J Comp Physiol A (1992) 170:545–563

Journal of Comparative Physiology A Sensory, Neural, and Behavioral Physiology

Opponent colour coding is a universal strategy to evaluate the photoreceptor inputs in Hymenoptera

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Accepted March 3, 1992

Summary. Behavioural tests were carried out with 9 hymenopteran insect species, which ranked certain sets of coloured stimuli according to their subjective similarity to a previously memorized stimulus. Kendall's τ coefficient is employed for the analysis of correlation between these similarity rankings and the colour distance rankings predicted by various models of neural colour computation. The models are based on the measured spectral sensitivities of photoreceptor colour types and use a variety of simple colour coding systems to derive hypothetical colour distances. The correlation between the predictions of the models and the behavioural results serves as a measure for the likelihood of existence of a colour coding system. In all species, the similarity rankings can be best explained by assuming that colour is coded on a perceptual level by two colour opponent mechanisms. Brightness differences are ignored, indicating that an intensity-coding sub-system is not used in colour discrimination by the insects investigated. The weighting factors of the colour opponent mechanisms differ between species in detail, but not in the principles involved. It is thus possible to employ a standard measure of perceptual colour distance (colour hexagon distance) to predict the capacities of colour discrimination adequately in all the tested insects.

Key words: Comparative colour vision – Opponent processes – Colour computation – Hymenoptera – Colour discrimination behaviour

Introduction

How is colour computed in the insect brain? How are the photoreceptor signals integrated in a neural colour coding system to generate the perception of colour? The ingenious studies of Backhaus and Menzel (1987), Backhaus et al. (1987) and Backhaus (1991) concerning the psychophysics of honeybee colour vision demonstrate how these questions can be tackled in animals that, unlike humans, cannot directly render informations about their colour perception. These analyses include the following basic steps:

1. Spectral inputs are calculated in terms of physiological receptor voltage signals (photoreceptor excitations), using intracellularly measured spectral sensitivity functions of single receptor cells as a basis (Backhaus and Menzel 1987).
2. The behavioural output of the unknown colour coding system is evaluated in terms of the perceptual distances between colours, developing methods to estimate these from the results of dual and multiple choice colour discrimination experiments (Backhaus et al. 1987).
3. Multidimensional scaling and least square fit procedures are used to infer the processes underlying the conversion of receptor excitations into a bee's percept of colour (Backhaus et al. 1987; Backhaus 1991).

Their results suggest that colour is coded using two sets of spectrally opponent mechanisms, each of which combines the inputs of three receptors with weighting coefficients that add up to zero. This model agrees with the properties of spectrally opponent bee neurons as characterized electrophysiologically by Kien and Menzel (1977), Hertel (1980), Riehle (1981), Hertel and Maronde (1987).

The problem with the third step of this analysis (multidimensional scaling and least square methods) is that it requires very extensive behavioural investigations. A 12×12 stimuli matrix discrimination experiment has to be conducted. In essence, this means that during the course of the tests each of the 12 stimuli has to occur as the training mark and the 11 others are tested for their similarity with the trained colour. Consequently, this investigation can only be carried out with species that can easily be trained and which can render a large quantity of behavioural data in a reasonably short time. Animals other than the honeybees can be much more difficult to train, do not recruit colony members to a feeding station

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equally reliably, or may collect food as non-social individuals. Nevertheless, a considerable body of colour discrimination data has been collected from such less favourable species. Therefore, we developed another method for inferring colour coding mechanisms from behavioural measures of colour discrimination. We compared the colour similarity rankings, determined behaviourally, with the colour distance rankings generated by different models of colour coding. These models processed receptor inputs that were determined using the measured spectral sensitivities of the different photoreceptor colour types. The most likely model of colour coding was then deduced by correlating model outputs, the colour distance rankings, with the behavioural rankings. Our findings suggest that all Hymenoptera so far tested use sets of two opponent mechanisms for colour coding.

Material and methods

The method of analysis presented here shall first be illustrated by an example (see Fig. 1). The unknown colour coding system in the animal is depicted as a black box, the well described inputs of which are the photoreceptor excitations with respect to the coloured stimuli 1–5 (Backhaus and Menzel 1987). In order to be able to determine the "system in the box" one needs an investigable output. The animal has to be forced to process known inputs and indicate the outcome. We use the behavioural performance in a colour discrimination test as the output. The animal has first to memorize one of the colour marks 1–5 (No. 1 in this example) and then rank the other 4 with regard to their perceived similarity to the learned stimulus (see below for experimental procedures). To determine the network between input and output (the colour coding system), the combination of the 3 input variables (receptor signals) must be varied in such a way that a colour distance measure is obtained which can explain the behavioural similarity ranking. To make the procedure clear, consider the example given in Fig. 1. Suppose the choice frequencies for the simultaneously presented stimuli 1–5 in the test are 45/9/23/11/36 choices, and one wants to find out, for example, whether the animal evaluates the receptor inputs by simply summing up the 3 photoreceptor excitations. These excitations, E(U), E(B) and E(G), are determined by applying the spectral sensitivities of the receptors to the spectral outputs of the stimuli 1–5 and are given in the following table.

Stimulus No.	Receptor excitations			Sum of excit.	"Colour distance" to stim. No. 1	Choices in test
	E(U)	E(B)	E(G)	$\sum E_i$	$\sum E_1 - \sum E_i$	n
1	0.1	0.2	0.1	0.4	0	45
2	0.5	0.5	0.5	1.5	1.1	9
3	0.6	0.6	0.9	2.1	1.7	23
4	0.9	0.6	0.3	1.8	1.4	11
5	0	0	0	0	0.4	36

The 5th column of this table denotes the absolute response values generated by this particular model of processing (summing receptor inputs). The corresponding colour distances are given in the 6th column and can be compared with the behavioural data in the 7th column. The next step of the analysis is to develop an appropriate method to determine the correlation between the colour distances predicted by the model (column 6) and the behavioural data (column 7). We can then ask 3 major questions. 1. How good is the correlation, and therefore, how probable is the model underlying the distance measure? 2. Is this correlation significant, in other words, how high is the probability that the respective co-efficient has been obtained by chance? 3. Is the correlation significantly better (or worse) than the correlation resulting from the distance scale generated by another model of coding?

In what follows we will use this type of procedure to test as many arbitrary colour computation models as possible (within tolerable limits of expenditure) and then test them for correlation with the behavioural data.

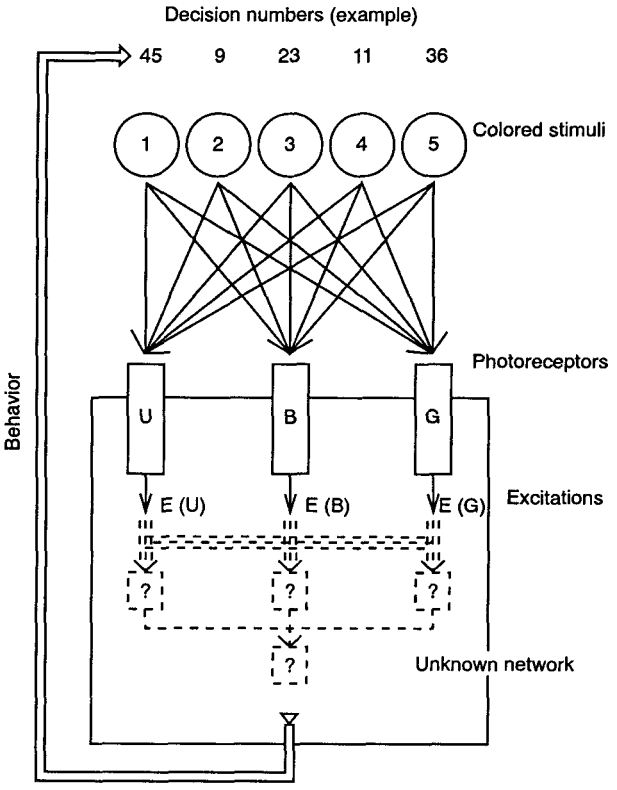


Fig. 1. The basic approach of this work as a "black box" – problem. The test animal (with an unknown colour computation system) is assumed to rank the colour marks 2–5 with respect to their subjective similarity to stimulus 1. The inputs to the unknown system, i.e. the receptor excitations, can be calculated for all 5 stimuli (see Methods). The behavioural similarity ranking is taken as the output of the system. How can the photoreceptor signals be processed in the unknown network so to generate differences from stimulus 1 that explain the behavioural response? In other words, the input and output of the black box are known. What processes in the black box can account for the input-output-relation?

1. The gathering of behavioural and electrophysiological data

The goal of this work was to gather all the available data in order to be able to investigate and compare as many species as possible. The electrophysiological (photoreceptor spectral sensitivity) and behavioural data (colour discrimination tests) are partially still unpublished, and since the test setups were not always the same, a brief description will be given. In those cases where the material and test procedures are published, reference will be made to the respective authors.

1.1. Electrophysiological data. Unless specified otherwise, all data are reviewed in abstract form by Peitsch et al. (1989). This survey of spectral types found that the majority of species have 3 spectral

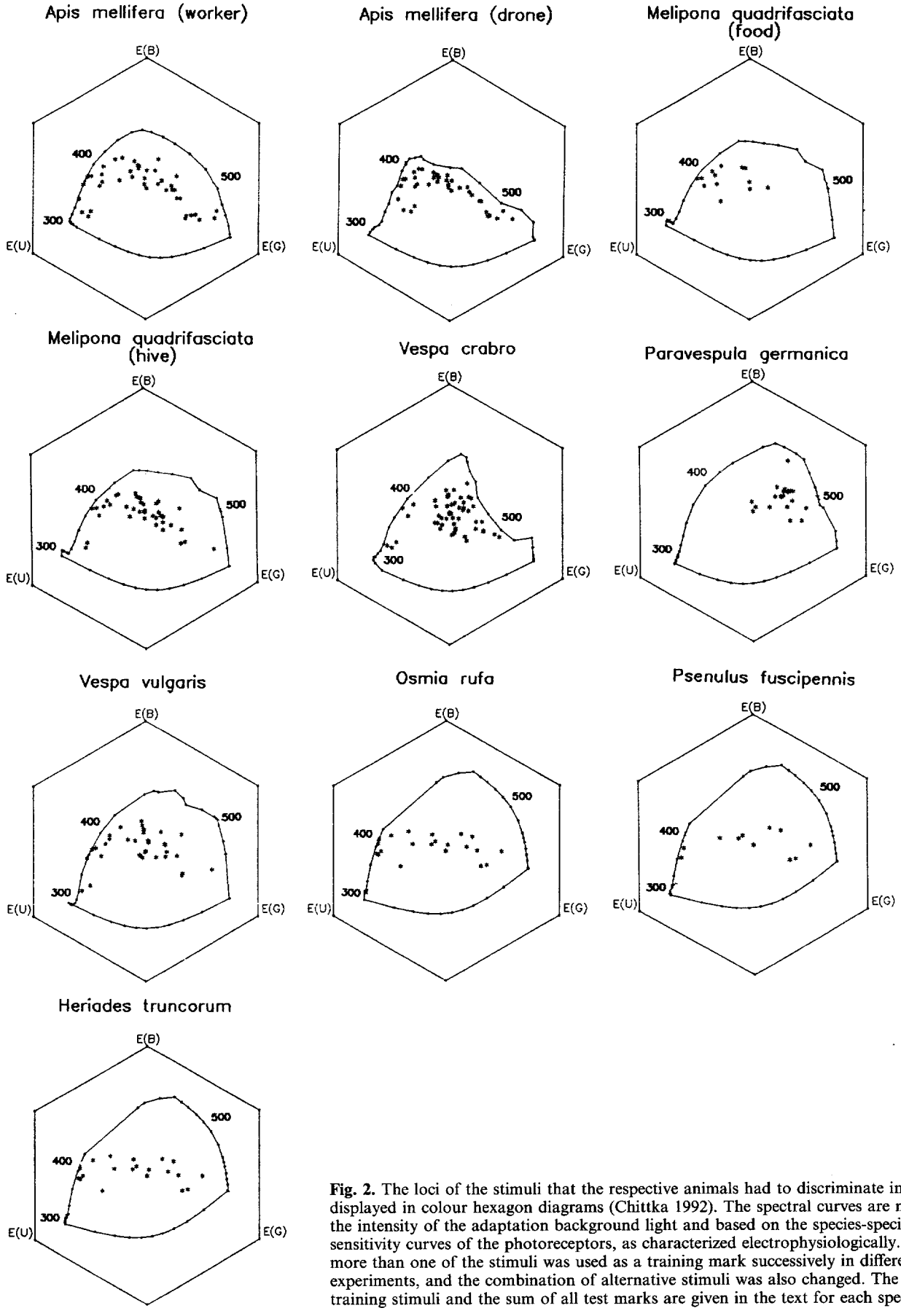


Fig. 2. The loci of the stimuli that the respective animals had to discriminate in the test are displayed in colour hexagon diagrams (Chittka 1992). The spectral curves are normalized to the intensity of the adaptation background light and based on the species-specific spectral sensitivity curves of the photoreceptors, as characterized electrophysiologically. In all cases, more than one of the stimuli was used as a training mark successively in different series of experiments, and the combination of alternative stimuli was also changed. The numbers of training stimuli and the sum of all test marks are given in the text for each species

