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Floral colours and the physiology of vision

SIR C V RAMAN

The world of flowers provides us with an illimitable variety of objects manifesting colour to our visual perceptions. How do these colours arise? The issues raised by this question would be regarded from entirely different points of view by men of science according to their professional interests. But the most fundamental issue of all is the relationship which exists between our visual perceptions and the spectral composition of the light which reaches our eyes from the material of the flower. This relationship can be studied by very simple methods which enable a great many cases to be rapidly surveyed and thereby permit of some conclusions of general validity to be reached. Such an investigation has occupied the author during these past few months and the results which it has yielded are of extraordinary interest and importance. Indeed, it appears that a radical reconstruction of our ideas regarding the physiology of vision and the perception of colour is called for in the light of the facts revealed by the investigation.

The colours of the spectrum, in other words, the sensations excited in our visual organs by the monochromatic radiations into which white light is split by a prism or a diffraction grating, form the natural and indeed the most appropriate standard of comparison with any observed colour and therefore also the basis of the language in which any observed colour should be described. But the distinguishable colours of the spectrum are very numerous, and a further difficulty is raised by the fact that many observable colours appear to our perceptions to differ fundamentally from any of the pure spectral colours. In these circumstances, the question of terminology complicates the task of describing the results of a study which seeks to specify the relationship between any perceived colour and the spectral composition of the light which gives rise to that sensation. Fortunately, however, it turns out that this difficulty is not insuperable and that the results of the study can be set out in readily intelligible terms.

The sensation known as purple is one that is readily recognised by all who are familiar with the subject of colour and we shall therefore begin by considering the origin of this sensation as revealed by the present investigation. It is appropriate that we consider first the case of a plant which is accessible to the widest possible circle of readers. Balsam is a well known garden plant which also goes by the name *Impatiens* by reason of the violent discharge of its seeds from the pod when ripe. The flowers appear along the entire stem of the plant. One of the known varieties of balsam advertised in the seedsmen's catalogues bears purple flowers.

Holding up the petals of this flower against the sky, a visual examination of the light emerging through it with a pocket spectroscope reveals that the petals exercise a powerful absorption in the spectral region between 560 and 590 mμ, the strength of such absorption visibly increasing as we proceed towards greater wavelengths and being greatest at 590 mμ. In other words, the petal absorbs the yellow region of the spectrum strongly, whereas the rest of the spectrum is let through the different regions therein exhibiting the same relative intensities as in the incident light. Another method of examination is to view the petal in sunlight by reflection instead of by transmission. The spectrum seen in this way represents the colour of the flower more nearly than the spectrum observed by transmission. Actually, however, in the particular case, there is no noticeable difference in the characters of the observed spectra.

As another noteworthy example of a purple flower may be mentioned here the blooms of the great forest tree known as *Lagerstroemia Flos-Regina*, the striking beauty of which in the flowering months has led to its being planted extensively as ornamental trees in gardens and in avenues. There are two varieties of this tree, one of which bears purple flowers and the other rose-coloured ones. We shall return to the second kind later on. The flowers of *Lagerstroemia* have very thin and delicate petals, but their colours are extremely striking. The spectral behaviour of the purple variety is the same as that of the balsam flowers described earlier. This is also true of numerous other flowers which exhibit a purple hue to our visual perceptions. The well-attested fact thus emerges that the weakening or removal of the yellow sector of the spectrum between 560 and 590 mμ from the light entering the material of the flower and re-emerging as scattered or diffused light results in the latter exhibiting to our visual perceptions the characteristic sensation of a purple colour.

In the foregoing paragraph, reference was made to the rose-coloured flowers borne by the second variety of *Lagerstroemia Flos-Regina*. Spectroscopic examination of these rose-coloured flowers reveals that their petals exercise an observable absorption in the spectral region between 510 and 570 mμ, the maximum of absorption being at 550 mμ. There is no sensible absorption at wavelengths less than 510 mμ or greater than 570 mμ. In other words, the petals of the rose-coloured flowers present a sensible absorption in the green sector of the spectrum, but allow the violet and blue as well as the yellow, orange and red parts of the spectrum, to come through freely. The manifestation of a rose-red colour to our perceptions is thus associated with the spectral behaviour just mentioned.

A rose-red colour is exhibited by numerous other flowers. A highly significant fact which has emerged from the studies made by the author with such flowers is that the saturation of the observed hue increases *pari passu* with increasing strength of the absorption manifested in the green sector, the rest of the spectrum retaining its characteristic of free transmission. In other words, the more nearly complete the absorption of the green is, the more nearly does the observed hue approach a spectral red in its visual characters. This feature is noticeable with many flowers, a particularly remarkable fact being that their perceived colour is red, despite the fact that the spectroscope shows the blue of the spectrum appearing with undiminished intensity relatively to the red, orange and yellow parts of the spectrum. In some cases, indeed, the perceived colour is indistinguishable from a pure spectral red, but the spectroscopic examination shows the blue coming through with no observable diminution in its intensity.

