

The colour hexagon: a chromaticity diagram based on photoreceptor excitations as a generalized representation of colour opponency

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Summary. A chromaticity diagram which plots the 3 photoreceptor excitations of trichromatic colour vision systems at an angle of 120° is presented. It takes into account the nonlinear transduction process in the receptors. The resulting diagram has the outline of an equilateral hexagon. It is demonstrated by geometrical means that excitation values for any type of spectrally opponent mechanism can be read from this diagram if the weighting factors of this mechanism add up to zero. Thus, it may also be regarded as a general representation of colour opponent relations, linking graphically the Young-Helmholtz theory of trichromacy and Hering's concept of opponent colours. It is shown on a geometrical basis that chromaticity can be coded unequivocally by any two combined spectrally opponent mechanisms, the main difference between particular mechanisms being the extension and compression of certain spectral areas. This type of graphical representation can qualitatively explain the Bezold-Brücke phenomenon. Furthermore, colour hexagon distances may be taken as standardized perceptual colour distance values for trichromatic insects, as is demonstrated by comparison with behavioural colour discrimination data of 3 hymenopteran species.

Key words: Colour vision – Chromaticity diagrams – Opponent processes – Colour computation – Bezold-Brücke phenomenon

Introduction

Colour is not a property inherent to the surface of objects. It is an evaluation of the spectral reflection of an object by the combined action of the spectral photoreceptor types and the nervous system. For the graphical representation of colour one therefore has to take into account, as far as possible, the characteristics of the colour coding mechanisms of the animal in question. With

trichromatic systems, it is common to plot colour loci on triangular chromaticity diagrams (see Rodieck 1973 for review). The trivariance values (tristimulus or quantum flux values) are determined by the respective animal's spectral sensitivity curves, which in turn depend on the stimulus intensities used to fulfill certain criteria in the receptor's cell potential (see Menzel et al. 1986 for a review of methods as applied to insect photoreceptors). This means that the variables are based on the input to the receptor (stimulus intensity). The tristimulus values are then normalized so that their sum equals unity (Backhaus and Menzel 1987, for reference to insect vision) and plotted at angles of 120° between the vectors.

This normalization makes colour loci independent of the intensity with which the respective stimuli are illuminated. The relations in a colour triangle cannot, therefore, account for a number of phenomena well known in human colour perception and also in bees (Backhaus 1991a, b), namely that every colour should shift towards the uncoloured point (i.e. black) at decreasing intensity, and very bright stimuli should also appear closer to "uncoloured" (i.e. white). Furthermore, the constancy of a colour locus with changing intensity contradicts the Bezold-Brücke phenomenon, the intensity dependent hue shift that occurs mainly at high intensity levels. This phenomenon exists in the honeybee (Backhaus 1991b) as well as in human psychophysics.

Another striking inadequacy of the triangular chromaticity diagram is that colours that actually lie outside the visible spectrum, e.g. a monochromatic red at 700 nm for honeybees, will have their colour loci in the green edge of the colour triangle, whereas actually it will of course appear uncoloured/black. This results from the circumstance that the quantum catch in the green receptor will be >0 (if only very little), whereas in the blue and uv-receptor it is 0; the normalization to unity will then shift the locus of the actually invisible colour into the periphery of the diagram and thus make it congruent to the locus of a saturated green of e.g. 550 nm. This problem shall be illustrated by an example in the Appendix.

Consequently, the subjective colour appearance of objects and perceptual colour distances may not be derived from colour loci in chromaticity diagrams (Schroedinger 1920a, b) based on effective quanta as variables; this also applies to the CIE chromaticity diagram (see Rodieck 1973 for the relation with the triangular representation of colour) and the diagram proposed by MacLeod and Boynton (1979).

The representation of colour can be modified by dealing with the values that the nervous system actually has to calculate with: the physiological graded potential of the photoreceptor cells. Once the hyperbolic transduction function (or the tanh log function, Naka and Rushton 1966) of the receptors is taken into account, one can perform linear transformations of the receptor signals and achieve very good predictions of psychophysical data (e.g. Valberg et al. 1986; Backhaus 1991a).

Both in humans and bees, most phenomena of colour vision can be explained best by assuming the evaluation of the initial 3 receptor signals in two spectrally opponent neural mechanisms. If the weighting factors of these spectral opponencies are known, chromaticity can be plotted in a two-dimensional diagram using as axes the two scales assigned to the respective spectrally opponent mechanism (Backhaus 1991a). The weighting factors for the opponent mechanisms have been determined for the honeybee (Backhaus 1991a) and in human psychophysics (Hurvich and Jameson 1955; Guth et al. 1980; Werner and Wooten 1979). They are, however, not known for a variety of animals (e.g. 40 hymenopteran insect species, see Peitsch et al. 1989), which by electrophysiological recordings have been characterized as trichromats. For all these cases, a chromaticity diagram would be desirable that is based on the physiological receptor excitations without any predictions about how the excitations are weighted in spectrally opponent processes.

Methods

The model calculations are based on the spectral sensitivity functions of honeybee photoreceptors as electrophysiologically characterized by Menzel et al. (1986), unless otherwise mentioned in the text.

It is assumed that the receptors are adapted such that they render half their maximum response when exposed to the adapting light (Laughlin 1981). The adaptation light is assumed to be the spectral reflection of an achromatic, medium grey background illuminated by natural daylight (normfunction D65).

The determination of the quantum catch (tristimulus values) in the photoreceptors with regard to the spectral composition of coloured stimuli and the illuminating light follows Backhaus and Menzel (1987). The transformation of effective quanta values into physiological receptor excitations is done according to:

$$E = V/V_{\max} = (R \cdot P)^n / ((R \cdot P)^n + 1) \quad (1)$$

(Naka and Rushton 1966; see also Lipetz 1971; Backhaus and Menzel 1987; Chittka et al. 1992 for reviews) where P is the photon flux in the receptor and R is the absorption resulting in half the maximum cell potential (Laughlin 1981). The exponent n differs slightly with the adaptation state and the species in question; it is assumed to be 1 in the model calculations (see Backhaus and Menzel 1987 for a more detailed review). If $V_{\max}$ is normalized

to 1, the receptor potential E can in principle reach any value from 0 to 1.

