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How and why are uniformly polarization-sensitive retinae subject to polarization-related artefacts? Correction of some errors in the theory of polarization-induced false colours

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Abstract

If the photoreceptors of a colour vision system are polarization sensitive, the system detects polarization-induced false colours. Based on the functional similarities between polarization vision and colour vision, earlier it was believed that a uniformly polarization-sensitive (insect) retina (UPSR)—in which receptors of all spectral types have the same polarization sensitivity ratio and microvilli direction—cannot detect polarization-induced false colours. Here we show that, contrary to this belief, a colour vision based on a UPSR is subject to polarization-related artefacts, because both the degree and the angle of polarization of light reflected from natural surfaces depend on wavelength. Our second goal is to correct certain errors in the theory of polarizational false colours. The quantitative estimation of the influence of polarization sensitivity on colour vision was recently motivated by the suggestion that certain *Papilio* butterflies detect such false colours. The theoretical basis of this subject is to calculate the colour loci in the colour space of a visual system from the quantum catches of polarization-sensitive receptors of different spectral types. Horváth et al. (J. Exp. Biol. 205 (2002) 3281) gave the first exact mathematical and receptor-physiological derivation of formulae for these calculations. Here we prove that the two formulae given earlier by others are inappropriate or erroneous. This, however, does not influence the validity of the experimental data and the principal conclusions drawn about the colour vision and polarization sensitivity in *Papilio* butterflies.

Keywords: Polarization vision; Colour vision; Polarization-induced false colours; Uniformly polarization-sensitive retina

1. Introduction

If the photoreceptors of a colour vision system are polarization sensitive, the system detects polarization-induced false colours which differ from the real colours determined by the spectral characteristics of objects (Wehner and Bernard, 1993). Such polarizational false colours are usually eliminated in insect eyes by a proper twist of the photoreceptors (e.g. Wehner et al., 1975) or by random microvilli orientations or by monochromacy of the polarization-sensitive receptors (e.g. Wehner and Bernard, 1993). After Kelber (1999a) and Kelber et al. (2001) had suggested that certain *Papilio* butterflies may detect polarization-induced false colours with their weakly polarization-sensitive colour vision system, the quantitative investigation of the influence of polarization sensitivity on colour vision became a biologically inspired topic.

In a uniformly polarization-sensitive (insect) retina (UPSR) the microvilli of receptors of different spectral types are uniformly oriented with the same angle β (e.g. $\beta_{UV} = \beta_B = \beta_G = \beta$) relative to the eye's dorsoventral meridians and the polarization sensitivity ratios P of receptors of different spectral types are also identical (e.g. $P_{UV} = P_B = P_G = P$). Based on the functional similarities between polarization vision and colour vision, earlier it was believed that a UPSR cannot detect polarization-induced false colours (e.g. Kelber et al., 2001, p. 2469, 2471, 2477). According to the anatomical and physiological data presented by Kelber et al. (2001),

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the existence of a UPSR cannot be excluded in *Papilio* butterflies. The first aim of this paper is to show that a UPSR can detect polarizational false colours, because both the degree and the angle of polarization of light reflected from natural surfaces depend on wavelength.

The theoretical basis of this subject is to calculate the colour loci in the colour space of colour vision systems from the quantum catches of polarization-sensitive receptors of different spectral types. First Wehner and Bernard (1993) calculated the polarization-induced false colours of a dandelion leaf detected by a hypothetical honeybee without receptor twist. They referred to a formula used by Bernard and Wehner (1977). Kelber et al. (2001) gave another expression to calculate polarizational false colours. Horváth et al. (2002) presented the first detailed mathematical and receptor-physiological derivation of a formula for polarization-induced false colours. The second aim of this work is to show that the two earlier formulae are inappropriate or erroneous. This, however, does not influence the validity of the published experimental data and the principal conclusions drawn about the colour vision and polarization sensitivity in *Papilio* butterflies.

2. Materials and methods

The reflection-polarization patterns of *Epipremnum aureum* (golden pothos, Aracea, Fig. 3A–C) were measured by imaging polarimetry in the blue (B), green (G) and red (R) spectral ranges at $\lambda_B = 450 \pm 40$ nm (wavelength of maximal sensitivity $\pm$ half bandwidth of the camera's CCD sensors), $\lambda_G = 550 \pm 40$ nm and $\lambda_R = 650 \pm 40$ nm. The method of video polarimetry is described in detail by Horváth and Varjú (1997).

The computation of the spectral loci of colours detected by a polarization- and colour-sensitive insect retina was performed as described by Horváth et al. (2002). Here we mention only that the quantum catches q_r of photoreceptors of spectral types $r\,(= R, G, B)$ were calculated from the formula (A.3) in Appendix A.1 for amplitude normalization of the absorption functions $A_r(\lambda)$ of receptors, while the quantum catches m_r for integral normalization were calculated from the formula (A.10) in Appendix A.2. Then the three coordinates M_R, M_G and M_B of the spectral locus of the detected colour within the equilateral R–G–B colour triangle are (Horváth et al., 2002)

$$M_R = q_R/(q_R + q_G + q_B), \quad M_G = q_G/(q_R + q_G + q_B), \quad M_B = q_B/(q_R + q_G + q_B) \tag{1}$$

for amplitude normalization, and

$$M_R = m_R/(m_R + m_G + m_B), \quad M_G = m_G/(m_R + m_G + m_B), \quad M_B = m_B/(m_R + m_G + m_B) \tag{2}$$

for integral normalization. The amplitude normalized absorption functions $A_r(\lambda)$ of the R, G and B photoreceptors are given in Fig. 1A, where functions are the same as those applied by Kelber et al. (2001). The relative intensities $I(\lambda)$ of the different colour stimuli *BL*, *GR* and *RE* in Fig. 2 are shown in Fig. 1B. These stimuli are the same as those used by Kelber et al. (2001). In the computation of patterns in Figs. 3D and 5 the values of intensity I, degree of linear polarization δ and angle of polarization χ at a given point of the patterns were taken from the *I*- , δ- and χ-patterns in Fig. 3A–C measured by video polarimetry. The calculation of the quantum catches q_r (for amplitude normalization) and m_r (for integral normalization) using these videopolarimetric data are described by Horváth et al. (2002). The functions $I(\lambda)$, $\chi(\lambda)$ and $\delta(\lambda)$ in Fig. 4 were obtained as follows: We took the $I(\lambda_r)$- , $\chi(\lambda_r)$- and $\delta(\lambda_r)$-values measured by video polarimetry in a typical point of the red spathe and green leaf of *Epipremnum aureum* at wavelengths $\lambda_B = 450$ nm, $\lambda_G = 550$ nm and $\lambda_R = 650$ nm. Then we fitted polynomials to the point-triplets $[I(\lambda_B), I(\lambda_G), I(\lambda_R)]$, $[\chi(\lambda_B), \chi(\lambda_G), \chi(\lambda_R)]$ and $[\delta(\lambda_B), \delta(\lambda_G), \delta(\lambda_R)]$ by the method of least squares. The microvilli directions β_R, β_G and β_B relative to the eye's dorsoventral meridians (Fig. 1C) and the polarization

