

Ways of coloring: Comparative color vision as a case study for cognitive science

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Abstract: Different explanations of color vision favor different philosophical positions: Computational vision is more compatible with objectivism (the color is in the object), psychophysics and neurophysiology with subjectivism (the color is in the head). Comparative research suggests that an explanation of color must be both experiential (unlike objectivism) and ecological (unlike subjectivism). Computational vision's emphasis on optimally "recovering" prespecified features of the environment (i.e., distal properties, independent of the sensory-motor capacities of the animal) is unsatisfactory. Conceiving of visual perception instead as the visual guidance of activity in an environment that is determined largely by that very activity suggests new directions for research.

Keywords: adaptation; color vision; comparative vision; computation; ecological optics; evolution; objectivism; ontology; qualia; sensory physiology; subjectivism

The study of color vision provides a microcosm of research in cognitive science: Each of the disciplines that compose cognitive science has made significant contributions to our understanding of color. Neuroscientists have had some success in uncovering the anatomical and physiological correlates of color vision in the visual system, primarily in primates (DeValois & DeValois 1975; Livingstone & Hubel 1984; Zeki 1983); cellular biologists have characterized the retinal basis of sensitivity (Brown & Wald 1964; Dartnall et al. 1983; Svaetichin & MacNichol 1958); molecular biologists have isolated and sequenced the genes for the three different types of color-sensitive photopigments in the human eye (Nathans et al. 1986); psychophysicists have contributed quantitative models for human visual performance (Hurvich 1985; Hurvich & Jameson 1957; Jameson 1985); cognitive psychologists have provided models of the structure of human color categories (Heider 1972; Rosch 1973); linguists have shown that human languages contain a limited number of "basic" color terms (Berlin & Kay 1969) and have provided models to derive these semantic universals from properties of the visual system (Kay & McDaniel 1978); researchers in computational vision and artificial intelligence have devised computational models and algorithms for color constancy (Gershon 1987; Hurlbert 1986; Land 1983; Maloney 1985; Maloney & Wandell

1986); and finally, philosophers have discussed the ontological status of color and its implications for theories of mind and perception (Hardin 1988; Hilbert 1987; Thompson 1989).

This target article is intended as a contribution to this ongoing interdisciplinary effort. We propose to offer here a new empirical and philosophical perspective on color vision, one based on recent experimental research in *comparative* color vision – studies of color vision in various animal species. We do not intend to provide a detailed scientific review of current research on this topic (see Goldsmith, 1990; Jacobs 1981; and Nuboer 1986). Rather, we wish to draw on this material, especially recent research on fishes, birds, and insects, to cast new light on some fundamental questions in visual perception, cognitive science, and the philosophy of mind.

Our presentation has three stages. In the first, we provide an overview of various types of explanation for color vision in contemporary visual science, showing how particular types of explanation have been used to motivate various views about what color *is*, that is, about the ontology of color. As we shall see, those who favor objectivism about color, the view that colors are perceiver-independent physical properties (Hilbert 1987; Matthen 1988), rely on computational vision, whereas those who favor subjectivism, the view that colors are internal sen-

sory qualities (Hardin 1988), rely on psychophysics and neurophysiology. In the second stage, we propose a broader comparative and evolutionary perspective on color vision. We present what we call "the comparative argument," which purports to show that an adequate account of color must be *experientialist* (unlike objectivism) and *ecological* (unlike subjectivism). In the third stage, we explore the implications of the comparative argument for vision research. We argue that the typical emphasis in computational vision on optimally "recovering" prespecified features of the environment (i.e., distal properties whose specification is thought to be independent of the sensory-motor capacities of the animal) is unsatisfactory. Instead, visual perception is better conceived as the visual guidance of activity in an environment that is constituted largely by that very activity. Here we present what we call an "enactive" approach to perception (proposed originally by Varela 1979; 1984; 1989; 1991a; and developed subsequently by Varela et al. 1991b). We then suggest some directions for further research that follow from our discussion.

1. Explanation in visual science and the ontology of color

1.1. Levels of explanation: A brief overview

A central concern in contemporary visual science (indeed throughout all cognitive science) is the relation among various levels of generalization and explanation. Following Churchland and Sejnowski (1988), we can distinguish several notions of "level" at work in cognitive science: levels of analysis, of organization, and of operation ("processing"). Because these notions will prove to be of use in our discussion of color vision, we review them briefly here.

In vision research, the notion of levels of analysis is most familiar from the work of Marr and Poggio (1977). In their framework, vision requires analysis and explanation at three different levels: (i) the level of computational theory; (ii) the level of algorithm; and (iii) the level of physical implementation. The computational level is an abstract analysis of the problem or task, which for early vision, according to Marr and Poggio, is the recovery of three-dimensional scenes from ambiguous two-dimensional projections, otherwise known as "inverse optics" (Marr 1982; Poggio et al. 1985). For color vision, the inverse optics problem is to recover the invariant surface spectral reflectances of objects in a scene. The algorithmic level is concerned with the specific formal procedures required to perform a given computational task. Finally, the level of physical implementation is concerned with how the algorithms are physically realized in biological or artificial systems.

It is well known that Marr (1982) claimed that these three levels of analysis were largely independent. In the study of biological vision, Marr also supposed that the algorithmic level corresponds to psychophysics and to parts of neurophysiology, whereas the implementational level corresponds to most of neurophysiology and neuroanatomy (1982, p. 26). This conception of explanation in visual science, especially as applied to the study of natural vision, has generated considerable discussion and debate. Among other things, many dispute Marr's (1982)

claim that the three levels of analysis are largely independent. Some favor a more "bottom up" approach to the explanation of visual processes, and some criticize Marr's assumption of optimality at the computational level, that is, that "what is being computed is optimal in some sense or is guaranteed to function correctly" (1982, p. 19) [see also Schoemaker, "The Quest for Optimality: A Positive Heuristic of Science?" *BBS* 14(2) 1991; and Anderson, "Is Human Cognition Adaptive?" *BBS* 14(3) 1991.] We do not intend to review all of these controversies here.¹ We mention them, rather, as pointers toward some of the issues that will arise shortly when we discuss models of color vision, and when we present our alternative "enactive" approach to visual perception in section 3.

In contrast to the notion of levels of analysis, the notion of levels of organization is relatively straightforward. In the nervous system, we find highly organized structures at many different scales from molecules to synapses, neurons, neuronal ensembles, neural networks, maps, systems, and so on. Each level has properties specific to it, which in turn require different techniques for their investigation. Such organizational complexity is certainly evident in color vision, ranging from the chemical properties of receptor photopigments to the network properties of retinal and cortical cells.

Finally, in addition to these levels of organization, we find many levels of operation in the nervous system. How these levels are to be assigned, however, is considerably less clear than it is for levels of organization. The typical procedure is to order the levels hierarchically from peripheral (lower) to central (higher) areas (measured in terms of synaptic distance from sensory stimulation), thereby suggesting that "processing" in the nervous system proceeds sequentially. We wish, however, to dissociate the notion of levels of operation from the idea that processing among the levels is sequential. If (as we and many others believe) "higher" levels can significantly affect the processing in "lower" levels, then the notion of sequential processing will be of limited application, or at least will have to be modified considerably. To cite just one example that is relevant for our discussion here: Although the visual system is typically described as carrying out sequential processing from retina to lateral geniculate nucleus (LGN) to visual cortex, it is also well known that there are massive back-projections from all areas of the cortex to the thalamic nuclei (Steriade & Deschenes 1985). In the case of the visual system, there are actually more fibers going down from the visual cortex to the LGN than go in the reverse direction (Robson 1983). This organization suggests that neuronal activity in central levels may considerably modulate the activity at peripheral levels, an idea that is also supported by some recent experiments (e.g., Varela & Singer 1987). We set this issue aside here. However the relations among levels of operation must ultimately be conceptualized, it is obvious that there are various levels to be distinguished. For example, in primate color vision, we need to understand at the very least the two-way interactions between operations in the retina, thalamus, striate (V1) and peri-striate (V4) visual cortex.

With these three notions of "level" in hand we can now turn specifically to color vision. In the remainder of section 1 we give a brief overview of the types of explanation offered for color vision, showing how they have been

used to motivate contrasting philosophical positions on the ontology of color.

