Color Vision in Honeybees: Metric, Dimensions, Constancy, and Ecological Aspects

Werner Backhaus, Annette Werner, and Randolf Menzel
Institut für Tierphysiologie, Neurobiologie, Freie Universität Berlin, Königin-Luise-Str. 28–30, D-1000 Berlin 33, FRG

Abstract. The color space of honeybees can be modeled with great precision since we know the spectral sensitivities of the three receptor types very accurately. The predictions of the model are met by color matching experiments (lower colorimetry), and by the judgment of the dissimilarity of colors (higher colorimetry) if we take the receptor noise as the limiting factor for perceptual distance judgment. The behavioral analysis with factorial (multidimensional) analysis reveals two perceptual dimensions; the total color distance is the sum of the absolute differences on the two perceptual scales (city-block metric). Color brightness is ignored by the bee in our training experiments. The dissimilarity between color pairs correlates well with the added differences of excitations of a UV-blue-green and a blue/UV-green color opponent system. The corresponding spectrally opponent neurons were found already several years ago. Color constancy is tested in a simultaneous, multi-color arrangement similar to that of Land's (21) "Mondrian" experiment. It is concluded that color constancy in bees is a consequence of antagonistic color coding, and that ratio-making operations are an essential part of this function. It can be quantized with the algorithm developed for human color constancy. Higher order color phenomena of color vision like asymmetric color discrimination between pairs of signals, color specific differences in learning acquisition, context specific discrimination of color signals are described. The phenomena indicate a central nervous representation of color and not just a neural coding of the inputs from the three spectral receptor types.

INTRODUCTION

The study of color vision in honeybees began with a historical controversy. V. Hess (13), an influential physiologist early this century claimed that bees are color blind because in his experiments their choice preference for colored lights or pigment paints resembled that of color blind people. He came to the conclusion: "At the present time there is not one single fact that would make the assumption even probable, that the bee has a color sense that is comparable to our own sense of color. In fact, my earlier experiments with spectral and glass lights, as well as my new experiments with colored paper, have finally shown this assumption to be unfounded. Considering also the results of previous experiments, all of which are easily reproducible, it is no longer possible to defend Sprengel's spiritual doctrine (Sprengel 1793) (see 45) which is concerned with the meaning of flower color with regards to insect visitation."

As so often in science, V. Hess was not completely wrong. Indeed his early experiments were actually correct and bees are color blind in the behavioral context in which he tested them. However, he made the important mistake to conclude that bees are, therefore, also color blind in other behavioral contexts e.g. at the feeding place. In addition, he made serious experimental mistakes when he tried to repeat V. Frisch's experiments. Hess tested the bees in their phototactic response when they tried to escape from an enclosure spontaneously to the light. We repeated these experiments under better controlled conditions and also found that bees direct their escape runs towards a light source only with respect to the effective photon flux without any indication of color effects (32). For example, mixtures of UV and green (or UV and blue or UV and violet) lights were chosen relative to monochromatic green light with a frequency which can be predicted by simple addition of the effective photon flux of each of the two mixed wavelengths. Apart from phototaxis, bees are also color blind in their optomotor response (16) and in the orientation of their flights along vertical contrast borders (scanning behavior) (25). Both these behaviors are dominated by the green receptors, whereas in phototaxis all three photoreceptors contribute about equally. Furthermore, bees are color blind in training experiments at low light intensities. For example, bees were trained to walk to one side (e.g. left) in a T-maze when a spectral light was presented from below at the decision point, and to walk to the other side (e.g. right) when the presented light was achromatic white. At low intensities of the spectral light the bees walked to the left, whereas at higher intensities they chose the right side. The spectral light thus appeared achromatic to the bees at lower intensities, and colored at higher intensities (28). This result is supported by the finding that free flying bees lose color vision at low ambient light before they are unable to visually control their flight behavior (27, 41).