Table 1. The numerical aspects of the test procedures for all the investigated species are listed

	Apis mellifera worker	*Apis mellifera* drone	*Melipona quadrifasciata* (hive)	*Melipona quadrifasciata* (food)	*Vespa crabro*	*Paravespula germanica*	*Vespa vulgaris*	*Osmia rufa*	*Psenulus fuscipennis*	*Heriades truncorum*
Number of training marks	5	3	10	12	5	5	6	13	6	13
Number of alternative marks	59	44	95	132	114	43	71	69	12	51
Number of decisions	7346	3205	34853	3419	15376	22846	7689	3768	298	2366

photoreceptor types, similar to the worker bee's with maxima of sensitivity at around 340, 440 and 540 nm. A manuscript publishing the spectral sensitivity curves of all species in detail is pending (Peitsch et al., in press).

1.2. Behavioural experiments. The coloured stimuli used in the tests were Schott filters on aluminium plates, combinations of such filters on aluminium plates or filters on coloured cardboards (Menzel and Lieke 1983). The filters need not be individually described because their calibrated spectral outputs were converted to receptor excitations (Backhaus and Menzel 1987). Thus the range of spectral contents can be judged from the scatter of loci in the appropriate tri-stimulus space, shown here (Fig. 2) using the recently developed colour hexagon (Chittka 1992). Correspondingly, Table 1 gives the number of training and test stimuli as well as the absolute number of choices obtained in the tests.

In all cases the colour stimuli measured 7 cm in diameter and had a central hole (Ø 1 cm). If the stimulus was to be memorized by the insects, this hole was connected to the hive/nest entrance during the training phase. Correct choices were thus rewarded by gaining access to the home site during the training phase (see below for details of test procedures). In one case *(Melipona quadrifasciata)* the animals were also trained and tested at the food source; here, they were rewarded with sugar water in the centre of the training mark. Unless otherwise mentioned, the stimuli were presented on an achromatic median grey background.

After a training phase of a few days, when a constant level of accuracy in colour discrimination (90–95% discrimination of very different stimuli) was assured, the tests were started. A set of stimuli (one of which was the originally trained stimulus) was presented and the number of times an animal chose each of them recorded. These choice frequencies were taken as a direct indication of the subjective difference of colours and were used to draw up a rank order of colour similarity.

The tests were repeated with constant stimuli combinations (in different spatial arrangements) until a sufficiently high number of choices for the tested stimuli had been achieved. When the training colour was changed, we always made sure that we trained new test animals, so that the last learned colour could not affect the choice behaviour in the new test situation.

1.2.1. The honeybee Apis mellifera *worker.* Data partially published by Menzel (1985), experimentalists: F. Franck, S. Menzel, S. Müller, K. Weber, experimentalists of unpublished data: L. Chittka, T. Echternacht, M. Hoffmann, K. Steinhauer. Receptor spectral sensitivities from Menzel et al. (1986).

Dual choice tests as described by Menzel and Lieke (1983) and 12-stimuli multiple-choice tests according to Backhaus et al. (1987) were performed, with the only difference that the bees tested here were not fed as a reward for correct choice at the training mark: the central hole of the colour signal provided access to the hive entrance by means of a plexiglass pipe system. Bees could use this access to the hive freely during training. In the test situation, the training marks (and thus the way to the hive) were closed, and the choice behaviour with respect to the respective 12 (or 2) test signals (one of which was equivalent to the trained one) was recorded. When too many homecoming bees had gathered in front of the test device, or the tested bees got tired and started sitting on the test plate, the test ended and the access to the hive was opened again. Detection of bees approaching a colour mark was done automatically by infrared light detectors (Menzel and Greggers 1983).

1.2.2. Apis mellifera *drone.* Data partially published by Menzel et al. (1988). experimentalists of unpublished data: L. Chittka, T. Echternacht, M. Hoffmann, K. Steinhauer.

Multiple choice tests were performed at the hive entrance. Since drones show a tendency to follow worker bees in search of their hive, they had to be tested separately from the workers. Thus, all the drone tests were prepared in the following way: some 40 drones were caught and kept in a dark cage. The hive entrance was then closed and the bees returning from foraging flights were captured until there were no more workers around the test device. This procedure took about 30 min; thereafter, the drones were set free. The choice behaviour of the now highly motivated test animals was recorded by three 8 mm movie cameras. Single exposures were taken every 5 s and the pictures were analyzed by counting the number of drones visible directly in front of the respective stimuli. Infrared detectors (Menzel and Greggers 1983) could not be used, because drones tend to land and walk around on the colour marks, so that one choice will be counted as several choices by the detectors. During the test phase, frequent permutations of stimuli were made, and the animals were sometimes blown off the test device after landing in order to obtain more behavioural data. After about 10 min, when drones were apparently too exhausted to be tested any further, the hive entrance was made accessible again.

1.2.3. The stingless bee Melipona quadrifasciata. Data partially published by Menzel et al. (1989). Receptor sensitivities from the same paper. Experimentalist of unpublished behavioural data: S. Rodrigues de Souza, using multiple choice test procedures at the feeding place as described by Backhaus et al. (1987).

1.2.4. The hornet Vespa crabro. Previously unpublished behavioural data. Experimentalists: W. Beier and H. Hertel. Dual choice tests (Menzel and Lieke 1983) and multiple choice tests (Backhaus et al. 1987) at nest entrance. No infrared detectors could be used for counting of choices in the tests, because hornets show a rather inaccurate flight behaviour when approaching the nest entrance. An observer had to count the choices and, since it is not possible for one experimentalist to survey all 12 stimuli, only two stimuli were displayed in the test. One of them was always equivalent to the training stimulus. Later, the number of simultaneously presented stimuli was increased to four. In all cases, the tested colour marks were chosen from the 12-stimuli set displayed in the learning phase.

1.2.5. The wasp Paravespula germanica. Data and experimental procedures for the nest entrance (dual choice) colour discrimination tests described by Beier and Menzel (1972).

1.2.6. The wasp Vespa vulgaris. Previously unpublished behavioural experiments at the nest entrance. The multiple choice test device described by Backhaus et al. (1987) was used. The choice behaviour in the test was monitored by means of a miniature camera. Pictures were taken every 5 s and were later evaluated by simply counting

the wasps that were visible directly in front of the colour marks. Experimentalist: J. Menzel

1.2.7. The solitary bee Osmia rufa. Colour discrimination data (dual choice tests at nest entrance) taken from Menzel et al. (1988). Receptor sensitivities from the same paper. Adaptation background: bamboo wood (as also in the following species).

1.2.8. The digger wasp Psenulus fuscipennis. Previously unpublished data. Experimentalist: E. Steinmann. Procedure in behavioural investigations see Menzel et al. 1988. Since no electrophysiological data were available, the spectral sensitivity functions of the receptors of *Osmia rufa* were inserted.

1.2.9. The solitary bee Heriades truncorum. Previously unpublished data. Experimentalist: E. Steinmann. Procedure in behavioural investigations see Menzel et al. 1988. Receptor spectral sensitivities see *Psenulus*.

2. Calculation of colour distances according to 1007 different models

The object is to determine a set of neural interactions that evaluates the spectral inputs (receptor signals) such that it can explain the choice behaviour in a colour discrimination test. For this purpose the spectral inputs will be systematically combined in many different ways to produce a large number of measures of colour distance. These modelled distances can then be compared with the behaviourally determined measures of colour similarity.

First, we will describe the principles involved in the calculation of colour distances according to the various models of colour coding. The particular models will be described in detail.

2.1. Computation of photoreceptor voltage signals. The calculation of receptor excitations generated by a given coloured stimulus is reviewed and explained in detail by Backhaus and Menzel (1987). Nonetheless, since this is an important logical step in the present analysis, it will be briefly outlined here.

The effective quantum catch P in a photoreceptor receiving a given coloured stimulus is determined by integrating over: 1) the spectral sensitivity curve $S(\lambda)$ of the receptor; 2) the daylight illumination curve (normfunction D65, $D(\lambda)$) and 3) the spectral reflection function of the respective colour stimulus $I_s(\lambda)$ according to

$$P = R \int_{300}^{700} I_s(\lambda)S(\lambda)D(\lambda)d\lambda \quad (1)$$

where R (the range sensitivity) depends on the adaptation state. The adaptation process is assumed to adjust each receptor's sensitivity such that it renders half its maximal response when stimulated by the light reflected from the background (Laughlin 1981). Under the condition that n equals 1 in equation 3 (see below), R is determined by the equation

$$R = 1/\int_{300}^{700} I_B(\lambda)S(\lambda)D(\lambda)d\lambda. \quad (2)$$

$I_B(\lambda)$ is the spectral reflection function of the background on which the stimuli are presented during the tests. The calculation of physiological receptor voltage signals (excitations E) from quantum catch values P is described by

$$E = P^n/(P^n + 1). \quad (3)$$

The exponent n is set to 1 in our model calculations (Backhaus and Menzel 1987, for details). Under these conditions, (3) is reduced to

$$E = P/(P + 1) \quad (4)$$

where E can theoretically obtain any value between 0 and 1. In the case when the receptor is stimulated by the adaptation light, P equals 1 and E is 0.5. For further reference, see Naka and Rushton (1966), Lipetz (1971).

2.2. Deriving colour distance from models of color coding. Every model evaluated stimuli by using one or more simple linear transformations of the form

$$A = aE(U) + bE(B) + cE(G) \quad (5)$$

where A is the signal generated by the transformation, a, b and c are the weighting factors and E(U), E(B) and E(G) are the receptor excitations. Transformations in which one or more of the weighting co-efficients were zero were considered.

The simplest models evaluated the receptor inputs by applying a single linear transformation (Eq. 5). For these one-dimensional models the colour distance between two stimuli, 1 and 2, is determined by calculating the signals A_1 and A_2 produced by the transformations of 1 and 2. The colour distance is given by the absolute difference

$$D_{(1-2)} = |A_1 - A_2|. \quad (6)$$

The more complicated (and realistic) models were 2- or 3-dimensional in the sense that they used 2 or 3 linear transformations of the type given in Eq. 5 to process receptor inputs. Each of these transformations will henceforth be termed sub-systems. To produce the measure of colour distance in a two- or three-dimensional model system, first the distances between two stimuli in the subsystems are calculated. The resulting values for colour difference are then summed according to a city-block metric. Thus, we get the equations (7) for the two-dimensional and (8) for the three-dimensional case:

$$D_{(1-2)} = |A_1 - A_2| + |B_1 - B_2| \quad (7)$$

$$D_{(1-2)} = |A_1 - A_2| + |B_1 - B_2| + |C_1 - C_2| \quad (8)$$

where B and C are the signals of the newly introduced subsystems according to (5). The city-block metric was chosen because its validity has been established in extensive analyses of colour computation in the worker bee's visual system (Backhaus et al. 1987).