The basic geometry of the colour hexagon

The receptor signals $E(U)$, $E(B)$ and $E(G)$ are plotted as vectors with angles of 120° between them. Since the receptor excitations are independent from each other and can have values between 0 and 1, the resulting diagram will have the outline of an equilateral hexagon. No point outside the borders of this hexagon can be reached if no vector can exceed 1 (see Fig. 1). This basic geometry has been presented by Küppers (1976, 1977), but his vectors are based on a spectrum cut into equal portions of non-overlapping primary colours and thus have nothing to do with the physiological sensitivity curves of the receptors nor with any kind of phototransduction process. The conversion of 3 vectors at angles of 120° into orthogonal X-Y-coordinates follows from the geometry in Fig. 2. The ordinate is then described by the equation:

$$\begin{aligned} y &= 1 \cdot E(B) - 0.5 \cdot E(U) - 0.5 \cdot E(G) \\ \Leftrightarrow y &= E(B) - 0.5 \cdot (E(U) + E(G)) \end{aligned} \quad (2)$$

whereas the values on the abscissa are determined by:

$$\begin{aligned} x &= -\sin 60^\circ \cdot E(U) + \sin 60^\circ \cdot E(G) \\ \Leftrightarrow x &= \sin 60^\circ \cdot (E(G) - E(U)) \\ \Leftrightarrow x &= \sqrt{3}/2 \cdot (E(G) - E(U)). \end{aligned} \quad (3)$$

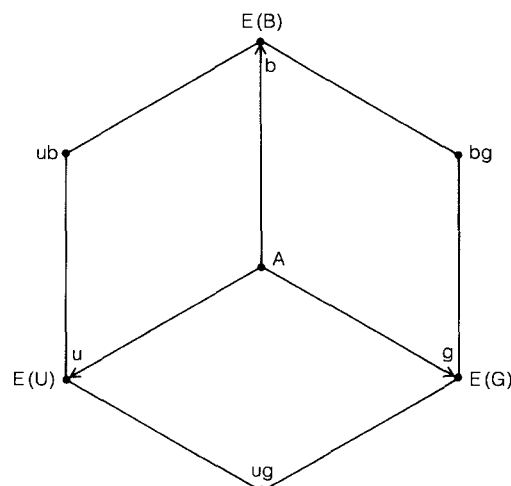


Fig. 1. The colour hexagon. The photoreceptor excitations are plotted at angles of 120° , the vectors starting from the point "A", which marks the locus of all uncoloured stimuli in the hexagon. The vector length can vary from 0 (no excitation) to 1 (maximal excitation), and the 3 vectors are independent from each other. The hexagonal outline of the diagram is thus determined by vector combinations with either one vector value of 1 and the two others of 0 or two vectors of 1 and the third of 0. Point u is characterized by the combination $E(U)/E(B)/E(G)=1/0/0$, ub is determined by $1/1/0$, b will be given by $0/1/0$ and so forth

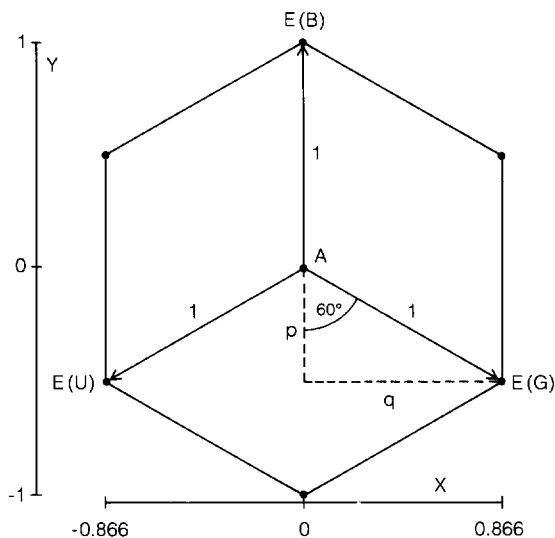


Fig. 2. The 3 vectors, lying at equal angles of 120° can readily be converted into orthogonal coordinates trigonometrically. All 3 vector directions are given with their maximal length of 1. For the determination of Y-coordinate values, the weight of the E(B)-vector in positive (upward) Y-direction equals unity; the weighting factors for both other vectors in negative (downward) direction are calculated as $p = \cos 60^\circ = 0.5$, because $\cos a = p/1$. The Y-coordinate in the colour hexagon is consequently: $y = 1 \cdot E(B) - 0.5 \cdot E(U) - 0.5 \cdot E(G)$. For the X-axis values, E(B) is of no influence. The weighting factors in X-direction (assigned to the straight line q) are given by $q = \sin 60^\circ = \sqrt{3}/2$, since $\sin a = q/1$. The X-coordinate may therefore be written as: $x = -\sin 60^\circ \cdot E(U) + \sin 60^\circ \cdot E(G)$

The colour hexagon represents excitation differences

Three independent variables cannot be plotted in a two-dimensional diagram without loss of information. The absolute values of receptor excitations cannot be read from the colour hexagon, no more than absolute numbers of effective quanta can be derived from the triangular chromaticity diagram. An infinite number of photoreceptor signal combinations will result in the same colour locus (see Fig. 3), but all these combinations have in common constant differences between excitations. The identity of the coordinates for excitation combinations with equal differences follows from Eq. (2) and (3). All 3 excitation values are raised (or diminished) by the value of k , which can have any value between $1 - E_{\max}$ and $-E_{\min}$, where $E_{\max}$ is the highest of the 3 receptor excitations and $E_{\min}$ the lowest. Under these conditions the excitation differences $E(U) - E(B)$, $E(B) - E(G)$ and $E(U) - E(G)$ remain constant, because $(E(U) + k) - (E(B) + k) = E(U) - E(B)$ and so forth. Consequently, (2) and (3) become:

$$y = E(B) + k - 0.5 \cdot (E(G) + k + E(U) + k) \quad (2b)$$

$$x = \sqrt{3}/2 \cdot (E(G) + k - E(U) - k), \quad (3b)$$

and it can easily be seen that k cancels itself in both equations, and the unchanged (2) and (3) will be regained. This means that the values on both coordinates will remain unchanged, if all receptor excitations are

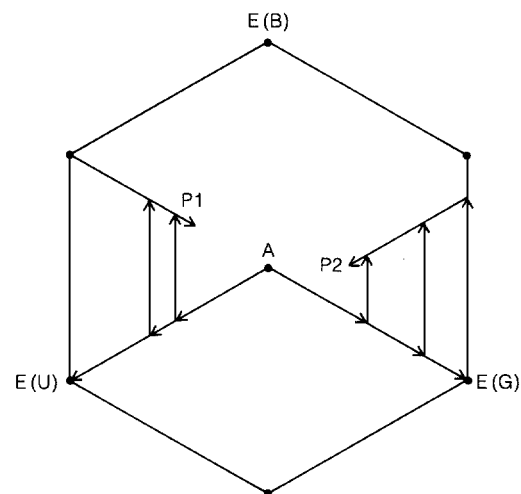


Fig. 3. An infinite number of excitation combinations will result in the same colour locus in the colour hexagon. Two points ($P1$ and $P2$) with 3 examples each are given in the figure. $P1$ can, for example, be defined by the following combinations: $E(U)/E(B)/E(G) = 1/1/0.5$ or $0.6/0.6/0.1$ or $0.5/0.5/0$. In all cases the colour locus remains unchanged. Three examples for the determination of point $P2$ are: $0.6/0.8/1$ or $0.4/0.6/0.8$ or $0.1/0.3/0.5$