Bees see color contrast at the feeding place and at the hive entrance. Since Frisch's (6) first experiments, color training experiments have been repeated many times with varying experimental arrangements. The result of these efforts is that their tri-chromatic color vision system, which partly consists of UV, blue and green receptors, is well documented with behavioral and electrophysiological experiments. Recently, quantitative models have been developed which try to explain the color matching and the color discrimination behavior on the basis of the properties of the photoreceptors and the visual interneurons. (30, 2, 3). We shall first outline the major arguments of these quantitative studies. Further aspects of the color vision in bees have been described particularly with respect to color constancy, and these shall be presented in the second part of this article. The perceptual dimensions of color vision in bees derived from multiple choice experiments and the interpretation of color opponent systems are presented in the following two chapters. Finally, the question of a connection between color memory and color categories (basic colors) is discussed. We shall demonstrate that color opponency, color constancy and categorical color coding are the basic features of the color vision system in bees.
Chromaticity Diagrams and Photoreceptor Properties

Daumer (5) showed in color mixture experiments with free flying bees, that the Gra"bmannian mixture laws formulated for human color vision (7) also apply to the color vision system of the bee. As an analogy to human color vision, he presented color mixtures in a chromaticity diagram for bees, i.e. the edges of a symmetric triangle represent three basic lights (primaries); the loci of light mixtures are constructed by dividing the straight line between the loci of two lights of the mixture into the same but inverse ratios of the light intensities used (center-of-gravity construction, see Fig. 1b). In particular, Daumer proved the continuity of a series of mixtures of UV and yellow ("bee-purple"), which have no correlating spectral light. Furthermore, he measured the proportions of complementary spectral lights that are necessary to produce metameric light mixtures (physical different but undistinguishable) to "bee-white".

Fig. 1 - a. The receptor plane as a section through the receptor space. The geometrical connection of the chromaticity coordinates p of the color stimulus f and the components P constituting the corresponding color stimulus vector F. b. Center-of-gravity construction of the mixture locus f_0 from the amounts M of the mixed color stimuli f_1 and f_2. The proportional relations hold for the chromaticity coordinates p as well. Geometrical distances are indicated by a line.

Equivalent to the chromaticity diagram, is the concept of a three dimensional color space where the three primaries are denoted as orthonormal basis vectors. The Gra"bmannian mixture rules are realized by vector addition. Fig. 1a shows the interpretation of the chromaticity diagram as a section through the color space. Brightness can be included in a color luminance space by multiplying the basis vectors by their luminance coefficients (43, 44). The brightness of a color is calculated as sum of the absolute values of the components of the color brightness vector (Abney's law).

The primaries can be changed to other lights, in general to all linear functionals of light intensity, e.g. absorbed photon fluxes; the loci of the lights change in different color spaces but the Gra"bmannian mixture laws (and Abney's law) hold (13). This allows the construction of a physiological color stimulus space (tristimulus space) (4, 42, 46). The primaries correspond to the photon fluxes P (tristimulus values) absorbed by each of the three receptors:

\[ P_i = \int_{-\infty}^{+\infty} s(\lambda) \alpha_i(\lambda) d\lambda \]

The spectral photon flux density (spectral intensity) as emitted or reflected from color signals; \( s \) are the spectral sensitivities of the three receptor types. "Bee-luminance" is assumed to be proportional to the sum of the tristimulus values, i.e. the "bee-brightness" only depends on the spectral sensitivities. The color stimulus space corresponds to the color luminance space. The corresponding physiological chromaticity diagram represents a plane of constant "bee-brightness" (constant totally absorbed photon flux). The chromaticity coordinates \( p \) are defined as:

\[ p_i = \frac{P_i}{P_{\text{total}}} \text{, thus} \]

\[ \sum_{i=1}^{3} p_i = 1 \]

Changes of photon fluxes absorbed by the three receptors cause perceptual changes in chromaticity and brightness. If the lights are changed in such a way that the total absorbed photon flux is kept constant, changes occur only in chromaticity. Variations of the total absorbed photon flux change the brightness of the color. Lights which are indistinguishable for the receptors cause matching colors. On the other hand, it is not obvious whether two lights, which are distinguishable for one or more of the receptors, will be judged as different colors. One may ask, therefore, what is the relationship between color difference and receptor properties?