1.2. Color space: Psychophysics and neurophysiology

In general, psychophysics and neurophysiology have taken as their point of departure what is known as "color space." This is the closed space formed by the three semi-independent dimensions of color known as hue, chroma or saturation, and value or brightness (Figure 1).² Hue obviously refers to the redness, greenness, yellowness, or blueness of a given color. Saturation refers to the proportion of hue in a given color relative to the achromatic (white-black) dimension: Saturated colors have a comparatively greater degree of hue, whereas desaturated colors are comparatively closer to gray. Brightness refers

to the achromatic or white-black dimension. In this space, colors can be seen to exhibit certain relations among themselves, such as the hue-opponency of red and green, and yellow and blue. These kind of relations compose what we call the *phenomenal structure of color space*, or simply the *phenomenal structure of color*.

How are we to explain the generation of this phenomenal structure? Why does (our) color space have this phenomenal structure and not some other? It is primarily this question that has motivated the psychophysical and neurophysiological study of color vision. Rather than review this enormous field, we present merely a few points that are relevant for our purposes in this paper.³ The basic idea is to provide a mapping from the phenomenal color space of Figure 1 into a new color space whose coordinates correspond to psychophysical and/or neurophysiological processes relevant for color vision. We call the axes of these new color spaces "color channels." Strictly speaking, channels are specified psychophysically and so are not isomorphic with unique neuronal pathways (Boynton 1988, p. 77), but we intend to use the term "channel" both in this psychophysical sense and somewhat more loosely to refer to underlying neurophysiological processes (such as color opponent receptive field properties) that can be studied at various levels of analysis, organization, and operation.

We should note that the following maps of color space are idealized. We do not intend to suggest that they provide full-fledged "linking propositions" needed to identify chromatic perceptual states and states of the visual substrate (see Teller 1984; 1990; Teller & Pugh 1983). Visual science is still far from being able to provide the full story of how the activity in multiple neuronal areas becomes integrated to form our experience of color. Our intention, however, is simply to provide some illustrations of the kinds of covariance that have been established between aspects of the phenomenal and the biological.

We begin with the three kinds of retinal cones, short-wave ($S^1 = S$), medium-wave ($S^2 = M$), and long-wave ($S^3 = L$), which respond with a differential sensitivity to wavelength according to the photopigment they carry in their outer segments (Figure 2a, bottom). At this level, we can construct a rudimentary map of color space whose coordinates correspond to the relative activity of the cones, which are present (in various proportions) at each point of the visual field. This map corresponds to a vector $\vec{s}_r = \langle S^1, S^2, S^3 \rangle(\vec{r})$, where \vec{r} is the surface coordinate. A convenient representation is a (Maxwell) triangle (Figure 2b) instead of a 3-D graph to depict the spectral loci of monochromatic lights: The three kinds of cone receptor appropriately adjusted in activation are required to match a test-light of any spectral composition and intensity. This property corresponds to the *trichromacy* of normal human color vision.

We refer to this mapping of color space as "rudimentary" because it takes into account only the relative absorptions of the cone photopigments. Postreceptor cells, however, both combine and compare (subtract) cone signals, thereby giving rise to three new types of color channels: two opponent chromatic channels (R-G, Y-B) and one nonopponent achromatic channel (Wh-Bk), which can be found in primates at the retinal and thalamic levels (Figure 2c). These new channels result, then, from

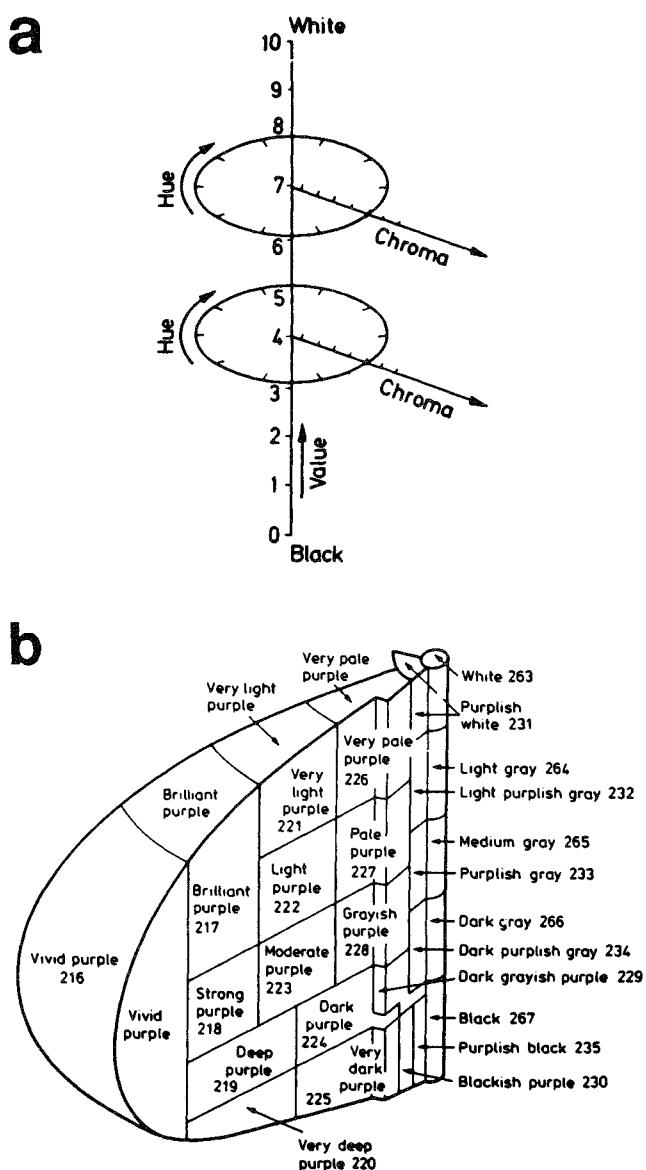
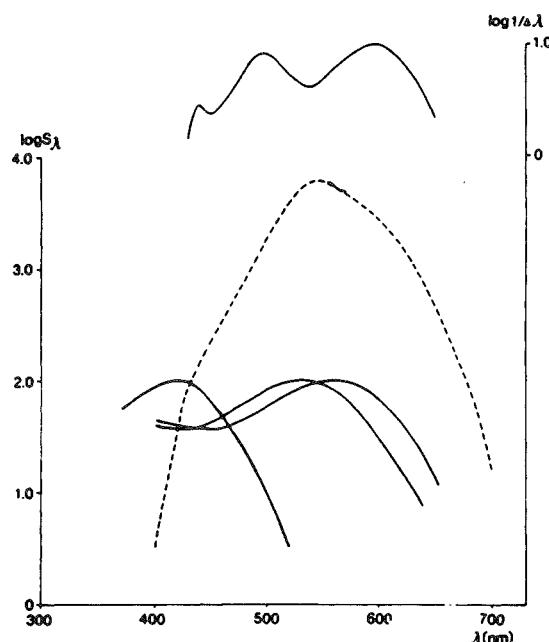
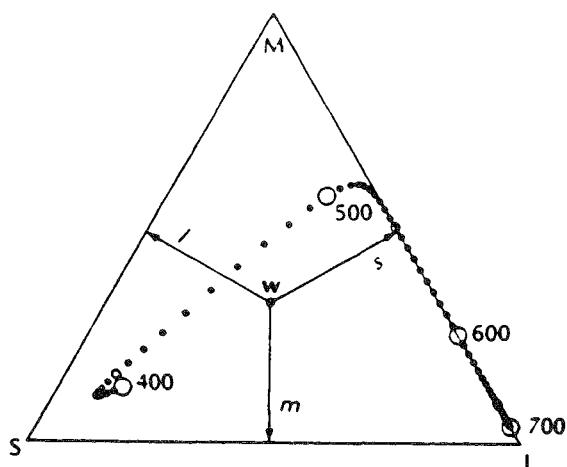


Figure 1. The phenomenal structure of human color space. (a) The three-dimensional space of hue, saturation or chroma, and brightness. We use here the standard Munsell color space. (b) A slice in color space for the purple sector (Munsell values 3P–9P), using the ISCC-NBS color names (or equivalent centroid numbers).

