Proc. Indian Acad. Sci. **A61** 267–271 (1965)

The new physiology of vision—Chapter XVI. Further studies of the retinal responses

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Received March 26, 1965

In the present chapter will be set out the results of the study of the functioning of the retina by the method which makes use of special colour filters as has been fully explained in the preceding chapter. Observations with thirty filters made with seven different dye-stuffs have already been described in that chapter. The results which emerged are sufficient by themselves to lead to definite conclusions. However, many more filters had been fabricated with several other dye-stuffs and it was considered desirable to complete the study making use of such of them as are suitable for the observations. The results obtained and set forth here confirm and in certain respects usefully supplement the earlier findings. The significance of these findings in relation to the structure and functioning of the retina will be discussed in the next chapter.

Filters of cotton blue: This dye-stuff incorporates itself smoothly into gelatine films, making admirably clear filters exhibiting a blue colour of which the depth is determined by the quantity of the dye taken up. Spectroscopic examination shows that the absorption by the dye is strongest in the yellow region of the spectrum, viz., at 580 mμ. The filters are completely transparent to the shorter wavelengths in the spectrum up to about 550 mμ. Beyond the yellow again there is a sensible absorption which results in the orange and red of the spectrum being much weakened.

When such a filter is held before the eye of the observer who views a brightly-illuminated white screen for a little while and the filter is then removed with the vision fixed at a particular point on the screen, a picture of the observer's retina flashes into view. The most conspicuous feature in the picture is a bright yellow disk which is an enlarged image of the fovea with a bright yellow spot at its centre and a distinctly brighter rim around its margin. Encircling the foveal disk appears an area of circular shape with a fairly well-defined outer margin. This has a diameter some four times greater than that of the foveal disk. The colour of this region is yellow with a slight greenish tinge. The rest of the screen displays a glow of which the yellow hue is readily distinguishable from the colours noticed in the regions which it surrounds.

Filters of coomassie brilliant blue: This dye-stuff when incorporated into gelatine films makes very satisfactory filters. Their colour as seen by transmitted light alters progressively from a light to a deep blue as the quantity of the dye taken up is increased. The filters prepared were transparent to the whole visible spectrum except in the region between 550 and 630 mμ. This region which includes the greenish-yellow, yellow and orange sectors is totally absorbed by the more heavily-dyed filters. In the observations made in the usual manner with such filters, the most conspicuous feature is the foveal disk with a bright spot at its centre and a bright rim around its margin. It exhibits a greenish-yellow colour. The foveal disk appears encircled by a circular region which is less luminous but much larger in area. This again appears surrounded by a field exhibiting an orange-yellow hue. From the observed features, it is evident that the foveal disk and the luminous area immediately surrounding it owe their origin to the absorption by the filter appearing between 550 and 590 mμ, while the orange-yellow glow appearing in the outer parts of the field arises from the spectral region between 590 and 630 mμ.

Filters of bromophenol blue: Three filters dyed to diffirent depths were obtained with this material, the colour exhibited by them in transmitted light showing the progression from a lighter to a deeper blue to be expected in the circumstances. Spectroscopic examination of the transmitted light showed with all the three filters, a band of complete extinction in the wavelength range between 590 and 630 mμ covering the orange sector of the spectrum. In addition, an absorption was also exhibited in the wavelength range between 560 and 590 mμ covering the greenish-yellow and yellow parts of the spectrum. This absorption was relatively weak in the first of the three filters, much stronger in the second filter and practically complete in the third filter.

The effects exhibited to the observer's vision with the three filters showed very clearly a progressive change. The foveal disk and the luminous area immediately surrounding it were only dimly seen with the first filter, were much stronger with the second and very conspicuous with the third. The colour exhibited by the foveal disk was a pale greenish-yellow and that of the area immediately surrounding it which was less luminous appeared to be the same. On the other hand, the outer parts of the field exhibited an orange-yellow hue.

Filters of coomassie violet: Excellent colour filters are produced by incorporating this dye-stuff into gelatine films. The colour of the light transmitted by the filters may be described as rose-red. Spectroscopic examination shows the filters to be completely transparent to all parts of the spectrum except the green in which there is an absorption band covering the wavelength range between 520 and 570 mμ, the strongest absorption being at 545 mμ. It is necessary to hold the filter in front of the eye for at least a couple of minutes on the first occasion before removing it in order to perceive the effect which results from its removal, viz., a

greenish-yellow glow covering the entire screen except the foveal area at the centre of the field. This latter area appears quite dim, the glow seen elsewhere being totally absent in it. The phenomenon can be seen again and again, merely by putting back the filter before the eye and then removing it.