The resolution of the color vision system in bees has been measured in behavioral experiments with respect to wavelength discrimination (11), brightness discrimination (29) and first saturation threshold that surrounds the white point (24). Since the concept of chromaticity diagram and color space is based on color matching judgments (metamerism), the results of color difference judgments cannot be predicted in a simple way from the differences of tristimulus values or chromaticity coordinates. In the case of "small field color vision" (one ommatidium, three receptor types 3 UV, 2 blue, 4 green receptors, 31, 34), the color vision system cannot resolve better than the photoreceptors. The resolution of the photoreceptors is limited by the fluctuations of the receptor potential. Each photon absorbed by the receptors is transduced into a unit of transmembrane currents, the sum of which is coded as the relative magnitude of the graded receptor potential:

\[ I(x,y) = \left( M_x(x,y) / M_x(0,0) \right) \]
The photon absorption process and the transduction process cause fluctuations of the receptor potential (shot noise and transducer noise) (23). These fluctuations were found to be independent of the magnitude of the potential (23) as we also observed in our intracellular recordings (34, Fig. 6). The fluctuation amplitude of the receptor potential never exceeds a boundary of 1.2% of the maximal potential, and this is identical with the 3 sigma interval when assuming (proved by eye), that the fluctuation is Gaussian distributed. One standard deviation s turns out to be 0.4% of the maximal response.

Fig. 2. (a) pind-scales calculated for variations in wavelengths (black dots) and variations of the white-spectral light mixtures (circles). The distance between the marked loci represents 10 pind steps. The closed curves (black dots) are calculated for white-spectral light mixtures that differ by 10% in the mixture coefficient. The radial curves (circles) are calculated for spectral and purple lights that differ by 10 nm and 10% in the green-UV mixture coefficient. The comparison of the probability transformed choice frequencies p with the pind scales derived from the receptor model, as each number gives a pair of color stimuli which have been tested in a dual forced choice discrimination test after training bees to one or the other choice stimulus: 1: BG12 (U = 219, B = 274, G = 274) vs. BG23 (U = 53, B = 274, G = 274); 2: BG18 (U = 270, B = 274, G = 274) vs. BG28 (U = 189, B = 274, G = 274); 3: BG28 + B4 (U = 146, B = 274, G = 274) vs. BG28 (U = 189, B = 274, G = 274); 4: BG28/2 (U = 274, B = 274, G = 107) vs. BG28 (U = 274, B = 274, G = 107); 5: BG28 + V3 (U = 274, B = 274, G = 274) vs. BG28 (U = 274, B = 274, G = 274). The unit of the ordinate corresponds to 5 nm of Helversen's function and to the reciprocal value of 38 pind steps per 10 nm in the model calculation.

What are the consequences of this limitation in accuracy of the light intensity coding in the receptor potentials with respect to the resolution of the bees color vision? To analyze the limitation of the perceptual just noticeable difference steps (pind) by the just noticeable difference steps in the receptors (rind), we stimulated stimulation of the receptors by changing mixtures of spectral light and white light which cause a constant total absorbed photon flux i.e. which only cause differences in chromaticness (see above). In the first series the mixture varied continuously in the wavelength of the spectral light changing the white-light proportion in 10% steps. In a second series, the mixture varied continuously in the white-light proportion whilst the spectral light changed in 10 nm steps (Fig. 2a). One rind step is reached if the variations of the mixtures cause a significant (50% threshold: 0.3% of $V_{max}$) change in at least one of the three receptor types (a dot denotes ten rind steps). As seen in

Fig. 2a. areas with high (many dots between the lines) or low resolution (few dots between the lines) do not correspond to areas where the lines are more or less dense. It is obvious from this calculation that there exists no simple relationship between color resolution and the geometrical distance of the loci of the stimuli in the chromaticity diagram. We found a very good agreement between the calculated resolution of the color vision system for spectral lights, as the number of pind's, and the spectral discrimination function as determined by Helversen (11) by training experiments (see 2, Fig. 2b).

