Colourful Objects Through Animal Eyes

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Abstract: To understand how bees, birds, and fish may use colour vision for food selection and mate choice, we reconstructed views of biologically important objects taking into account the receptor spectral sensitivities. Reflectance spectra of flowers, bird plumage, and fish skin were used to calculate receptor quantum catches. The quantum catches were then coded by "red," "green," and "blue" of a computer monitor; and flowers, birds, and fish were visualized in "animal colours." Calculations were performed for different illumination conditions. To simulate colour constancy, we used a von Kries algorithm, i.e., the receptor quantum catches were scaled so that the colour of illumination remained invariant. We show that on land this algorithm compensates reasonably well for changes of object appearance caused by natural changes of illumination, while in water failures of von Kries colour constancy are prominent. © 2000 John Wiley & Sons, Inc. Col Res Appl, 26, S214–S217, 2001

Key words: color vision; color constancy; reflectance spectra; flowers; fish skin; bird plumage

INTRODUCTION

Most of what we see in the natural environment comprises brown and green backgrounds, among which colourful patterns of plants and animals may be concealed or flamboyantly displayed. These colour signals have been evolved for eyes different from ours. Plants often use brightly coloured flowers to advertise a reward of nectar and pollen to the insects and birds that pollinate them. Birds use colourful plumage to attract mates. Similarly, colourful patterns of fish skin are used to communicate with other fish. Animals also use coloured patterns to protect themselves—a coloured pattern may help conceal or disguise an animal, or advertise that it is toxic.

Colours convey information, and to make a correct food or mate choice animals need to perceive colours constantly in varying illumination. Several experimental studies have shown that animals can compensate for changes of colour caused by changes of illumination spectra.[1] However, colour constancy fails when illumination colour saturates. One of the first proposed models of colour constancy, a von Kries transformation, assumes that signals of photoreceptors are scaled so that colour of illumination remains invariant. Such an algorithm can be implemented by receptor adaptation, and so invokes the simplest physiological mechanism; no special-purpose neural circuitry is required. Although it is not known which algorithm of colour constancy animals use, the von Kries model yields predictions that agree with results of behavioral experiments.[2,3] Generally, von Kries transformation does not lead to perfect colour constancy, and here we ask how well this transformation may compensate for changes of colour.

We consider flower colours as seen by bees, bird colours seen by birds, and colours of coral reef fish for fish eyes. Colour can be quantified by a set of receptor quantum catches, which, in turn, can be calculated for any light stimulus if receptor spectral sensitivities are known. Receptor spectral sensitivities in animals' eyes differ substantially from ours and, thus, our colour perception says little about colour appearance for animals. We have 3 types of receptors

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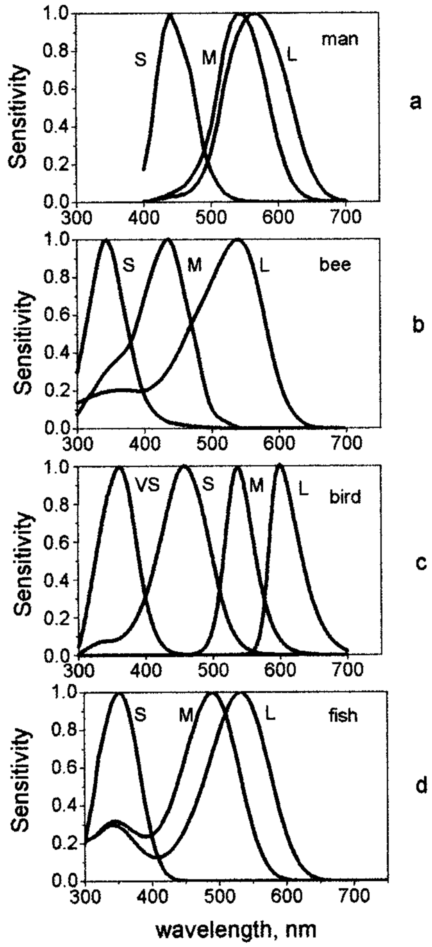

FIG. 1. Receptor spectral sensitivities of (a) man; (b) honeybee *Apis melifera*; (c) a passerine bird *Leiothrix lutea*; and (d) a marine fish *Pomacentrus.* Sensitivities of man are Smith and Pokorny fundamentals[12]; the honeybee's sensitivities were obtained by intracellular recording[4]; the bird's and fish's sensitivities are the results of optical modeling[13] based on spectra of cone pigments,[14,6] oil droplets,[14] and ocular media[14] (Marshall *et al.*, unpublished).

