Commentary/Thompson et al.: Ways of coloring

important, LO is consistent with the thesis that animals of different sorts could perceive the same color distinction in different ways. For example, an animal might see some color distinction we see but see it in terms of hues that we do not see just as Thompson et al. claim. It follows that LO is consistent with the claim that the content of the color distinctions we see depends on the nature of our nervous systems in an analytically way (a way that goes beyond the mechanics of fixing the reference of our color terms), so that, for example, redness is not a physical property of objects. The possibility of hue inversion suggests this, as do Thompson et al.'s considerations of perceptual differences between animals. (Here LO cannot be fleshed out with an account of redness, but see Averill 1985.)

If color distinctions are an objective feature of the world (and thus independent of our nervous systems), but redness is dependent on the human nervous system, then the ontological question is not, "Are colors physical properties?" but rather, "What features of colors are physical properties?"

Conclusions from color vision of insects

Werner Backhaus and Randolf Menzel
Institut für Neurobiologie, Freie Universität Berlin, 1000 Berlin 33, Germany
Electronic mail: 9907@dbotz01.bitnet

Contribution of philosophy to color science. The discussion of the philosophical conflicts between objectivism and subjectivism as presented throughout the target article appears, in the context of evolutionary and ecological aspects of color vision, to be confusing rather than providing coordinates for orientation. What Thompson et al. call objectivism with respect to color ("color is objective insofar as the colors of objects do not depend on how they appear to observers, or even whether or not there are any observers," Hilbert, 1987, p. 119) appears to be more or less the view of "naive" realism ("the simplest form of the view that sense perception is direct awareness of external things; that we do actually perceive objects in the 'external world'." Flew, 1984, p. 240). The philosophical conflict Thompson et al. describe occurs because we experience our sensations not as located inside ourselves but as located at the positions of the objects outside that emit or reflect light (phenomenology of color, e.g., Bergson, 1982, p. 1). On the other hand, we know from psychophysical and neurophysiological investigations that color is created somewhere in the brain, although the exact location of this process is still unknown, and we even have no idea what entities the sensations called color are. Because the scientific and philosophical discussion of color should not go beyond our actual knowledge (see also Hardin, 1985, p. 60) it is not at all a matter of taste or philosophical viewpoint where colors can be thought to be located. In short, colors appear only at first (naive) glance to be located in objects; closer inspection shows that colors are produced in the brain (see Corinn, 1975, for remaining possible philosophical positions compatible with scientific results, pp. 217-46 for falsification of naive realism).

Color vision is well described as a causal structure (the physical stimuli cause the sensations called colors). This allows a unique indication of colors and a unique description of the relations between colors occurring on different levels by measurable quantities: (1) physically by spectral reflectances and illumination spectra (or functions of those) or by functions of light intensity (e.g., chromaticity and color designation diagrams) or (2) physiologically in terms of absorbed photon fluxes (chromaticity diagrams), (3) physiologically by describing the neuronal coding system (e.g., color opponent coding), (4) psychophysically by describing the relations between colors (subjective color spaces and color order systems) and the relation of those (e.g., color differences) to the physical dimensions of the stimuli (e.g., intensity, wavelength), and (5) psychologically and linguistically by describing colors verbally (e.g., color names).

Thus, color indication systems are based either on terms describing the outer world (the aim of science) or on terms describing sensations (the aim of psychology and color vision). Both ways of indicating color vision are better described simultaneously on all these "levels" or only on one does not appear to be a philosophical matter; rather it is dictated by appropriateness to the scientific (or practical) problem to be solved. So there appears to be no need to give the well-defined term "color" (see e.g., Halsey 1989) an additional meaning ("color, in this account, is the disposition objects have to reflect varying percentages of the incident light." Hilbert, 1987, p. 119), which only gives rise to confusion of scientific terms, as shown in the target article.