The dissimilarity of colors can be measured as the minimal number of pind steps (10, 44). The paths of most similar colors follows (in general) curved lines in the chromaticity diagram. We derived an approximation procedure to find the shortest (minimal number of pind steps)
mixture line between two colors (2). In Fig. 2c, the shortest mixture lines are drawn for a starting point at pure spectral lights in 10nm intervals and increasing proportions of white light. The model predicts that bees trained to a 1:1 mixture M of white and spectral light should judge a spectral light of longer wavelengths \( S_B^A \) more similar than the spectral lights used for the mixture (Bezold-Abney hue shift). The hue shift occurs more or less to longer and shorter wavelengths respectively, and is caused by the nonlinearity of the transduction function of the receptors. The Bezold-Abney shift has still to be demonstrated for bees.

The application of the receptor model to natural objects, which reflect light varying in all physical parameters, makes a further assumption necessary. Natural objects do not adjust the lights so that only chromaticness changes. A change from one light to another causes changes in the potentials of the three receptors. The color vision system has to derive a measure of color distance from the differences in the potentials. We investigated two different possibilities for the color vision system to compute a neuronal representation of a color distance measure. 1) The maximum information about changes in absorbed photon fluxes is obtained when the system determines the response steps separately in each receptor as a difference in receptor potential weighted by a factor for converting rjd to pjnd, and then simply adding the weighted differences as a dissimilarity measure. 2) Since the transduction function \( \text{with } n = \text{a} \) is approximately a logarithmic function \( V/V_{\text{max}} \), the receptor channels can be subtractively connected to make the resulting excitation independent of changes in intensity. The dissimilarity measure can simply be represented as the difference in excitation of a cell. The non-linearity of the transduction process causes the linear dissimilarity measure to appear from the measurements as complicated functions of the chromaticity coordinates (curved similarity lines in the chromaticity diagram), since color measurements can only be performed in terms of light intensities or absorbed photon fluxes respectively.

The first possibility predicts that the bee weights brightness differences equal to differences in hue and saturation. The second possibility predicts that the bee weights differences in chromaticness higher, and that differences in brightness do not contribute to the dissimilarity of colors. We found a much better correlation of the choice behavior with the second measure (two dimensional) than with the first measure (three dimensional). Fig. 2d shows the correlation of the z-values of the measured choice proportions of Apis with the second jnd measure (two dimensional) for color distance. The scatter is homogeneous around the regression line. The same was found for the stingless bee Melipona (35).

Thus bees ignore differences in brightness when trained to colors (not specially trained to brightness differences). Color distance is dominated by the receptor properties spectral sensitivity, phototransduction, and noise. The independency of intensity differences is taken into account in the model by the simple assumption that the receptor potentials are linearly subtracted. This model predicts that the nonlinear transduction process makes the linear (neuronal) dissimilarity measure appear very complex in psychophysical experiments. The resulting curved similarity lines in the chromaticity diagram should be directly measurable as Bezold-Abney hue shift.

Color Contrast and Color Constancy

Color contrast effects can be demonstrated by training bees to one of several color signals on a grey background and presenting the same color signals on different backgrounds during a test situation (36, 37). The colors used by Neumeyer differed in hue along a blue-yellow axis, and the backgrounds surrounding the colormarks were either grey, yellow or blue. If the background color was changed from grey to blue, the bees shifted their choice behavior to more blue colors, whereas if it was changed to yellow they chose more yellow colors. The hue shift was also induced by a small colored ring surrounding the color mark, even if the colored ring was separated from the color mark by a thin black annulus.