The term "city-block metric" can briefly be explained by means of a graphical representation. Suppose you have a two-dimensional diagram with two orthogonal axes X and Y and two points determined by the values x_1/y_1 and x_2/y_2. The familiar Euclidian distance between the two points can be measured directly with a ruler. It may also be calculated using the equation:

$$D_{(1-2)} = \sqrt{(x_1 - x_2)^2 + (y_1 - y_2)^2}. \quad (9)$$

In order to obtain the distance according to a city-block metric instead of the Euclidian metric, one has to "go around the corner", very much like one does in a modern city with a rectangular layout, to get from one point to another. In terms of the graphical representation, this means that to bridge the distance between the two points, one first follows the one axis and then the other. The total distance between the two points equals the sum of the distances on both axes:

$$D_{(1-2)} = |x_1 - x_2| + |y_1 - y_2| \quad (10)$$

Returning to our model calculations, this corresponds to equation (7). The same considerations hold for the three-dimensional case.

2.3. The range of models investigated. By systematically varying the weighting factors a, b and c, we were able to evaluate the colour distances of 1007 different models. In the following account of these models the weighting factors are always positive and the sign of the interaction between receptor excitations is specified in the equations. This convention makes explicit the distinction between the summation of inputs and antagonism between inputs (spectral opponency).

Our 1007 models cover a wide range of possible interactions. The colour distances between trained and tested stimuli were calculated according to the following models:

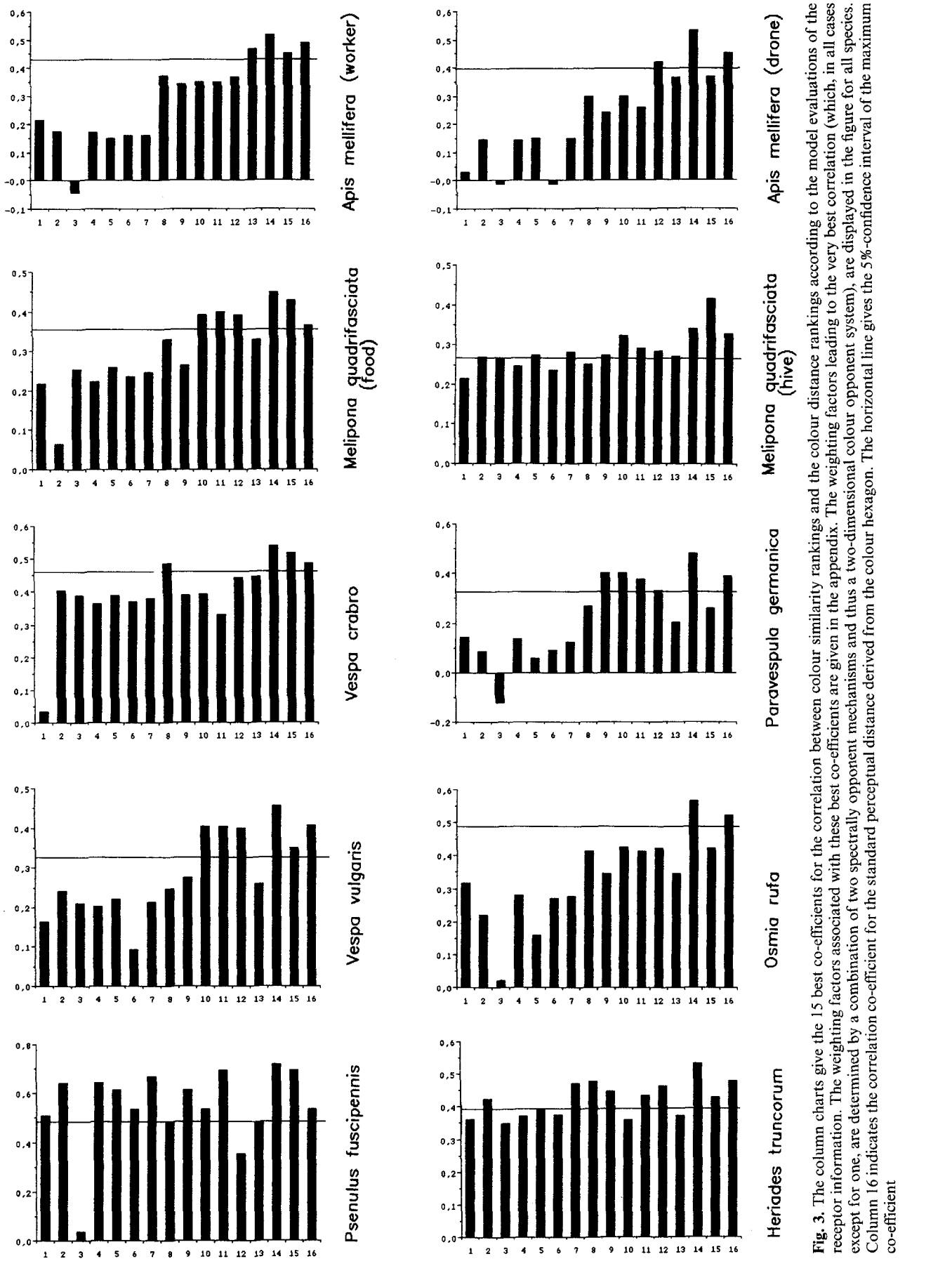


Fig. 3. The column charts give the 15 best co-efficients for the correlation between colour similarity rankings and the colour distance rankings according to the model evaluations of the receptor information. The weighting factors associated with these best co-efficients are given in the appendix. The weighting factors leading to the very best correlation (which, in all cases except for one, are determined by a combination of two spectrally opponent mechanisms and thus a two-dimensional colour opponent system), are displayed in the figure for all species. Column 16 indicates the correlation co-efficient for the standard perceptual distance derived from the colour hexagon. The horizontal line gives the 5%-confidence interval of the maximum co-efficient

2.3.1. One-dimensional systems without spectral opponency

	Number of possibilities when weighting factors are varied	Number of correlation co-efficients in column charts
1. E(U)	1	1
2. E(B)	1	1
3. E(G)	1	1
4. aE(U)+bE(B)	20	1 of 20
5. aE(B)+bE(G)	20	1 of 20
6. aE(U)+bE(G)	20	1 of 20
7. aE(U)+bE(B)+cE(G)	125	1 of 125

In 4, 5 and 6, the weighting factors are varied as follows: first a was kept constant at 0.5 and b was varied from 0.1 to 1 in 0.1-steps and then b was held constant and a was varied. In 7, all 3 factors are varied freely from 0.1 to 0.9 in 0.2-steps.

The reduced number of correlation co-efficients that are going to be plotted in column charts (Fig. 3) is also displayed in all the tables.

Note that these are all-positive-input, intensity coding systems, which do not allow colour discrimination.

2.3.2. One-dimensional systems with spectral opponency

	Number of possibilities	Number of plotted co-efficients
8. aE(U)−bE(B)	20	1 of 20
9. aE(B)−bE(G)	20	1 of 20
10. aE(U)−bE(G)	20	1 of 20
11. aE(G)−bE(B)−cE(U)	11	1 of 11
12. aE(U)−bE(G)−cE(B)	11	1 of 11
13. aE(B)−bE(G)−cE(U)	11	1 of 11

Gain factors in 8, 9 and 10 are varied as described above. In 11, 12, and 13, a is kept constant at 1, and b is raised from 0 to 1 in 0.1-steps, whereas c is diminished from 1 to 0 at the same time. For these model systems (11–13), we assumed that the weighting factors were such that the signal generated by equal receptor input was zero, as found in the worker bee (Backhaus 1991).

2.3.3. Two-dimensional systems (consisting of two different, spectrally opponent sub-systems)

	Number of possibilities	Number of plotted co-efficients
14. aE(G)−bE(B)−cE(U) and aE(U)−dE(G)−eE(B)	121	
aE(G)−bE(B)−cE(U) and aE(B)−dE(G)−eE(U)	121	
aE(B)−bE(G)−cE(U) and aE(U)−dE(G)−eE(B)	121	1 of 363

These are the 3 possible combinations of the mechanisms listed under 11–13.

2.3.4. Three-dimensional systems (consisting of two spectrally opponent and one non-antagonistic, intensity coding sub-system)

	Number of possibilities	Number of plotted co-efficients
15. aE(G)−bE(B)−cE(U) and aE(U)−dE(G)−eE(B) and fE(U)+gE(B)+hE(G)	121	
aE(G)−bE(B)−cE(U) and aE(B)−dE(G)−eE(U) and fE(U)+gE(B)+hE(G)	121	
aE(B)−bE(G)−cE(U) and aE(U)−dE(G)−eE(B) and fE(U)+gE(B)+hE(G)	121	1 of 363

These are the combinations of the systems given in 14 with a third, intensity coding sub-system. The gain factors f, g and h are kept constant at 2/3 = 0.666, so that all 3 mechanisms can produce differences between 0 and 2 and thus have equal weight. The equality of the weighting factors in the brightness coding sub-system follows Abney's additivity law of brightness (Abney 1913). This law purports that the intensity of an additive mixture is equal to the sum of the intensities of its components. Physiologically, it can be taken as the sum of the 3 photoreceptor excitations. An intensity coding mechanism should follow this rule, because otherwise the brightness dimension would become interdependent with chromaticity.

The set of models and weighting factors considered here (systems 1–15) produce 1007 different predictions of colour distance. Such predictions have then to be compared with the behaviourally determined colour similarity.

3. Processing of behavioural data

The numbers of times animals chose test colours relative to trained colours must be converted into a measure of the perceived similarity between colours. For reasons given below, in section 4 of the methods (correlation analysis), both behavioural data and colour distance values have to be transformed into ranks.

For the data sets we are considering, a number of different training colours were used. To improve the reliability of the data, we would like to be able to compare the similarity between test colours, irrespective of the particular training colours used. To this end the data have to be normalized before ranking. The mode of normalization is arbitrary since ranks are afterwards assigned to the values. Here, we will normalize the number of choices for the training stimulus to 100. The procedure shall be illustrated by the following example: assume, that in one experiment the test animal chose the training stimulus T1 100 times and the alternative colour A1, 25 times; in another test, the choice frequencies are 50 for the trained stimulus T2 and 25 for the alternative A2.

Tested stimulus	T1/T2	A1	A2
Relation of choices	–	100/25	50/25
Normalized ratio	100	100/25	100/50
Rank	1	3	2

This means, that A2 is judged more similar to T2 than A1 to T1. Rank 1 is thus alloted to both T1 and T2; there will be only one rank for all training stimuli, since the choice numbers are normalized to the same value. The similarity ranking becomes: T (1); A2 (2); A1 (3).

For some species, data from different test procedures, i.e. dual/multiple choice tests, will be combined (*Apis mellifera* at the hive and *Vespa crabro*). In these cases it has to be assumed that the choice proportions do not differ significantly with regard to the test mode. This has been shown explicitly only for the honeybee at the feeding site by Backhaus et al. (1987).

4. Correlation analysis

To correlate one with the other, the choice frequencies (the number of times a particular colour was chosen) from the behavioural tests and the modelled colour distance values have to be transformed into ranks, since the data are not normally distributed and linearity of the regression of one variable on the other can not be taken for granted.

The measure of correlation in this paper will be Kendall's τ (Kendall 1938), mainly because it allows the determination of a much narrower confidence interval than the better known Spearman rank correlation co-efficient r_s; the importance of a small confidence interval will become clear in the result section.

The calculation and application of this co-efficient has been described in detail and very comprehensibly in a text book by Kendall (1948); consequently, reference will be made here to the respective page numbers (pattern: K.p. 1, with K for Kendall, p for page/pages) in the latest issue of this book available to the authors (4th edition, 2. impression, 1975).

The calculation of τ itself is explained on K.p. 3–6. Note that Spearman's r_s is always greater than τ (often about 50%, K.p. 12) and it has to be kept in mind that it has a different scale and represents a rather different measure of correlation.

If ties (equal values) are present, then the "mid-rank method" has to be applied (K.p. 34); τ then must be calculated according to K.p. 35–36.

The calculation of the significance level of τ is explained on K.p. 49–55; in case of the occurrence of ties, see K.p. 55–56.

The determination of the variance of τ, and thus the confidence interval, follows Daniels and Kendall (1947) and is also described in K.p. 87–91. Throughout this paper, 5%-confidence intervals are used.

Note that correlation co-efficients may not be compared directly if the number of ranks (n) is different.