Phototransduction and color coding. Thompson et al. give the impression that opponent coding would be directly related to photon fluxes absorbed in the photoreceptors rather than to photoreceptor cell potentials. To adequately describe color vision systems physiologically, it is necessary to take the measured nonlinear transduction process of the photoreceptors into account (e.g., humans, Rodieck 1973; macaques, Valberg et al. 1986; honeybees, Backhaus & Menzel 1987. Backhaus 1991). Otherwise, color vision models will be oversimplified because they do not describe the color coding for stimuli at different intensities (Bezold-Brücke effect).

Color opponent coding in the bee. Figure 3c in the target article was derived from a figure that was provided as a courtesy from W. B. to R. M. for a short report (Menzel 1989). The full treatment of the color opponent coding (COC) system of the bee is presented in Backhaus (1988, 1991; reviews: Backhaus et al. 1987, Menzel & Backhaus 1989, 1991). The example in Figure 1 shows how to derive the color difference measure between two stimuli graphically from the diagram according to the city-block metric of the color space that gives the same results as the calculation by the color difference formula. The description of color vision and color choice behavior of the bee, of which the opponent coding system is an essential part, has been confirmed by comparison with data from independent experiments, and thus has the status of a theory (Backhaus, in press).

The relationship of opponent coding to unique colors. Whether color opponent coding "channels" are isomorphic to unique (opponent) colors cannot be assumed a priori as suggested in the target article; it has to be shown empirically. Provided that the color similarity judgment (decision behavior) of the bee does in fact rely on opponent colors, the empirical data about the color vision system of the bee suggest that the amounts of these opponent colors must be linearly related to the neuronal opponent coding system. This results from the very good fit of the several predictions based on the excitations of the color opponent coding system to measured data (Backhaus, in press; Menzel & Backhaus 1991). A nonlinear relation between the coding system and the unique colors can be excluded, because an additional step in the linear part of the processing chain of color information must be linear to maintain the fits.

Wavelength discrimination. The form of the wavelength discrimination function depends on the steepness of the potential/wavelength function of the photoreceptors, showing regions of best discrimination for wavelengths at which the changes in potential caused by changes in wavelength are greatest (Backhaus 1991, Backhaus & Menzel 1987). The crossing points of the receptors' spectral sensitivities have no physiological meaning, although they are suggestive from a graphical point of view (Figure 2a,b). The wavelength discrimination functions for trichromatic color vision systems, for example, can have more than two regions for best discrimination because the potential/wavelength functions can in general have several regions of greatest steepness (honeybee, Figure 2c; see also Menzel & Backhaus 1991, Figure 4a-e; human, e.g., Wright & Pitt 1934). The minima shift in location on the wavelength scale and in value as shown in Figure 2c. So it is not possible to conclude from the measured number of ranges of best wavelength dis-
Commentary/Thompson et al.: Ways of coloring

Figure 1 (Backhaus and Menzel). Geometry of the color opponent coding (COC) diagram presenting chromaticity (hue and saturation) of color stimuli (from Backhaus 1991). The excitations of the two opponent coding systems A, B caused by a color stimulus are linearly related to the respective cell excitations E of the three photoreceptor cell types (u, b, g): A = -9.86E_u + 7.70E_b + 2.16E_g, B = -5.17E_u + 20.25E_b - 15.08E_g. Presented are the loci of equally bright monochromatic lights in 10 nm steps and the mixtures of the lights of the ends of the visible spectrum (400 nm and 550 nm), the purple line in 10% steps, which closes the spectral curve. The example shows how the subjective color difference (d = 2) between two stimuli S_1 and S_2 is derived graphically from the diagram according to the city-block metric of the color space by counting the concentric squares around S_1 when approaching S_2 on a straight line or by calculation from the color difference formula: d(S_1, S_2) = |A_1 - A_2| + |B_1 - B_2|

crimination how many photoreceptors are actually involved in color vision (nor can one conclude this from the form of the behavioral spectral threshold function). To answer the question about the number of photoreceptors involved in color vision, a detailed analysis of behavioral data is necessary (Backhaus, submitted).