A particular kind of color contrast effect has been found in pattern discrimination experiments (33). A vertically arranged circular pattern consisting of two half circles with two different colors is readily discriminated from a similar but differently oriented pattern. The sensitivity to the change in orientation of the pattern depends on the color of the half-circles. For example, there is a change in the upper field of view if the area is UV light reflecting. The spatial dependence is reversed for a bluish-green appearing area; a similar antagonism was observed for blue and yellow. Although this orientation specific color effect is not yet well understood, it demonstrates clearly a combined spatial-chromatic antagonism along the vertical axis.

Connected with color contrast is the ability of a color vision system to see the color of objects unchanged while the illuminating light changes both in intensity and/or spectral composition, a phenomenon called "color constancy" (10) or "color transformation" (15). In humans, the effect of color constancy is particularly impressive in an experimental arrangement which Land (21) calls the "Mondrian-experiment": the "Mondrian" arrangement is composed of many rectangular colored plates with different reflectance coefficients. The arrangement is equally illuminated by three adjustable light beams containing light of long, middle, and short wavelengths respectively. When the intensities of the illuminating light beams are changed, the colors of the Mondrian areas remain the same or change very slightly. Slow receptor adaptation is unlikely to be involved because the colors appear to be the same even when the arrangement is illuminated for 100 msec (22). It is concluded, therefore, that color constancy results from neural processes in the retina and cortex (retinex-theory). The color of an area in such an arrangement is determined not only by the photon flux coming from this area but also depends on the relative photon fluxes of the whole arrangement. An adequate way to describe color in this context is the representation as points in a retinex three-space composed of three (short-, middle-, and longwave) designators on orthogonal axes. The contributions of the photon fluxes of all areas to the
three designators corresponding to the color of an area are computed independently from each other according to the retinex algorithm. Starting at random positions in the arrangement, all logarithms of the relative photon fluxes (above a threshold) of one waveband of every two neighboring areas are summed on the way to the area in question. The designators of the area are the average of these sums. The procedure converges quickly; only a few paths have to be considered. Overall changes in illumination do not change the designators and, therefore, do not change the color appearance of the arrangement.

Fig. 3 - A multicolored checkerboard arrangement ("Mondrian") is illuminated from behind by a mixture of the three wavelength bands (UV max=340nm, blue max=440nm, green = 550nm). The numbers of the "Mondrian"-areas indicate the types of glass filters.

A similar experiment was carried out in order to study the color constancy of bees (17, 48). Freely flying bees were trained to collect a sucrose solution from one of 13 colored filters, which were arranged like a checkerboard (Fig. 4). This arrangement was illuminated from behind by three broadband light beams (UV, blue, green), whose spectral composition was matched to the spectral properties of the three color receptors in the bee eye. After training the bee to discriminate one color from all the others, the three light beams were changed in such a way that one of the unrewarded filters transmitted the same amounts of the photon fluxes of the three light beams as did the rewarded filter during training. If the color of a filter would be determined by the photon flux passing through it, the bee should choose this filter. As Fig. 3 shows, the bee still preferred the trained filter despite the fact that the spectral composition of the transmitted photon flux changed considerably, and that the actual signals in the photoreceptors changed accordingly.

Fig. 4 - Performance of color constancy, tested for four color matches between violet and blue-green colors. In all cases, the distribution of choices between training (O) and matching color remained almost constant during training illumination (first double block of every experiment) and during matching illumination (second double block of every experiment).

A convenient way to explain the independency of color appearance from the actual photon flux of the three light beams is to assume a ratio making principle which adjusts the neural representation of a color such that each color representation is expressed in relative terms of the photon fluxes from all other areas in the visual field. A neuronal correlate for such a process may be seen in (double) opponent cells which combine spatial and chromatic opponency in their response properties (22, 49). Simple color opponent cells with overlapping receptive fields of their antagonistic responses (U'B"G"; B'U"G") have been recorded in the visual system of the bee many times (see below; Hertel and Maronde, this vol.); recent investigations have also been carried out on double opponent cells with a UV-green antagonism combined with spatial antagonism. Centre-surround double opponency is not known from any insect visual interneuron, but more complex combinations of spatial and chromatic contrast have been found (17). Such neurons are equally suitable for the proposed mechanism of ratio making if they exist in many positions of their receptive fields. It might well be that only a limited number of such neurons exist with particular positions of their
receptive fields, in which case one should expect color constancy to be limited to certain arrangements of color areas in the visual field. An indication for preferred combinations of chromatic and spatial contrast comes from the color pattern experiments described above. More experiments with the “Mondrian” are required to investigate whether or not color constancy is limited to certain spatial and chromatic combinations, and to determine the range of variations in Illumination where color constancy holds.