Results

1. Correlation of behaviour with 15 different basic models

The methods given in the preceding section were applied to 10 sets of behavioural data (9 species, but two different test contexts in *Melipona*). In each case we set out to find which of our basic 15 types of model colour computation system best accounted for the behavioural performance. We first adjusted the parameters in each type of model (1–15) to find the set of weighting factors that gave the best fit. We then compared the performances of the best of each type to see which model was most satisfactory. In every case, the performance was assessed in terms of the coefficient of correlation between the outputs of a model (the colour distance) and the behavioural ranking of colour similarity. The 15 best correlation co-efficients (one for each type of model) are given in the column charts (Fig. 3 – columns 1–15). These column charts show that, for almost all species, a two-dimensional (i.e. consisting of two subsystems) opponent model of colour vision (column 14) worked best. The correlation is highly significant in all cases ($P < 0.0001$ (!) in all species except *Psenulus*, where $P < 0.001$).

The likelihood that a particular model was capable of producing the observed behavioural rankings of colour similarity is indicated by the 5% confidence interval (the horizontal line in each column chart). In every case more than one model falls within this confidence limit.

There are two basic reasons for this observation. One relates to the similarity of different colour distance measures and will be explained below (section "Common

Table 2. The table gives the weighting factors of the two opponent processes A and B with which a colour distance measure is obtained that predicts the behavioural results best. They may be assigned to the respective axes A and B in the colour hexagon symbols of Fig. 7 and the colour opponent diagrams of Fig. 8. In order to allow better comparisons of the colour opponent diagrams (Fig. 8) with the colour hexagon plots (Fig. 2), we chose the axes A and B such that, basically, the uv edge of the spectral curve would be on the lower left part of the colour opponent representation (Fig. 8), the blue edge should be in the upper part, and the green edge should be in the lower right edge. In order to follow this convention, we had to reverse all signs in some of the equations. This simply means that one axes is "turned around"; the distance proportions are not changed by this procedure. The respective equations are marked with an asterisk (*) in the end

Apis mellifera worker						
A =	−1	E(U) +	0.8	E(B) +	0.2	E(G) (*)
B =	−0.5	E(U) +	1	E(B) −	0.5	E(G)
Apis mellifera drone						
A =	−1	E(U) +	0.6	E(B) +	0.4	E(G) (*)
B =	0.2	E(U) +	0.8	E(B) −	1	E(G) (*)
Melipona quadrifasciata food						
A =	−0.4	E(U) −	0.6	E(B) +	1	E(G)
B =	−1	E(U) +	1	E(B) −	0	E(G)
Melipona quadrifasciata hive						
A =	−0.7	E(U) −	0.3	E(B) +	1	E(G)
B =	−0.3	E(U) +	1	E(B) −	0.7	E(G)
Vespa crabro						
A =	−1	E(U) +	0.8	E(B) +	0.2	E(G) (*)
B =	−0.4	E(U) +	1	E(B) −	0.6	E(G)
Paravespula germanica						
A =	−1	E(U) +	0.5	E(B) +	0.5	E(G) (*)
B =	0.1	E(U) +	0.9	E(B) −	1	E(G) (*)
Vespa vulgaris						
A =	−0.4	E(U) −	0.6	E(B) +	1	E(G)
B =	−1	E(U) +	1	E(B) −	0	E(G)
Osmia rufa						
A =	−0.2	E(U) −	0.8	E(B) +	1	E(G)
B =	−0.8	E(U) +	1	E(B) −	0.2	E(G)
Psenulus fuscipennis						
A =	−0.8	E(U) −	0.2	E(B) +	1	E(G)
B =	−0.2	E(U) +	1	E(B) −	0.8	E(G)
Heriades truncorum						
A =	−1	E(U) +	0.2	E(B) +	0.8	E(G)
B =	−0.5	E(U) +	1	E(B) −	0.5	E(G)

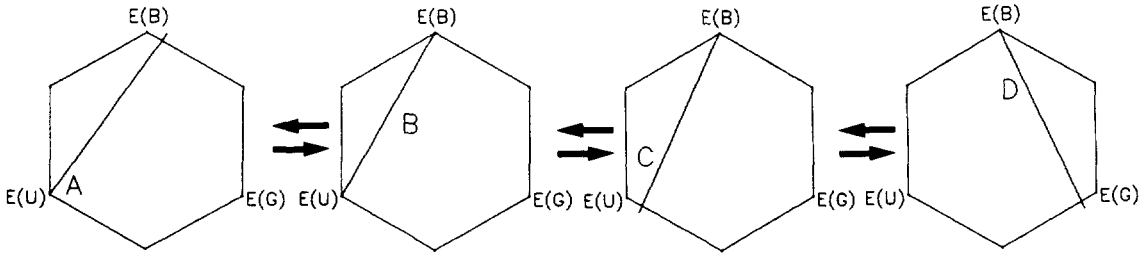


Fig. 4. This examplary series of colour opponent axes demonstrates that a blue-"uv-green" spectrally opponent mechanism (*C*) may actually be more similar to a uv-bluegreen mechanism (*A*) than to another blue-"uv-green" mechanism (*D*) with different weighting factors. A is related to C by only a slight variation of the weighting factors. For further interpretation see text

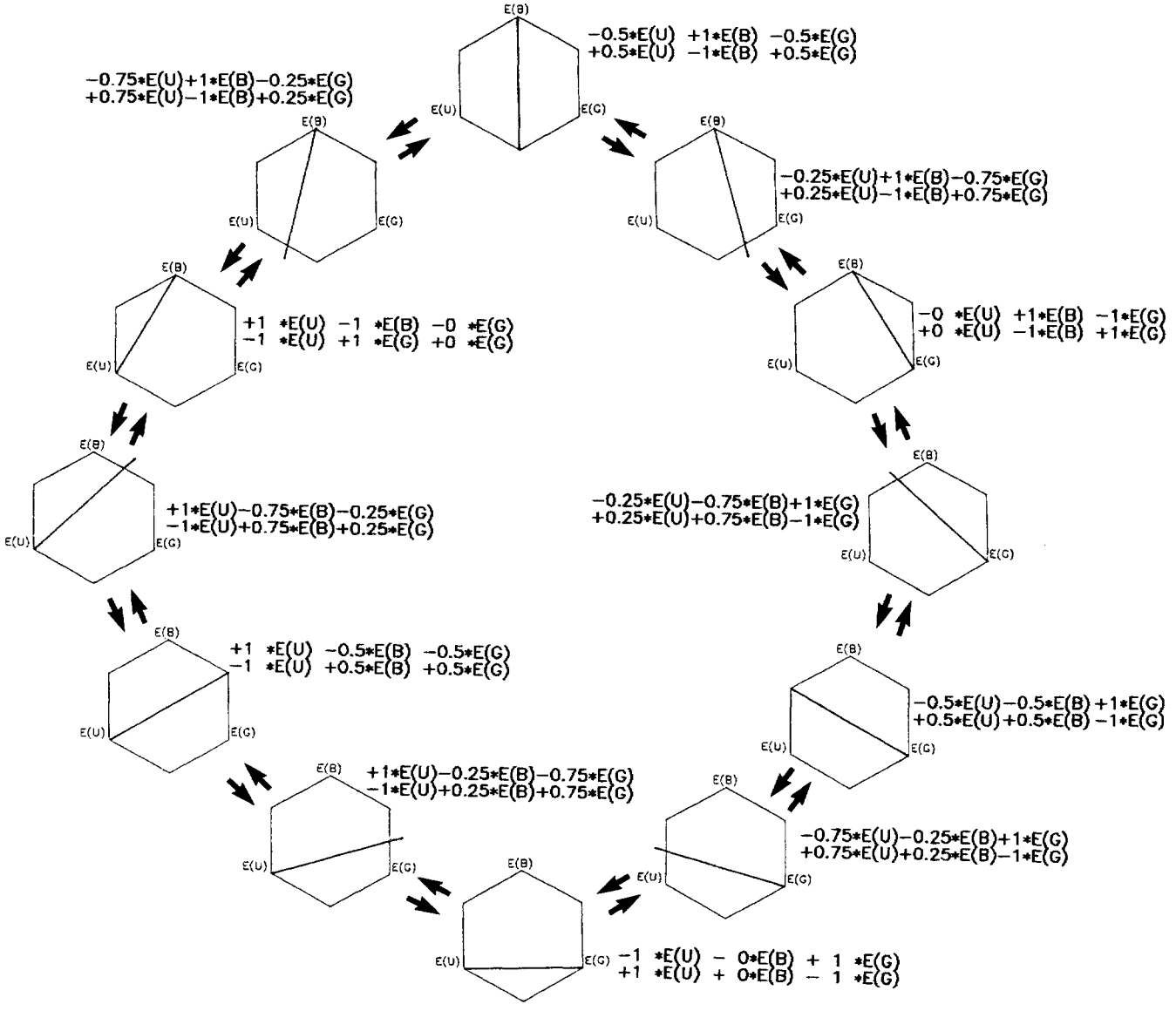


Fig. 5. All spectrally opponent mechanisms are interrelated and pass into each other if the weighting factors are changed. As demonstrated by Chittka (1992), colour opponent axes may be drawn through the colour hexagon, and the step from trichromacy to colour opponent relations can thus be comprehensibly illustrated. For certain weighting factors, a "− + −"-type-mechanism will merge into a "+ − −"- or "− − +"-type spectrally opponent mechanism (or vice versa). The two possibilities for the weighting factors associated with the opponent mechanisms are given next to the respective colour hexagon symbols