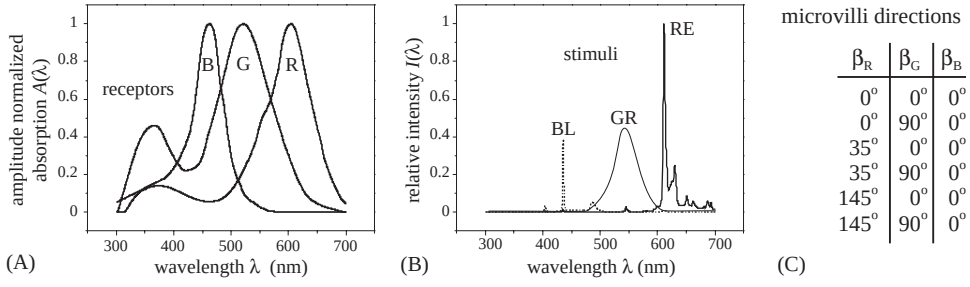


Fig. 1. (A) Absorption functions $A(\lambda)$ of the B, G and R photoreceptors in the butterfly *Papilio xuthus* being maximally sensitive in the blue, green (with a secondary maximum in the UV) and red (with a secondary maximum in the UV, too) spectral ranges (after Kelber et al., 2001). (B) Relative intensities $I(\lambda)$ of the nearly monochromatic stimuli *BL* and *RE* used in the feeding experiments conducted by Kelber et al. (2001) with *Papilio xuthus* and the spectrum of the stimulus *GR* applied in the oviposition experiments of Kelber et al. (2001) with *Papilio aegeus*. (C) The microvilli directions β_R, β_G and β_B relative to the eye's dorsoventral meridians of the red, green and blue photoreceptors found by Kelber et al. (2001) in *Papilio xuthus*.

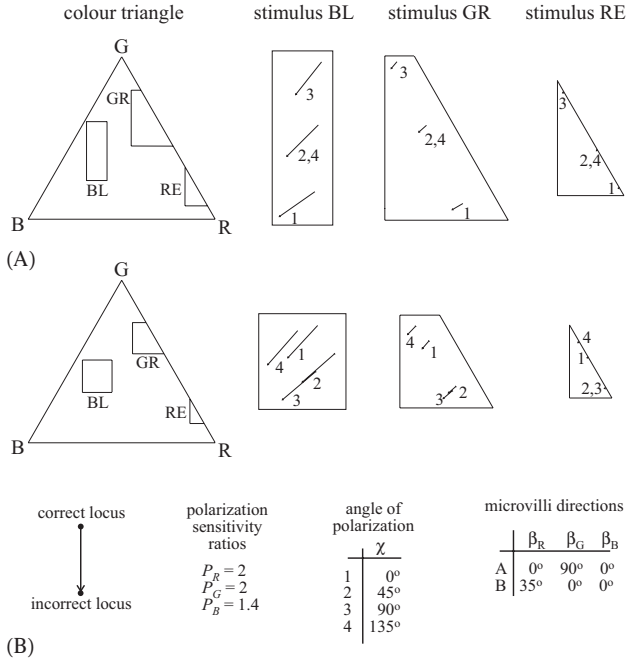


Fig. 2. Comparison between the spectral loci of detected colours calculated from the incorrect formula q_r^{KE} (A.2) and the correct formula q_r^{HE} (A.5) for the amplitude normalized quantum catch q_r of polarization-sensitive photoreceptors of spectral type r for stimuli *BL*, *GR* and *RE* (Fig. 1B) with angles of polarization $\chi = 0°$, 45°, 90° and 135° in case of two (A, B) different configurations of the microvilli directions β_R, β_G and β_B of the red (*R*), green (*G*) and blue (*B*) receptors within the equilateral colour triangle. Microvillar configurations (β_R, β_G, β_B) and polarization sensitivity ratios ($P_R = 2$, $P_G = 2$, $P_B = 1.4$) were chosen according to the parameters of receptors of type 1 defined by Kelber et al. (2001). The arrows start from the spectral loci calculated using the correct formula q_r^{HE}, while the arrowheads point to the loci calculated using the incorrect formula q_r^{KE}. In the second, third and fourth columns from left enlarged parts of the colour triangles are shown with the same magnification.

sensitivity ratios P_R, P_G and P_B of the red, green and blue receptors were chosen according to the characteristics of the photoreceptors found by Kelber et al. (2001) in the butterfly *Papilio xuthus*. Our logical policy was that since only the formula of Horváth et al. (2002) is supported by exact derivation, we considered it correct, until it is proven to be unreliable. Further mathematical and computational details are presented in the Appendices A.1, A.2 and A.3.

3. Results

In Appendix A.1 it is shown that the polarization sensitivity function $S_r^{BE}(\lambda)$ — where r is the spectral type of the receptors—defined by Bernard and Wehner (1977) is inappropriate for calculation of polarization-induced false colours, and the formula q_r^{KE} of Kelber et al. (2001) to describe the quantum catch for totally linearly polarized light [with degree of linear polarization $\delta(\lambda) = 1$ and angle of polarization $\chi(\lambda) =$ constant] is erroneous. Polarizational false colours can be correctly calculated from the formulae of the quantum catch q_r^{HE} derived by Horváth et al. (2002) and given by Eq. (A.3) in Appendix A.1. Fig. 2 demonstrates the differences in the spectral loci of detected colours calculated from the formulae q_r^{KE} and q_r^{HE} for stimuli *BL*, *GR* and *RE* in Fig. 1B with angles of polarization $\chi = 0°$, 45°, 90° and 135° in case of two different configurations of the microvilli directions β_R, β_G and β_B of the red, green and blue receptors with the low polarization sensitivity ratios $P_R = 2$, $P_G = 2$, $P_B = 1.4$ found in *Papilio xuthus* by Kelber et al. (2001). Quite similar results were obtained for other microvilli directions β_R, β_G, β_B shown in Fig. 1C. The arrows in the colour triangles of Fig. 2 represent the errors in positioning the spectral loci of colours when using the formula q_r^{KE} for the receptor's quantum catch. For stimulus *BL* relatively large colour differences occur at all angles of polarization and for all configurations of the microvilli directions. At stimulus GR these colour differences are small, while for stimulus *RE* they are negligible. We conclude that using this incorrect formula inevitably results in some errors, the magnitude of which depends on the angle of polarization of the stimulus and the microvilli directions of the receptors. Such quantitative errors should be eliminated in future studies by the use of the correct formula mentioned.

All incorrect loci in Fig. 2 are shifted toward the blue corner of the colour triangle relative to the correct loci. This can be explained by the fact that the red and green receptors have higher polarization sensitivity ratio ($P_R = P_G = 2$) than the blue ones ($P_B = 1.4$). In Appendix A.1 it is shown that the relation between the erroneous correction factor C_{KE} and the correct factor C_{HE} is $C_{KE} = C_{HE}/P_r$. Thus, since $P_B < P_R = P_G$, the blue component M_B of the detected colour will be larger if the colour locus is calculated by using C_{KE} instead of C_{HE}. If $P_R < P_G = P_B$ or $P_G < P_R = P_B$ were the case, then all incorrect loci in Fig. 2 would be shifted toward the red or green corner with respect to the correct loci. The smaller the lowest P_r-value, the larger the shift toward the r corner of the colour triangle.