The ethological approach to color vision. We are very sympathetic to the ethological approach exemplified in Thompson et al.'s last section, although the replacement of "ethological" by "enactive" appears superfluous and is unnecessarily dogmatistic. It is also disturbing that an important distinction for any evolutionary argument is neglected, namely, that between ultimate and proximate mechanisms. The first one refers to evolutionary processes based on genetic variability and natural selection, and works over evolutionarily relevant periods of time. In the case of color vision, ultimate mechanisms have led the sensory-neural systems to incorporate the information about the spectral (and other physical) properties of relevant objects. As a result, the proximate mechanisms appear as the genetically controlled design principles of the whole visual system from the spectral sensitivities of the receptors to the specific neural motor commands. Because relevant objects are often but not always biological systems themselves, with their own potential of ultimate mechanisms, the mutual relationship may be described in part as a codetermining relationship. It is an exaggeration, however, to argue that all environmental factors are evolutionarily shaped by the organism (e.g., the spectral reflection of green leaves has certainly not coevolved with the visual system but

Figure 2 (Backhaus and Menzel). Relationship between photoreceptor spectral sensitivity and wavelength discrimination.
(a) Spectral sensitivity functions of honeybee photoreceptors (best estimate functions, from Menzel & Backhaus 1989). (b) Comparison of the measured spectral discrimination curve (dashed, crosses) of von Helversen (1972) with the spectral discrimination curve (solid, stars) derived by simulation of this experiment with the color opponent coding (COC) model for the measured range (from Backhaus 1991). (c) Spectral discrimination (one over color difference D per 10 nm, adaptation to daylight normfunction D65) as predicted from the color opponent coding (COC) model for the honeybee (from Backhaus 1991) for equally bright monochromatic lights at different levels of relative brightness Q. Q = 0.1: - - - - , Q = 0.5: --- ---, equally bright to the adaptation light Q = 1: - ---, Q = 5: - - - - , Q = 10: - - - - - . The third minimum in the UV-region becomes dominant over the second around 400 nm at higher intensities (Q = 10).
results from the ultimate mechanisms of the photosynthetic machinery.

Ethology, and in particular neuroethology, have a long standing and productive history in providing compelling evidence for the processes involved in coadaptive mechanisms (e.g., Erber et al. 1989). Unfortunately, Thompson et al. do not present any in-depth analysis or any convincing example for this concept as applied to color vision. In essence, it should be possible to derive the informational processes in the sensory-neural system from the physical properties of the biologically relevant signals that have to be best discriminated; and, in reverse, the properties of good discriminable signals (e.g., the spectral reflection must be derivable from the properties of the sensory-neural system. It is true that the approach of Barlow (1982) and Buchsbaum and Gottschalk (1983) is of little help here, because their analysis does not allow specific predictions. If their general engineering attitude is replaced by the neuroethological approach, however, the results should be rewarding.

Such a strategy was recently used successfully in an attempt to understand the adaptive value of the color vision system of flower visiting hymenopteran species. We measured the spectral reflection functions of flowers and leaves in more than 500 insect-pollinated plant species of Israel (Menzel & Shmida, in preparation), and used the spectra to search for the optimal triple set of spectral input functions on the basis of chlordane norm-functions, which apply well to hymenopteran photoreceptors. The criterion for optimal color information is based on the color discrimination between each flower and its natural background under daylight illumination. The measure for color discrimination is derived from the COC model developed for the honeybee (Figure 1). We find that the positions of the maxima of the sensitivities of the three spectral receptor types on the wavelength scale can indeed be predicted from the floral spectral reflectances (Chittka et al. 1990; Chittka & Menzel, submitted) and that agree very well with the positions of the maxima found in more than 40 flower visiting hymenopteran species (Peitsch et al. 1989). It is now possible to examine basic questions such as: (1) Why (on the basis of ultimate mechanisms) is there mostly only one longwave receptor type (max. > 500 nm) if the eye contains a UV-receptor? (2) Why are the maxima of the two longwave receptors very close together on the wavelength scale if there is no UV-receptor? (3) What constraints are imposed by the absolute and the spectral distribution of the illuminating light flux? (4) How does the spectral matching between the predominant background and one of the receptor types (Lythgoe 1979) influence the color vision system? (5) What is gained by tetrachromatic color vision (Chittka & Menzel, in preparation)?