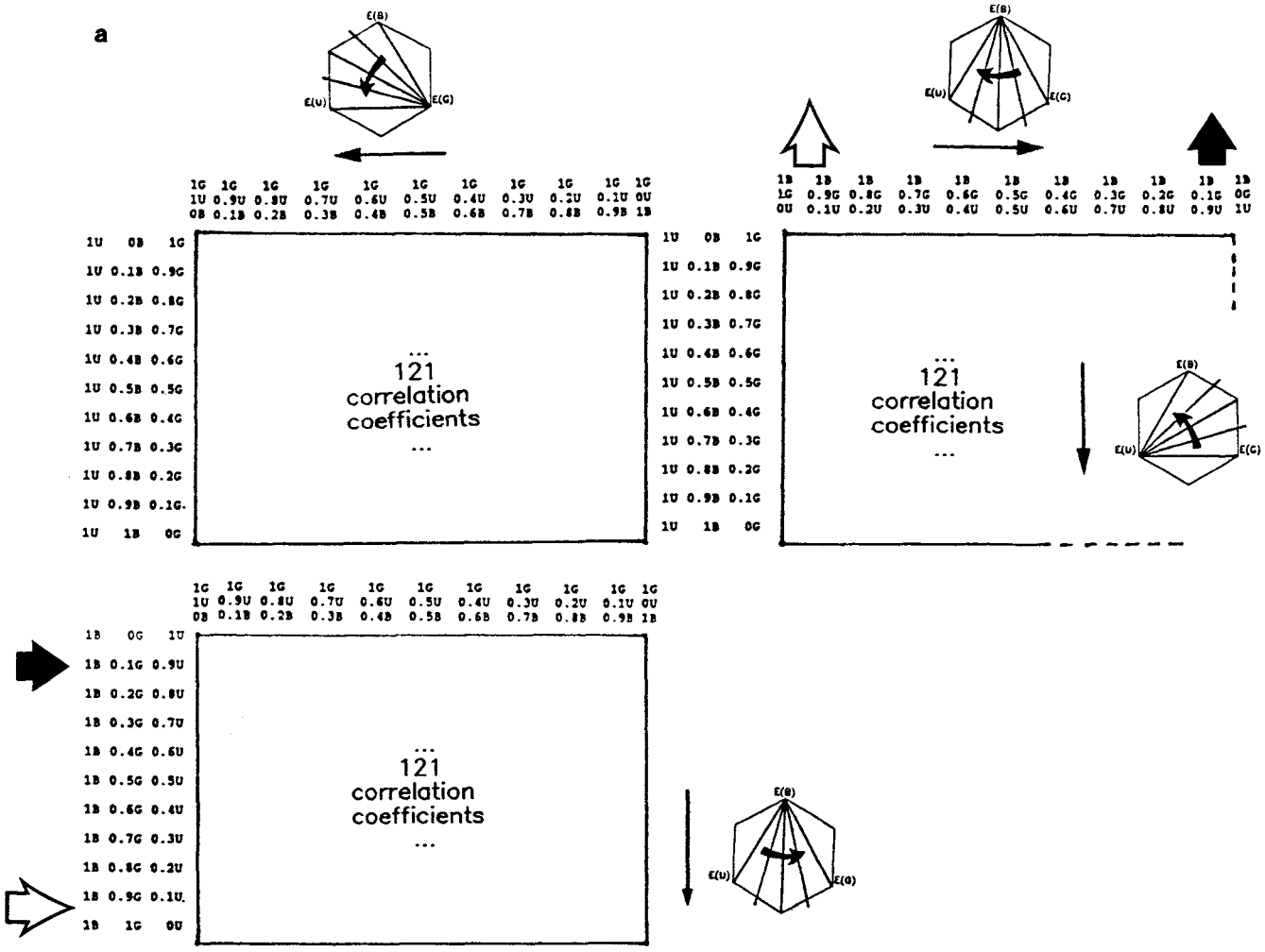


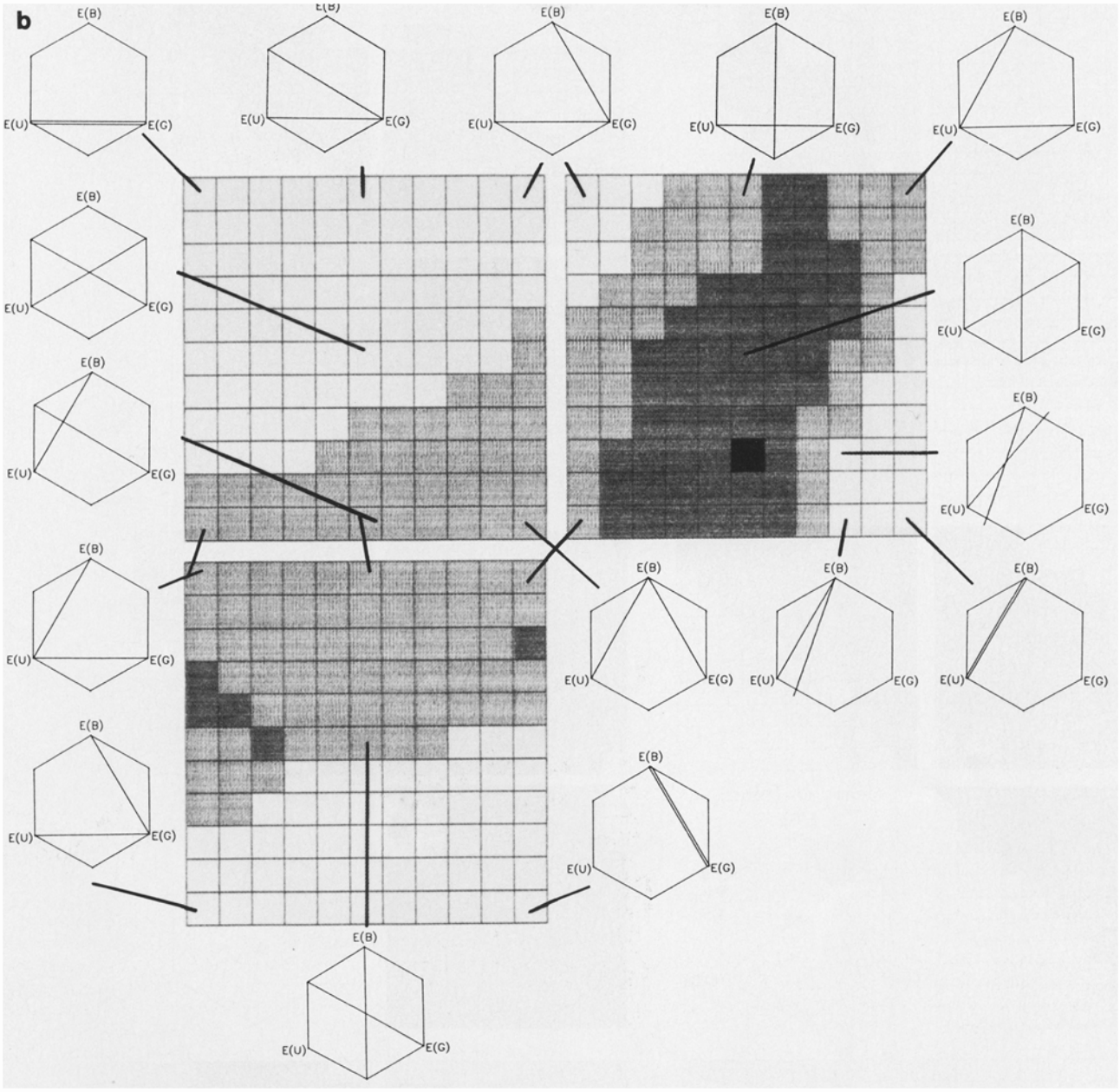
Fig. 6. **a** The set of 3 matrices specifying the combinations of opponent sub-systems used in the two-dimensional model (14). Note that the matrices are connected in the sense that each shares common rows or columns with the two others. Where this connection cannot be made directly, by placing the matrices next to each other, it is indicated by pairs of *thick arrows*. The colour hexagons illustrate the systematic change in position of the axis determined by the neighbouring row or column. **b** The three 11 × 11 matrices of correlation coefficients are presented graphically using plots termed "grey-scale-diagrams"; in this example, *Apis mellifera's* colour vision at the hive entrance is concerned. The black field marks the optimum of correlation, the grey area gives the 5%-confidence interval around the maximum coefficient. The area with coefficients that lie within half the confidence interval under the optimum is marked dark grey. A selection of colour hexagons demonstrates the axes assigned to particular fields in the grey-scale-diagrams. For all the other fields, the corresponding axes can readily be derived by comparison with **a**

principles..."). The other reason relates to the behavioural experiments. Each of the behavioural studies generated a moderately small data set that is, from the nature of colour discrimination tests, subject to considerable random variation. This random variation reduces the accuracy of predictions about the system underlying the behaviour, so lowering the confidence limits. This effect is demonstrated by the results obtained from the least reliable data set *(Psenulus)*. Relatively few decisions contributed to this data and only 12 different colour stimuli were used. With 12 scattered data points the 5% confidence limit includes almost all models. Nonetheless, here as elsewhere, model 14, the two-dimensional opponent system, works best. Note that correlations, by their very nature, never prove the existence of a model but only indicate the likelihood that it can account for the data. In this sense it is remarkable that, with one exception, a two-dimensional opponent model was always the most likely among the wide range tested.

In only one case (*Melipona* at hive entrance) does the three-dimensional model system (column 15) account best for the choice behaviour. Nevertheless, the correlation coefficient for the two-dimensional case (column 14) is the second highest. It is also not significantly lower than the co-efficient for the three-dimensional model; consequently, it may not be excluded on the basis of the confidence interval. Therefore, we tend to interpret this exception as a result of statistical scatter.

The weighting factors assigned to the respective best co-efficients for all models 1–15 are listed in the Appendix. The weighting factors that yield the best correlation among the possibilities for the two-dimensional opponent systems (model 14) are charted in Table 2.

For a spectrally opponent mechanism with given

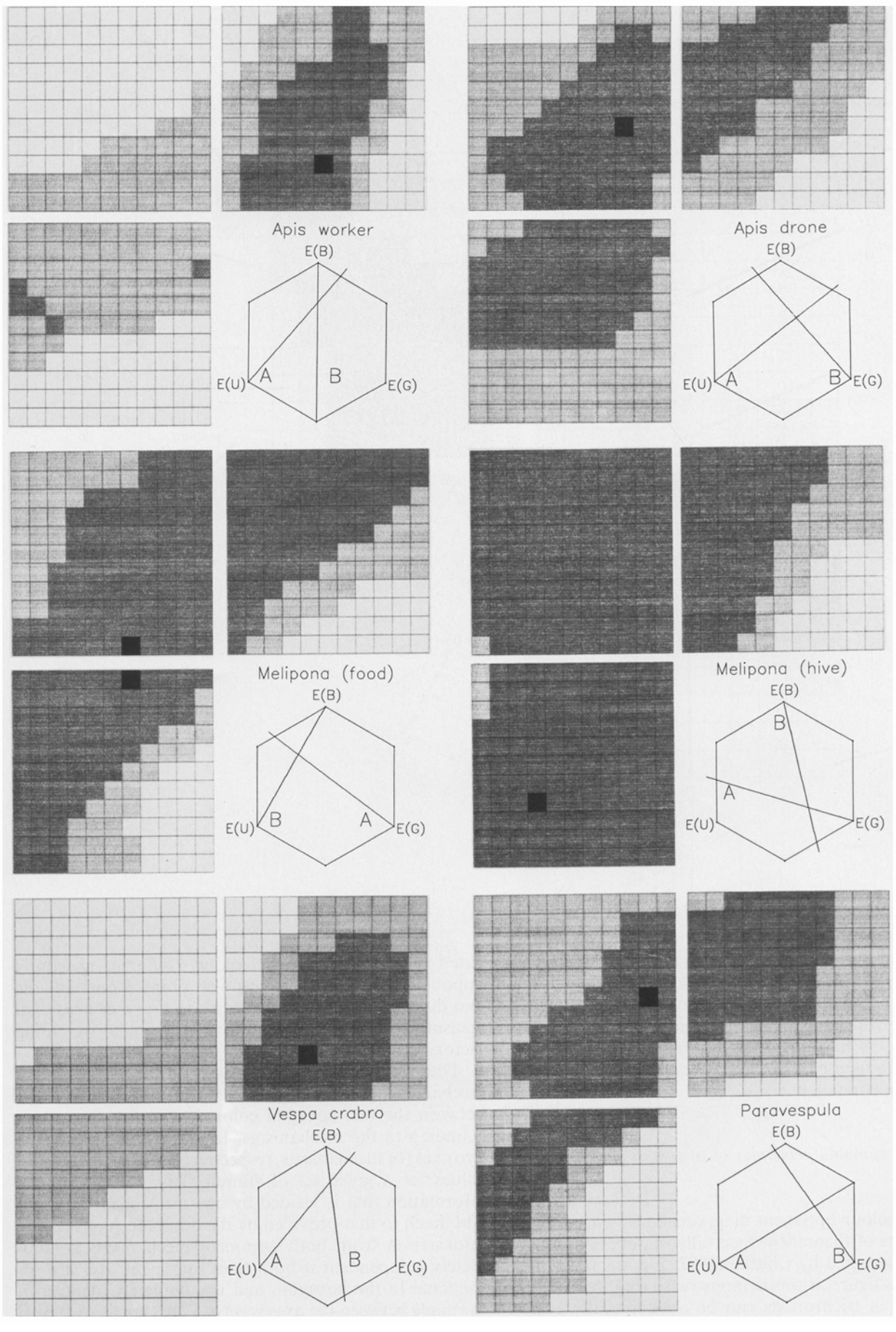


weighting factors, a colour opponent axis may be drawn through the colour hexagon (Chittka 1992). Thus, in correspondence with Table 2, the optimal set of two colour opponent axes for each species is depicted in a hexagon (insets in Fig. 7). In this representation, the derived combinations of colour opponent mechanisms can easily be compared.

2. Are there common principles of opponent coding in all species?

A series of colour opponent diagrams based on various combinations of theoretical spectrally opponent mechanisms was presented by Chittka (1992, Fig. 6). With reference to this figure, it was demonstrated that the colour information in trichromats can be unequivocally evaluated by any combination of two different spectrally opponent mechanims. It was also pointed out that the two-dimensional system decreases to a one-dimensional measure if both mechanisms have very similar weighting factors.