In Appendix A.3 we prove that if the degree $\delta(\lambda)$ and/or the angle $\chi(\lambda)$ of linear polarization of the stimulus is wavelength-dependent, the colours detected by a uniformly polarization-sensitive retina (UPSR) differ from the real colours detected by a polarization-blind retina (PBR) with $P_B = P_G = P_R = 1$. Consequently, a UPSR can detect polarization-induced false colours, contrary to the earlier belief. This phenomenon is demonstrated and visualized in Figs. 4 and 5, based on the measured polarization patterns in Fig. 3.

Figs. 3A, B and C show the patterns of the intensity I, degree of linear polarization δ and angle of polarization χ of *Epipremnum aureum* (golden pothos, Aracea) measured by video polarimetry in the red, green and

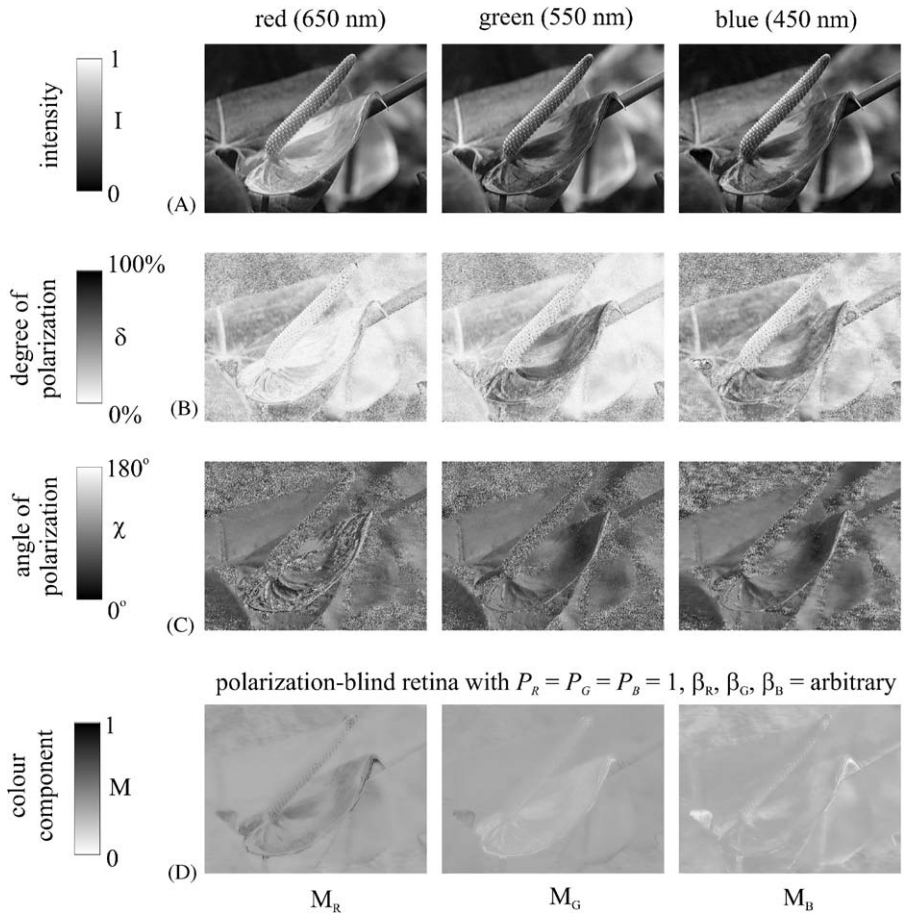
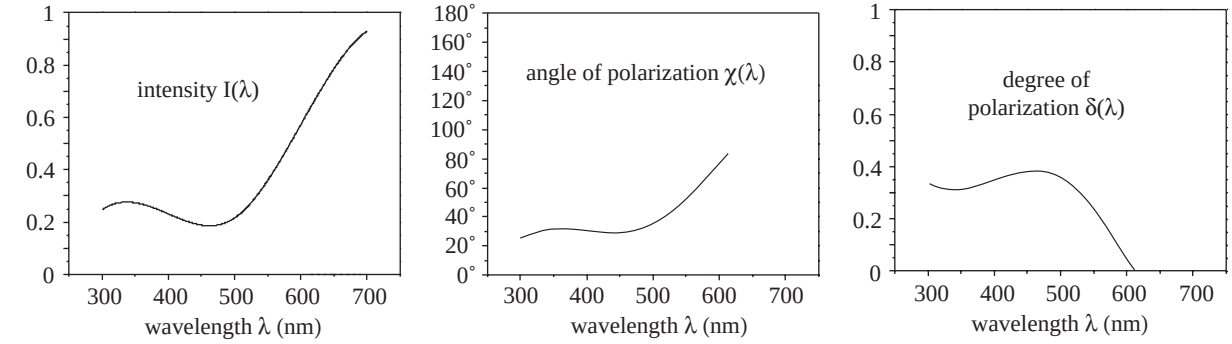


Fig. 3. (A–C) Patterns of the intensity I, degree of linear polarization δ and angle of polarization χ of *Epipremnum aureum* (golden pothos, Aracea)—illuminated by light from a clear sky from above through glass panes of a greenhouse—measured by video polarimetry at wavelengths 650, 550 and 450 nm. (D) Patterns of the red, green and blue components M_R, M_G and M_B of the colour of *E. aureum* detected by a polarization-blind retina with polarization sensitivity ratios $P_R = P_G = P_B = 1$ and microvilli directions β_R, β_G, β_B = arbitrary, where M_r ($r = R, G, B$) are the coordinates of the spectral locus in the equilateral colour triangle.

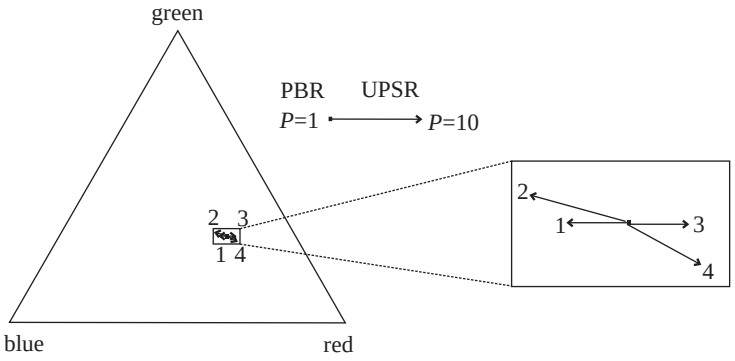
blue. According to the rule of Umow (1905), in a given spectral range the lower the intensity of reflected light the higher the degree of polarization δ of light reflected from a plant surface (see also e.g. Horváth et al., 2002; Horváth and Varjú, 2003). This is the reason why the red spathe of *E. aureum* is so weakly polarized in the red, and its green leaves in the background are least polarized in the green (Fig. 3B). Fig. 3D displays the patterns of the red, green and blue components M_r of the colour of *E. aureum* detected by a polarization-blind retina.