(henceforth S for short-, M for middle-, and L for long-wavelength receptors), which are sensitive from blue to red in the spectrum [Fig 1(a)]. By comparison, bees also have 3 receptors, but these peak in the green, blue, and UV part of the spectrum[4] [Fig. 1(b)]. Birds typically have four receptors. In addition to S, M, and L receptors, they have "very short-wavelength" receptors (VS), which may peak either in UV or in violet part of the spectrum[5] [Fig 1(c)]. Due to cone filters—coloured oil droplets—spectral sensitivities of S, M, and L receptors in birds are narrower then in humans or bees.[5] Some fishes (including goldfish) have four receptors, but many fishes, including some of the colourful species that live on coral reefs, have only 2 or 3, where the S receptor may peak either in the UV, violet, or blue part of the spectrum[6] [Fig. 1(d)].

Colour depends on both reflectance and illumination spectra. In terrestrial habitats, typical illuminations are standard daylights[7] (normal light: D65; blue-sky-dominated light: D75; sun-dominated light: D55) and greenish illumination filtered by leaves in forest [Fig. 2(a)]. In water, absorption and scattering of light is wavelength-dependent. Therefore, illumination spectra in water change rapidly with depth and also depend on whether an object is illuminated from above or by side light [Fig. 2(b)]. Also, in water, light is absorbed and scattered on the path from the object to the eye. Hence, colours may change with the distance from which objects are viewed. Generally, colour constancy in water should be more difficult than in air, and we consider terrestrial and aquatic habitats separately.

METHODS

To calculate quantum catches, we use the following equations. In air, quantum catches, Q_i, are given by

$$Q_i = k_i \int R_i(\lambda)S(\lambda)I(\lambda)d\lambda, \tag{1}$$

where i = L, M, S, (VS) denoting the spectral type of a receptor, $R_i(\lambda)$ denotes receptor spectral sensitivities, k_i are the scaling factors, $S(\lambda)$ and $I(\lambda)$ denote surface reflectance and illumination spectra, respectively, and integration is performed over the range where visual system is sensitive. Mathematical formulation of von Kries colour constancy is straightforward — the scaling factors, k_i , depend on illumination spectra:

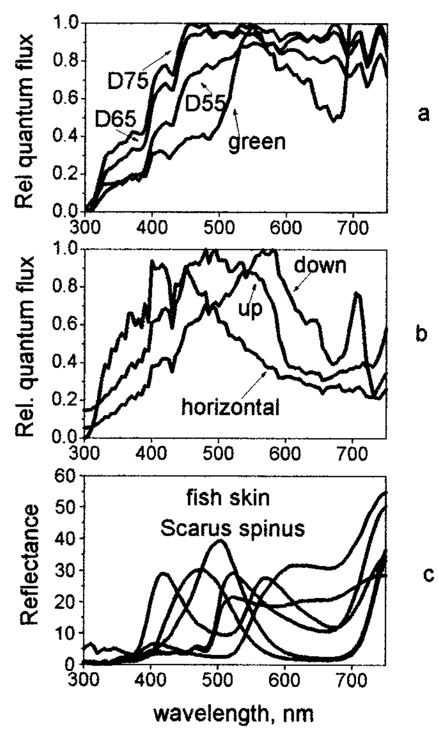

FIG. 2. Illumination and reflectance spectra. (a) Typical daylight illuminations[7] D65, D55, D75, and green illumination as measured in rain forest[10]. (b) Underwater illuminations (depth 1 m) measured with a 15° beam in horizontal, vertical up, and vertical down directions (noon time, Great Barier reef, August 1997). (c) Reflectance spectra of skin of a reef fish *Scarus spinus*.