The difference between two spectrally opponent mechanisms can be estimated by measuring the angle between the two hexagon colour opponent axes corresponding to the mechanisms. If this angle is small, the two axes (or mechanisms, respectively) will render similar values for a given set of stimuli. This means that the information that is yielded by one mechanism does not add much to that provided by the other mechanism. The information from both opponent mechanisms is completely independent if both their opponent axes are orthogonal in the hexagon, and is completely identical if the angle between the axes is zero. Thus, it was suggested


Apis worker
E(B)
E(U)
A
B
E(G)
Apis drone
E(B)
E(U)
A
B
E(G)
Melipona (food)
E(B)
E(U)
B
A
E(G)
Melipona (hive)
E(B)
B
A
E(U)
E(G)
Vespa crabro
E(B)
E(U)
A
B
E(G)
Paravespula
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E(U)
A
B
E(G)

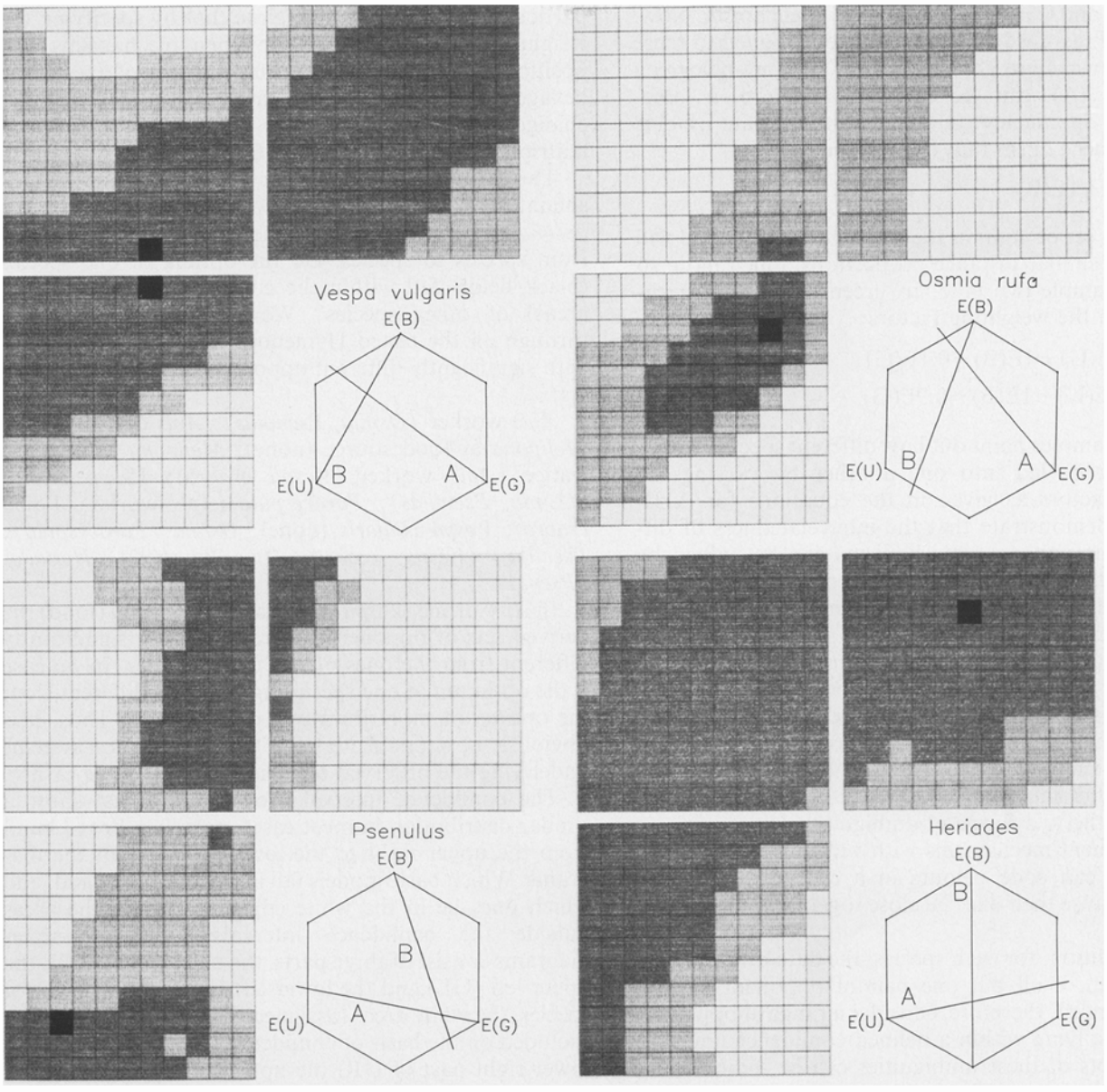

Fig. 7. The grey-scale-diagrams of all 9 species (*Melipona* in two behavioural contexts) are presented for comparison. The sets of opponent processes that yield the highest correlation *(black fields)* are different in all species, but the confidence intervals have a similar shape, namely a broad band connecting the upper right and the lower left edges of the diagrams. Certain parts of the matrices are outside or in the periphery of the confidence intervals in most cases. The hexagon insets show the axes specified by the most likely pair of opponent mechanisms, corresponding to a black entry in the matrix and equations A and B in Table 2

that natural colour coding systems should use opponent mechanisms that differ significantly in their orientations within the hexagon.

Our data allow us to test this hypothesis. Comparing the species-specific sets of axes drawn through the colour hexagon (insets of Fig. 7), one finds that they all make angles greater than 40°. Without emphasizing the evaluation of the angles, the tendency is clear. Thus the predicted independence of the opponent processes holds for all species.

Apart from this common characteristic, the weighting factors for the opponent processes which best predict the behavioural data differ widely between species (see Table 2, insets Fig. 7), but are they really significantly different i.e. mutually exclusive? In order to answer this question, one first has to go a little further into the theory of opponent colour coding. We can then take a closer look at the distribution of correlation co-efficients among all the two-dimensional systems tested.

Consider first the following two spectrally opponent mechanisms and compare them with the respective graphs (A and C) in Fig. 4

$$A = \quad 1 \quad E(U) - 0.9E(B) - 0.1E(G)$$

$$C = -0.9E(U) + 1 \quad E(B) - 0.1E(G)$$

At first sight, these seem to be completely different mechanisms because A is a uv-bluegreen spectrally opponent

mechanism and C is a blue-"uv-green" mechanism. Now, looking at Fig. 4, we find that the axes assigned to these two mechanisms are actually similar. The uv-bluegreen opponency (A) can be transformed into a blue-"uv-green" opponency (C) via an intermediate uv-blue opponent mechanism that follows the equation

$$B = 1E(U) - 1E(B)$$

For a given set of stimuli, the mechanisms A and C will also render similar distance proportions, much more so than for example two blue-"uv-green" opponent mechanisms with the weighting factors:

$$C = -0.9E(U) + 1E(B) - 0.1E(G)$$

$$D = -0.1E(U) + 1E(B) - 0.9E(G)$$

These examples point out how different spectral opponencies can be led into one another by varying the weighting factors as given in the equations for A–D. They also demonstrate that the interrelatedness of different colour opponent mechanisms can be judged by comparing their respective hexagon colour opponent axes much better than by comparison of the weighting factors themselves.

We find that, in general, all such mechanisms may be understood as interrelated and can be merged into each other by systematically changing the weighting factors (Fig. 5). What are the implications for the results of the correlation analysis?

The results must be assessed in a way that takes account of the two forms of ambiguity.

a) Opponent mechanisms with very different weighting factors can code colours in a remarkably similar fashion because their axes lie close together in the colour hexagon.

b) In addition, for each species, the data do not allow for exclusion of all but one pair of opponent mechanisms. One must, therefore, consider a range of opponent mechanisms, lying within a defined confidence limit.

The effects of these ambiguities can be indicated by presenting the range of possible weighting factors that can account for a particular set of behavioural data and seeing how this range relates to the positions of the axes in the hexagon.

We are considering the most satisfactory model, 14, a two-dimensional colour opponent system. This system computes colour distances using pairs of opponent sub-systems chosen from models 11–13. The range of plausible sub-systems can be assessed by examining the extent to which the outputs of the complete set of models correlate with behavioural measures of similarity. This distribution of correlation co-efficients is presented in the 3 11×11 matrices. These tabulate the weighting factors of all of the pairs of opponent mechanisms that were modelled (Fig. 6a). Each element in the matrix displays the correlation co-efficient for the pair of model opponent mechanisms specified by a row and column. To help visualise the distribution of correlation co-efficients, their magnitudes are displayed using a grey-scale. This plot specifies the position of the model which yields the best correlation, and the distribution of models lying within particular confidence limits. Note that by specifying the weighting factors of a pair of opponent mechanisms each position in a matrix also determines a pair of axes in the hexagon. The positions and orientations of these axes change systematically as one moves across the three matrices, as illustrated in Fig. 6b.

The grey-scale-diagrams for all species (Fig. 7) consolidate the notion that the weighting factors for the *optima* of correlation (black fields) are rather different from species to species. Do the optima of one species (black fields) fall within the confidence intervals (grey areas) of other species? We will go systematically through all the tested Hymenoptera, listing the species with significantly different opponent processes in brackets:

Apis worker *(Osmia, Psenulus); Apis* drone (none); *Melipona* at food source (none); *Melipona* at hive entrance (*Apis* worker, *Vespa crabro*); *Vespa crabro (Osmia, Psenulus); Paravespula* (*Apis* worker, *Vespa crabro*); *Vespa vulgaris* (none); *Osmia (Paravespula); Psenulus* (*Vespa crabro, Apis* worker); *Heriades (Psenulus)*.

In *Apis* drone, *Vespa vulgaris* and *Melipona* (food) the derived sets of opponent processes are not significantly different from the ones of *any* other species. In no case is the optimum of one species significantly different from the optima of more than two other species. Thus, it is obviously not possible to tell if the colour vision systems underlying the observed behaviour are the same or not.

The confidence interval areas (grey areas) show a similar distribution in most cases, namely a broad band from the upper right to the lower left edge of the diagrams. Which basic models fall inside this grey band, and which ones lie in the white edges that mark the areas outside the confidence intervals? The grey-scale-diagrams consist of three parts, the upper right (UR), the upper left (UL) and the lower left (LL) matrix. In most species, the white areas (assigned to models which can be excluded on the basis of confidence intervals) occupy the lower right part of UR, the upper left edge of UL and the lower right part of LL. If these parts are not white, they are light grey, i.e. they are located in the periphery of the confidence interval.

The extreme edges of these white areas denote combinations of opponent mechanisms with identical weighting factors, i.e. ineffective systems that have reverted to the one-dimensional condition. The white areas near these edges must be approaching this condition, as illustrated by the small angles made between axes in the colour hexagons associated with these areas (Fig. 6a, b). Thus, the distribution of confidence intervals suggests that, as one might expect, systems with a tendency to revert to one-dimensionality are avoided. The favoured models fall within a range that makes better use of a two-dimensional system.