Consider a typical point of the red spathe and the green leaf of *E. aureum* in Fig. 3. The graphs in Fig. 4 show the experimentally predicted wavelength-dependent intensity $I(\lambda)$, angle of polarization $\chi(\lambda)$ and degree of polarization $\delta(\lambda)$ of light reflected from these points. In the colour triangles of Fig. 4 the arrows represent the differences between the colours detected by a UPSR and a PBR at different values of the uniform microvilli directions $\beta_R = \beta_G = \beta_B$ in the UPSR. For both the spathe and leaf the colour differences are relatively small and depend on the microvilli direction. However, Fig. 4 demonstrates well that a UPSR can detect polarization-induced false colours.

Fig. 5 shows the patterns of difference $\Delta M_r = |M_r^{UPSR} - M_r^{PBR}|$ ($r = R, G, B$) between the components of colours of *E. aureum* (Fig. 3) detected by a UPSR and a PBR calculated for two different values of the uniform microvilli directions $\beta_R = \beta_G = \beta_B$ in the UPSR. Large and small ΔM_r–values mean strong and weak false colour effect, respectively. In other words, Fig. 5 displays how the polarization-induced false colours detected by a UPSR differ from the real colours detected by a PBR shown in Fig. 3D. Similar results were obtained for other values of the uniform microvilli directions $\beta_R = \beta_G = \beta_B$. At $\beta_R = \beta_G = \beta_B = 35°$ (Fig. 5A) usually only weak polarizational false colours are induced in the UPSR in all three spectral ranges. The false colours are weakest in the green for both the red spathe and green leaves. In the red the spathe, while in the blue the spathe and the leaves possess relatively strong false colours. At $\beta_R = \beta_G = \beta_B = 145°$ (Fig. 5B) usually strong polarizational false colours are induced in the UPSR in all three spectral ranges. The false colours



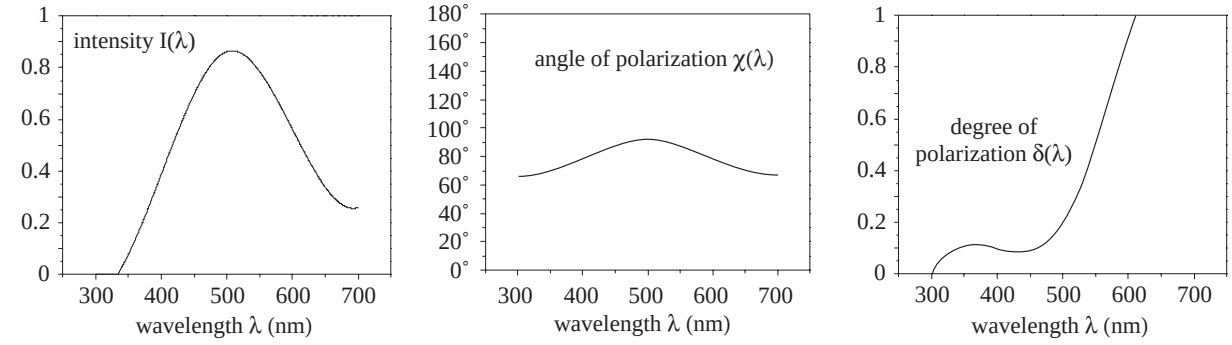
red spathe



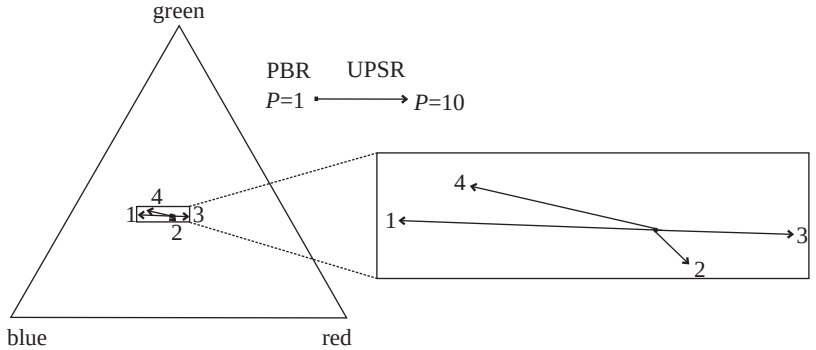
UPSR microvilli directions

	$\beta_R = \beta_G = \beta_B$
1	0°
2	35°
3	90°
4	145°

(A)



green leaf



UPSR microvilli directions

	$\beta_R = \beta_G = \beta_B$
1	0°
2	35°
3	90°
4	145°

(B)

Fig. 4. Differences between the colours of a plant surface—a red spathe (A) and a green leaf (B)—detected by a uniformly polarization-sensitive retina (UPSR) and a polarization-blind retina (PBR) calculated for four different values of the uniform microvilli direction $\beta_R = \beta_G = \beta_B$ of the red, green and blue receptors. The polarization sensitivity ratio of the UPSR is $P_R = P_G = P_B = P = 10$, while for the PBR it is $P_R = P_G = P_B = P = 1$. The intensity $I(\lambda)$, degree $\delta(\lambda)$ and angle $\chi(\lambda)$ of polarization of reflected light are shown in the graphs. In the equilateral colour triangles the arrows start from the spectral loci of colours detected by the PBR, while the arrowheads point to the loci of colours detected by the UPSR. In the immediate vicinity of the colour triangles their enlarged parts are shown with the same magnification.

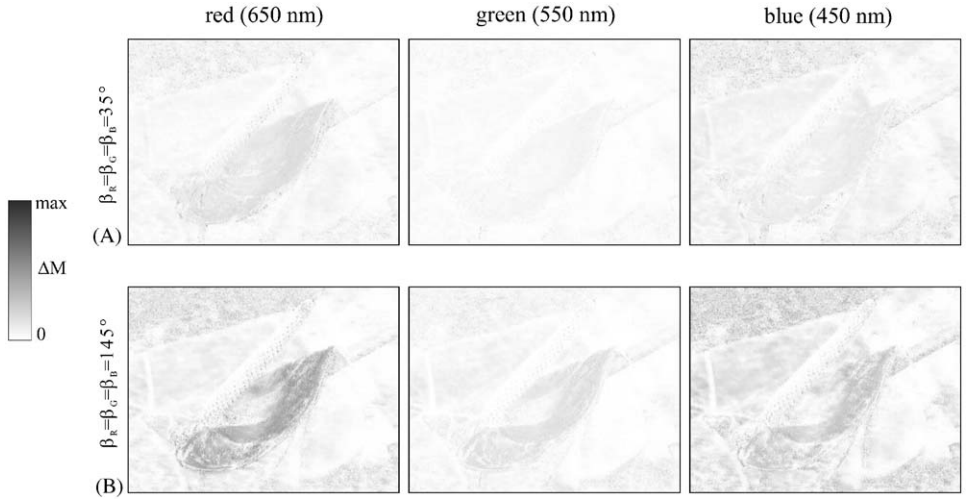


Fig. 5. Patterns of the difference $\Delta M_r = |M_r^{UPSR} - M_r^{PBR}|$ ($r = R, G, B$) between the components (M_R, M_G, M_B) of colours of *Epipremnum aureum* (the reflection–polarization patterns of which is shown in Fig. 3) detected by a uniformly polarization-sensitive retina (UPSR, with polarization sensitivity ratios $P_R = P_G = P_B = 10$ and microvilli directions $\beta_R = \beta_G = \beta_B = \beta = 35°$ or $\beta = 145°$) and a polarization-blind retina (PBR, with $P_R = P_G = P_B = 1$ and β_R, β_G, β_B = arbitrary). The ΔM_r-values are normalized to the maximal difference ΔM_{max} (shaded by dark grey) obtained throughout all difference patterns.

are weakest in the green for both the spathe and leaves. The spathe has strongest false colours in the red, while the leaves in the blue. From these we conclude that depending on the microvilli direction as well as on the spectral and polarizational characteristics, a UPSR detects weaker or stronger polarization-induced false colours.