$$k_i = \frac{1}{\int R_i(\lambda)I(\lambda)d\lambda}. \qquad (2)$$

Consequently, the response of a receptor to the illuminant is by definition unity. In water, quantum catches depend on the distance to an object, z, and the following equations are valid:

$$Q_i(z) = k_i \int R_i(\lambda)G_S(\lambda, z)d\lambda, \qquad (3)$$

where the spectrum of light entering the eye, $G_S(\lambda,z)$, depends on the reflectance spectrum of a viewed surface, $S(\lambda)$. This dependence is given by

$$G_S(\lambda, z) = I(\lambda)S(\lambda)\mathrm{Exp}[-\alpha_1(\lambda)z] + I^0(\lambda)(1 - \mathrm{Exp}[-\alpha_2(\lambda)z]), \qquad (4)$$

where $\alpha_1(\lambda)$ and $\alpha_2(\lambda)$ denote, respectively, narrow beam and scatter attenuation coefficients, $I^0(\lambda)$ is the background space light.[8] The first term in Eq. (4) describes attenuation of the light on the way from a surface to the eye; the second term describes the light that, due to scatter, is added to light between a reflecting surface and the eye. One consequence of the light scatter is a veiling effect, which reduces contrast, and changes colour appearance in much the same way as fog on land.

An image of an object as seen through the animal's eyes can be represented by a set of quantum catches corresponding to each point of the image. To show quantum catches, we use the colours of a computer monitor, and, in the case of trichromatic vision, "blue," "green," and "red" of the monitor correspond to quantum catches of S, M, and L receptors, respectively. To show a pattern as it is seen through a tetrachromatic eye, we make two images: in the first one "blue," "green," and "red" code, respectively, quantum catches of S, M, and L receptors; in the second one "blue" and "green" code S and M quantum catches, "red" codes the VS receptor. It is important to note that we do not know how animals perceive colours—the code we use shows only the information from which the nervous system may form colour. Generally, the larger the changes in receptor signals, the larger are the changes in colour appearance. Therefore, inspection of images, where quantum catches are coded with colours, allows us to judge whether or not an object's appearance changes strongly, but we make no inferences about colour appearance.

To obtain reflectance spectra in each point of the image, we used two methods. (I) Flower views were reconstructed from the images recorded with a UV-sensitive camera through coloured filters.[9] The set of filters were selected so that the error of reconstruction of previously measured 1056 flower reflectance spectra was minimal. (II) To reconstruct images of birds and fishes, we measured reflectance spectra[10] of feathers or fish skin from different body regions. Coloured photographs of animals were examined, and a relation between colours in photographs and type of reflectance spectra was established. Special-purpose software was used to substitute the colours in the photograph with the colour code for receptor quantum catches. Brightness was adjusted in accordance with differences in spectra between the sensitivity of human luminosity vision and receptor sensitivities in animals.

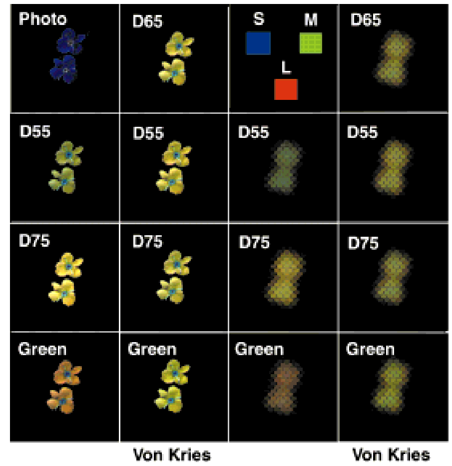

FIG. 3. Flowers of *Veronica chamaedrys* seen through the eye of a honeybee. Left upper corner: A coloured photograph. Reconstructed images show the quantum catches of the S, M, and L receptors in false colours. Left panels: Flower as it can be seen from a very close distance. Right panels: A projection onto the ommatidium array[9] of flowers viewed from a distance of 8 cm. Each hexagon indicates an ommatidium. Iluuminations are indicated in each panel. Compare the images obtained under the standard D65 illumination with those obtained at different illminations before and after correction by von Kries transformation.