a



b



c

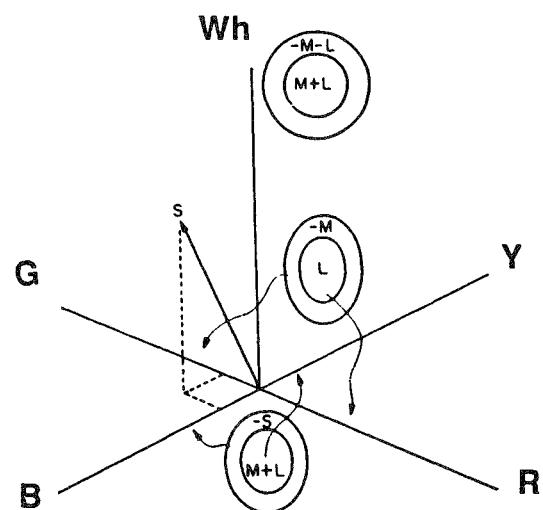
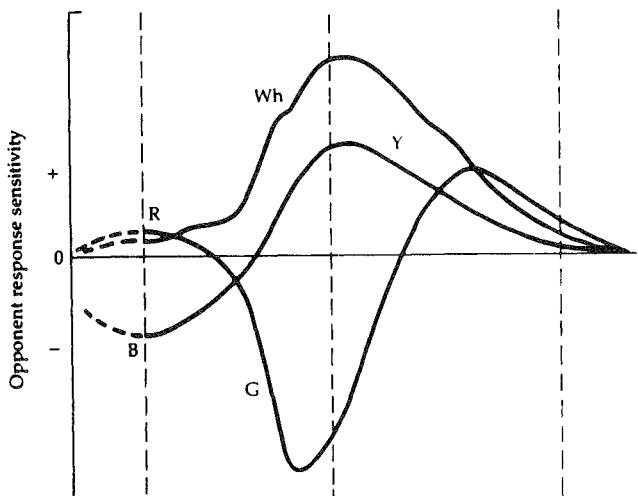


Figure 2. Biological mappings of human color space at various levels. (a) The spectral absorption of human cone pigments and the overall photopic sensitivity curve for humans (in discontinuous lines). In the upper part a plot of the wavelength discrimination curve (reciprocal of the just noticeable difference in wavelength necessary for wavelength discrimination). Modified from Nuboer (1986). (b) For any light, the relative Long/Medium/Short wave length absorptions (L , M , S) can be plotted as relative activity on a Maxwell triangle with orthogonal axes l , m , s of unit length. The loci of pure spectral colors are shown calculated by normalizing the pigment spectra for equal

areas and computing the quantum catch. Equal absorption for all three areas is labelled as w . From Goldsmith (1990). (c) On the left, opponent neural system obtained by the weighted excitatory and inhibitory responses between retinal elements. On the right, a diagram showing how each of these channels can be used to provide a set of axes for color space. The Wh-Bk (White-Black) channel receives excitatory input mostly from L and M cones, whereas the two antagonistic channels receive both excitatory and inhibitory inputs: $+L - M$ for the R-G (Red-Green) channel, and $(M + L) - S$ for the Y-B (Yellow-Blue) channel. From Hurvich (1981), and Ingling and Tsou (1977).

d

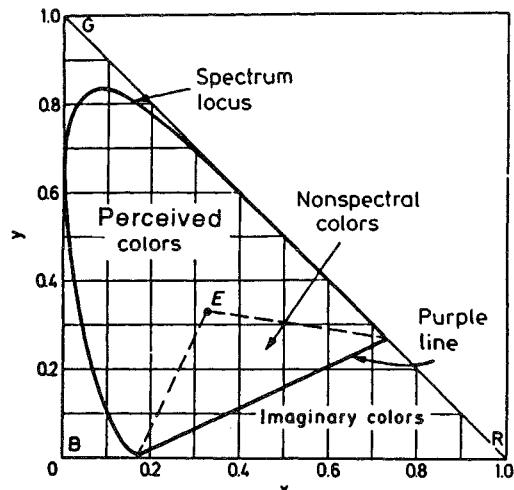


Figure 2(d) Chromaticity diagram computed from the three CIE (Commission Internationale de l'Eclairage) 1931 color matching functions. As in (b) the relative activities have been normalized so that two values suffice to locate all points in this modified triangle.

linear combinations of the receptor activations, which can be written vectorially as $\vec{c}_r = M \cdot \vec{s}_r$, $\vec{c}_r = \langle C^1, C^2, C^3 \rangle (\vec{r})$, with $C^1 = Wh-Bk$, $C^2 = R-G$, $C^3 = Y-B$. The matrix M for constructing the channels is at the core of various color vision theories (Wyszecki & Stiles 1982); we return to provide an algorithm for its determination below in section 2. These three color channels proper can be used to provide a set of axes for color space (Figure 2c). This diagram thus displays the trivariate of human color vision mapped onto the three dimensions of color space at the physiological level.

This mapping, too, has limitations, for it relies on an analogy between the existence of opponent colors and the existence of chromatically opponent cells, which though obviously promising nonetheless neglects many details of the fit between properties of color perception and the properties of these peripheral cells (Hood & Finklestein 1983; Teller 1990). It also does not take into account the multilevel neuronal interactions in the visual pathway that somehow constitute our entire experience of color (Livingstone & Hubel 1984; Zeki 1983).

To obtain axes more appropriate for this level we need to use psychophysical global response functions. The functions chosen will depend on which aspect of color experience we are interested in quantifying more precisely, for example, chromatic sensitivity, discrimination, or color mixing (see Wyszecki & Stiles 1982). For our purposes here, one useful standard set comprises the empirically determined CIE (Commission Internationale de l'Eclairage) color-matching functions $\langle x, y, z \rangle (\lambda)$, which specify the well-known human chromaticity diagram (Figure 2d). To project our three-dimensional color space into this two-dimensional plane we equalize for brightness. At the center is the achromatic neutral (white/gray) point; movements away from the point indicate an increase in saturation, with the maximally saturated hues along the periphery. In this chromaticity diagram, we find complementary colors at the opposite ends of the

space, the pure spectral locus at the outermost boundary, and the purple range as "nonspectral" loci. Thus any color we perceive can be matched in this space by an appropriate value of the underlying channels (global response functions). It should be made clear that although strictly speaking the CIE diagram is a *stimulus* space, the stimuli are useful in characterizing color experience by mapping its extent, and so the CIE diagram can be read as a mapping of one aspect of color experience. (This point will also apply to the relation between the stimulus spaces and color perception in other animals as discussed below).

These color-matching functions were derived mostly for purely psychophysical and industrial purposes and so are not particularly useful as a guide to underlying neuronal processes. Nevertheless, they do provide a more precise and quantitative way of mapping some aspects of the phenomenal structure of color space. It should be noted that alternative color channels motivated by computational algorithms (Land 1983) and perceptual and neurobiological data (Zeki 1980; 1983; 1985) have been proposed by taking into account the global integration properties of visual mechanisms, because a local description (i.e., independent of the rest of the visual field) violates perceptual evidence and neurophysiological data. For example, Land (1983) proposes three lightness "indicators," which result from discarding the illuminant from the receptor activity after long-range integration of local values.

We have now provided enough illustrations of the various neurophysiological and psychophysical mappings of color space for this target article. Henceforth, we will use the term "color space" to refer to this kind of composite representation in which the phenomenal structure of color and the structure of the visual system covary. For our purposes here, then, color space refers to the following multilevel description:

- (i) receptor space: the raw array of local activity under given illumination conditions in a scene;
- (ii) "lightness" indicator space: the globally integrated activity at various levels after discarding the illuminant from the receptor space via lateral interactions;
- (iii) physiological channels space: the local activity of subtraction and addition of integrated values to conform to antagonistic mechanisms obtained from indicator values;
- (iv) psychophysical channel space: the perceptual, high-level integration into separable mechanisms, obtained on the basis of the underlying physiological activity relevant to color channels;
- (v) phenomenal space: the color appearance space of hue, saturation, and brightness.

The main task of the psychophysical and neurophysiological study of color vision is to uncover the appropriate biological processes underlying all these levels and to formulate, test, and establish the "linking propositions" needed to relate the various levels (Teller 1984; 1990; Teller & Pugh 1983). As a matter of general principle, however, it is clear that the phenomenal structure of color covaries with the structure (and, as we shall see later, the ecological interactions) of the perceiver. If we wish to explore this fact, we should determine whether and how changes in the structure (and ecological interactions) of the perceiver can be correlated with changes in the phenomenal structure that color exemplifies. This is the main task of this target article.

1.3. Computational color vision

A full explanation of color vision requires that we also understand how color appearances remain relatively stable or constant in natural light environments – a phenomenon known as *color constancy*. Computational color vision is particularly concerned with this phenomenon. Because the retinal activity from a given point hopelessly confounds the illumination with the reflectance properties of surfaces, the core problem is to disentangle these variables and assign colors that correlate with surface properties.