4. Discussion

Although it does not influence the validity of the experimental data about the colour vision and polarization sensitivity in *Papilio xuthus* and *P. aegeus* butterflies, the theoretical calculations of Kelber et al. (2001) are erroneous, independently of the normalization method. Hence, these computations remain incorrect even if they take into account any type of normalization (e.g. receptor adaptation), since they apply an incorrect formula for the quantum catch of polarization-sensitive receptors. Since the colour discrimination ability of *P. xuthus* and *P. aegeus* is unknown, at present it is unpredictable whether the calculated colour differences (due to the usage of an erroneous formula) are large enough to be detected by these species. Note, however, that these colour differences are of quantitative rather than qualitative nature. Thus, the principal conclusions drawn by Kelber et al. (2001) are not affected.

In this work, we concentrated on the influence of polarization sensitivity on the colour vision of *P. xuthus* and *P. aegeus*, to which equilateral colour (R–G–B) triangles were applied by Kelber (1999b) and Kelber et al. (2001). Bernard and Wehner (1977) as well as Wehner and Bernard (1993), for example, also used colour triangles. Kelber (1999b) and Kelber et al. (2001) have shown that although *P. xuthus* and *P. aegeus* have a pentachromatic colour vision system, the behavioural data obtained for these species can be explained also with the assumption of a trichromatic system. Horváth et al. (2002) showed the soundness of their trichromatic polarization-sensitive retina model. In order to demonstrate that a UPSR detects polarization-induced false colours and the formula of Kelber et al. (2001) is incorrect, it is enough to assume a trichromatic system. Quite similarly, a tetra- or pentachromatic UPSR, for instance, also detects polarizational false colours, independently of the dimension of the colour space.

According to Eq. (A.7), for a uniformly polarization-sensitive retina (UPSR) with constant polarization sensitivity ratio P and microvilli direction β, the quantum catch q_r^{UPSR} of receptors of spectral type r is proportional to $\int A_r(\lambda) S_r^{UPSR}(\lambda) I(\lambda)\, d\lambda$, where $S_r^{UPSR}(\lambda) = P[1 + \delta(\lambda)] + 1 - \delta(\lambda) - 2\delta(\lambda)(P - 1)\sin^2[\chi(\lambda) - \beta]$ is the polarization sensitivity function using the nomenclature of Bernard and Wehner (1977). For a polarization-blind retina (PBR) with $P = 1$, the sensitivity is $S^{PBR} = 2$, independently of the wavelength λ and the receptor's spectral type r. As we proved in Appendix A.3, a UPSR detects polarization-induced false colours if the degree $\delta(\lambda)$ and/or the angle $\chi(\lambda)$ of polarization of the stimulus depends on λ. These polarizational false colours depend on the sensitivity $S_r^{UPSR}(\lambda)$. If in a given part of the spectrum the E-vector direction of the stimulus is parallel ($\parallel$) to the microvilli of the UPSR, i.e. $\chi(\lambda) = \beta$, then $S_r^{UPSR\parallel}(\lambda) = P + 1 + (P - 1)\delta(\lambda)$. In this case the higher the $\delta(\lambda)$, the higher is the $S_r^{UPSR\parallel}(\lambda)$. The difference between the

quantum catches for the UPSR$\parallel$ and the PBR is $\Delta q_r^{\parallel} = |q_r^{UPSR\parallel} - q_r^{PBR}| \sim |\int A_r(\lambda)[P+1+(P-1)\delta(\lambda)]I(\lambda)\,d\lambda - \int A_r(\lambda)I(\lambda)\,d\lambda|$. The larger is the difference $\Delta q_r^{\parallel}$, the more strongly the polarizational false colours differ from the real colours. According to the Umow rule, if the intensity $I(\lambda)$ is high, the degree of polarization $\delta(\lambda)$ is low, and thus the sensitivity $S_r^{UPSR\parallel}(\lambda)$ is also low. This phenomenon therefore results in small $\Delta q_r^{\parallel}$, i.e. a weak polarizational false colour effect. This is the reason, why the polarization-induced false colours detected by a UPSR differ only slightly from the real colours when in a given spectral range the angle of polarization is nearly parallel to the microvilli direction (Figs. 4 and 5).

If in a given spectral range the E-vector is perpendicular ($\perp$) to the microvilli, i.e. $|\chi(\lambda)-\beta| = 90^\circ$, then $S_r^{UPSR\perp}(\lambda) = P+1-(P-1)\delta(\lambda)$. In this case the higher is $\delta(\lambda)$, the lower is $S_r^{UPSR\perp}(\lambda)$. The difference between the quantum catches for the UPSR$\perp$ and the PBR is $\Delta q_r^{\perp} \sim |\int A_r(\lambda)[P+1-(P-1)\delta(\lambda)]I(\lambda)\,d\lambda - \int A_r(\lambda)I(\lambda)\,d\lambda|$. If $I(\lambda)$ is high, $\delta(\lambda)$ is low (according to the Umow rule), and thus $\Delta q_r^{\perp}$ is relatively high, consequently, the polarizational false colour effect is stronger. This explains, why the polarization-induced false colours detected by a UPSR differ strongly from the real colours when in a given part of the spectrum the E-vector is approximately perpendicular to the microvilli (Figs. 4 and 5).

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Appendix

A.1. Erroneous and correct formulae for calculation of polarization-induced false colours

In the literature on polarization vision three different formulae have been published for the calculation of polarization-induced false colours. The expression of polarization sensitivity $S_r(\lambda)$ of a receptor of spectral type r (e.g. $r = UV$: ultraviolet, or B: blue, or G: green) applied by Bernard and Wehner (1977) is:

$$\begin{aligned} S_r^{BE}(\lambda) &= 1 + [(P_r-1)/(P_r+1)]\delta(\lambda)\cos[2\chi(\lambda)-2\beta_r] \\ &\equiv \{P_r[1+\delta(\lambda)] + 1 - \delta(\lambda) - 2\delta(\lambda)(P_r-1) \\ &\quad \times \sin^2[\chi(\lambda)-\beta_r]\}/(P_r+1), \end{aligned} \tag{A.1}$$

where the superscript "*BE*" refers to Bernard et al., λ is the wavelength of light, $\delta(\lambda)$ is the degree of linear polarization, $\chi(\lambda)$ and β_r are the angle of polarization and the direction of the receptor microvilli, respectively, relative to the eye's dorsoventral meridians, and P_r is the polarization sensitivity ratio of the receptor. The quantity S_r must not be confused with the polarization sensitivity ratio P_r, frequently called as *PS*-value: if the electric field vector (simply E-vector) of totally linearly polarized incident light is parallel to the longitudinal axes of the microvilli, a polarization-sensitive photoreceptor of type r absorbs P_r-times the number of photons as in the case when the E-vector is perpendicular to the microvilli.