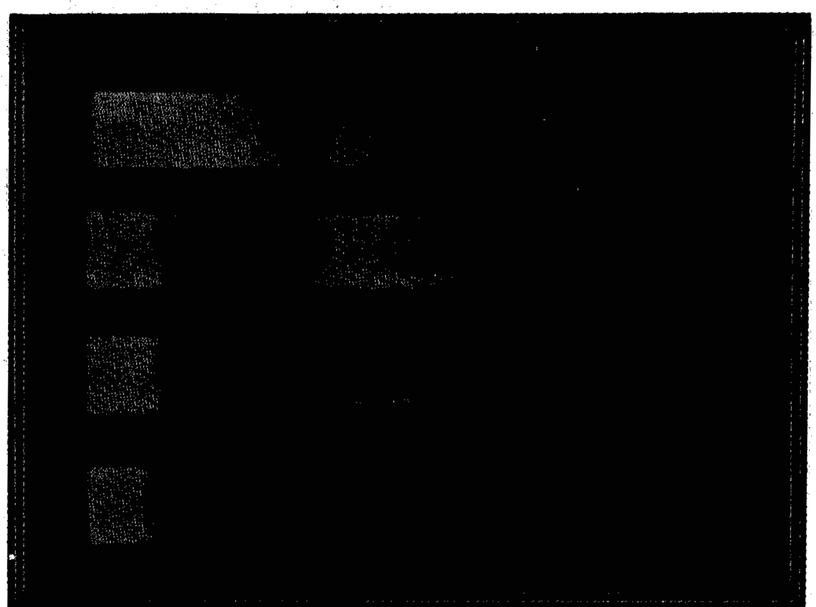
The facts set forth above are so remarkable in themselves and so different from what the current beliefs regarding the origins of colour would indicate that it appeared desirable to present to the reader some evidence of an objective nature supporting the statements made on the basis of subjective observations. In the course of the author's investigations, indeed, numerous spectrograms were recorded of the light transmitted through various flower petals. A complication that presented itself in this work was the non-uniform sensitivity of the panchromatic film employed to record the spectrograms. This shows up as a very pronounced minimum of recorded intensity in the green region. In consequence of this, the photographic record of the transmission spectra is not as satisfactory an indication of the real behaviour of the flower petal as could be desired. Nevertheless, the records are not altogether useless for the purpose in view.

Figure 1 in the accompanying reproduction exhibits three spectrograms recorded with three different exposures of the light of a tungsten filament lamp (filtered through $CuSO_4$ solution) and transmitted through the petal of a purple balsam flower. Above them appears a comparison spectrum of the light source. The red end of the spectra appears at the extreme left in each case, while the blue and violet regions stretch out to the right. The sharp cut-off seen visually at 590 mμ and the rapid decrease in the absorption at smaller wavelengths are both clearly shown in the spectrograms.

Figure 2 reproduces the absorption spectra (recorded in a similar manner) of the petal of a polyantha rose. This was chosen for the reason that its red colour was of nearly saturated hue. On a comparison with figure 1, it will be seen that the absorption in figure 2 begins at a greater wavelength and extends over nearly the whole of the green sector. It is significant that the blue and violet regions of the spectrum appear in the transmitted light without any observable indications of absorption.

Numerous flowers the colour of which appears blue to our visual perceptions were also studied. It was a noteworthy fact that none of those so far examined exhibited any localised increase of intensity in the regions of shorter wavelengths in the spectrum. On the other hand, the spectroscope showed very clearly that the observed colour had its origin elsewhere in the spectrum. We may mention here three flowers exhibiting a blue colour which were studied in some detail, viz., the flowers of the avenue tree *Jacaranda mimosifolia*, the flowers of the climbing plant *Thunbergia grandiflora*, and the clusters of blue flowers of the well known shrub *Plumbago capensis*. In each of these cases, the most conspicuous feature of the spectrum was an absorption band from 560 to 590 mμ covering the yellow region.

(1)



(2)