Dimensions of color perception

Multiple color choice experiments as in the “Mondrian arrangement” are also suitable for analyzing the perceptual dimensions of color vision. In these experiments the color marks are presented as small (50 or 70 mm²) discs on a grey background and are so far apart (more than 20 cm) that the individual test bee views each test color signal independently. Twelve different signals are presented simultaneously. Each of the twelve signals was trained in turn using a new bee for each new signal and the choice behavior of all twelve colors determined in many tests. Metric (46) and nonmetric (19) multidimensional scaling procedures can be applied to the dissimilarities derived from the choice frequencies (8, 46). The dissimilarities are easily reproduceable from only two subjective scales by the city-block metric (sum of the absolute differences on the scales) (3).

Although the light reflected by the color signals differed in intensity over a wide range, brightness did not correlate with any of the two scales (nor with a third scale). The bee ignores differences in brightness in this color choice situation, and this is in good agreement with the findings of Daumer (3) and Helversen (11). Fig. 5a shows the twelve color stimuli used in the experiment. The subjective color loci with the two scales as components are presented in Fig. 5a. The two configurations are topographically equal to each other.

The subjective color scales can be interpreted in two ways: 1) The scales correlate with a UV/blue-greenness and blue/greenness dimension. The similarity measure can be represented neurally as the sum of the differences in the excitations of two opponent color systems. 2) The scales correlate with a hue and saturation dimension. The similarity measure has to be calculated by the nervous system in a complicated way from the receptor potentials as absolute sum of the differences in saturation S and hue H derived as $\Delta S = \sqrt{\text{UV} - \text{BG}}^2 + (\text{UV} - \text{BG})^2$ and $\Delta H = \arctan\left(\text{UV} / \text{BG}\right)$ from the excitations of the respective color opponent system UVG (14).

Color Opponency

We tested the first hypothesis which is supported by our receptor model and which assumes linear subtraction of the receptor potentials (see above). We calculated the coefficients as the least square solution of the general linear equation (without assuming anything about opponency) of the two scale values A and B (Fig. 5a) obtained for twelve colors of the multiple choice experiment (see above) and the corresponding three receptor excitation E.

caused by the twelve color stimuli (Fig. 5b).

$$A = -10.0 E^U + 2.3 E^B + 3.0 E^G$$

$$B = -7.9 E^U + 21.0 E^B - 14.2 E^G$$

The result is that scale A corresponds to a UV/blue-green opponent system, and that scale B corresponds to a blue/purple opponent system. The reproduced subjective color loci from the receptor excitations are shown in Fig. 5c. We found that the derived subjective scales A' and B' are very sensitive to changes of the coefficients (e.g. rank changes occur because of the nonlinearity of the transduction function). On the other hand the coefficients change very little if the sample is reduced by two of the color stimuli. Thus the nervous system can obtain the color dissimilarity measure as the sum of the absolute differences in the excitations in the
two opponent systems when two color stimuli are presented after each other, or simultaneously, at different areas in the visual fields. Since the sum of the coefficients is not equal to zero, our opponent color model predicts the dependence of color on the light intensity (Bezold-Brücke effect). Both the light intensity dependent and the wavelength dependent (Bezold-Abney) hue shift are a consequence of color opponency. Both dependencies have yet to be measured.