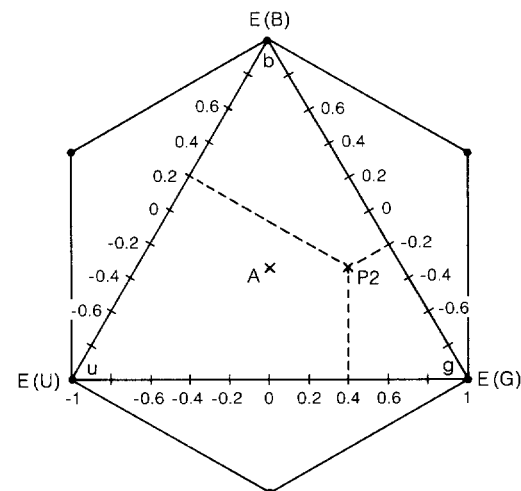


Fig. 4. Excitation differences can be derived from scales drawn through the colour hexagon. When the extreme points u , b and g are connected, then the resulting axes can be given values between -1 and 1 . The colour locus of $P2$ is the same as in Fig. 3. The excitation differences defined by the respective sets of excitations can easily be read from the axes

increased or decreased by the same value. For a given point in the colour hexagon (with all the possible excitation combinations that define it) it follows that the differences $E(U) - E(B)$, $E(B) - E(G)$ and $E(U) - E(G)$ (or vice versa) are constant in any case. In comparison to the triangular chromaticity diagram where constant ratios (i.e. quotients) between effective quanta numbers define the respective colour loci, one can state that in the colour hexagon, the relevant parameters for constancy of colour loci are excitation differences. These differences can be read from axes put through the colour hexagon as illustrated in Fig. 4.

The colour hexagon as a generalized colour opponent diagram

It has been shown that a locus in the colour hexagon denotes specific receptor excitation differences ($E(U) - E(B)$, $E(B) - E(G)$ and $E(U) - E(G)$). Consequently, excitation values for two-input-mechanisms ("+/−"-type) can be derived as described above.

It will now be demonstrated that it is also possible to read excitation values for three-input-mechanisms (i.e. $a \cdot E(U) + b \cdot E(B) + c \cdot E(G)$, where one of the factors a , b and c has the reverse sign of the two others, i.e. "+/−/−" or "−/+/−" or "−/−/+"-type) directly from the colour hexagon.

A basic requirement of the following considerations is that the sum of the weighting factors (a , b and c) associated with the receptor signals is zero. This condition is found to be accomplished in honeybees (Backhaus 1991 a), but it is only approximately met in psychophysical investigations of human colour vision (Hurvich and Jameson 1955; Werner and Wooten 1979; Guth et al. 1980). Nevertheless, for several reasons given in the Discussion section of this paper, the weighting factors should add up to values close to zero. The assumption thus appears to be a legitimate approximation.

If the net excitation $E_{(ant.)}$ values of three-input spectrally antagonistic mechanism are to be read from the colour hexagon, then it has to be shown that they can be derived from X-Y-coordinates of the hexagon. This can be done as follows:

$$\begin{aligned} E_{(ant.)} &= a \cdot E(U) + b \cdot E(B) + c \cdot E(G) \\ \Leftrightarrow E_{(ant.)} &= a \cdot E(U) + b \cdot E(B) - (a + b) \cdot E(G), \quad (4) \\ \text{since } a + b + c &= 0. \end{aligned}$$

From (2) and (3), it can be derived that:

$$\begin{aligned} E(U) &= E(G) - 2/\sqrt{3} \cdot x \\ \text{and } E(B) &= y + E(G) - x/\sqrt{3}. \end{aligned}$$

Consequently, (4) becomes:

$$\begin{aligned} E_{(ant.)} &= a \cdot (E(G) - 2/\sqrt{3} \cdot x) \\ &\quad + b \cdot (y + E(G) - x/\sqrt{3}) - (a + b) \cdot E(G) \end{aligned}$$

which can be reduced to:

$$E_{(ant.)} = -x/\sqrt{3} \cdot (2a + b) + b \cdot y. \quad (5)$$

It may therefore be concluded that all the information available to spectrally opponent mechanisms is given by colour loci in the hexagon, since the excitation values for any colour opponent mechanism with given weighting factors a , b and c can be derived from X-Y-coordinates in the colour hexagon. The coordinates themselves are determined by the 3 photoreceptor excitations. If axes assigned to such opponent mechanisms are to be drawn through the hexagon, so that excitation values $E_{(ant.)}$ can be read directly from them, the respective linear equation $y = m \cdot x + n$ for the line defining such an

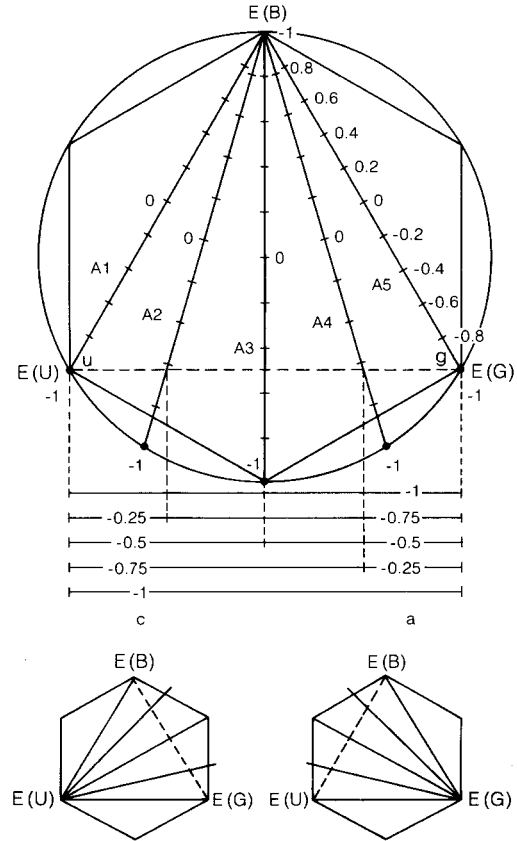


Fig. 5. The construction of colour opponent axes assigned to spectrally opponent mechanisms can be derived from (6). Suppose one is dealing with a mechanism of the type $a \cdot E(U) + b \cdot E(B) + c \cdot E(G)$ (where $b=1$ and a and c are negative). For convenience, this axis should run through the end point of the $E(B)$ -vector ($x=0, y=1$). The straight line ug then has to be intersected by the axis at a point that divides its entire length into the portions equal to the weighting factors. The examples given here are the axis corresponding to the following mechanisms:

- A1: $-1 \cdot E(U) + 1 \cdot E(B) - 0 \cdot E(G)$
- A2: $-0.75 \cdot E(U) + 1 \cdot E(B) - 0.25 \cdot E(G)$
- A3: $-0.5 \cdot E(U) + 1 \cdot E(B) - 0.5 \cdot E(G)$
- A4: $-0.25 \cdot E(U) + 1 \cdot E(B) - 0.75 \cdot E(G)$
- A5: $0 \cdot E(U) + 1 \cdot E(B) - 1 \cdot E(G)$

The construction of axes for mechanisms with weighting factor $a=1$ or $c=1$ is done equivalently, as illustrated in the insets. The central point of each axis corresponds to the value 0, and the ending points -1 and 1 lie on the circle's outline (which follows $x^2 + y^2 = 1$), so that all possible points in the hexagon can be covered by the axes. The derived axes may be subdivided into scale units and the excitation values for the corresponding type of spectrally opponent mechanism can be read from them

axis follows from:

$$m = \frac{b - 0.5 \cdot (a + c)}{(\sqrt{3}/2) \cdot (c - a)} \quad \text{and} \quad n = y_1 - \frac{\sqrt{3} \cdot b \cdot x_1}{-2 \cdot a - b}$$

as can be derived from (2) and (3) by simply replacing the excitations by their weighting factors. x_1 and y_1 are the coordinates of any point that one wants the axis

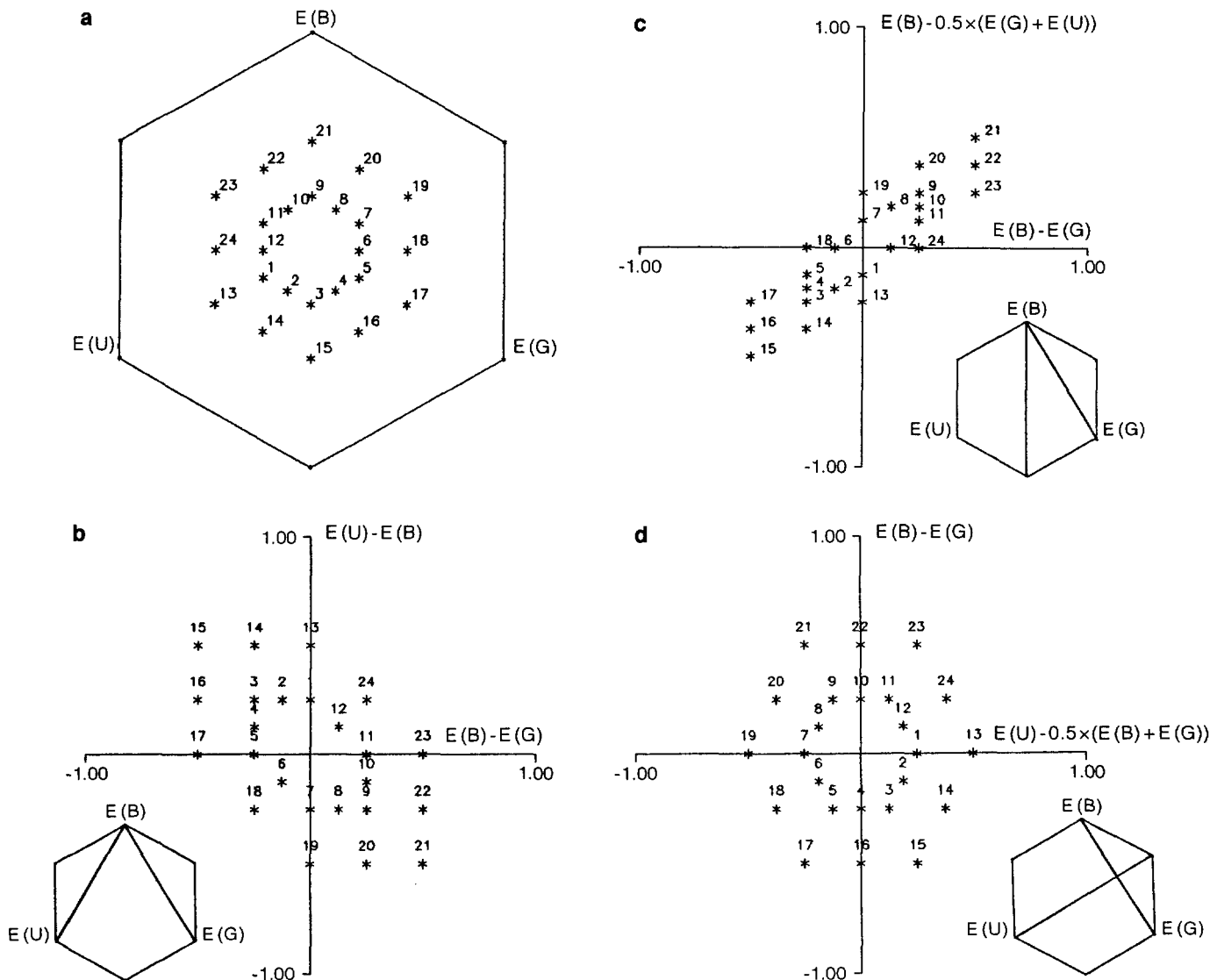


Fig. 6. **a** A set of 24 hypothetical colour stimuli, the loci of which are symmetrically distributed over the hexagon. **b–d** The loci of the same stimuli in 3 different two-dimensional colour opponent diagrams. The respective mechanisms are illustrated by means of colour hexagon symbols and axes drawn through them. The chro-

matic information is coded unambiguously in all these diagrams, but the distance proportions between stimuli differ quite largely between the various combinations of spectrally opponent mechanisms

to be put through for convenience reasons. The linear equation for a colour opponent axis with given weighting factors is thus:

$$y = \frac{b - 0.5 \cdot (a + c) \cdot x}{(\sqrt{3}/2) \cdot (c - a)} + y_1 - \frac{\sqrt{3} \cdot b \cdot x_1}{-2a - b}$$

which may be transformed into:

$$y = \frac{\sqrt{3} \cdot b}{-2a - b} \cdot (x - x_1) + y_1. \quad (6)$$

This is the equation for any axis assigned to a mechanism with given weighting factors that is supposed to run through point x_1/y_1 . The construction of such axes is actually very easy, as is illustrated in Fig. 5.

The colour hexagon can therefore be understood as a general colour opponent diagram, since its proportions can be regarded as representations of all possible kinds of colour opponency (with mechanisms the weighting factors of which follow $a + b + c = 0$).

