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Floral colours and the physiology of vision— Part XI. A review of the results

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The special role played by the yellow sector of the spectrum between 566 and 589 m μ in the physiology of vision is a fact of observation which emerges very clearly from the studies described in this memoir. The sensory impression produced by the ensemble of polychromatic radiations which form the visible spectrum is profoundly influenced by this range of wavelengths if present, and is modified in a remarkable fashion when it is removed or weakened by absorption. A further result established by the study is that, in general, the sensory impression produced by polychromatic radiation can by no means be described as the result of a simple superposition of the effects of the individual parts of the ensemble. The weakening or even complete suppression of the effects of some parts of the spectrum by those of the others in certain circumstances is a fact of observation. We shall deal with these matters in some detail, confining ourselves to a statement of what is actually observed in various cases.

The region of the yellow in the spectrum of polychromatic radiation makes its presence felt in the colours of the leaves and flowers of numerous plants. Indeed, in a great many cases, it is the colour which is actually perceived. Spectroscopic examination reveals that yellow of a richer hue is observed when the violet and blue sectors appearing between 400 and 500 m μ are completely eliminated, while the rest of the spectrum is freely transmitted. If, on the other hand, there is also a sensible transmission of wavelengths less than 500 m μ , the colour perceived is a paler yellow. As an illustration of a flower exhibiting the richer hue, we may mention the shrub *Caesalpinia pulcherrima*, one of the two known varieties of which bears a profusion of vividly coloured yellow flowers. The absorption spectrum of a petal of this variety is reproduced as figure 1 in plate I along with comparison spectra of the light-source employed. The cut-off in the spectrum covers not only the violet and the blue, but also the green up to 520 m μ .

As the violet and blue sectors of the spectrum are of low luminous efficiency, it is not surprising that their elimination has but little effect on the brightness of flowers. Indeed, yellow flowers are usually quite brilliant, It is significant that even when most of the green sector is cut out, this continues to be the case. An

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excellent illustration of this is furnished by the flowers of the shrub *Calendula*, the petals of which absorb the violet and blue and also the green completely up to $550 \text{ m}\mu$, while the rest of the spectrum is unaffected. The flowers appear of a bright orange-yellow hue. We may compare them with those of the well-known tree *Cordia sebestina* which bears showy clusters of flowers of a rich orange hue. The violet, blue and green sectors of the spectrum are completely cut out by the petals of this flower, while the yellow sector from 565 to 590 m μ is enfeebled. The striking difference in colour as well as its diminished brightness as compared with the flowers of *Calendula* are clearly due to the partial elimination of the yellow radiations. A more complete elimination of the yellow sector results in a further striking change of colour from orange to red coupled with a further enfeeblement of luminosity. This is well illustrated by the flowers of numerous other trees and shrubs.

The highly remarkable fashion in which the yellow sector of the spectrum influences our visual perceptions of light and colour becomes evident when we study various cases in which that sector is partially or wholly excluded by absorption. As has been shown in the second part of this memoir, the familiar green colour of vegetation arises in that fashion. To convince himself of this, an observer may compare the spectra of sunlight filtering through two leaves of the same tree held side by side, one of them being a mature green leaf and the other a leaf which has turned a golden-yellow prior to its falling off. Alternatively, he may view a green field filled with growing young plants through a pocket spectroscope and compare it with the spectrum of the sky above it as seen through a yellow filter which cuts out the blue and the violet. The visible range is the same in the two cases, viz., 510 to $650 \,\mathrm{mu}$, but the spectroscope reveals the weakening or elimination of the yellow sector in the spectrum of the green leaves. Indeed, it is clear from such observations that our perception of the green colour results from the elimination of the yellow sector. It is also evident that when the yellow is eliminated, the visual effect of the green masks or suppresses the visual sensation due to the red which is already weakened to some extent in the spectrum of the green leaves.

Another highly noteworthy phenomenon discovered in the present investigation is that when the yellow sector in the spectrum of white light is weakened or wholly eliminated, the polychromatic radiation which is left over manifests itself to our visual sensations as exhibiting a *purple* colour. Several examples of flowers exhibiting this effect have been given in the earlier parts of the memoir. Perhaps the most striking case is that of the flowers borne by one variety of the tree *Lagerstroemia Flos Regina* described in the fourth part of the memoir. The purple colour of its petals is a conspicuous phenomenon and is indeed responsible for the magnificent appearance presented by this great tree when it is in full flower. As the purple colour of each flower in a bunch fades away day after day, so also does the absorption in the yellow which is its origin.