In what follows, the ideas we present naturally take a mathematical form, which cannot be simplified without losing some important features. The nonmathematical reader can skip the formulae, however, without losing the basic points we need for our argument here. (Our presentation throughout this section is indebted to the more detailed treatment in Hurlbert 1989, ch. 3).

Most computational models simplify the overall situation by considering only the surface reflectance (or albedo), which depends on object properties, not on viewing geometry, as in [1]:

$$I(\lambda, \vec{r}) = \rho(\lambda, \vec{r})E(\lambda, \vec{r}) \quad [1]$$

where I is the irradiance, λ is wavelength, E is the surface illumination, and ρ is the reflectance, and \vec{r} , as before, is the surface coordinate. The irradiance affects an array of sensors which have a specific nonlinear response function $R^i(\lambda)$, $i = 1, \dots, n_{recep}$, comprising a number of different cone classes (e.g., for primates $n_{recep} = 3$). Under these conditions the raw receptor response corresponding to a point \vec{r} from a surface is the integral:

$$S^i(\vec{r}) = \int_{\text{visible window}} d\lambda R^i(\lambda)\rho(\lambda, \vec{r})E(\lambda, \vec{r}) \quad [2]$$

We have written “visible window” simply to indicate the extent of the wavelength sensitivity depending on the species being considered. For primates, this “visible” range is approximately 400–700 nm; for insects it shifts down to approximately 310–590 nm; in birds it broadens to approximately 350–720 nm.

As we mentioned above, the computational approach to color constancy is a prime example of inverse optics – the recovery of what are taken to be objective attributes of three-dimensional scenes from ambiguous two-dimensional projections. In the case of color vision, the problem is to discard the source illuminant E and retain the invariant spectral reflectances ρ of object surfaces given only the retinal activity S . This problem – like inverse optics problems generally – is underscored or ill-posed. (Poggio et al. 1985). To solve an ill-posed problem one must restrict the class of admissible solutions by introducing constraints; these constraints are said to “regularize” the problem. In the case of color vision, a combination of empirical evidence and task-level analysis has shown that these constraints are basically of three kinds: (i) low-dimensional models of lights and reflectance; (ii) global computations; and (iii) spatial segmentation.

1.3.1. Low dimensionality. Naturally occurring illuminants and object reflectances can be described as lying within a low-dimensional space: A few basis functions, when added together in the correct proportions, suffice to

span the entire diversity of actual lights and reflectances. Formally expressed this becomes:

$$\begin{aligned} E(\lambda, \vec{r}) &= \sum_{j=1}^{n_{illum}} \varepsilon_j(\vec{r})E_j(\lambda) \\ \rho(\lambda, \vec{r}) &= \sum_{k=1}^{n_{reflec}} \zeta_k(\vec{r})\rho_k(\lambda) \end{aligned} \quad [3]$$

where E_j and ρ_k are basis functions, and ε_j and ζ_k are spatially varying coefficients. On the basis of empirical evidence from measurements of typical ambient conditions and object reflectances, n_{illum} and n_{reflec} are usually taken to be 3 or at most 6 (Maloney 1985). It is typically further assumed that illumination is quite uniform over space,

$$E(\lambda, \vec{r}) = E(\lambda), \varepsilon_j(\vec{r}) = \varepsilon_j \quad [4]$$

and that reflectance is invariant under changes in viewing geometry (i.e., a Lambertian reflection model). Thus, computational color vision is fundamentally constrained by the low dimensionality of *both* the stimuli and the receptor types, because these are known to come in small numbers.

Under these conditions the irradiance equation [2] takes the general form:

$$S^i(\vec{r}) = T^{ik}(\varepsilon)\zeta_k(\vec{r}) \quad [5]$$

where

$$T^{ik}(\varepsilon) = \sum_j \varepsilon_j \tau_{jik}, \tau_{jik} = \int d\lambda R^i(\lambda)\rho_k(\lambda)E_j(\lambda) \quad [6]$$

The matrix, $T^{ik}(\varepsilon)$ (which Maloney calls the “light transformation matrix”), depends on the illuminance and reflectance basis functions, the sensory sensitivities, which are fixed, and the illuminant, which is variable. Clearly, since this matrix and the $\zeta_k(\vec{r})$ are, in general, not entirely known, the equations are underdetermined, and to find solutions further constraints need to be introduced. These take various forms. For example, Buchsbaum (1980) requires that a weighted average of all reflectances in a given scene be known. In contrast, Maloney and Wandell (1986), and Yuille (1984), assume that there is at least one more sensor type than there are reflectance components. This assumption obviates the need for the previous ones, and exploits instead the various sensors at each location. For instance, using only photoreceptors, these algorithms would recover constant colors for materials that can be described using no more than two basis functions. Finally, D’Zmura and Lennie (1986) introduce eye movements and light adaptations to recover illuminants.

1.3.2. Global computations. The foregoing discussion focused on the quality of the light signals and the number of receptors, but it did not take into account the way the local activity of a photoreceptor, $S^i(\vec{r})$, is not the most significant variable. More relevant to account for color constancy and chromatic induction is the interaction of receptor activity over distant places in the visual scene, which transforms luminance (a quantity which expresses a local level of activity) into “lightness,” $L^i(\vec{r})$, a level of activity closer to reflectance (and one that is relative to

other levels of activity in the scene). These global interactions can all be understood as a manifestation of the lateral interactions and reentrant circuits typical of both the retina and parts of the visual system, which lead to internally specified values rather than raw sensory values.

There are a number of equivalent “lightness” algorithms (Hurlbert 1986). In general, though, lightness algorithms proceed by (i) taking a differential of values of the intensity over different locations of space; (ii) applying a threshold operation that eliminates small values because of smooth changes in the illumination and retains large values resulting from abrupt changes in reflectance at the borders between patches; and (iii) integrating the result of this operation back into reflectance values for each position in space. For example, one of the first algorithms, proposed by Horn (1974), obtains lightness by simulating a diffusion of the activity of one receptor over the entire layer. Mathematically, this is expressed as a solution to the Poisson equation on the receptor activity:

$$\nabla^2 L^i(\vec{r}) = \theta[\nabla^2 S^i(\vec{r})] \quad [7]$$

where $\theta[.]$ is a thresholding operation performed on the Laplacian operator ∇^2 , which embodies the neural lateral interactions. When the sensor array is finite, and surrounded by a constant boundary condition, [7] can be solved explicitly. More recently, global computations have been approached by noticing that each sensory receptive field has an excitatory center and an inhibitory periphery that can be seen as a filter for the light signal. It is also known that these receptive fields have various sizes and degrees of steepness. Thus, a family of recent algorithms assumes that the sensor array is convolved through a center-periphery profile at each point of the visual scene (Land 1986) and at various scales (Hurlbert 1986). In this case:

$$L^i(\vec{r}) = \int_{\text{Scale range}} d\mu \int_{\text{Region}} d\vec{q} \Theta[\nabla^2 G(\vec{r} - \vec{q}; \mu) S^i(\vec{q})] \quad [8]$$

where G is a Gaussian function, with a continuum of parameters μ . The Laplacian of G is roughly equivalent to a difference of Gaussians (DOG function), similar to receptive fields. Expression [8] degrades when approximated in the discrete case, but sums over ten scales of μ yield reasonable lightness values for so-called “Mondrian” scenes (displays consisting of about 100 different colored papers arranged arbitrarily that resemble the paintings of Piet Mondrian).

1.3.3. Spatial segmentation. Even with low-dimensional constraints and network global computations, reflectances are still underdetermined. One missing key element is the way a scene is segmented into the relevant patches on which the calculation of reflectance will be performed. Some extra assumptions about surfaces (abruptness of change, distributed averages, etc.) must therefore be brought to bear. These assumptions in part miss the purpose of color vision, which is presumably important in object discrimination and identification (D’Zmura & Lennie 1986), a point to which we return in later sections. The overall effect of segmentation is to make reflectance values correspond not to local scene coordinates r , but to regions σ , yielding lightness values

over *regions*, L_σ^i , $\sigma \in \Sigma$. One of the better known segmentation algorithms is the one from Rubin and Richards (1982; 1988), which seeks to determine where material changes occur in a scene using only spectral intensity responses in separate points on the retina. For example, we can state this idea by considering two different receptors, which will have a spectral crosspoint on opposite sides of an edge when:

$$[S^i(\vec{r}_1) - S^i(\vec{r}_2)][S^j(\vec{r}_1) - S^j(\vec{r}_2)] < 0 \quad [9]$$

If the product is negative, one channel increases while the other decreases. Such a crosspoint will be produced only by material changes, under such simplifying assumptions as uniform illumination. In addition, one can consider the signs of the slopes of each response function (opposite slope sign condition). There are conditions in which these algorithms will not segment a scene into material discontinuities but will give false positives because of shadows, occlusions, or illuminant variations.