How can colour be coded? The effects of different combinations of spectrally opponent mechanisms on colour distance proportions

It has been demonstrated that the colour hexagon represents all of the information evaluated by spectrally opponent units. Since the colour hexagon is a plane, this means that chromaticity can be coded unequivocally by any combination of two axes. Axes in the colour hexa-

gon correspond to particular spectral opponent mechanisms. This means that any combination of two spectrally opponent mechanisms can code chromaticity. The consequences of using different combinations of opponent mechanisms to code colour will be illustrated by a series of examples (see Fig. 6). A symmetrical "cloud" of colour loci is displayed in the hexagon (upper left). For comparison, the same set of stimuli is also depicted in 3 colour opponent diagrams. The axes' labels denote the weighting factors of the assumed colour opponent mechanisms. In addition, the hexagon insets display the respective combination of colour opponent axes.

The figure demonstrates that any combination of two spectrally opponent mechanisms unequivocally codes loci in the hexagon that are not congruent. There is no combination of axes corresponding to such mechanisms which combines separate loci into a single point.

The differences between the possible combinations of opponent mechanisms lie in the extension and compression of certain spectral areas. The comparison of distance proportions between colour loci in the three colour opponent diagrams of Fig. 6 clearly shows that, depending on which mechanisms are assumed, certain loci move closer together (and thus will be perceived as being more similar) whereas in other spectral regions the distances increase (and consequently discrimination will be better).

It is obvious that a combination of colour opponent processes such as in Fig. 6 (upper right) is less likely to be found in a natural colour coding system. What is it that makes this combination less favourable than the other ones?

Comparing the hexagon insets that display the colour opponent axes which correspond to the axes of the colour opponent diagrams, one finds that the angle between the hexagon axes is small in this case (30° , Fig. 6, inset upper right). If the angle between the axes is very small, this means that both the corresponding mechanisms have similar weighting factors. Consequently, the mechanisms will yield similar values for a given sample of stimuli. Consider the extreme case in which both axes would correspond to mechanisms with the exact same weighting factors. In this case all stimuli would lie on a straight line in a colour opponent diagram, i.e. the system is now one-dimensional. The example in Fig. 6 (upper right) is a case where this condition is approached. The "stimulus cloud" shows a tendency to contract to a "stimulus line" because both mechanisms render similar values. It is clear that this solution is inappropriate for colour coding, because the information from both mechanisms is highly interdependent. In other words, there is a great deal of redundancy present and this compromises coding efficiency.

The opposite extreme is found in Fig. 6 (lower right), where the colour hexagon axes are orthogonal. In this case the information from one mechanism is completely independent from the other, i.e. redundancy is minimized. The stimulus cloud is evenly stretched out, and one does not find a particular weighting of certain spectral parts. From the point of view of information processing (Buchsbaum and Gottschalk 1983), this is opti-

mal, but it doesn't mean that the hexagon axes actually *have* to be orthogonal when assigned to mechanisms in natural colour coding systems. An animal might well be interested in extending certain spectral parts on a perceptual level at the expense of having to compress other parts of its subjective colour plane. Nonetheless, if not orthogonal, the angle between the hexagon colour opponent axes should certainly be larger than in Fig. 6, upper right.

Intensity-dependent changes of colour loci

Backhaus (1991 a) has demonstrated that the colour loci in a colour opponent diagram, as derived for the honeybee, change as a function of relative intensity. It was then demonstrated that such changes actually exist on the perceptual level of the honeybee (Backhaus 1991 b).

These effects are based on the nonlinear phototransduction process in the receptors and can be observed in any model which uses photoreceptor excitations, such as the colour hexagon (Fig. 7). The loci of a series of representative monochromatic colours are plotted at 8 different relative brightness values between $Q=0.01$ and $Q=1000$. $Q=1$ denotes the intensity to which the receptors are assumed to be adapted. Please compare this figure with Fig. 6 in Backhaus (1991 a), where the intensity dependent shifts of the same monochromatic lights are plotted in a two-dimensional colour opponent diagram. This comparison nicely illustrates the differences between a colour space based on particular opponent processes of one species and a generalised colour space such as the hexagon. The "loops" generated by variation of the intensity of different monochromatic lights have similar shapes in both diagrams. Since, however, in the honeybee colour opponent space the blue-"uv-green" axis has a stronger weight than the uv-bluegreen axis, the distance proportions are more extended in the direction of the first axis, whereas in the colour hexagon the two directions are equally weighted.

The curves clearly display that there will be an optimum transmission intensity range around the adaptation level; far above and below that, the distances between spectral colours degenerate and finally collapse into the uncoloured point. This observation explains a well known perceptual phenomenon: colours illuminated by an intensity far below adaptation light will appear as more similar to black, and colours lit at very bright intensities will also be judged as less saturated (i.e. closer to the locus of all uncoloured stimuli).

Note that not only does the distance from the uncoloured point change, but loci deviate significantly from a straight line connected to the uncoloured point, particularly when they are more intense than the adapting background. This indicates that the colours will change their subjective hue depending on relative intensity, a phenomenon well known as Bezold-Brücke shift in human psychophysics. Figure 8 illustrates how the receptor signals at increasing intensity contribute to the shift of one monochromatic colour as an example; at low relative brightness, all receptors will respond with an excita-