The second expression was used by Kelber et al. (2001) to describe the quantum catch q_r of a receptor of spectral type r for totally linearly polarized light stimuli with $\delta(\lambda) = 1$ and $\chi(\lambda) = \chi =$ constant:

$$\begin{aligned} q_r^{KE} &= C_{KE}\int_0^{\infty} A_r(\lambda)I(\lambda)\,d\lambda \quad \text{with} \\ C_{KE} &= [P_r - (P_r-1)\sin^2(\chi-\beta_r)]/P_r, \end{aligned} \tag{A.2}$$

where the superscript/subscript "*KE*" refers to Kelber et al. $A_r(\lambda)$ is the relative absorption of the receptor, $I(\lambda)$ is the intensity of light and factor C_{KE} corrects for the polarization sensitivity of the receptor.

The third formula was applied by Horváth et al. (2002) for the quantum catch q_r of a photoreceptor of spectral type r:

$$\begin{aligned} q_r^{HE} = k\int_0^{\infty} &\{P_r[1+\delta(\lambda)] + 1 - \delta(\lambda) - 2\delta(\lambda)(P_r-1) \\ &\times \sin^2[\chi(\lambda)-\beta_r]\}\, A_r(\lambda)I(\lambda)\,d\lambda, \end{aligned} \tag{A.3}$$

where the superscript "*HE*" refers to Horváth et al. and k is a constant. Horváth et al. (2002) gave an exact mathematical and receptor-physiological derivation of their formulae; thus expression (A.3) can be considered reliable until it is proven to be incorrect.

In order to compare the formula (A.2) with Eqs. (A.1) and (A.3), let us replace $\delta(\lambda) = 1$ and $\chi(\lambda) = \chi =$ constant into Eqs. (A.1) and (A.3):

$$\begin{aligned} S_r^{BE}(\delta=1,\chi) &= 2[P_r - (P_r-1) \\ &\quad \times \sin^2(\chi-\beta_r)]/(P_r+1), \end{aligned} \tag{A.4}$$

$$\begin{aligned} q_r^{HE}(\delta=1,\chi) &= C_{HE}\int_0^{\infty} A_r(\lambda)I(\lambda)\,d\lambda \quad \text{with} \\ C_{HE} &= 2k[P_r - (P_r-1)\sin^2(\chi-\beta_r)]. \end{aligned} \tag{A.5}$$

If $P_r \gg 1$, the expression of $S_r^{BE}(\delta=1,\chi)$ can be approximated by

$$\begin{aligned} S_r^{BE}(\delta=1,\chi,P_r\gg 1) &\approx 2\{1 - [(P_r-1)/P_r] \\ &\quad \times \sin^2(\chi-\beta_r)\} = 2C_{KE}. \end{aligned} \tag{A.6}$$

There are two problems with the correction factor C_{KE}:

- The polarization sensitivity ratio P_r in *Papilio xuthus* ranging from 1.3 to 2 is so weak, that the condition $P_r \gg 1$ is not satisfied. Hence, for the weak polarization sensitive *Papilio xuthus* the formula q_r^{KE} (A.2) cannot be applied.
- The correction factors C_{KE} in Eq. (A.2) and C_{HE} in Eq. (A.5) are different, and their relationship is: $C_{KE} = C_{HE}/(2kP_r)$. Since the constant $2k$ will be eliminated during the calculation of the loci of polarization-induced false colours, practically the final relationship is: $C_{KE} = C_{HE}/P_r$. The factor $1/P_r$ is not due to a difference in normalization, because Kelber et al. (2001) used amplitude normalization and the formula $q_r^{HE}(\delta = 1, \chi)$ (A.5) is valid also for amplitude normalization. The formula q_r^{KE} (A.2) is erroneous, if the polarization sensitivity ratios P_r of receptors of distinct spectral types are different, which is the case in *Papilio xuthus*, for example, in which $P_{UV} = 1.3 - 1.5, P_B = 1.3 - 1.5, P_G = 2, P_R = 2$. The formula q_r^{KE} (A.2) leads to the same result as $q_r^{HE}(\delta = 1, \chi)$ (A.5) only, if the polarization sensitivity ratios P_r of receptors of different spectral types are equal: $P_{UV} = P_B = P_G = P_R = P =$ constant. Then the constant $2kP$ will be eliminated during the calculation of polarization-induced false colours, and thus $C_{KE} = C_{HE}$.

A similar problem occurs with the formula $S_r^{BE}(\lambda)$ (A.1). Using the terminology of Bernard and Wehner (1977), the formula q_r^{HE} (A.3) can be rewritten as follows:

$$q_r^{HE} = k \int_0^\infty S_r^{HE}(\lambda) A_r(\lambda) I(\lambda)\, d\lambda \quad \text{with}$$

$$S_r^{HE}(\lambda) = P_r[1 + \delta(\lambda)] + 1 - \delta(\lambda) - 2\delta(\lambda)(P_r - 1)\sin^2[\chi(\lambda) - \beta_r]\}, \tag{A.7}$$

where $S_r^{HE}(\lambda)$ is the polarization sensitivity. Comparing (A.1) with (A.7), we can see that

$$S_r^{BE}(\lambda) = S_r^{HE}(\lambda)/(P_r + 1). \tag{A.8}$$

However, there is a problem with the formula $S_r^{BE}(\lambda)$ (A.1):

- The polarization sensitivities $S_r^{BE}(\lambda)$ and $S_r^{HE}(\lambda)$ differ by a factor of $1/(P_r + 1)$, which could be explained by the different normalizations performed by Bernard and Wehner (1977) and Horváth et al. (2002). However, independently of the type of normalization, it is evident that the loci of (real or polarization-induced false) colours should be calculated from the quantum catches q_r of the different receptor types r, rather than from the polarization sensitivities $S_r(\lambda)$. $S_r(\lambda)$ is involved in the determination of the locus of the detected colour only indirectly as a factor of the integrand in the expression of q_r. In other words, any colour is essentially determined by the q_r-values, rather than by the S_r-values. Consequently, if any kind of normalization is made, q_r has to be normalized instead of S_r. Mathematically speaking, such a normalization is allowed only for the complete integral $\int_0^\infty A_r(\lambda)I(\lambda)S_r(\lambda)\, d\lambda$ and not for the integrand $A_r(\lambda)I(\lambda)S_r(\lambda)$. Note, that $S_r^{BE}(\lambda)$ leads to the same result as $S_r^{HE}(\lambda)$ only, if the polarization sensitivity ratios P_r of receptors of different spectral types are equal, $P_r = P =$ constant, because then the constant factor $1/(P + 1)$ will be eliminated during the calculation of polarization-induced false colours, and thus $S_r^{BE}(\lambda) = S_r^{HE}(\lambda)$.