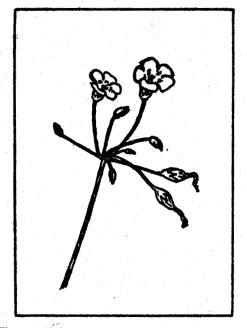


Figure 1. Flowers of Oxalis acetosella (reddish-purple).



Figure 2. Flower of Barleria gibsonii (azure-blue, also reddish purple).

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A long list could be compiled of flowers which exhibit a purple colour by reason of the partial or complete extinction of the yellow by absorption. The depth or degree of saturation of the purple hue is found to depend greatly on the strength of such absorption. It will suffice here to mention a few examples. The common weed known botanically as *Oxalis acetosella* bears small reddish-purple flowers which very clearly exhibit the absorption in the yellow, as is shown in the spectra reproduced as figure 2 in plate IV of part X of the preceding part of the memoir. The garden plant, known familiarly as *Balsam* and botanically as *Impatiens*, is another illustration. There are numerous known varieties of balsam, in some of which the flowers exhibit a purple colour. The balsam flowers which are a vivid purple exhibit a complete extinction of the yellow, the band of absorption covering the entire region of wavelengths between 590 and 550 m μ . Figure 1 in plate II reproduces this effect. Other varieties of balsam in which the purple is less vivid also exhibit the absorption in the same region of the spectrum but less strongly.

Another result of great interest which has emerged from the present investigation relates to the origin of the blue colour exhibited by numerous flowers. In every case of the kind which has been studied, it is found that the yellow sector in the spectrum has either been completely eliminated or else has been greatly weakened by absorption. Indeed, that a definite relationship exists between the depth of the blue colour and the strength of the absorption in the yellow is indicated by the cases studied.

To the numerous examples of blue flowers of which the spectroscopic behaviour has been discussed earlier in the memoir, we may add yet another. This is the shrub *Plumbago capensis* which is a very attractive hedge-plant bearing a profusion of pale blue flowers all the year round and is a familiar sight in Indian gardens (figure 3 in the text). The absorption of the yellow by its flowers is weak and is only just noticeable in the spectrum of the light transmitted by a single petal. But when we hold a few flowers together, the blue colour of the light which penetrates through the mass becomes conspicuous. Examining this light through a pocket spectroscope, a well defined absorption band can be seen in it in the yellow, still another band in the red and a fainter band in the green.

The intense blue of the cornflower (*Centaurea cyanus*) presents a striking contrast with the pale blue of *Plumbago capensis*. The spectroscope reveals the origin of its colour to be an intense absorption band covering the spectral region from 560 to 620 m μ , in other words, both the yellow and the orange sectors of the spectrum. But the rest of the spectrum, including not only the violet and the blue but also the green and red sectors, does not manifest any weakening by absorption. Thus, the chromatic behaviour of the blue cornflower closely parallels that of the "Morning Glory" or *Ipomea learii* discussed in the third part of this memoir. That in these cases, the colour of the flower appears to our perceptions as a saturated blue must be considered highly remarkable. The only possible interpretation of the facts of observation appears to be that in these

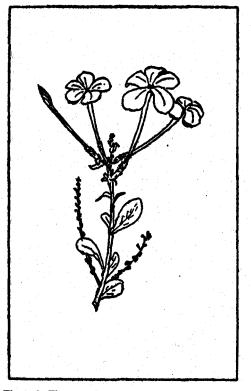


Figure 3. Flowers of Plumbago capensis (azure-blue).

cases, the visual sensation excited by the unextinguished red as well as the entire green of the spectrum is masked or suppressed by the sensations excited by the blue and violet sectors.