3. A perceptual colour distance measure for all species?

Two-dimensional colour opponent diagrams as developed by Backhaus (1991) for the honeybee, were derived for all species using the weighting factors from

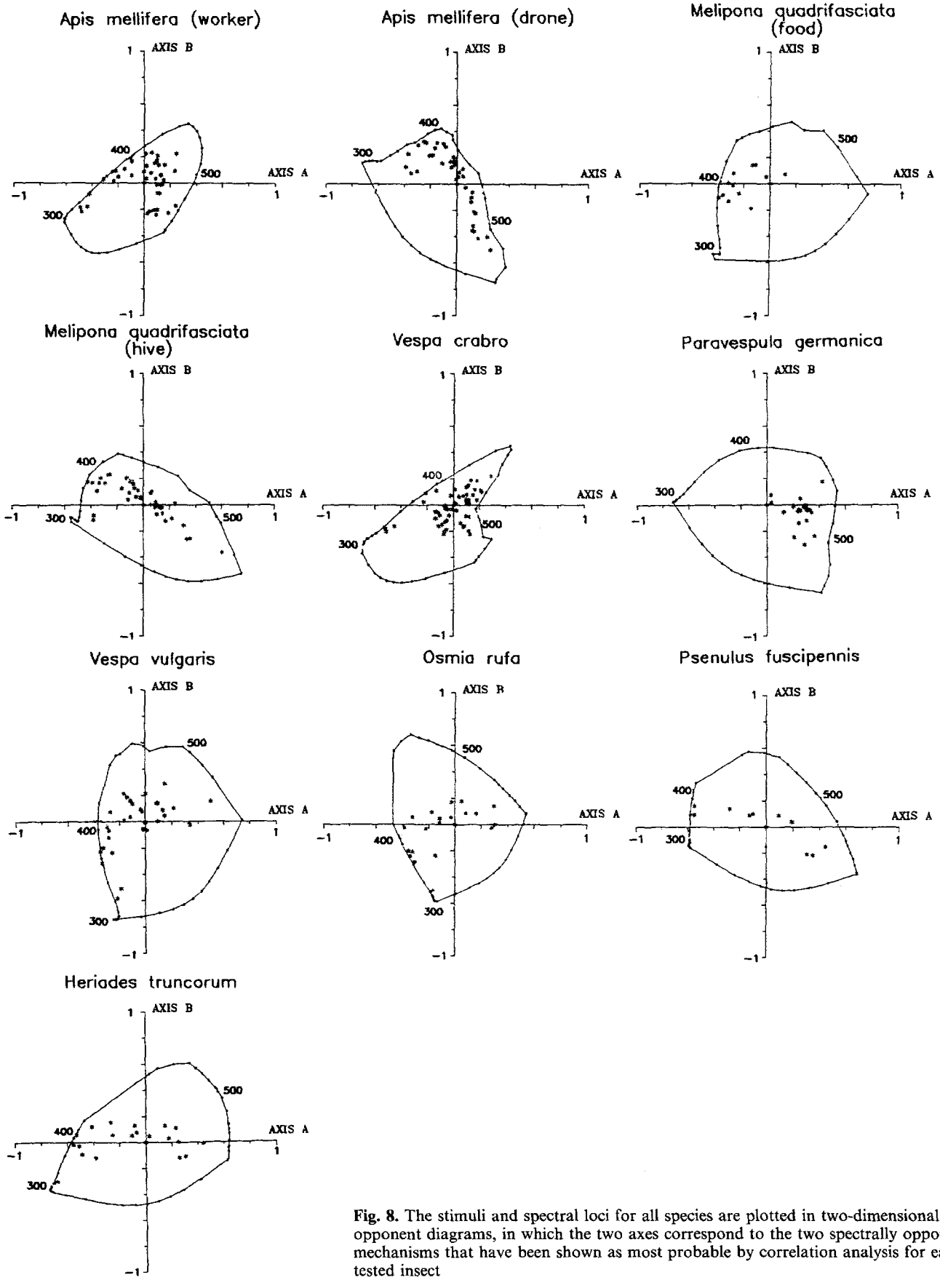

Fig. 8. The stimuli and spectral loci for all species are plotted in two-dimensional colour opponent diagrams, in which the two axes correspond to the two spectrally opponent mechanisms that have been shown as most probable by correlation analysis for each tested insect

Table 2. The values on the axes A and B were calculated by simply inserting the receptor excitation values for each stimulus into the equations A and B of Table 2.

The colour opponent diagrams (Fig. 8) illustrate how the derived opponent mechanisms affect the distribution and distance proportions of the stimuli used in the colour discrimination tests. The initially uninterpreted (and unweighted) relations in the colour hexagon (compare Fig. 2 with Fig. 8) are extended in certain spectral domains and compressed in others in the colour opponent diagrams. However, the deformations are small; in most cases one finds little difference in the shape of the spectral locus and the scatter of stimuli between Figs. 2 and 8. This indicates on a graphical level that the hexagon provides us with a satisfactory standardized colour space for all species.

A colour opponent diagram based on the specific opponent processes as derived for one species will illustrate the colour space of this species best. However, for some purposes it may be inconvenient or inadequate to use a different colour opponent diagram for each different species. This concerns all cases in which one wants to investigate the influences of different sets of photoreceptor colour types on the properties of the colour space *independently* of the particular mode of opponent coding. The hexagon distances have been successfully applied to compare the spectral discrimination functions of some 40 Hymenoptera (Peitsch et al. 1992) and to determine an optimal photoreceptor set for coding of natural objects as derived from a systematic variation of the receptor properties (Chittka and Menzel, unpublished). Since all the extensions and compressions of distances are deformations of the initially unweighted information in the hexagon, it is proposed, that the hexagon distances themselves should be used as a standard for assessing colour differences. For this purpose, the applicability of the colour hexagon distance proportions for the prediction of the behavioural data has to be tested.

The correlation of behavioural ranks with standard (hexagon) distance ranks is given by column 16 in the column charts (Fig. 3). The correlation is, of course, always worse than the one with the derived best fit distance measure, but it is the only scale that supplies reliably high correlation coefficients in all species and almost always is the second or third best. All other correlation coefficients are determined by different weighting factors for different species (see Appendix tables), whereas the hexagon distance is the only measure that is kept constant for all species. Bearing this in mind, the consistently good correlation of behavioural similarity rankings with the colour hexagon distance in all species is remarkable. We conclude that the colour hexagon distances may well be employed as a standard measure for perceptual colour distance for the trichromats under consideration.

4. A simple neuronal network

Since colour computation follows the same basic scheme of two-dimensional opponent coding in all the species, a network diagram is presented, which illustrates how the receptor information might be evaluated in the brain (Fig. 9). The model suggests that the receptors feed into two spectrally opponent channels. Every given colour stimulus will then be defined by two excitation values in the respective spectrally opponent sub-systems; these values have to be compared with the values of a memorized stimulus saved in the "memory unit". The calculated differences must then be rectified to equal sign, and simply have to be added up (city-block metric). If the sum of differences equals zero, the actual stimulus and the memorized colour will be judged identical; with increasing values of the sum of differences, the given colour will be perceived more and more dissimilar to the training colour (and less choices will be observed in a behavioural similarity test).

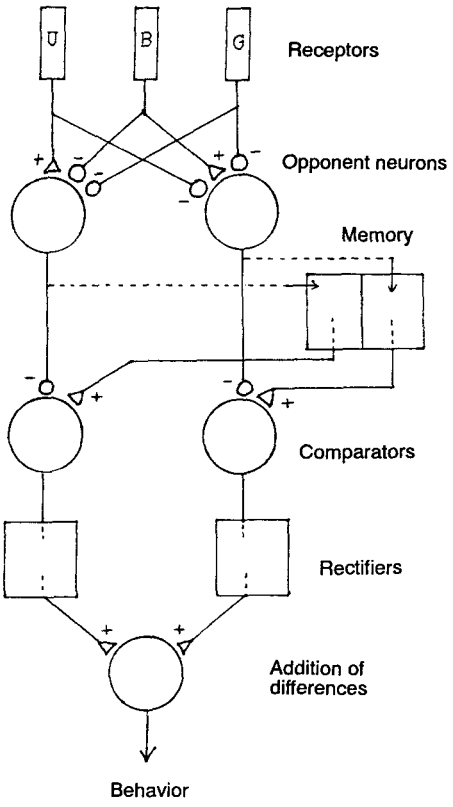

Fig. 9. Opponent colour coding as derived for the tested Hymenoptera may be realized using a rather simple network. The model describes the evaluation of the receptor signals in two colour opponent sub-systems. There has to be a comparator to calculate the differences between memory signals (memorized colour stimulus) and actual colour opponent values (any coloured stimulus). These differences must first be rectified and then added up, since the difference of two colours is computed as the sum of the differences on both colour opponent scales (city block metric). The more the value in the last sub-system differs from zero, the more should the respective stimulus be judged dissimilar from the trained one in colour discrimination tests

Discussion

1. Restrictions applied to the modelled systems

The variation of weighting factors in the analysis is subject to the following restrictions. 1. The weighting coef-

ficients in the opponent processes add up to zero, as is the case in the honeybee (Backhaus 1991, see also Chittka 1992 for a discussion). 2. The rather big step size (0.1 steps in most simulations) is justified by the fact, that, as the width of confidence intervals shows, a more exact determination of weighting factors would not be useful; 3. the opponent processes in the two- and three-dimensional simulations have equal weight and 4. the weighting factors in the intensity-coding sub-system in the three-dimensional simulation are not varied (Abney 1913, see Methods). The restrictions also have the practical purpose of reducing the scale and complexity of modelling and evaluation.

2. *Statistical analysis*

The behavioural data described here, together with the relatively large confidence intervals that rank correlation methods imply, are obviously not suited to the demands of determining the weighting factors in colour computation systems exactly. Thus, we must restrict ourselves to basic questions. Do the respective animals possess opponent colour coding? If so, is it a two- or three-dimensional system, and what sort of design principles are involved?

As often in statistics, the available methods are compromises, and no approach will suit the problem perfectly. The methods described by Backhaus et al. (1987) and Backhaus (1991) require very extensive behavioural data which are not available for any species other than the honeybee worker. Furthermore, the least square fit procedure (Backhaus 1991) will only determine the model system which accounts *best* for the scales as derived from the behavioural data. One can determine a model distance measure which is most likely, but exclude none which is less likely.

The correlation analysis described here will supply reasonable results with less behavioural data. Not only is the most likely model system determined; a whole range of possibilities of colour coding are considered. Conclusions are drawn about which *basic* colour computation systems are likely and which systems may be excluded on the basis of confidence intervals.

Nonetheless, the present study is to a large degree based on the pioneering works of Backhaus and Menzel (1987), Backhaus et al. (1987) and Backhaus (1991). Quite a few of their results are used as restrictions for the models tested here, i.e. they were not varied critically. These are the choice of the city-block metric and the assumption that equal receptor signals result in a neutral (zero) signal in the opponent processes.

This makes evident a basic problem with methods that do not result in *one* unequivocal solution. Once one starts *varying* the parameters, an infinity of models can be generated theoretically. Since it is not practical to calculate and evaluate these, one needs reasonable restrictions for the variation. If these restrictions have to be based on the results obtained by other methods, then it is clear that they cannot replace these methods.

3. *Comparison of results*

When comparing the results of the correlation analyses for the different species, one has to consider the large differences in experimental conditions. The experiments were not originally designed to be comparable and to be subject to the analysis described here. Different numbers and sets of test and training stimuli were used, the adapting backgrounds and illuminations varied between several test animals and the training and test situations and contexts were not always the same. The methods used to record the animal's behaviour in the tests developed in the course of time, and had to be adapted to the respective species behaviour and to the experimental context.

Despite the differences in behavioural experiments, the analysis basically yields similar results in all the insects investigated. The evaluation of the three receptor inputs in two colour opponent sub-systems appears to be universal among trichromatic Hymenoptera. In all cases, such models correlate with the behavioural data on a very high significance level. The tested species are thus equipped with a neural colour coding system that can evaluate the chromatic information from an input system with three photoreceptor types unequivocally (see also Chittka 1992).

The optimal weighting factors of the spectrally opponent mechanisms are different between all species in detail, but the differences are mostly not significant as could be demonstrated by means of confidence intervals. The main similarity between the systems is that the two mechanisms should be different from each other to a certain degree, thus avoiding the degeneration of the two-dimensional system to a one-dimensional measure.

It has been pointed out that the evolutionary tuning of the weighting factors in colour opponent mechanisms should provide a powerful means to weight the receptor information according to species-specific eco-physiological demands (Chittka 1992). We must now conclude that the width of confidence intervals in the present study sets the limit to the analysis of such an investigation of the evolutionary optimization. The confidence intervals include a large range of different colour coding systems. The common principle of all the systems within the confidence intervals (grey areas in Fig. 7) remains the "degree of orthogonality" of the hexagon colour opponent axes that can be graphically assigned to the opponent coding sub-systems, but there are no significant differences between species with respect to this criterion.

Another feature of hymenopteran colour processing is the apparent lack of an intensity coding sub-system in colour discrimination tasks. This is in concurrence with the findings of Daumer (1956), von Helversen (1972) and Backhaus et al. (1987), who found that honeybees ignore intensity differences in colour discrimination tasks at the feeding site.

4. *Standard colour opponent distance*

No particular set of weighting factors can be unequivocally associated with data from colour discrimination

tests. The possible combinations of spectrally opponent mechanisms with different weighting factors represent a continuum with distance proportions that can match each other to a high degree. Furthermore, if one bears in mind that both behavioural data and statistical methods are susceptible to incertainties, it must be concluded that deriving a single set of defined weighting factors from such tests might be useful for model calculations and graphical presentations, but is definitely an oversimplification. Since a whole continuum of mechanism combinations has to be considered as theoretically underlying the behavioural data, it is not possible to characterize the underlying mechanisms exactly.