Another model for segmentation is provided by D’Zmura and Lennie (1986). In this model, mechanisms of light adaptation (“a multiplicative change in sensitivity in the independent cone mechanisms followed by an adaptive linear transformation of scaled cone signals at color-opponent sites” [p. 1670]), combined with eye movements that expose the eyes to the average light reflected from the field of view, are used to evaluate and discount the illuminant, thereby recovering reflectance designators. This scheme does not rely on a prior segmentation of the scene. Instead, the designators are transformed to yield estimates of hue, which is, compared to saturation and lightness, relatively independent of object shape and viewing geometry. These hue estimates can then be used in the task of segmentation.

These three elements – low-dimensional constraints, global integration, and scene segmentation – must come together for artificial systems to regularize the ill-posed problem of recovering reflectance. Since the assumptions introduced are about the natural world, they can be expected to fail when they are not satisfied in the world. For example, with a few exceptions (e.g., D’Zmura & Lennie 1986) most current computational algorithms do not perform well in the presence of significant specular components; the algorithms require a virtually uniform illumination, and the collection of surface reflectances must average to the same “gray” in every scene.

Our purpose is not to provide a comprehensive discussion of computational color vision. Enough has been said to indicate that there are at present different approaches to color vision, which focus on different respective kinds of color phenomena: On the one hand, we have computational theories of color constancy, on the other hand, psychophysical and neurophysiological investigations of a range of such chromatic phenomena as constancy, contrast, color matching, color blindness, and so on. At the present stage of research, the question of how these approaches to color vision might be related does not admit of a clear and nonpartisan answer. Only a handful of studies explore possible links among the various levels of analysis and kinds of phenomena – for example, Zeki’s (1980; 1983; 1985) neurophysiological studies of the cortical mechanisms underlying color constancy, or Buchsbaum & Gottschalk’s (1983) formal analysis of opponent color mechanisms. This question does raise a number of

conceptual and empirical issues, however, which in turn have considerable implications for the ontology of color.

1.4. Current ontologies

To discern these issues consider that human color vision exhibits only *approximate* color constancy. Many factors can affect constancy; among the best documented are the effects of sensitivity to the spectral quality of the illumination (Helson 1938; Helson & Jeffers 1940; Judd 1940). As Jameson and Hurvich (1989, p. 7) note in a recent review: "Departures from perfect color constancy with changes in the spectral quality of illumination . . . imply that perceived contrast between objects of different surface reflectance varies with the level and kind of illumination in which they are seen and to which the visual system is adapted."

From the standpoint of the computational level of analysis, the approximate constancy of human color vision is not surprising. For example, in Maloney & Wandell's (1986) model, surface reflectance can be completely recovered only if there are more sensor types than degrees of freedom in reflectance. Since naturally occurring reflectances require 3 to 6 degrees of freedom for their full specification (Maloney 1985) and human color vision is trichromatic (3 receptor types), Maloney & Wandell's model predicts that there are chromatic differences among naturally occurring surface reflectances that cannot be detected by a trichromatic system (assuming, of course, that no other kind of disambiguation is available).

So far, then, we have an overall agreement between psychophysics and computational vision. The problems arise when we ask how the approximate constancy of natural color vision is to be *explained*. It is in the kind of answer given to this question that we find the motivation for current views on the ontology of color.

Starting from the computational level of analysis as outlined above, we assume that the function of color vision is the achievement of color constancy, defined as the recovery of the invariant surface spectral reflectances in a scene. We then are led to explain approximate color constancy as a departure from ideal or perfect color constancy, the implication being that such a departure constitutes a visual shortcoming or error (cf. Maloney & Wandell 1986, p. 32). Obviously, once such a conceptual framework is in place, it is natural to suppose that color is simply the property of surface spectral reflectance. Thus, consider the following passage from Maloney (1985):

The analyses of Chapter 2 [those presenting finite-dimensional linear models of lights and reflectances] used data appropriate to human environments and suggested that what we call color corresponds to an objective property of physical surfaces. Depending on the lights and surfaces present in a scene, we succeed or fail in estimating these properties. Failures of color constancy, from this viewpoint, can be considered as visual illusions. We misestimate true color as we might misestimate true height in an Ames room (p. 119).⁴

We might wonder, however, whether this "top-down" computational approach, although consistent with the approximate constancy of natural color vision, should be accorded the status of an explanation. If we wish to design a visual system that exhibits complete constancy, and the system exhibits only approximate constancy, then we are

justified in saying that the system does not perform optimally, that it fails to achieve the task *for which it was designed*. But because natural color vision presumably resulted from evolutionary tinkering involving "trade-offs" rather than optimal design, why should the approximate constancy of natural color vision be explained by appealing to such a strong, engineering notion of optimality? Furthermore, even if natural color vision is in some sense optimal (relative to a given species and its niche), it might exhibit approximate constancy for biological and ecological reasons that preclude designating this kind of constancy as involving visual error. For example, most computational approaches seem to assume that color vision is concerned primarily with the reflecting properties of surfaces. As a result, illumination conditions are treated merely as something to be "discounted" in the task of recovering reflectance. Natural color vision appears to be concerned with illumination conditions in their own right, however, for these provide indications about weather conditions, time of day, and so forth (Jameson & Hurvich 1989). To emphasize color constancy at the expense of sensitivity to the illumination in its own right would therefore seriously prejudge the behaviors that natural color vision serves.

Consider, then, what happens if we proceed in a more "bottom-up" direction by taking the performance of natural color vision and its biological embodiment as our reference point. Here our point of departure is color space and its dimensions. That color constancy is only approximate provides an example of how these dimensions (hue-saturation-brightness) can shift depending on the state of the perceiver and the conditions of viewing. We therefore give more attention to the local, context-dependent features of perception than to the high-level, physically invariant properties of the environment. Furthermore, because our point of departure is color understood phenomenally, we are less likely to play favorites among the different ways colors can be encountered. For example, afterimage colors as well as surface colors require explanation. These both count as genuine color phenomena because they exhibit the three dimensions of hue, saturation, and brightness. It therefore becomes natural to identify color with this phenomenal structure. And because this structure does not reduce to properties of either light waves or surface reflectance (more on this later), we will probably be led to embrace subjectivism. Thus, consider the following passage from the conclusion of Zeki's (1983) pioneering study of cortical cell responses to both surface colors and after-image colors:

The results described here . . . suggest that the nervous system, rather than analyze colors, takes what information there is in the external environment, namely, the reflectance of different surfaces for different wavelengths of light, and transforms that information to construct colors, using its own algorithms to do so. In other words, it constructs something which is a property of the brain, not the world outside. (Emphasis in original, p. 764)

If we compare the above passage from Maloney (1985) with this remark of Zeki's, we can see that despite the considerable advances made in the study of color vision in recent years, disagreement remains among vision researchers on the ontology of color. Ontology is more the specialty of philosophers, but they do not agree either. In

fact, the two positions just outlined, with their respective links to computational vision and to neurophysiology, correspond precisely to the most recent discussions by philosophers: Hilbert (1987) and Matthen (1988) defend objectivism largely on the basis of computational color vision (Maloney & Wandell's model and Land's retinex theory); Hardin (1988) defends subjectivism largely on the basis of neurophysiology and psychophysics (opponent-process theories).

Two basic claims constitute Hilbert's version of objectivism. First, the centerpiece of his position is the typical objectivist claim that we must distinguish between color as an objective property of the world and color as we perceive it. For Hilbert, each objective color is identical with a distinct spectral reflectance. Objects that have identical surface spectral reflectances have the same color; objects that have different surface spectral reflectances have different colors. Second, Hilbert claims that since our color perception and color terms are indeterminate with respect to surface reflectance, they give us only "anthropocentrically defined colors and not colors themselves" (p. 27). For Hilbert, "red," "green," "yellow," and "blue" do not name determinate spectral reflectances; rather, they name indeterminate kinds of spectral reflectance whose specifications are arbitrary from a purely physical standpoint, but nonetheless of interest in relation to the structure of the human visual system. Hilbert accordingly calls his position "anthropocentric realism."