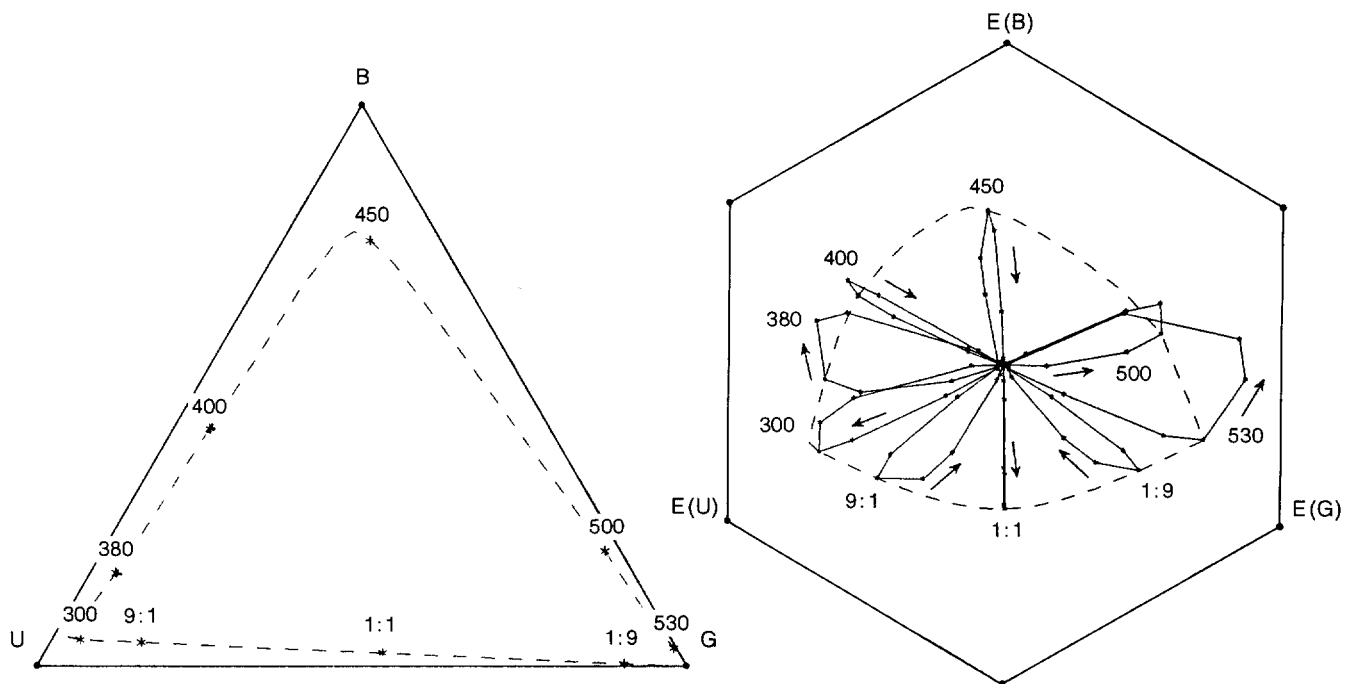


Fig. 7. Left figure: the position of 9 representative monochromatic lights in the colour triangle and the spectral locus. Right graph: the shift of the same colours as a function of intensity relative to the adaptation light. In the uv-green part the mixture values denote the ratio of combinations of the 300 nm and 550 nm monochromatic lights. At longer wavelengths, it is not possible to continue the spectral curve at constant relative brightness (Backhaus 1991a). The *arrows* illustrate the direction of intensity increase. The *points* mark the following intensities: $Q=0.01/0.1/0.5/1/5/10/100/1000$, where $Q=1$ corresponds to the intensity of the adaptation light. The *dashed line* gives the spectral curve at background

(adaptation light) intensity. In most cases the colour loci shift more or less linearly from the "uncoloured" locus to an optimum distance and start shifting "sideways" (i.e. towards different hues) at intensities above the adaptation light (Bezold-Brücke phenomenon). The optimal signal transfer will be in an intensity range between half and 5 times the one of the adaptation light, whereas below and above that the spectral loci collapse into the uncoloured point. The figure may be directly compared to Fig. 6 in Backhaus (1991a), where the exact same colours with the same relative intensity values are given in a two-dimensional colour opponent diagram based on the weighting factors derived for the honeybee

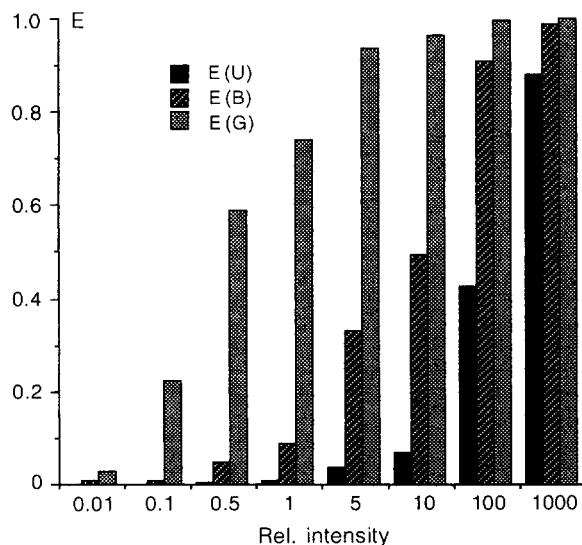


Fig. 8. The change of the 3 photoreceptor excitations with respect to the relative intensity is given for one representative monochromatic light (530 nm) in detail. The columns denote the absolute value of the receptor signals $E(U)$ (left column), $E(B)$ (middle column) and $E(G)$ (right column). The intensity values plotted on the abscissa are the same as in Fig. 7. Note that all these excitation sets will have the same colour locus in the triangular chromaticity diagram

tion close to 0; the colour will therefore appear as black (uncoloured). At intensity levels close to the adaptation light, the signal of the green receptor dominates strongly over the two other inputs and the colour will thus appear as a saturated green. At a stronger illumination, the blue receptor starts to contribute more (and the green receptor already asymptotes to the saturation level), and the colour perception will consequently shift towards blue-green; finally all receptors are approaching their maximal response of 1 and the colour will appear more and more whitish (achromatic), because the responses cancel each other in every hypothetical type of opponent process.

Colour hexagon distances as perceptual colour differences

A diagram that is meant to represent colour distance proportions that are as close as possible to perceptual measures should be based on the properties of the colour coding mechanisms of the animal in question. Numerous insects, and in particular Hymenoptera (Peitsch et al. 1989; Menzel and Backhaus 1991) have 3 types of photoreceptors and, by analogy with the worker bee (Backhaus 1991a), one might expect their colour vision to be based on opponent coding. Can one use the colour