RESULTS AND DISCUSSION

A flower as it is seen through the eye of a bee in different illumination conditions is shown in Fig. 3. Spatial resolution of a bee's compound eye is significantly lower then ours. The compound eye of a bee is formed by ommatidia in a hexagonal lattice. Each ommatidium contains all three spectral types of the photoreceptor cells. Resolution of a compound eye is defined by interommatidial angles and by the acceptance angle of a single ommatidium.[11] Examination of projections of flowers onto a compound eye of a bee[9] (Fig. 3, right panel) shows that bees cannot resolve details of flower pattern from a long distance. Unlike our camera-type eye, the compound eye may only resolve well at very close distance, and bees can, theoretically, see fine patterns of a flower only when they sit on it (Fig. 3, left panel). Changes of illumination yield a notable shift in quantum catches. However, if corrected by the von Kries algorithm, it is difficult to see any differences between a flower illuminated by standard D65 light and that illuminated by different natural lights. In the case of a bird looking at a bird (Fig. 4) colour is practically invariant after correcting by the von Kries algorithm. Birds have receptor sensitivities narrowed by oil droplets, which make von Kries colour constancy particularly effective.[10] Generally, our observations indicate that in terrestrial habitats von Kries mechanism of colour constancy compensates reasonably well for changes of illumination.

Figure 5 shows a fish as seen through fish eyes. Although illumination spectra in water change strongly, von Kries colour constancy works well, if the fish is viewed from a short distance, when scatter and absorption in water does not play a role. However, von Kries colour constancy fails, if the fish is viewed from a distance. In the latter case, the spectrum of the light entering the eye is further modified by wavelength-dependent absorption and scatter, and the simple coefficient rule as postulated by von Kries no longer compensates for changes in the colour.

Our conclusions are based on inspection of images obtained by modeling quantum catches of the eyes that might naturally view them. A more accurate study would compare the shifts of colour with colour thresholds. Analysis of a large body of plumage colours shows that, for some plumage colours, the shifts do not exceed thresholds, while colour constancy fails for others.[10] The strongest colour shifts are, in average, yielded by change of illumination from the standard daylight (D65) to green light of sunlight filtered through leaves.

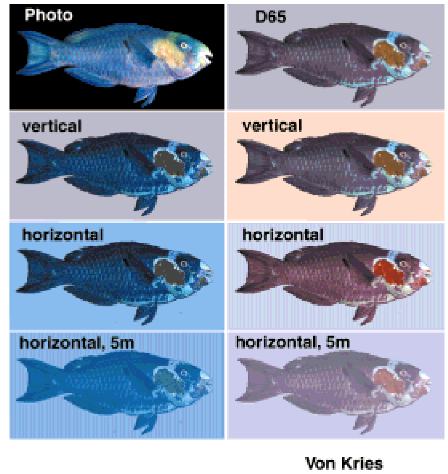

FIG. 5. A reef fish *Scarus spinus* as seen through the fish eye. (See legend to Fig. 3.) Background colours correspond to the spectra of background light.

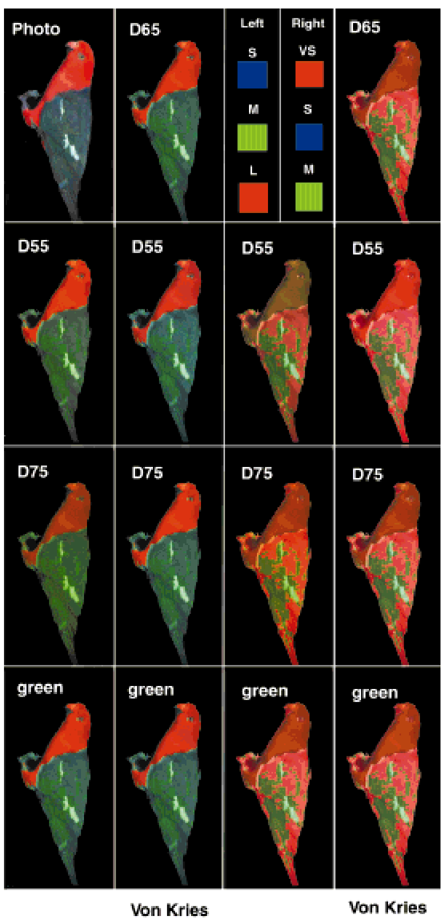

FIG. 4. A king parrot as seen through the eye of a bird. Left upper corner: A coloured photograph. Right panels: The quantum catches of S, M, and L receptors are coded by "blue," "green," and "red," respectively. Left panel: The quantum catch of VS receptor is coded by "red," S and M receptors are coded, respectively, by "blue" and "green." (See legend to Fig. 3.)

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