The model calculations explain the results of the color choice experiments and support strongly opponent color coding mechanisms. Neuronal correlates of the predicted opponent mechanisms have been recorded from the second and third visual neuropile (medulla, lobula) in the bee brain (17, 12, 39, see also Hertel and Maronde this volume). As Fig. 6 shows, two main classes of chromatic opponency are found: an antagonism between UV / blue and green, and one between blue / UV and green ("purple").

Memories for Colors and Color Categories
There is some evidence that the choice behavior depends on the behavioral context, i.e. that the information represented by the color vision system is used selectively by the bees like in human color vision, where color naming uses different color attributes (hue names, saturation, red/greenness, blue/yellowness, brightness) depending on the kind of experiment and the instructions given by the experimenter (14, 38, 9). Besides color discrimination and color distance experiments, in which the judgment of the bee is based on the dimensions UV/blue-greenness and blue/purpleness, there exist other behavioral aspects which are better explained by hue and saturation as perceptual dimensions.

Colors are meaningful signals to the bee. They mark a food source or the entrance to the hive. The meaning of the color signal is derived from the information gathered by the species through the evolutionary process and by the learning processes of an individual animal. The choice behavior towards a color signal is not only determined by perceptual aspects but also by the meaning of it. In honeybees, the individual learning process is so strong that the choice behavior can be manipulated by training procedures. In such a situation, most of the information available to the nervous system to discriminate colors is actually used and this permits the kind of psychophysical analysis as described above. However, under certain conditions the bias of the evolutionary predispositions shines through the individual learning process. For example, the acquisition of spectral colors as food markers is faster for violet and slower for bluish-green (Fig. 7a) (26). This is independent of the photon flux and of the

Fig. 6 - A summary of all kinds of spectrally opponent neurons recorded in the visual system of the honeybee. Except for the very lowest trace (UV-off, B-on, G-off) all neurons display tonic spectral opponency. The lowest trace gives an example for a phasic opponent neuron. The neuron UV^B^-G^+ in the middle of the figure has been marked intracellularly (courtesy of S. Schäfer). It receives input from the proximal medulla and projects to the distal dorsal lobula. (From 12, 17 and unpublished data).
wavelength used as an alternative color in the dual choice test. Colors of low saturation are learned slower than those of high saturation (5, 24), although they are very well discriminated (24). Achromatic white is very hard to train at all (5, 24, 26).

Asymmetries in the choice behavior are an additional indicator for color biased behavior. Fig. 6 gives an example of a matrix of twelve color signals which were all trained individually and tested against the other 11 signals. If only the perceptual distance between the colors A and B would determine the choice behavior it should not matter whether A or B was trained. It is obvious from Fig. 7b that significant asymmetries exist, and that they indicate an improved choice for the more saturated colors.

Color discrimination may also depend on the behavioral context. We found a particular interesting example in the stingless bee, Melipona quadrifasciata (Fig. 7c), which distinguishes bluish-green colors much better at the hive entrance than at the feeding station (35). No such large differences were found in Apis mellifera (30). The preferred choice of color signals which is not overcome by learning is of much greater importance in Melipona than in Apis. For example, the asymmetries mentioned above are more pronounced in Melipona, and the response/function of color signals tested than in Apis (35).

A bias towards certain colors may indicate a neural process which categorizes the color signals into a small number of unique or basic colors. We have not yet collected enough data throughout the whole color space of the bee to determine these basic colors, but we believe that the analysis of asymmetries, as in Fig. 7, will give us the answer.

CONCLUSION
Seventy years of active research on color vision in bees has revealed a large body of knowledge at various levels of neural integration and behavioral analysis. The accurate determination of the spectral sensitivity functions of the three receptor types enables us to construct a receptor model of color vision. This in turn allows to make predictions about color mixing (lower colorimetry) and the dissimilarities of colors (higher colorimetry), if we take the receptor noise as the limiting factor for perceptual difference judgment. The behavioral analysis with multifactorial (multidimensional) analysis has revealed the perceptual dimensions of color vision in bees. The perceptual dimensions UV/blue-greenness and blue/purpleness are not separately affected by single variations of the physical parameters of wavelength or white proportion as performed in conventional color discrimination experiments. The dissimilarity between two colors correlates well with the added differences of excitations of a UV/blue-green and a blue/purple color opponent system.