Matthen (1988) defends a similar view by first developing a theory of perceptual content. In his view, perceptual states have content because they have the function to detect things of a certain type. Matthen then argues on the basis of Land's retinex theory (Land 1977; 1983) that the function of color vision is to detect surface reflectance. Because Matthen identifies the contents of types of chromatic perceptual states with the distal property they supposedly have the function to detect, he is naturally led to claim that color simply is that distal property, namely, surface reflectance.

Hardin (1988), on the other hand, develops an extensive argument against objectivism, which consists of two basic points: First, surface spectral reflectance is only one of the many kinds of stimuli that can give rise to color experience; second, the properties of color – for example, the uniqueness and binariness of hue and hue-opponency – cannot be found in properties of the (distal or proximal) physical stimuli for color vision. The second is the more important point, for it consists in the claim that there is no mapping from physical stimuli to phenomenal color space that is sufficient to ground objectivism. As we saw above, however, there are mappings from color space to the visual system at various levels of organization and operation. Hardin relies precisely on these kinds of mappings, especially opponent-process theories, to support his subjectivist view that there are no "extradermal" colored objects; there are only chromatic perceptual states. In his words: "Colored objects are illusions, but not unfounded illusions. We are normally in chromatic perceptual states, and these are neural states . . . We are to be eliminativists with respect to color as a property of objects, but reductivists with respect to color experiences" (pp. 111–12).

We refer to these two positions as "computational

objectivism" and "neurophysiological subjectivism," respectively, thus highlighting the link between current color ontologies and explanation in visual science. The debate between these two positions has so far proceeded with computational objectivists downplaying the phenomenal structure of color and neurophysiological subjectivists responding by emphasizing the context-dependent, approximate constancy of human surface color perception.

Our intention in the remainder of this target article is to move beyond this debate by offering a broader empirical and philosophical perspective grounded in comparative color vision. Before we proceed, let us lay our cards on the table. With respect to the debate as outlined so far, we are fundamentally in agreement with Hardin's claim that "every attempt . . . to type-identify chromatic sensory states in terms of their stimuli is fundamentally misguided" (1989, p. 3). Nonetheless, we believe that Hardin's neurophysiological subjectivism is far too restrictive, for there are dimensions of color vision that do not yield to analysis purely in terms of the neurophysiological structure of the perceiver. These dimensions are, we argue, ecological. Hardin (1990) has recently begun to emphasize some of these dimensions, but we believe he has not gone far enough. On the other hand, although computational objectivism does emphasize the environmental context of color vision, it usually does so in a profoundly unbiological and uneccological way by making animal-independent, distal properties the ultimate point of reference.

2. The comparative argument

2.1. Overview

Two pervasive phenomena of natural color vision form the basis for the comparative argument:

1. Animals whose neural apparatuses have little in common beyond the peripheral photoreceptor level (e.g., insects, fishes, birds, and primates), and that inhabit considerably diverse environmental contexts, nonetheless possess color vision.

2. Despite this commonality, color vision varies across species and animal groups. Among the most salient variations are the *type* (dimensionality) and *amount* (sensitivity) of color vision and its neural substrates. These variations imply different phenomenal color spaces, some of which are incommensurable.

These two phenomena constrain any attempt to explain color vision and the ontology of color. Our claim is that they constrain such a theory to be *experientialist* and *ecological*: Color can be understood only in relation to the visual perception of a given individual or species (contrary to objectivism); but such visual experience can be understood only in the context of its ecological embodiment (contrary to subjectivism).

Consider (1) first. Why do so many species of invertebrates, nonmammalian vertebrates, and mammals possess color vision? To answer we must appeal not only to comparative physiology, but also to the evolutionary histories of seeing animals (probably at several levels of selection), to common features among the diverse environmental contexts of color vision, and to changes in the

environment that are a function of animal-environment coevolution (we mention examples later).

These ecological dimensions of color vision have generally been taken to support computational objectivism. Among computational visual scientists, the argument (which usually goes unstated) is that because color vision is biologically pervasive, the evolution of color vision must consist in various species devising their own unique “solutions” to the information-processing problem of recovering surface reflectance in their respective environments. Among philosophers, this argument takes the form we reviewed above: The contents of perceptual states are to be type-identified by the (distal) properties they have the function to detect; the function of color vision is to detect surface reflectance; therefore color can be identified with surface reflectance (Matthen 1988).

In this section, we argue at some length against this view on the basis of (2) above, which develops into three related points:

(i) The properties of color, especially of different and sometimes incommensurable color spaces, cannot be modelled on the basis of properties of physical stimuli like surface reflectance. Hence color cannot be identified with surface spectral reflectance.

(ii) Given considerable variation in the dimensionality and sensitivity of color vision, and given a role for color vision in determining the boundaries of surfaces, the segmentation of the visual scene and therefore of what counts as a distinct surface to be perceived may in fact be relative to the structure of the perceiving animal. Thus surfaces may themselves be relational like color, providing no animal-independent anchor for objective color as surface spectral reflectance.

(iii) Natural color vision is concerned not just with detecting surfaces but also with a variety of other tasks in various terrestrial, aquatic, and aerial contexts. Among these are the discrimination of illumination conditions and the generation of a set of perceptual categories that have “cognitive significance” for animals in a variety of interactions. For these reasons, it is a mistake to suppose that the one and only (or even primary) function of color vision is the recovery of surface spectral reflectance.

Because each of these points rests on the idea of differences in color space, we begin by discussing the evidence for the existence of different kinds of color space among perceiving animals.

2.2. The color space of other animals

It is tempting to assume that our visual abilities provide the norm for understanding color vision. This assumption might be justifiable if humans – or our primate relatives – were unique in possessing color vision. In reality, however, color vision is widespread throughout the animal world. Indeed, it seems that virtually every animal class has some species with trichromatic vision (Jacobs 1981, p. 153). But it would also be a mistake to take trichromacy as the norm. Many animals are *dichromats* (e.g., squirrels, rabbits, tree shrews, some fishes, possibly cats and dogs, some New World monkeys); others appear to be *tetrachromats* (e.g., goldfish, the Japanese dace, turtles), perhaps even *pentachromats* (pigeons, ducks).

Before discussing the evidence for higher dimensional color spaces, it is important to consider how color vision

also varies considerably in its amount or sensitivity as determined by the spectral sensitivity, wavelength discrimination, and colorimetric purity functions. By measuring these functions for various animals, one can compare their overall sensitivities to spectral stimuli, their abilities to discriminate on the basis of wavelength, and whether spectral stimuli appear more or less saturated.

Each of these functions will differ for color vision of different dimensionality. The wavelength discrimination curve is of particular interest here, for it can also be taken as an indication of the type of color vision system: A maximum or minimum is expected where there is a crossover between two primary responses. For example, our three primaries are revealed in our wavelength discrimination curve, which has two maxima (Figure 2a, top). These maxima correspond to the two regions in the spectrum where our hue discrimination is finest (580nm and 470nm). The curve for the goldfish, however, shows three regions of best hue discrimination at 610nm, 500nm, and 400nm (Neumeyer 1985, 1986). This finding suggests that the goldfish has four active primaries and so is potentially a tetrachromat (Crawford et al. 1990; Neumeyer 1988). In contrast, the wavelength discrimination curve for the pigeon shows four regions of best hue discrimination at 390nm, 450nm, 540nm, and 600nm (Emmerton & Delius 1980), suggesting that the pigeon has five active primary mechanisms, and so is potentially a pentachromat. Three of the minima not including the one at 390nm in the UV region are shown in Figure 4c (Palacios et al. 1990a).

The three functions also differ among animals that have color vision of the same dimensionality, among “normal” and “anomalous” individuals, and even among “normal” individuals. To cite examples of each kind of variation: (i) Humans and forager honey bees are both trichromats, but bee color vision is shifted toward the ultraviolet, with the points of best hue discrimination at about 400nm and 490nm (Menzel 1979; 1989), as can be seen in Figure 3, which also shows the receptor-level and the opponent channel color space for these insects. (ii) For normal human trichromats, spectral sensitivity peaks at about 555nm; the spectral sensitivity of deuteranomalous trichromats, however, is shifted toward longer wavelengths, whereas that of protanomalous trichromats is shifted toward shorter wavelengths. (iii) Finally, each of the three functions can differ slightly among “normal” individuals: For example, men and women appear to differ in their color mixtures (Neitz & Jacobs 1986).