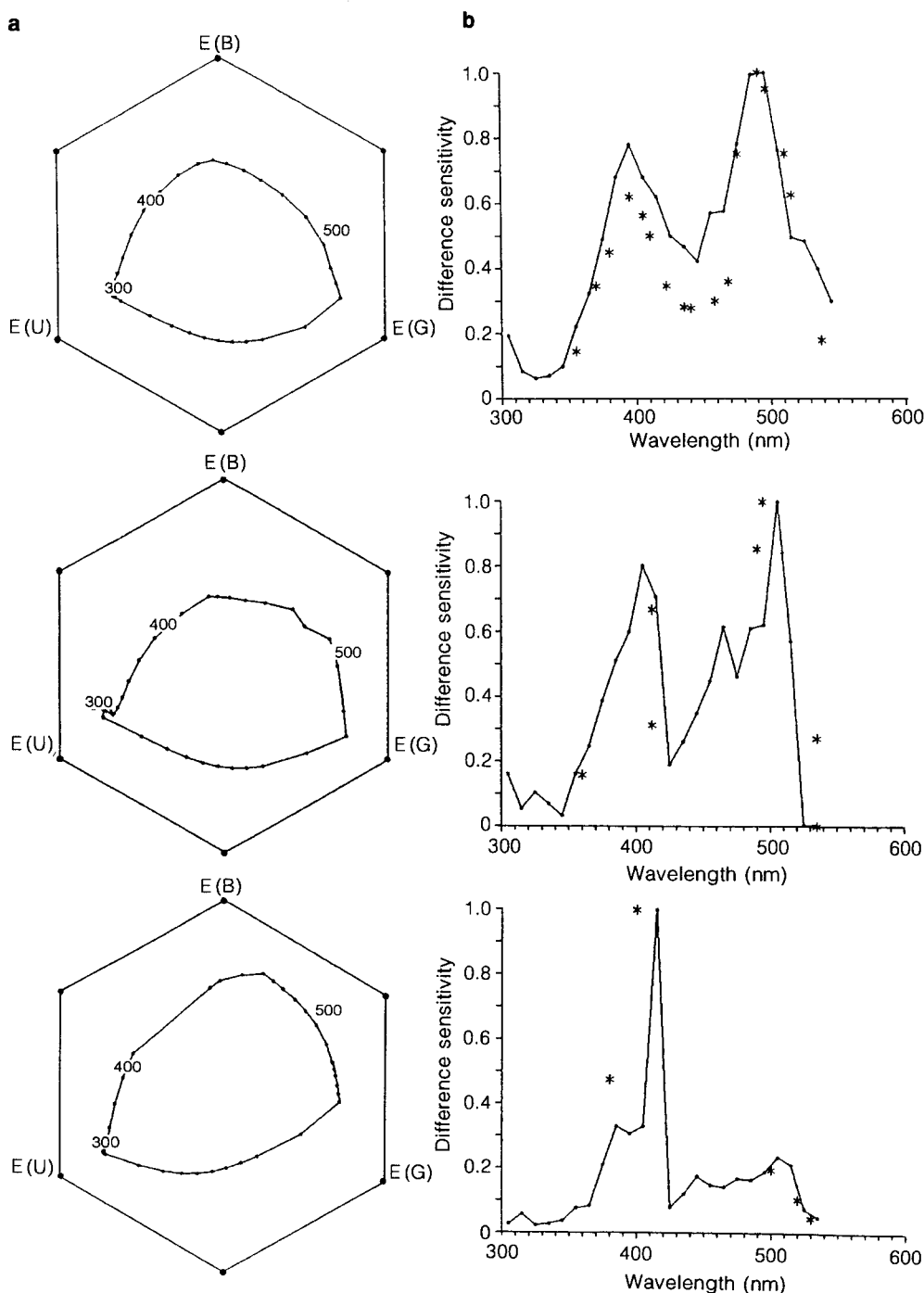


Fig. 9. **a** (left side) gives the spectral curves at adaptation light intensity (see Methods) of the 3 trichromatic insect species *Apis mellifera* (top), *Melipona quadrifasciata* (middle) and *Osmia rufa* (bottom) in the colour hexagon. The long wavelength point at which the uv-green mixture line starts is determined by the wavelength at which the green receptor is saturated and the contributions of the uv and blue receptors approach zero (Backhaus 1991a). **b** (right side) Spectral discrimination (inverse $\Delta\lambda/\lambda$) curves calculated from 10 nm steps of monochromatic light distances (according to equation (7)) in the colour hexagon for the same animals. The stars mark the spectral discrimination values for the respective species from behavioural investigations (literature quoted in the text). All curves are normalized to a maximum of unity

hexagon to provide standardized measures of colour distances in these species, that approximate to perceptual differences but make no assumptions about the precise values of the weighting factors used by spectrally opponent mechanisms? This possibility is explored by using the colour mechanisms. This possibility is explored by using the colour hexagon distances to predict spectral discrimination data and comparing these predictions with published behavioural measurements. Three Hymenoptera are used, namely the honeybee *Apis mellifera* (von Helversen 1972), the stingless bee *Melipona quadri-*

fasciata (Menzel et al. 1989) and the solitary bee *Osmia rufa* (Menzel et al. 1988). For *Apis* and *Melipona*, the data were collected in colour discrimination tasks at the food source, whereas *Osmia* was tested at the nest entrance. The distance between two colour loci 1 and 2 in the colour hexagon is derived as follows:

$$D_{(1-2)} = \sqrt{(x_1 - x_2)^2 + (y_1 - y_2)^2}.$$

Replacing X and Y according to the Eqs. (2) and (3) results in the following relation:

$$D_{(1-2)} = \sqrt{\left\{ \left(\sqrt{3}/2 * (E(G)_1 - E(U)_1) - (\sqrt{3}/2 * (E(G)_2 - E(U)_2) \right)^2 \right.} \\ \left. + \left\{ (E(B)_1 - 0.5 * (E(G)_1 + E(U)_1) - (E(B)_2 - 0.5 * (E(G)_2 + E(U)_2) \right\}^2 \right.} \\ \Leftrightarrow D_{(1-2)} = \sqrt{0.75 * \{E(U)_2 - E(U)_1 + E(G)_1 - E(G)_2\}^2 + \{E(B)_1 - E(B)_2 + 0.5 * (E(U)_2 - E(U)_1 + E(G)_2 - E(G)_1)\}^2} \quad (7)$$

Equation (7) is the hexagon colour difference formula. The model calculations which lead to the presentations in Fig. 9 are based on the spectral sensitivity functions of the respective insect species as electrophysiologically characterized (Menzel et al. 1986, 1988, 1989). The colour hexagon spectral distances supply a good prediction of the wavelength positions of maxima and minima of the behavioural spectral discrimination function in all 3 investigated species (Fig. 9). The vertical deviations (particularly in *Apis*) seem tolerable if one bears in mind that a *standard* measure is applied to all 3 species.

Discussion

The geometrical inferences of this paper indicate that spectral information can be coded unambiguously by means of any two combined spectrally opponent mechanisms if the number of input variables is 3. This confirms on a geometrical basis the considerations of Buchsbaum and Gottschalk (1983) who demonstrated on the basis of information theory that the evaluation of the 3 receptor signals is most effectively achieved by means of two spectrally opponent mechanisms for coding chromaticity (and one achromatic channel for coding intensity). The present paper demonstrates the arbitrariness of the mode of coding. To be unequivocal, there must be two different opponent processes, but it does not matter what weighting factors they have, nor if they evaluate 2 or 3 receptor signals antagonistically. The particular values of weighting factors determine the extent to which particular spectral areas are compressed or expanded. Consequently, the mode of opponent colour coding can be adapted phylogenetically to favour an organism's particular ecophysiological demands. This idea can be tested by comparing the colour coding systems of different animals (Chittka et al. 1992).

The geometry of the colour hexagon as a general opponent colour diagram is based on the assumption that the weighting factors in spectrally opponent mechanisms add up to zero. This is the case in honeybees (Backhaus 1991a); it also holds if the explanation of behavioural data in colour similarity tests for 8 other hymenopteran species is concerned (Chittka et al. 1992), although it has not been tested critically there. In humans, it is only approximately true (see above), and especially in the blue-yellow colour opponent mechanism a considerable deviation is found in the existing literature (Hurvich and Jameson 1955; Werner and Wooten 1979; Guth et al. 1980). Nonetheless, there are several good reasons for believing that colour opponent mechanisms should at least tend to follow this rule. Backhaus (1991a) has shown that such an organisation of the opponent mechanisms minimizes the Bezold-Brücke-shift. Furthermore, equal excitation of all 3 receptors should result in a neu-

tral (0-) excitation of the colour opponent mechanisms and therefore an uncoloured perception. The further the sum of the weighting factors deviates from zero, the more would one observe an intensity-dependent chromatic change of uncoloured stimuli (i.e. for example "grey" would become "coloured" in case the intensity is varied).