Filters of phloxine: Two filters had been prepared with this dye, one of them being more strongly dyed than the other. Spectroscopic examination shows the absorption by the phloxine filters to be exclusively in the green of the spectrum, there being complete transparency in other parts. The more deeply-dyed filter shows a complete cut-off of the spectral region from 535 to 570 mμ coupled with a strong absorption from 500 to 535 mμ. The less heavily-dyed filter shows a strong absorption in the wavelength range from 540 to 565 mμ. Both filters give effects generally similar to those observed with the coomassie-violet filters and briefly described above.

Colour filters of fast green: A set of five filters prepared with this dye-stuff exhibit the characters best suited for such studies, viz., perfect transparency over an extended region of the spectrum and a complete extinction in other regions. The filters show a regular progression of the colour as seen by transmitted light, viz., from a bright blue for the most heavily-dyed to a greenish-blue for the most lightly dyed. Spectroscopic examination shows a complete cut-off of all wavelenghts greater than 560 mμ by the first filter. With the second filter, the cut-off has shifted to 580 mμ and with the third to 590 mμ. The fourth filter shows nearly perfect transparency up to 590 mμ while the orange and red regions have begun to appear in the transmitted light, a strong absorption showing itself in the red between 620 and 670 mμ. With the fifth and last filter, only this absorption can be seen, the rest of the spectrum being transmitted freely.

The yellow foveal disk with a bright spot at its centre and a bright rim is the most conspicuous effect observed with the first filter. It is less concpicuous with the second filter and only with difficulty observable with the third and fourth filters. It is not visible with the fifth filter. A similar sequence of changes is observed in respect of the circular area which surrounds the foveal disk. On the other hand, the glow seen over the rest of the screen following the removal of the filter is a conspicuous feature in all cases. There is a clearly noticeable change in the colour of this glow, an orange yellow with the first filter, an orange with the second and third filters, an orange red with the fourth and just red with the fifth and last filter.

Colour filters of brilliant green: The four filters exhibiting a green colour by transmitted light prepared with this dye-stuff showed effects of a distinctive character, arising from the circumstance that they exhibit absorption at both ends of the spectrum. The absorption in the region of the shorter wavelengths extends up to 450 mμ and is conspicuous with the heavily-dyed filters, but is also

noticeable with those more lightly dyed. In the region of long wavelengths, the yellow, orange and red sectors are completely absorbed by the heavily-dyed filter. The filters which are more lightly dyed exhibit little or no sensible absorption in the yellow. Their absorption is principally in the orange and the red where a dark band manifests itself in the wavelength range from 620 to 670 mμ.

The yellow foveal disk with its usual accompaniments is quite conspicuous in observations made with the most heavily-dyed filter of the set. It is much less so with the second filter and scarcely observable with the third and fourth filters. Very striking also is the rose-red glow which appears covering the whole field following the removal of the filter in all cases. This phenomenon is clearly the result of the superposition of the glows produced by the parts of the spectrum at both its ends which are absorbed by the filter and which impinge on the retina when it is removed.

Colour filters of tropaeolin: Three filters were prepared with this dye-stuff which by transmitted light exhibited respectively a golden yellow colour, a deep yellow and an orange-yellow hue respectively. The first of the three filters showed a cut-off of the shorter wavelengths in the spectrum upto 450 mμ and a noticeable absorption up to 500 mμ. With the second filter, the cut-off has shifted to 490 mμ with a perceptible absorption up to 510 mμ. The third filter exhibits a cut-off at 500 mμ and an appreciable absorption up to 520 mμ.

Observations with these three filters showed the effects already noticed with the auramin-yellow filters and described in the preceding chapter. Following the removal of the filter from before the eye of the observer, he notices a coloured glow over the screen, this however being definitely absent at the centre of the field in a circular area corresponding to the projection of the fovea of his retina on the screen. The colour of the glow is violet for the first, blue for the second filter and bluish-white for the third, the brilliancy of the glow increasing in that order. A dark spot at the centre of the foveal disk is very clearly seen. There are also indications of a radial structure in the foveal area.

Colour filters of acridene orange: Four filters were prepared with this dye-stuff. By transmitted light they exhibit a light orange hue in the case of the first filter, and progressively deeper orange hues for the others in the series. Spectroscopic examination showed that the first filter extinguishes all the shorter wavelengths in the visible spectrum up to 525 mμ. The wavelength of cut-off shifts to 535 mμ for the second filter, to 545 mμ for the third filter and to 550 mμ for the fourth.

The effects observed with the first of the acridene orange filters are very similar to those exhibited by the third of the series of tropaeolin filters. In particular, the darker region at the centre of the field corresponding to the fovea was quite clearly seen. With the more heavily dyed filters of the series, this central region is less well-defined and less clearly observable. The appearance of the screen following the removal of the filter does not indeed differ very much from its appearance in the absence of the filter. A short-lived bright glow with a hint of blue in it is all that is actually observed.