The corresponding spectrally opponent neurons were already described ten years ago. The properties of these neurons are interpreted to underlie also the observed phenomena of color contrast and color constancy.
However, there exist parameters measured in the bee's color choice behavior which are not explainable in relation to the one dimensional dissimilarity measure. White is learned very slowly, whilst spectral colors are learned much faster depending on the color range. It is possible that the speed and acquisition level of color learning depends on the saturation and hue of colors, which are other color attributes than UV-blue-greenness and blue/purpleness. Asymmetries in color discrimination seem to correspond to distinct areas in the color plane (basic colors). The memory of colors induces distortions in the perceptual representation of remembered colors, which in turn leads to generalization processes biased to certain colors. This bias is not very pronounced in the honeybee and its influence on color perception experiments can be overcome by a symmetrical arrangement of all the color discrimination tests. Although of relatively small effect, the color bias may be interpreted to indicate the existence of unique or basic colors in bees. These colors have still yet to be determined.

The knowledge of the opponent system in the color coding of bees offers a convenient way of describing the color of natural objects, which are important for the orientation of the bee (flowers, natural background etc.). The application of such a system would facilitate the elucidation of co-evolutionary relationships between flowers and bees, and the ecological constraints of the chromatic light climate in which bees live. In contrast to von Hoff, whom we cited at the beginning of this paper, we can conclude that the results presented here not only give further support to Sprengel's spiritual doctrine, but that we now also have the possibility to present this doctrine in the form of a quantitative investigation.

REFERENCES


(2) Backhaus, W.; and Menzel, R. in press. Color distance derived from a receptor model of color vision in the honeybee. Biol Cybern.


and peripheral mechanisms of colour vision, eds. D. Ottoson, S. Zeki, pp. 211-223, London:
MacMillan Press.

(31) Menzel, R.; and Blakers, M. 1976. Colour receptors in the bee eye morphology and


(33) Menzel, R.; and Lieke, E. 1983. Antagonistic color effects in spatial vision of the honey

sensitivity of photoreceptors in the insect compound eyes: Comparison of species and

(35) Menzel, R.; Ventura, D. F.; Werner, A.; and Backhaus, W. Submitted. Spectral
sensitivities of single photoreceptors and color vision in the stingless bee, Mellipona
quadridascata. J Comp Physiol.

(36) Neumeyer, C. 1980. Simultaneous color contrast in the honeybee. J Comp Physiol 139:
165-176.

(37) Neumeyer, C. 1981. Chromatic adaptation in the honeybee: Successive color contrast and

Soc Am 58: 19-22.

(39) Riehle, A. 1981. Color opponent neurons of the honey bee in a hetero-chromatic flicker


(41) Rose, R.; and Menzel 1981. Luminance dependence of pigment color discrimination in


Physik 63: 397-426; 427-456.

(44) Schrödinger, E. 1920. Grundlinien einer Theorie der Farbenmetrik im Tagessehen. Der
Farbenmetrik II. Teil: Höhere Farbenmetrik (eigentliche Metrik der Farbe). Ann Physik
63: 481-520.

(45) Sprengel, C. K. 1793. Das entdeckte Geheimnis der Natur im Bau und in der


(47) Werner, A. in press. Farbkonstanz der Honigbiene - ist die Biene ein Retinex-Tier?
Verh Dtsch Zool Ges.

(48) Werner, A. in press. Die Biene in einem "Mondrian-Experiment" - Farbkonstanzleistung

(49) Zeki, S. 1984. Colour pathways and hierarchies in the cerebral cortex. In Central and
peripheral mechanisms of colour vision, eds. D. Ottoson, S. Zeki, pp. 19-44, London:
MacMillan Press.