Now that we have introduced the idea of variations in the dimensionality and sensitivity of color vision, we can turn to what these variations tell us about color space. We focus first on color vision in birds, for as J. K. Bowmaker remarked some years ago: “The true culmination of the evolution of color vision in vertebrates is probably to be found in the highly evolved diurnal animals, perhaps best represented by diurnal birds, and it is within these species that we should look for color vision significantly more complex than our own and utilizing more of the available spectrum” (1980b, p. 196).

As we mentioned above, evidence that is now being accumulated indicates that such diurnal birds as the pigeon and the duck are at least tetrachromats, perhaps even pentachromats (Jane & Bowmaker 1988; Burkhardt 1989; Chen et al. 1984; Goldsmith 1990; Palacios 1991;

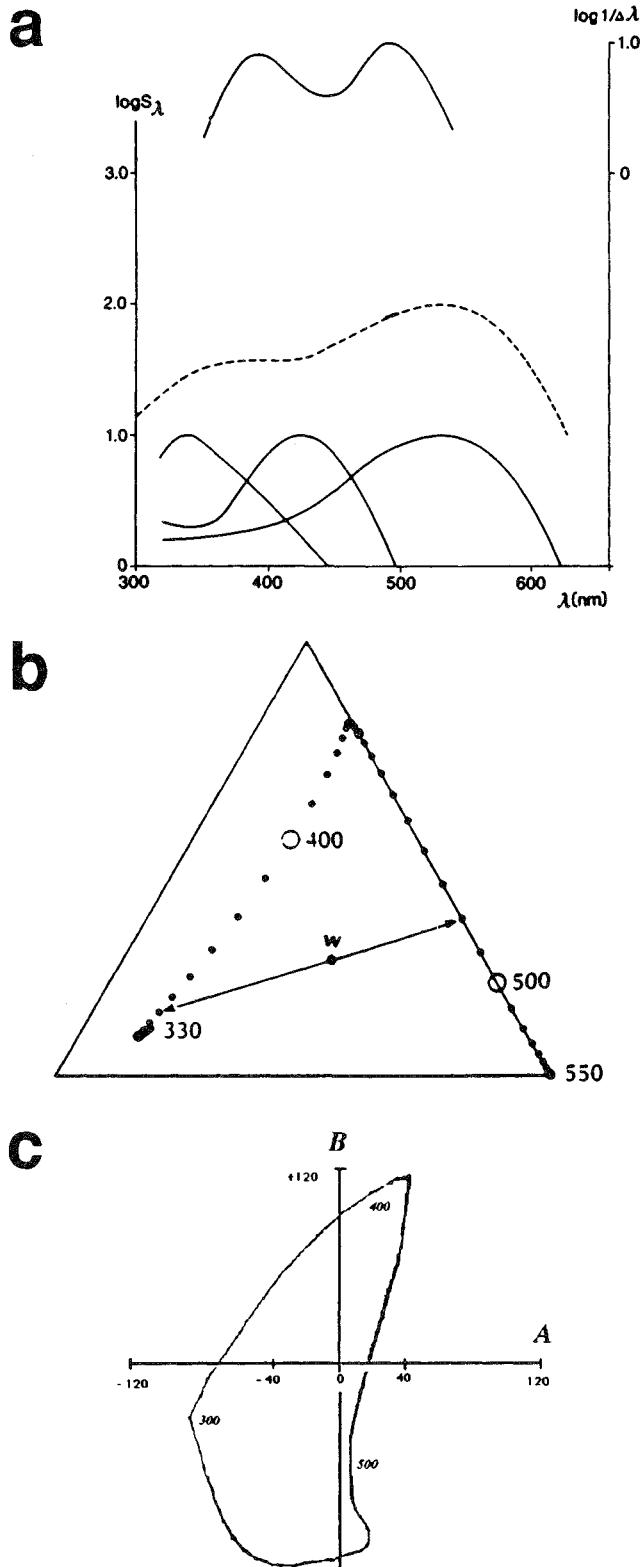


Figure 3. The honey bee: an alternative trichromatic color space. (a) Spectral sensitivities of the three pigments present in the forager honey bee's retina (*Apis mellifera*), with the overall sensitivity curve (discontinuous line) and the two-peaked wavelength discrimination function. Modified from Nuboer (1986). (b) Maxwell triangle for photoreceptor activities, indicating the spectral loci. Compare with Figure 2b. From Goldsmith (1990). (c) Chromaticity diagram for constant brightness, calculated on the basis of two antagonistic channels postulated for the bee from physiological findings: $A = +\text{UV} - \text{B} - \text{G}$; $B = \text{UV} - \text{B} + \text{G}$. From Menzel (1989).

Palacios & Varela, in press; Palacios et al. 1990b; Varela et al. 1991a). This evidence is derived from a variety of experiments with species ranging over various families within each order. The evidence also pertains to several levels, from the photoreceptor and retinal constitution, to the neurophysiological, and psychophysical or behavioral levels.

To begin at the retinal level, five different types of cone-oil droplet combinations have been described in the retinas of various birds such as pigeons, ducks, and penguins; passerines have at least four such combinations (Bowmaker 1977; Chen & Goldsmith 1986; Chen et al. 1984; Jane & Bowmaker 1988). As can be seen from Figure 4a, the "visible" spectral range available to diurnal birds includes that available to humans, but it also extends considerably further into the short-wave region. Indeed, it is now generally agreed that many birds have color vision in the near-ultraviolet region. For example, Wright (1972) found that the removal of an ultraviolet component changes the color of certain stimuli for the pigeon; and Goldsmith (1980) found that hummingbirds can distinguish near-ultraviolet light (370nm) from darkness, and from white light lacking wavelengths below 400nm. Humans cannot perform either of these tasks.⁵

The cones in the avian retina, unlike those in mammals and insects, also possess oil droplet inclusions, which appear to act as cut-off filters, thereby increasing in number the combination of receptor sensitivities (Bowmaker 1980b). Oil droplets are also found in the retinas of some fishes, amphibians, and reptiles. In the pigeon retina, for example, there are up to four types of colored oil droplets in combination with three types of cone photopigment for the long-wave region alone (Figure 4b) (Bowmaker 1977). Furthermore, this information about retinal organization is regional, because in birds like the pigeon there are two foveal regions that mediate different behavioral roles (Bloch & Martinoya 1983; Maldonado et al. 1988); evidence indicates that sensitivity and discrimination are different in these two visual regions (Nuboer & Wortel 1987; Remy & Emmerton 1989). These regional differences increase even more the complexity of pigeon color vision, for the color perceived depends on the visual field being attended.

Turning now to psychophysics, wavelength discrimination curves, as we have already mentioned, show four distinct minima (Emmerton & Delius 1980; Palacios et al. 1990a). Color-mixture experiments for the pigeon provide direct evidence for tetrachromacy (Palacios & Varela 1991; Palacios et al. 1990b). A definitive proof of pentachromacy would require five-way color-mixture experiments, which have yet to be performed.