All the data gathered in this study are compatible with trichromatic Hymenoptera using opponent processing and, therefore, with the representation of colour distances within the colour hexagon. Thus when a species is trichromat with known photoreceptor spectral sensitivities one can use the unweighted colour hexagon to determine the approximate perceptual distance between colours by assuming that it uses opponent processing. The actual distances will, of course, require a detailed analysis of colour coding, but the hexagon provides a rough approximation that is suitable for those cases where a detailed investigation is not feasible.

Conclusion

The analysis developed here uses a statistical method that enables one to determine a colour computation system on the basis of rather limited behavioural colour discrimination data. The basic requirement of the analysis is a knowledge of the inputs and the outputs of the unknown system, namely the spectral sensitivity functions of the receptors and the similarity judgments exhibited in a colour discrimination test. The method can be universally applied and should be applicable to a wide range of species.

Acknowledgements. We thank the students T. Echternacht, F. Franck, M. Hoffmann, J. Menzel, S. Menzel, S. Müller, S. Rodrigues de Souza, K. Steinhauer and K. Weber for collecting data in the very labourious experiments and Dr. A. Handl and Dr. R. Schwabe for statistical advice. The friendly cooperation and helpful comments of our collegues Prof. Dr. D. Fix Ventura, Dr. W. Backhaus, M. Dittrich and D. Peitsch are greatly appreciated. We are also grateful to A. Nedlina-Chittka for help with the English and to A. Klawitter for changing some of the figures into a presentable shape. Simon Laughlin invested so much work as a referee, that we actually considered making him a co-author, but then he would not have been eligible to referee the manuscript. This work was supported by grants from the Deutsche Forschungsgemeinschaft (DFG) to Prof. Dr. R. Menzel.

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Appendix tables

The tables give the weighting factors for the models 1–15 that fit the behavioural similarity rankings best. These are the weighting factors assigned to the columns 1–15 in Fig. 3. The weighting factors associated with column 14 are displayed in Table 2

Apis mellifera worker

1.	1	*E(U)		(also in all the following tables)				
2.	1	*E(B)		(see above)				
3.	1	*E(G)		(see above)				
4.	0.5	*E(U)	+	0.1	*E(B)			
5.	0.5	*E(B)	+	0.1	*E(G)			
6.	0.5	*E(U)	+	0.1	*E(G)			
7.	0.9	*E(U)	+	0.1	*E(B)	+	0.1	*E(G)
8.	0.4	*E(U)	−	0.5	*E(B)			
9.	0.5	*E(B)	−	0.5	*E(G)			
10.	0.5	*E(U)	−	0.6	*E(G)			
11.	1	*E(G)	−	1	*E(U)	−	0	*E(B)
12.	1	*E(U)	−	0.4	*E(B)	−	0.6	*E(G)
13.	1	*E(B)	−	0.6	*E(U)	−	0.4	*E(G)
15.	1	*E(U)	−	0.2	*E(B)	−	0.8	*E(G)
and	1	*E(B)	−	0.6	*E(U)	−	0.4	*E(G)
and	0.66	*E(U)	+	0.66	*E(B)	+	0.66	*E(G)

16. Colour hexagon distance (as in all following tables)

Apis mellifera drone

4.	0.1	*E(U)	+	0.5	*E(B)			
5.	0.8	*E(B)	+	0.5	*E(G)			
6.	0.5	*E(U)	+	0.1	*E(G)			
7.	0.1	*E(U)	+	0.9	*E(B)	+	0.1	*E(G)
8.	0.5	*E(U)	−	0.4	*E(B)			
9.	0.5	*E(B)	−	0.6	*E(G)			
10.	0.5	*E(U)	−	0.7	*E(G)			
11.	1	*E(G)	−	1	*E(U)	−	0	*E(B)
12.	1	*E(U)	−	0.6	*E(B)	−	0.4	*E(G)
13.	1	*E(B)	−	0.8	*E(U)	−	0.2	*E(G)
15.	1	*E(U)	−	0.3	*E(B)	−	0.7	*E(G)
and	1	*E(B)	−	0.9	*E(U)	−	0.1	*E(G)
and	0.66	*E(U)	+	0.66	*E(B)	+	0.66	*E(G)

Melipona quadrifasciata (food source)

4.	0.5	*E(U)	+	0.1	*E(B)			
5.	0.1	*E(B)	+	0.5	*E(G)			
6.	0.1	*E(U)	+	0.5	*E(G)			
7.	0.1	*E(U)	+	0.1	*E(B)	+	0.9	*E(G)
8.	0.5	*E(U)	−	0.5	*E(B)			
9.	0.5	*E(B)	−	0.5	*E(G)			
10.	0.5	*E(U)	−	0.5	*E(G)			
11.	1	*E(G)	−	0.8	*E(U)	−	0.2	*E(B)
12.	1	*E(U)	−	0	*E(B)	−	1	*E(G)
13.	1	*E(B)	−	1	*E(U)	−	0	*E(G)
15.	1	*E(G)	−	0.9	*E(U)	−	0.1	*E(B)
and	1	*E(U)	−	0.3	*E(B)	−	0.7	*E(G)
and	0.66	*E(U)	+	0.66	*E(B)	+	0.66	*E(G)

Melipona quadrifasciata (hive entrance)

4.	0.1	*E(U)	+	0.5	*E(B)			
5.	0.1	*E(B)	+	0.5	*E(G)			
6.	0.1	*E(U)	+	0.5	*E(G)			
7.	0.1	*E(U)	+	0.7	*E(B)	+	0.3	*E(G)
8.	0.1	*E(U)	−	0.5	*E(B)			
9.	0.5	*E(B)	−	0.5	*E(G)			
10.	0.3	*E(U)	−	0.5	*E(G)			
11.	1	*E(G)	−	0.9	*E(U)	−	0.1	*E(B)
12.	1	*E(U)	−	0	*E(B)	−	1	*E(G)
13.	1	*E(B)	−	0	*E(U)	−	1	*E(G)
15.	1	*E(G)	−	0.2	*E(U)	−	0.8	*E(B)
and	1	*E(U)	−	0.7	*E(B)	−	0.3	*E(G)
and	0.66	*E(U)	+	0.66	*E(B)	+	0.66	*E(G)

Vespa crabro

4.	0.1	*E(U)	+	0.5	*E(B)			
5.	0.5	*E(B)	+	0.1	*E(G)			
6.	0.1	*E(U)	+	0.5	*E(G)			
7.	0.1	*E(U)	+	0.9	*E(B)	+	0.1	*E(G)
8.	0.5	*E(U)	−	0.5	*E(B)			
9.	0.5	*E(B)	−	0.1	*E(G)			
10.	0.1	*E(U)	−	0.5	*E(G)			
11.	1	*E(G)	−	0.9	*E(U)	−	0.1	*E(B)
12.	1	*E(U)	−	0.9	*E(B)	−	0.1	*E(G)
13.	1	*E(B)	−	0.9	*E(U)	−	0.1	*E(G)
15.	1	*E(U)	−	0.9	*E(B)	−	0.1	*E(G)
and	1	*E(B)	−	0.4	*E(U)	−	0.6	*E(G)
and	0.66	*E(U)	+	0.66	*E(B)	+	0.66	*E(G)

Paravespula germanica

4.	0.5	*E(U)	+	0.1	*E(B)			
5.	0.5	*E(B)	+	0.1	*E(G)			
6.	0.5	*E(U)	+	0.1	*E(G)			
7.	0.9	*E(U)	+	0.7	*E(B)	+	0.1	*E(G)
8.	0.5	*E(U)	−	0.4	*E(B)			
9.	0.5	*E(B)	−	0.3	*E(G)			
10.	0.6	*E(U)	−	0.5	*E(G)			
11.	1	*E(G)	−	0.6	*E(U)	−	0.4	*E(B)
12.	1	*E(U)	−	0.9	*E(B)	−	0.1	*E(G)
13.	1	*E(B)	−	0.1	*E(U)	−	0.9	*E(G)
15.	1	*E(G)	−	0.3	*E(U)	−	0.7	*E(B)
and	1	*E(U)	−	0.5	*E(B)	−	0.5	*E(G)
and	0.66	*E(U)	+	0.66	*E(B)	+	0.66	*E(G)

Vespa vulgaris

4.	0.1	*E(U)	+	0.5	*E(B)			
5.	0.7	*E(B)	+	0.5	*E(G)			
6.	0.5	*E(U)	+	0.1	*E(G)			
7.	0.1	*E(U)	+	0.9	*E(B)	+	0.5	*E(G)
8.	0.5	*E(U)	−	0.4	*E(B)			
9.	0.5	*E(B)	−	0.2	*E(G)			
10.	0.6	*E(U)	−	0.5	*E(G)			
11.	1	*E(G)	−	0.7	*E(U)	−	0.3	*E(B)
12.	1	*E(U)	−	0	*E(B)	−	1	*E(G)
13.	1	*E(B)	−	0.4	*E(U)	−	0.6	*E(G)
15.	1	*E(U)	−	0.8	*E(B)	−	0.2	*E(G)
and	1	*E(G)	−	0.2	*E(B)	−	0.8	*E(U)
and	0.66	*E(U)	+	0.66	*E(B)	+	0.66	*E(G)

Osmia rufa

4.	0.5	*E(U)	+	0.1	*E(B)			
5.	0.5	*E(B)	+	0.1	*E(G)			
6.	0.5	*E(U)	+	0.1	*E(G)			
7.	0.9	*E(U)	+	0.1	*E(B)	+	0.1	*E(G)
8.	0.6	*E(U)	−	0.5	*E(B)			
9.	0.9	*E(B)	−	0.5	*E(G)			
10.	0.4	*E(U)	−	0.5	*E(G)			
11.	1	*E(G)	−	0.9	*E(U)	−	0.1	*E(B)
12.	1	*E(U)	−	0.4	*E(B)	−	0.6	*E(G)
13.	1	*E(B)	−	0.3	*E(U)	−	0.7	*E(G)
15.	1	*E(U)	−	1	*E(B)	−	0	*E(G)
and	1	*E(B)	−	0.9	*E(U)	−	0.1	*E(U)
and	0.66	*E(U)	+	0.66	*E(B)	+	0.66	*E(G)

Psenulus fuscipennis

4.	0.7	*E(U)	+	0.5	*E(B)			
5.	0.5	*E(B)	+	0.1	*E(G)			
6.	0.5	*E(U)	+	0.2	*E(G)			
7.	0.5	*E(U)	+	0.9	*E(B)	+	0.5	*E(G)
8.	0.1	*E(U)	−	0.5	*E(B)			
9.	0.5	*E(B)	−	0.1	*E(G)			
10.	0.5	*E(U)	−	0.1	*E(G)			
11.	1	*E(G)	−	0.4	*E(U)	−	0.6	*E(B)
12.	1	*E(U)	−	0	*E(B)	−	1	*E(G)
13.	1	*E(B)	−	0.6	*E(U)	−	0.4	*E(G)
15.	1	*E(U)	−	0.5	*E(B)	−	0.5	*E(G)
and	1	*E(G)	−	0.6	*E(U)	−	0.4	*E(B)
and	0.66	*E(U)	+	0.66	*E(B)	+	0.66	*E(G)

Heriades truncorum

4.	0.2	*E(U)	+	0.5	*E(B)			
5.	0.1	*E(B)	+	0.5	*E(G)			
6.	0.5	*E(U)	+	0.1	*E(G)			
7.	0.7	*E(U)	+	0.1	*E(B)	+	0.1	*E(G)
8.	0.2	*E(U)	−	0.5	*E(B)			
9.	0.5	*E(B)	−	0.1	*E(G)			
10.	0.1	*E(U)	−	0.5	*E(G)			
11.	1	*E(G)	−	0.9	*E(U)	−	0.1	*E(B)
12.	1	*E(U)	−	0.5	*E(B)	−	0.5	*E(G)
13.	1	*E(B)	−	1	*E(U)	−	0	*E(G)
15.	1	*E(U)	−	0.4	*E(B)	−	0.6	*E(G)
and	1	*E(B)	−	0.7	*E(U)	−	0.3	*E(G)
and	0.66	*E(U)	+	0.66	*E(B)	+	0.66	*E(G)