In summary, from the above analysis we conclude, that the formula q_r^{KE} (A.2) is erroneous and the polarization sensitivity $S_r^{BE}(\lambda)$ (A.1) is inappropriate for calculation of polarization-induced false colours. Polarizational false colours can be correctly calculated from the exact formulae of the quantum catch q_r^{HE} described by (A.3), (A.5) or (A.7).

A.2. Amplitude and integral normalizations of receptor absorption functions

In the literature on polarization-affected colour vision, there are two different conventions to give the absorption functions $A_r(\lambda)$ of photoreceptors of different spectral types r:

(1) When the absorption functions $A_r(\lambda)$ have equal amplitudes $A_r^{\max}(\lambda) = 1$, the convention is called "amplitude normalization".
(2) When the absorption functions $A_r(\lambda)$ have equal integrals $\int_0^\infty A_r(\lambda)\, d\lambda = 1$, the convention is called "integral normalization".

At amplitude normalization the formula q_r^{HE} (A.3) has to be used. The integral normalization corresponds to the assumption that the quantum catches of receptors of different spectral types are the same if the incident light is unpolarized $[\delta(\lambda) = 0]$ and physically white $[I(\lambda) =$ constant$]$. This has the consequence that "physical (or optical) white" coincides with "physiological (or perceptional) white". In other words, the locus of both physical and physiological white is positioned at the colourless centre of the equilateral colour triangle of a colour vision system. In this case the receptor absorptions $A_r(\lambda)$ are normalized by setting their integral to 1, that is the quantum catches q_r of receptor type r should be divided by the quantum catch

$$q_r^{white} = kI_{white}(P_r + 1)\int_0^\infty A_r(\lambda)\, d\lambda \tag{A.9}$$

of the receptor for unpolarized $[\delta(\lambda) = 0]$ and physically white light $[I(\lambda) = I_{white} =$ constant$]$. Hence, the quantum catch for integral normalization is (Horváth et al.,

2002):

$$m_r = q_r^{HE}/q_r^{white} = \left[\int_0^\infty \{P_r[1+\delta(\lambda)] + 1 - \delta(\lambda) - 2\delta(\lambda)(P_r - 1)\sin^2[\chi(\lambda) - \beta_r]\} A_r(\lambda) I(\lambda)\,\mathrm{d}\lambda\right] / \left[I_{white}(P_r + 1)\int_0^\infty A_r(\lambda)\,\mathrm{d}\lambda\right]. \quad (A.10)$$

Although in Fig. 1A we gave the R, G, B receptor absorption functions with the same amplitudes, this does not mean that we prefer amplitude normalization. We displayed amplitude-normalized sensitivities simply as a common graphic representation also used by Kelber et al. (2001), for instance.

A.3. Mathematical analysis of the uniformly polarization-sensitive retina (UPSR)

The following quotation, for example, demonstrates well the misbelief that a uniformly polarization-sensitive insect retina (UPSR) cannot detect polarization-induced false colours: "*For polarisation vision and colour vision to be independent, spectral receptor types should be insensitive to polarisation or share the same polarisation preference angle Φ and the same polarisation sensitivity ... Second, all long visual fibres have vertically oriented microvilli, and this would make colour vision independent of polarisation... This means that all three receptor types have Φ = 0°. Polarisation angle has no influence on colour*". (Kelber et al., 2001, pp. 2469, 2471, 2477.) Here Φ is the polarization angle to which the receptor responds maximally (i.e. the microvilli direction).

Assuming integral normalization and using Eqs. (A.3) and (A.10), let us calculate and compare the spectral loci of colours detected by a PBR and a UPSR. According to our definition, an insect retina is polarization-blind, if the polarization sensitivity ratio of all spectral receptor types is $P_r = 1$, that is, if none of the receptors are sensitive to polarization (see also Horváth et al., 2002, Horváth and Varjú, 2003). From Eq. (A.3) the quantum catch for a PBR with $P_r = 1$ is:

$$q_r^{PBR} = 2k\int_0^\infty A_r(\lambda) I(\lambda)\,\mathrm{d}\lambda. \quad (A.11)$$

Using Eq. (A.10), the integral normalized quantum catch for a PBR is:

$$m_r^{PBR} = [1/I_{white}]\int_0^\infty A_r(\lambda) I(\lambda)\,\mathrm{d}\lambda \Big/ \int_0^\infty A_r(\lambda)\,\mathrm{d}\lambda. \quad (A.12)$$

In order to make our formulae simpler, we introduce the following designation:

$$\langle a, b_1, b_2, \ldots, b_n\rangle := \int_0^\infty a(\lambda)b_1(\lambda)b_2(\lambda)\ldots b_n(\lambda)\,\mathrm{d}\lambda \Big/ \int_0^\infty a(\lambda)\,\mathrm{d}\lambda, \quad (A.13)$$

where each function $a, b_1, b_2, \ldots, b_n$ inside the brackets $\langle\,\rangle$ depends on λ, and refers to the corresponding function under the integrals. We omit the constant factor $1/I_{white}$ (or set it as unit, since I_{white} is arbitrary) further on, because it will be eliminated during the calculation of polarization-induced false colours. Thus Eq. (A.12) can be written in the simpler form:

$$m_r^{PBR} = \langle A_r, I\rangle. \quad (A.14)$$

According to Horváth et al. (2002), the coordinates of a spectral locus of the colour detected by a PBR in the colour triangle are:

$$M_i^{PBR} = m_i^{PBR}/{}_r\Sigma m_r^{PBR} = \langle A_i, I\rangle/{}_r\Sigma\langle A_r, I\rangle, \quad (A.15)$$

where indices i and r refer to the spectral type. The same calculations hold for a UPSR containing equally polarization-sensitive receptors with uniformly oriented microvilli, when P_r and β_r can be replaced by P and β, being independent of the spectral type r.

I. First consider the very special case designated by UPSR[χ,δ], when both the degree δ(=constant) and the angle χ(=constant) of linear polarization of the stimulus are independent of wavelength λ.

In this case the quantum catch is:

$$q_r^{UPSR[\chi,\delta]} = C''\int_0^\infty A_r(\lambda) I(\lambda)\,\mathrm{d}\lambda \quad \text{with}$$

$$C'' = k[P(1+\delta) + 1 - \delta - 2\delta(P-1) \times \sin^2(\chi - \beta)]. \quad (A.16)$$

This expression is similar to Eq. (A.11), and since constants become eliminated in the final formula (A.15), we obtain the same colour loci coordinates as those for a PBR:

$$M_i^{UPSR[\chi,\delta]} = \langle A_i, I\rangle/{}_r\Sigma\langle A_r, I\rangle = M_i^{PBR}. \quad (A.17)$$

- Hence, if χ and δ are independent of λ, a UPSR[χ,δ] detects the same real colours as a PBR.