In conclusion, we believe that the neuroethological approach is indeed most promising if it is possible to define what the evolutionarily relevant environment might have been (ultimate mechanisms), and if the assumptions necessary for the model calculations can be well supported by an understanding of the proximate mechanisms of color vision.

**Problems with explaining the perceptual environment**

Aaron Ben-Ze`ev

Department of Philosophy, University of Haifa, Haifa 31999, Israel

Electronic mail: rphb301@haifauxm.bitnet

Moses led the people of Israel for 40 years through the desert and ended up viewing the promised land from a distance. Thompson, Palacios and Varela, in their *Ways of coloring*, lead us through 40 interesting pages (manuscript size) and end up viewing the promised perceptual environment from a distance: they do not really present a positive philosophical account of their proposed approach. Let me say at the outset that I sympathize with their view and find the target article valuable and informative. Despite the controversial character of the topics discussed by the authors, I have hardly any criticism of what they say. On the contrary, their excellent target article deserves considerable praise for its clarity, logical reasoning, and the plausible position it presents. To reiterate the points on which I agree with the authors would exceed the thousand words allocated for this commentary. My criticism then concerns what they omit. The authors discuss various advantages and flaws of subjective and objective approaches to perception in a very relevant and convincing manner, leading us to believe that the presentation of a better approach will follow. No such thing happens. The authors' positive account is very short and hardly goes beyond the statement that the perceptual environment is largely determined by the perceiver's activity.

Thompson et al. place their view in relation to subjective and objective views of perception. Put crudely, subjectivism conceives of colors (and perceptual qualities in general) as a property of the perceiver, whereas objectivism conceives of them as a property of an independent object. The authors refer to recent sophisticated versions of these views and demonstrate their shortcomings convincingly. Once the difficulties at the two poles are presented, the road is open for an alternative. Gibson's ecological approach is a good example of such an alternative. Despite its affinity to Gibson's, the authors wish to place their approach closer to the subjective pole, arguing that a novel tenet of their view—in comparison with that of Gibson and others—that they treat the perceptual environment "not simply as the ecological setting for animal activity, but also as something determined by that very activity" (sect. 3).

Although I agree that the perceptual environment is to a certain extent determined by the perceiver's activity, I do not think this is a novel position. Gibson himself holds this view, arguing that an affordance (which is what we perceive) is "neither an objective property nor a subjective property, or it is both if you like. . . . It is equally a fact of the environment and a fact of behavior. It is both physical and psychological, yet neither" (Gibson 1979, p. 129). I admit that Gibson does not sufficiently elaborate this position and sometimes even contradicts himself precisely because he does not wish to drift too much toward the subjective pole (see Ben-Ze'ev 1984, 1989). Hence Thompson et al. are justified in claiming that with regard to Gibson's view we need to shift the reference point for understanding perception "from the environment to the structure of the perceiving animal" (sect. 3; see also Ben-Ze'ev 1988). The authors' own presentation, however, although more consistent than Gibson's, also lacks the requisite conceptual elaboration of such a problematic position. Nor is the authors' position novel in philosophy. Aristotle already claimed that "the property of the sensible object and that of the sense is one and the same activity, and yet the distinction between their being remains" (*On the soul*, 429b26). Kant also thought that the perceiver's structure determines the perceptual content. Both Aristotle and Kant held this position without assuming (as the subjective position does) that the perceptual environment is in the head. They also realized that the great complexity introduced by their position has to be faced by a complex conceptual framework. Thompson et al. have not attempted to outline such a framework.

The lack of a positive philosophical account for the authors' own approach surfaces in other ontological and epistemological issues. Thus, they rightly claim that the perceptual environment is neither in our head nor is it a property of the physical world, but there is no account of the alternative. It seems to me that the most promising alternative—used by Gibson and others—is the one that takes the notion of different levels of organization into account. To put it briefly: The perceptual environment exists on a psychological level of explanation that presupposes the physical existence of both the perceiver and the world (Ben-Ze'ev 1984, 1991, 1992). Various formulations are possible in