In order to determine the weighting factors in human colour opponent processes exactly, one would have to take into account graded photoreceptor voltage signals and adaptation processes. Should such an investigation still yield a strong deviation of the weighting factors' sum from zero, then the hexagon would have this one disadvantage in common with the colour triangle and the CIE diagram. In these "traditional" chromaticity diagrams a stimulus is also plotted in the center (neutral point) in the case of 3 equal tristimulus values. If two of these values are equal, the stimuli will lie on a line which is neutral with respect to these two variables. This means that in this mode of plotting chromaticity, as well as in the hexagon, an equal weighting of the receptor variables is implied.

The other advantages of the colour hexagon are not affected. The mode of plotting excitations presented here accounts for a number of phenomena which cannot be explained on the basis of a triangular (or CIE-) chromaticity diagram. This concerns the perceptually smaller distance of very bright and very dark colours (with respect to the adaptation level) to the perceptual impression "uncoloured" (i.e. black or white). The intensity-dependent change of hue that occurs mainly at high relative brightness levels (Bezold-Brücke phenomenon) also has to be predicted for animals other than humans and honeybees with different kinds of colour opponent processing. All these phenomena are based on the nonlinear transduction function of the receptors and the further evaluation of their signals in spectrally opponent mechanisms (Backhaus 1991a, b).

If such intensity-dependent effects are observed in a colour hexagon, they will also occur in any type of colour opponent mechanism and thus in any colour plane based directly on specific colour opponent mechanisms, because all possible opponencies are included in the hexagon. The hexagon will show the unweighted effects, whereas in a colour opponent diagram based on orthogonal axes according to the actual mechanisms (as derived for the honeybee by Backhaus 1991a), the perceptual phenomena can be explained quantitatively. Note that the *precise* perceptual distance proportions can only be read from a diagram that shows the hexagon relations interpreted by two actual spectrally opponent mechanisms and a defined metric assigned to it. The metric (either a city-block- or a Euclidian metric, see Chittka

et al. (1992) for an explanation of these terms) defines the way in which the nervous system calculates with the differences in outputs of the opponent channels to determine a difference in colour. If the exact mechanisms and/or the metric are unknown, then the Euclidian metric is more appropriate for perceptual colour difference estimations because the axes may be freely rotated (Backhaus 1991a). In a city-block-metric based on the hexagon coordinates the applicability would be restricted to systems with axes similar to these coordinates; the city-block-metric is the less general measure.

Colour hexagon distance proportions can be employed as satisfactory approximations of perceptual colour difference as demonstrated by comparing behavioural spectral discrimination data of 3 trichromatic insect species with the distances of monochromatic colours predicted for them in the hexagon. These results also indicate that the respective species possess a colour opponent system that consists of two spectrally opponent mechanisms; this question, however, will be scrutinized in the subsequent paper (Chittka et al. 1992). It should be noted that care has to be taken concerning the derivation of perceptual colour differences for humans, because here the intensity coding channel contributes to the total colour difference. Such a channel, however, is not found in hymenopteran colour vision (Daumer 1956; von Helversen 1972; Backhaus et al. 1987; Chittka et al. 1992).

A chromaticity diagram is presented which takes into account the nonlinear phototransduction process in the receptors and does not make any predictions about exactly how the nervous system weights the receptor information. The proportions of the diagram therefore represent a level closer to perception, since it deals with the variables the nervous system has to work with. The loss of one dimension in the hexagon (3 variables in a two-dimensional plane) is compensated by the fact that any two of the remaining dimensions (colour opponent axes) may be regarded as corresponding to two spectrally opponent mechanisms as actually found in humans, bees and many other trichromats (Chittka et al. 1992). The diagram thus unifies graphically the Young-Helmholtz and Hering theories of colour vision. It uses the 3 receptor signals as variables and also represents all possible mechanisms of colour opponency.

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Appendix

The following example demonstrates why the perceptual differences between colours may not be judged from loci in the colour triangle. The distance between two monochromatic lights (550 and 700 nm) for the honeybee will be considered both in this diagram and the colour hexagon. 550 nm should appear as a saturated green to the honeybee, because the green receptor is maximally stimulated, whereas the other two receptors will not be excited at this wavelength. 700 nm should be outside the visual spectrum of the

honeybee (and thus appear as black/uncoloured), but might yield a very small value in the green receptor in model calculations. Consider the following idealized quantum catch values for the two monochromatic lights:

550 nm: $U=0$; $B=0$; $G=1$

700 nm: $U=0$; $B=0$; $G=0.01$.

Before being transformed into the colour triangle coordinates, the quantum catch values are normalized such that their sum equals unity:

$u = U/(U + B + G) \Rightarrow u_{550} = 0$ and $u_{700} = 0$

$b = B/(U + B + G) \Rightarrow b_{550} = 0$ and $b_{700} = 0$

$g = G/(U + B + G) \Rightarrow g_{550} = 1$ and $g_{700} = 1$.

This normalization results in two identical sets of values, which would thus result in identical coordinates in the colour triangle. Calculating the Euclidian distance between the two, one would find a honeybee colour distance of zero between green and black (uncoloured).

Using photoreceptor voltage signals instead of normalized quantum catch values, we get the following results (a simplified version of Eq. (1) is employed for the calculation of excitations. See Chittka et al. (1992):

$E(U) = U/U + 1 \Rightarrow E(U)_{550} = 0$ and $E(U)_{700} = 0$

$E(B) = B/B + 1 \Rightarrow E(B)_{550} = 0$ and $E(B)_{700} = 0$

$E(G) = G/G + 1 \Rightarrow E(G)_{550} = 0.5$ and $E(G)_{700} = 0.0099$.

From Eq. (7) it follows that the perceptual distance between the two monochromatic lights is $D_{(1-2)} = 0.47$. (The maximum possible value for a distance in the hexagon is 2, the distance between two opposite corners.) This is a more reasonable value for two colours that should be as different as green and black (uncoloured). This extreme example was employed to demonstrate how gross the errors can be when colour distances are derived from the triangular diagram. The errors might be smaller with other pairs of stimuli, but will occur at any intensity level and in any spectral area. It follows that it is in no case possible to estimate a perceptual colour distance, a hue or a saturation value from the colour triangle. (Note, for example, that our 700 nm monochromatic light (honeybee black/uncoloured) would appear as maximally saturated in the triangular chromaticity diagram!)

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