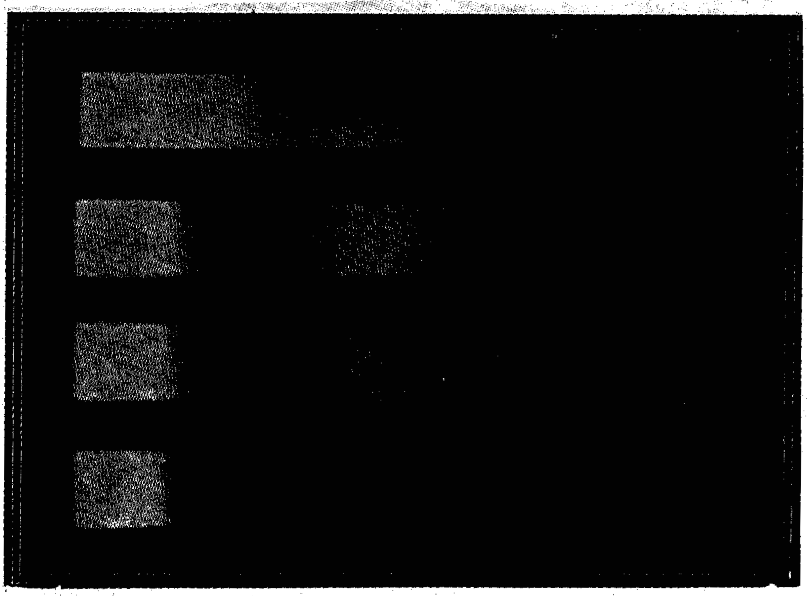


Figure 1 and 2. **1.** Absorption spectra of purple balsam (with comparison spectrum) **2.** Absorption spectra of red rose (with comparison spectrum).

That this did not result in the flowers appearing of a purple colour is due to the fact that in each case, an additional absorption band was noticeable which diminished the observable intensity in the orange-red parts of the spectrum.

Of particular significance is the behaviour of the flowers of the climbing creeper known botanically as *Ipomea learii* and popularly as the "Morning Glory". The absorption of this flower appears in a restricted region of the spectrum, the wavelength region between 560 and 590 mμ having a distinctly lowered intensity, while the region between 590 and 630 mμ is strongly absorbed. In other words, the yellow and orange sectors of the spectrum are partly or wholly eliminated, but the violet, blue, green and red sectors appear with undiminished intensity. That in these circumstances, the flower exhibits a deep blue colour without even a trace of any achromatic sensation being overlaid on it is quite remarkable.

Another interesting case is that of the tree *Solanum grandiflorum* popularly known as the large-flowered nightshade or potato tree. Spectroscopic examination reveals that its flowers exhibit an absorption band covering the yellow region of the spectrum. This is indeed a characteristic feature exhibited by all the blue flowers so far examined by the author. That the Solanum flowers exhibit a highly saturated bluish-violet colour instead of appearing as purple may be ascribed to the presence of an additional absorption band in the orange-red which diminished the observable intensity of that part of the spectrum.

From the facts set forth above, it is clear that the yellow sector of the spectrum covering the small wavelength range between 560 and 590 mμ plays an extraordinarily important role in the physiology of vision. Its presence in full strength, any reduction in its intensity, or its total extinction in the light from the object which reaches the observer's eye have enormous effects on the colour sensations experienced by him.

A detailed study has been made by the author of the origin of the characteristic green colour of vegetation. The usual explanation given of it is that the absorbing pigments present in green leaves eliminate the blue as well as the red parts of the spectrum, leaving us with the green, thereby accounting for the observed colour. Spectroscopic examination of the light which filters through green leaves shows this explanation to be untenable. The shorter wavelengths in the spectrum are indeed eliminated in the passage of light through a leaf, the carotenoid pigments playing the leading role in this respect. This is evident from the appearance of a fairly well-defined absorption limit at about 510 mμ. On the other hand, the characteristic absorption bands of the chlorophyll pigments appear at the red end of the spectrum. The contribution of the extreme red to visual luminosity is quite small. Hence the absorption by the chlorophylls in that region can have no sensible effect on the observed colour of green leaves. Actually, the entire spectrum between the wavelength limits 510 and 650 mμ, is transmitted. Hence, according to the ideas current at the present time, even a mature green leaf should appear of a golden yellow hue and not a bright green or a dark green as is actually the case.

The green colour of leaves thus confronts us with a basic problem in the physiology of vision. The clue to its solution is furnished by the fact that there is an observable diminution in the intensity of the yellow sector of the spectrum between 570 and 590 mμ in its passage through the leaf. This diminution is just noticeable in the case of tender leaves exhibiting a green colour tinged with yellow. It is easily seen with mature leaves which appear of a full green hue, while the absorption in that region is almost complete in the case of leaves exhibiting a dark green colour. It is clear that it is this absorption which determines the observed colour of the leaf. The rest of the spectrum between 590 and 650 mμ which passes through the leaf and can be seen through a spectroscope appears to have no effect on the perceived colour of the green leaf.

The present communication is essentially a recital of facts. It is evident that these facts are irreconcilable with the idea that the colour sensations produced by polychromatic radiation can be computed by arithmetic or algebraic processes involving only additions or subtractions. It is clear also that they require an alternative approach in which the concept is introduced of the masking in certain circumstances of the sensations produced by one part of the spectrum by those produced by another part. With the aid of that concept, it becomes possible to understand why a flower may appear of a full red colour but that it nevertheless transmits blue light freely, or why again, a leaf appears green despite the fact that a great deal of red light passes through it unabsorbed. But we shall not enter here into any detailed discussion of these interpretations of the observed facts.