of rods at that point on the retina. Turning, therefore, to the foveal colour sensations, we find that there are some differences between light- and dark-adaptation. The most striking result is the difficulty experienced by the observers in the recognition of blue-green when dark-adapted. In ten out of the twenty experiments this colour was called green on looking straight at the patch. The filters were made by me, and I was well aware of the difficulty found by the other observers in recognizing the blue-green and yet, knowing this, I also made mistakes with this colour. No difficulty was experienced in the light-adapted eye and green was never called blue-green. There were also some differences in the description of the yellow filter on direct fixation. It was usually called greenish-yellow in the light- and pale yellow in the dark-adapted eye.

It is surprising that in view of the amount of work which has been done on colour matching there appears to be practically none on the hue discrimination of the eye under different conditions of adaptation. Dreher (1911) working on the peripheral retina, appears to have found that a wider section of the spectrum is called yellow by the dark-adapted than by the light-adapted retina. From Baird's (1905) results it is obvious that his subjects got confused in the recognition of certain colours by the near peripheral retina. Thus at 10 degrees his green was often called yellow-green; his violet, blue; and his purple, purple-red. It is a pity that these workers did not extend their observations to the fovea. Basevi (1890) has claimed, however, that the fields of vision for colours are increased by dark-adaptation, but it is obvious that in his experiments dark-adaptation was very incomplete, in fact he says that they did not succeed if the darkness was too complete.

This colour confusion could be explained by assuming that the mechanism for colour perception (cones) becomes less sensitive during dark-adaptation and evidence from the critical frequency of flicker supports this view. Two other factors must, however, be taken into consideration. One of these is that the rods become very sensitive during dark-adaptation and the hue discrimination of the cones becomes difficult in the presence of the intense achromatic rod response. One would not expect this to affect the fovea unless the observers had been of the type described by

Abney and Watson (1916) as having relics of night-vision at the fovea, a condition for which no evidence was found. The other factor is the complication introduced by the presence of coloured pigments within the eye, namely, macular pigmentation and haemoglobin. Brücke (1851) has shown that light entering the eye through the sclera is sufficient to adapt the retina to red. In the light-adapted series, therefore, one might have been dealing with a red-adapted retina in which case the colour sensations in the dark would have been slightly different; orange and yellow would have appeared redder; green, yellower; blue-green, less saturated; blue, violet and purple, redder. There is a certain amount of evidence that changes in this direction do occur. Baird (1905) found that green was often called yellow-green and we found that a filter which appeared yellow-green in the light appeared yellow in the dark. Fick (1888) found that yellow appeared redder in dark adaptation and that the phenomenon was more marked in the peripheral retina. Dreher (1911) also found that yellow appeared redder in the periphery than at the fovea, a fact suggesting that the phenomenon may be connected with the blood vessels at the site of the retinal image in which case there would be no change of hue at the fovea since there are no blood vessels there. On the other hand some of the colour changes described in the literature cannot be accounted for by the presence of haemoglobin. Baird found that violet was often called blue by the dark-adapted peripheral retina whilst Peters (1904) found that green was sometimes called blue in the dark especially after a long period of dark-adaptation. In our experiments blue-green was often called green even at the fovea, but green was never called blue-green. This cannot be explained by the presence of haemoglobin since blue-green is only desaturated by the addition of light of the colour of haemoglobin. Whatever the true explanation the fact remains that colours are liable to be incorrectly named when the subject is dark-adapted. In the case of blue and green the colour appears very desaturated when viewed at angles greater than 5 degrees and it is not possible to guess the colour of the test-patch. These phenomena are not generally recognized. From the point of view of those occupations where the recognition of coloured lights is important it would be desirable to have further information on the effect of dark-adaptation on the perception of small feebly illuminated coloured light sources.

Of the five subjects used in these experiments four gave results which agreed very well one with another, and these subjects also gave the same results in the experiments on the critical frequency of flicker. From evidence which has been published elsewhere (Lythgoe and Tansley, 1929 *b*), we concluded that the fifth subject was probably partially night-blind. The condition might have been due to deficient powers of dark-adaptation or else to a greater proportion of cones to rods than is normal in the peripheral retina. The peripheral colour sensations of this subject were qualitatively the same as those of the other subjects and there was the characteristic desaturation of colours in dark-adaptation indicating that the condition was present in a mild form. For red, orange and yellow, however, this subject's colour fields in light-adaptation were slightly larger than those of the other subjects, and the conclusion seems to be that her peripheral retina was well supplied with the colour perceiving mechanism. Unfortunately, however, the differences from the normal were only slight and it is not possible to draw any definite conclusions.

Summary

(1) Experiments were made with a view to determining the influence of the adaptation of the eye on hue discrimination in the central and peripheral parts of the retina.

(2) During dark-adaptation colour sensations are much desaturated and also hue discrimination is less acute.

(3) The possible causes of this diminished acuteness of hue discrimination are discussed. It is due either to: (*a*) the suppression of the mechanism of colour perception during dark-adaptation; (*b*) swamping of the sensation by an achromatic rod response; or (*c*) the presence of pigments within the eye. The results do not point unequivocably to any one of these causes.

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