II. In the second, more general case designated by UPSR[χ], let the angle of polarization χ (=constant) be independent of λ, but let the degree of polarization $\delta(\lambda)$ be dependent on λ.

In this case the quantum catch is:

$$q_r^{UPSR[\chi]} = C_1\int_0^\infty A_r(\lambda) I(\lambda)\,\mathrm{d}\lambda + C_2\int_0^\infty A_r(\lambda) I(\lambda)\delta(\lambda)\,\mathrm{d}\lambda, \quad (A.18)$$

where C_1 and C_2 are constants. Now the integral normalized quantum catch becomes:

$$m_r^{UPSR[\delta]} = C_1'\langle A_r, I\rangle + C_2'\langle A_r, I, \delta\rangle, \quad (A.19)$$

where C_1' and C_2' are constants. Then the formula for the colour locus coordinates is:

$$M_i^{UPSR[\chi]} = (C_1'\langle A_i, I\rangle + C_2'\langle A_i, I, \delta\rangle)/ (C_{1\,r}'\Sigma\langle A_r, I\rangle + C_{2\,r}'\Sigma\langle A_r, I, \delta\rangle). \quad \text{(A.20)}$$

A UPSR[χ] would detect the same colour as a PBR only, if there were a mathematically identical equivalency between Eqs. (A.15) and (A.20). The existence or lack of such an equivalency is difficult to prove in the current form of Eqs. (A.15) and (A.20). Consider a polarization vision system, which has three spectral classes of polarization-sensitive receptors being sensitive in the red, green and blue part of the spectrum, for example, which is a reliable model also for the pentachromatic *Papilio xuthus* as it was shown by Kelber et al. (2001). The identical equivalency ($\equiv$) requires that it should be satisfied for each colour channel. Consider the conditional equivalency ($?\equiv$) between Eqs. (A.15) and (A.20) for the red receptors, for instance: $M_R^{PBR} ? \equiv M_R^{UPSR[\chi]}$. Using Eqs. (A.15) and (A.20), this condition is:

$$\langle A_R, I\rangle/(\langle A_R, I\rangle + \langle A_G, I\rangle + \langle A_B, I\rangle) ? \equiv (C_1'\langle A_R, I\rangle + C_2'\langle A_R, I, \delta\rangle)/[C_1'(\langle A_R, I\rangle + \langle A_G, I\rangle + \langle A_B, I\rangle) + C_2'(\langle A_R, I, \delta\rangle + \langle A_G, I, \delta\rangle + \langle A_B, I, \delta\rangle)]. \quad \text{(A.21)}$$

Performing several simple algebraic transformations in Eq. (A.21) and then reverting from the bracket convention to the integral convention according to Eq. (A.13), we obtain the condition:

$$\int A_R I \int A_G I\delta \int A_B + \int A_R I \int A_G \int A_B I\delta ? \equiv \int A_R I\delta \int A_G I \int A_B + \int A_R I\delta \int A_G \int A_B I, \quad \text{(A.22)}$$

where the dependency on λ of functions $A_R(\lambda)$, $A_G(\lambda)$, $A_B(\lambda)$, $I(\lambda)$, $\delta(\lambda)$, the infinitesimal increments $\mathrm{d}\lambda$ under the integrals and the upper (infinity) and lower (zero) limits of the integrals are hidden for the sake of easier comprehensiveness.

Similar equations can be obtained for receptors of other spectral types. Since functions $A_R(\lambda)$, $A_G(\lambda)$, $A_B(\lambda)$, $I(\lambda)$ and $\delta(\lambda)$ are independent of one another, the integrals cannot be transformed further; thus Eq. (A.22) is the simplest and only condition of the identical equivalency of Eqs. (A.15) and (A.20). It is obvious that identical equivalency is satisfied only if δ (= constant) is independent of λ, since in this case δ can be put in front of the integrals and hereby Eq. (A.22) becomes an equivalency: it is then the formerly discussed UPSR[χ,δ]. If $\delta(\lambda)$ depends on λ, the identical equivalency is not satisfied in Eq. (A.22).

- From this we conclude that a UPSR[χ] detects different colours from the real colours percieved by a PBR. Consequently, a UPSR[χ] detects polarization-induced false colours.

III. In the third, most general case of a UPSR, both the degree $\delta(\lambda)$ and the angle $\chi(\lambda)$ of linear polarization depend on wavelength λ.

In this case, introducing the designation $\sin^2[\chi(\lambda) - \beta] = \Psi(\lambda)$, the integral normalized quantum catch of a UPSR can be written as:

$$q_r^{UPSR} = C_1\int_0^\infty A_r(\lambda)I(\lambda)\,\mathrm{d}\lambda + C_2\int_0^\infty A_r(\lambda)I(\lambda)\delta(\lambda)\,\mathrm{d}\lambda + C_3\int_0^\infty A_r(\lambda)I(\lambda)\delta(\lambda)\Psi(\lambda)\,\mathrm{d}\lambda, \quad \text{(A.23)}$$

where C_1, C_2 and C_3 are constants. The coordinates of the spectral locus of a colour detected by a UPSR is:

$$M_i^{UPSR} = (C_1'\langle A_i, I\rangle + C_2'\langle A_i, I, \delta\rangle + C_3'\langle A_i, I, \delta, \Psi\rangle)/ (C_{1\,r}'\Sigma\langle A_r, I\rangle + C_{2\,r}'\Sigma\langle A_r, I, \delta\rangle + C_{3\,r}'\Sigma\langle A_r, I, \delta, \Psi\rangle), \quad \text{(A.24)}$$

where C_1', C_2' and C_3' are constants. Similarly as above, we seek for an identical equivalency between Eqs. (A.24) and (A.15). Consider again the red receptors, for example, for which, after simple algebraic transformations, we obtain the simplest form of the equivalency condition:

$$C_2'\int A_R I\left(\int A_G I\delta \int A_B + \int A_G \int A_B I\delta\right) + C_3'\int A_R I\left(\int A_G I\delta\Psi \int A_B + \int A_G \int A_B I\delta\Psi\right) ? \equiv C_2'\int A_R I\delta\left(\int A_G I \int A_B + \int A_G \int A_B I\right) + C_3'\int A_R I\delta\Psi\left(\int A_G I \int A_B + \int A_G \int A_B I\right). \quad \text{(A.25)}$$

Here, identical equivalency is satisfied only if both δ and Ψ are independent of the wavelength λ, that is they are constant. Since Ψ is dependent on λ through $\chi(\lambda)$, Ψ = constant means χ = constant. Hence, if $\delta(\lambda)$ and $\chi(\lambda)$ depend on λ, as it is usual in nature, then the identical equivalency in Eq. (A.25) is not satisfied.

- From this we conclude that if the degree δ and angle χ of polarization of the stimulus is independent of the wavelength λ, a UPSR detects the same colours as a PBR. However, since $\delta(\lambda)$ and $\chi(\lambda)$ usually depend on λ, a UPSR generally detects different colours from

the real colours percieved by a PBR. Consequently, a UPSR usually detects polarization-induced false colours.

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