Why the extinction of the yellow sector has the effect of exciting a purple sensation in the case of some flowers, while in other cases the observed result is a blue sensation, is an issue which obviously needs elucidation. An answer to this question is forthcoming in terms of the observed spectroscopic behaviour of the flowers themselves. A "purple" sensation is evidently one in which the observer is conscious simultaneously of the visual effects of the two parts of the spectrum lying on either side of the maximum of luminous efficiency in the yellow. Indeed, that the extinction of the yellow sector should result in exciting the sensation of "purple" is not altogether surprising. But if the extinction of the yellow be accompanied by other changes in the distribution of intensity in the spectrum, the sensation of "purple" may be modified in the sense that the sensory effect of the part of the spectrum on one side may dominate over the sensory effect of the part of the spectrum on the other side and may even mask or suppress it altogether. In

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Figure 4. Flowers of Phlox drummondi (various colours).

other words, we may have a "purple" in which the red is dominant or a "purple" in which the blue is dominant and may indeed be the colour that is actually perceived.

It will suffice here to mention three cases illustrative of the remarks made above. The first is that of the well-known garden shrub *Phlox drummondi* (figure 4 in the text). This has numerous varieties exhibiting colours and colour patterns of various sorts in its flowers. To the spectroscopist, the examination of these varieties with a view to ascertain how the spectral composition of the floral colours determines their physiological impact in an interesting exercise. Two of the flowers of *Phlox* examined by the author showed highly contrasting characters, one of them appearing a rich red and the other a purplish-blue. Closer examination, however, indicated that they should both be classed as "purples", but of different sorts. The characteristic absorption band in the yellow was exhibited by both, but the red end of the spectrum appeared more intense with one and relatively weak in the other, evidently as the result of a specific absorption effective at that end.

Still another example is furnished by the flowers of the shrub *Barleria* which is a common sight in Indian gardens. The shrub bears azure-blue flowers, while another variety bears reddish-purple flowers. In both cases, the colour is primarily ascribable to an absorption of the yellow portion of the spectrum, the

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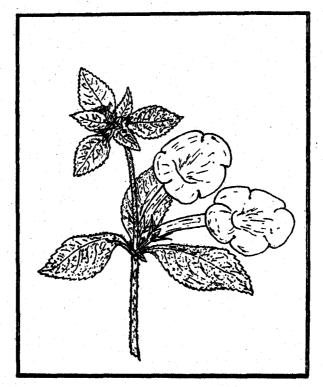


Figure 5. Flowers of Achimenes grandiflora (purplish blue, also purplish red).

differences being in the relative intensity of the blue and red sectors of the spectrum.

The third example we shall mention is that of the garden shrub Achimenes grandiflora which bears a profusion of flowers of large size. These are justly admired for their beauty of colour (see figure 5 in the text). A purplish-blue is the most frequently exhibited hue, but there is also a variety which bears flowers of a red colour. Flowers of both sorts show the absorption in the yellow characteristic of "purple" flowers. In both cases also, the red end of the spectrum is conspicuous. But it is much more brilliant in the case of the red than with the blue flowers.

The pomegranate flower illustrated in figure 6 in the text has six petals which are of a rich orange-red hue. Spectroscopic examination of the light which penetrates through them shows that the range of wavelengths between 490 and $550 \, \mu\mu$ (in other words, the green sector of the spectrum) is extinguished by absorption, but that the spectral regions on either side of this absorption band are transmitted more or less freely. The wavelengths less than $590 \, \mu\mu$ show some weakening of intensity, while still greater wavelengths show no indications of such weakening. The observed colour of the petals is thus satisfactorily accounted

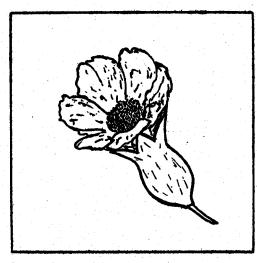
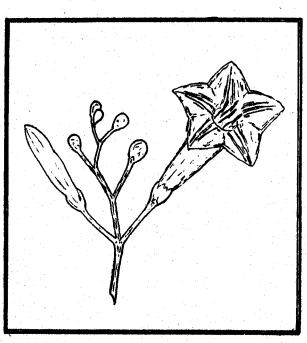
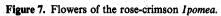
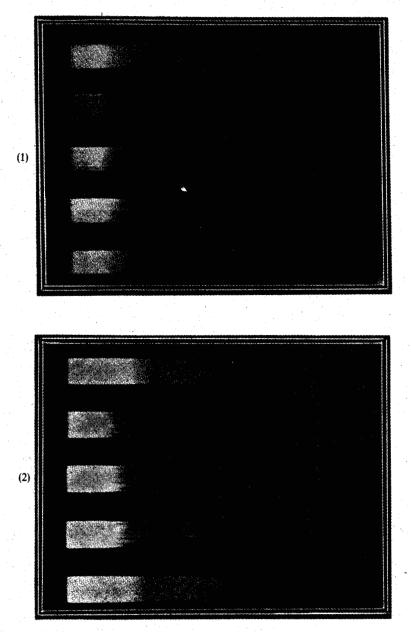


Figure 6. Flower of the pomegranate tree (orange-red).

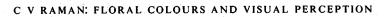


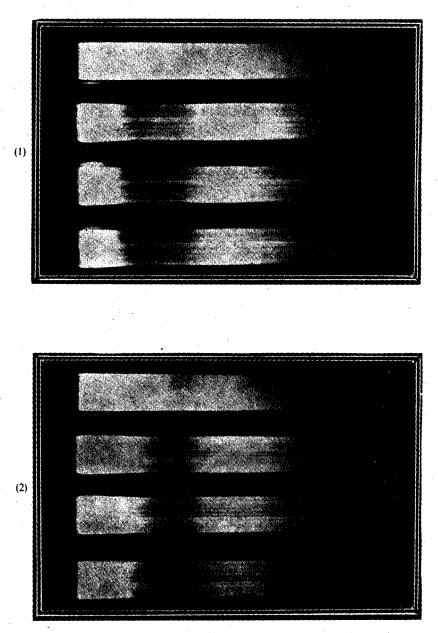




Figures 1 and 2. 1. Absorption spectrum of yellow flower (*Caesalpinia pulcherrima*) with comparison spectra 2. Absorption spectrum of orange-yellow lily with comparison spectra.

Plate I





Figures 1 and 2. 1. Absorption spectra of petal of purple Balsam flower with comparison spectrum. 2. Absorption spectra of petal of crimson flower of *I pomea horsfalliae* with comparison spectrum.

Plate II

for. But a noteworthy feature is that light of wavelengths less than $490 \text{ m}\mu$ (in other words, the blue part of the spectrum) also makes an appearance in the transmission by the petals (see figure 2 in plate III of part IX reproduced with the ninth part of the memoir). But no indication of any admixture with blue appears in the colour of the petals. The observed orange-red hue of the petals is what we should expect on the basis of the transmission of the yellow, orange and red regions of the spectrum. The petals are vividly chromatic and present no suggestion of any unsaturation in their hue. We are thus led by the facts to conclude that the radiations appearing in the yellow, orange and red sectors of the spectrum mask the visual effect of the blue region transmitted by the petals of the pomegranate flower.

Figure 7 represents a flower and some buds of the creeper Ipomea horsfalliae which is remarkable for the bright colour as well as for the profusion of the flowers which it bears. (An excellent reproduction in colour of its foliage and flowers appears facing page 125 of Mr Cowen's book Flowering Trees and Shrubs in India which has been mentioned earlier). The flower has five thick ribs which hold together the thinner membranes between them which allow more light to come through. The light which penetrates the membranes shows a complete extinction of the green of the spectrum. But both the red and the orange as well as the blue-violet are transmitted freely as in manifest from the spectra reproduced as figure 2 in plate II. It is clear that the light appearing in the region of greater wavelengths suppresses the visual effects of the shorter wavelengths coming through the petals. Such masking or suppression of the visual effect of the blue and violet regions in the spectrum by those of the red, orange and yellow when the green has been excluded by absorption occurs with numerous other flowers. Indeed, we have already in the earlier parts of the memoir discussed in detail several cases of the kind in which this effect determines the observed colour of the flower.

Summary

The results emerging from the study of the individual cases have been brought together in this part of the memoir and illustrated by further examples. In particular, the special role in the physiology of vision played by the yellow region of the spectrum and the remarkable manner in which its presence or absence determines the character of the sensory impressions produced by polychromatic radiation are described. It also emerges that in certain circumstances, the sensory effect of the two parts of the spectrum on either side of the yellow may be masked or suppressed, one by the other, or *vice versa*.