There is unfortunately little evidence at present about the neural basis for avian chromatic channels in general (see Maturana & Varela 1982; Varela et al. 1983). It is nevertheless possible to form an educated guess about the possible shape of the pigeon's color channels, comparable to those shown in Figures 2c and 3c for humans and bees, respectively. The basic idea, introduced by Buchsbaum and Gottschalk (1983), is to obtain the weighted combination of mutual excitation and inhibition that maximally decorrelates the primary photoreceptor responses (see Appendix A). In their original calculations, Buchsbaum and Gottschalk (1983) used the Vos-Walraven primary responses for humans, which are psy-

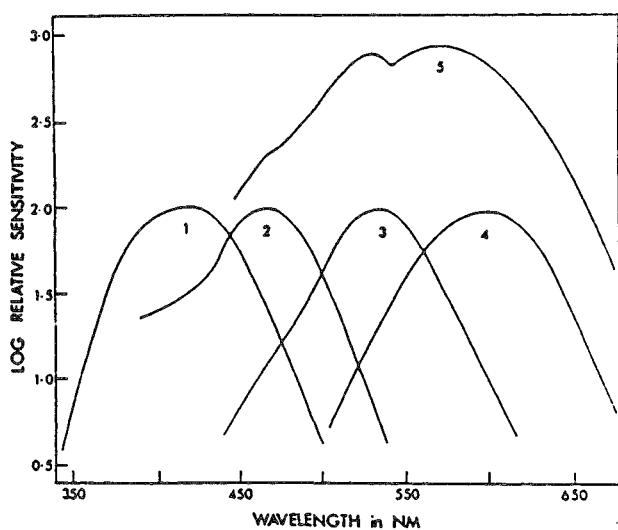
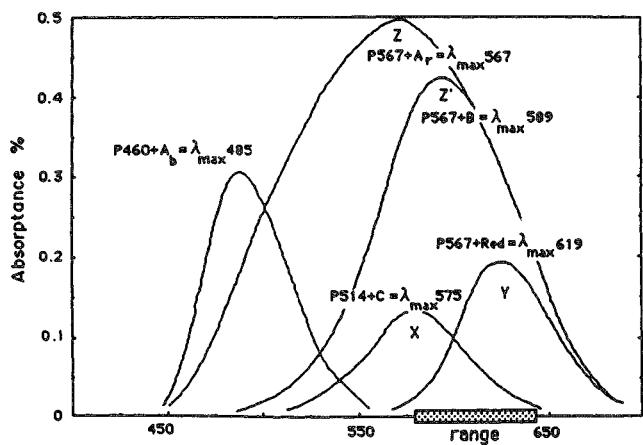
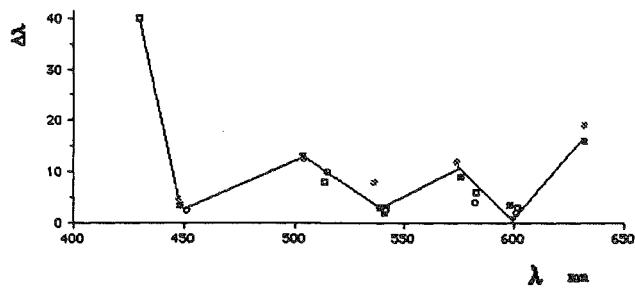
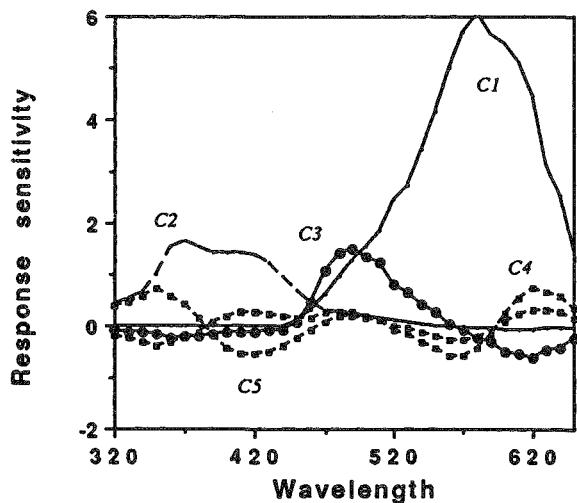
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Figure 4. The color hyperspace of diurnal birds. (a) Relative spectral sensitivities of the five major cone classes of the mallard duck (*Anas platyrhynchos L.*), calculated by taking into account both oil droplet and ocular media absorption. The fifth curve has been shifted up one log unit arbitrarily for clarity. From Jane and Bowmaker (1988). (b) The cone photopigments (maxima at 460nm, 514nm, and 567nm) and oil droplet (50% cutoff transmission at 476nm, 476nm, 554nm, 610nm, and 570nm, respectively) combinations actually present in the pigeon's retinal "red" field. The sector designated "range," the long-wave window 580–640nm, is compatible with trichromacy according to color-mixture data. From Palacios, Martinoya, Bloch and

Varela (1990), based on data from Bowmaker (1977). (c) A behavioral determination of the wavelength discrimination function for the pigeon (*Columba livia*) not including the UV region, showing three conspicuous minima. Data from Palacios, Bonnardel & Varela (1990a). (d) Proposed chromatic opponent channels for the pigeon, based on weighted subtractions and additions that maximally decorrelate primary responses (see text). The primary responses considered were maxima at 360nm, 415nm, 520nm, 580nm, and 620nm. These channels can adequately predict the known photopic sensitivity, wavelength discrimination curve, and color mixture in pigeons. From Palacios (1991).

chophysically derived. The resulting channels correspond remarkably well with the Wh-Bk (White-Black), R-G (Red-Green), and Y-B (Yellow-Blue) channels known to the psychophysicist, and to color-opponent profiles at the retinal or geniculate level known to the neurophysiologist.

We have applied this same procedure to other species, as explained in Appendix A. Unlike the human data, the animal data are incomplete; at present, the best one has to

work with are raw microspectrophotometric data. The proposed channels can be validated by their capacity to predict known behavioral evidence, such as sensitivity, discrimination, and color mixture. In Figure 4d we show the result of the decorrelation of the primary responses of the pigeon, thereby giving a set of putative channels. These channels adequately predict the known data on sensitivity, wavelength discrimination, and color mixture (Palacios 1991). We typically find that we need five

channels to account for the available data: one achromatic luminance channel (C1) and four color-opponent channels (C2, C3, C4, C5) with different zero crossings (Figure 4d).⁶

It is important to realize that such an increase in chromatic dimensionality does not mean that pigeons exhibit greater sensitivity to the monochromatic hues that we see. For example, we should not suppose that since the hue discrimination of the pigeon is best around 600nm, and since we see a 600nm stimulus as orange, pigeons are better at discriminating spectral hues of orange than we are. Indeed, we have reason to believe that such a mapping of our hue terms onto the pigeon would be an error: In an experiment designed to determine whether and how pigeons group spectral stimuli into hue categories, Wright and Cummings (1971) found that pigeons treat wavelengths to either side of 540nm as falling into different hue categories, whereas humans do not. As Jacobs (1981, p. 118) notes in his discussion of this experiment: "Among other things, this result strongly emphasizes how misleading it may be to use human hue designations to describe color vision in non-human species."

This point can be made even more forcefully, however, when it is a difference in the *dimensionality* of color vision that we are considering. An increase in the dimensionality of color vision indicates a fundamentally different kind of color space. We are familiar with trichromatic color spaces such as our own, which require three independent axes for their specification, given either as receptor activation or as color channels (Figure 2). A tetrachromatic color space obviously requires four dimensions for its specification. It is thus an example of what can be called a *color hyperspace*.

The difference between a tetrachromatic and a trichromatic color space is therefore not like the difference between two trichromatic color spaces: The former two color spaces are *incommensurable* in a precise mathematical sense, for there is no way to map the kinds of distinctions available in four dimensions into the kinds of distinctions available in three dimensions without remainder. One might object that such incommensurability does not prevent one from "projecting" the higher-dimensional space onto the lower; hence the difference in dimensionality simply means that the higher space contains more perceptual content than the lower. Such an interpretation, however, begs the fundamental question of how one is to choose to "project" the higher space onto the lower. Because the spaces are not isomorphic, there is no unique projection relation. Furthermore, to pass from one space to another, one needs to specify the appropriate axes (color channels), which differ according to the animal (even for animals that have color vision of the same dimensionality).

To mark this kind of difference in color space, consider the color space of the forager honey bee, which we presented in Figure 3 above. If bees are able to enjoy the experience of hue, the hues they perceive are likely to be different from ours, because they match wavelengths to which we are also sensitive with lights drawn from the near-ultraviolet region of the spectrum, which we cannot see. In spite of this difference, there is a sense in which bee color space and human color space can be said to be commensurable, for the dimensionalities of the spaces

are the same, and so a precise correspondence can be provided between these two perceptual spaces. In the case of tetrachromats or pentachromats such a correspondence is not possible.

This incommensurability can be more easily envisioned with the help of the evidence for tetrachromacy in teleost fishes, especially the goldfish (Neumeyer 1988). In Figure 5a, we present the pigment triangle for the goldfish, which should be compared with the previously presented triangles for humans (Figure 2b) and the bee (Figure 3b). Here the familiar Maxwell triangle has been doubled to accommodate the additional coordinate needed to map spectral loci. This representation was first proposed by Neumeyer (1988) for goldfish and independently by Burkhardt (1989) for the color vision of birds. We also reproduce here Goldsmith's (1990) suggestive rendering of the same idea as a pigment *tetrahedron* for an "imaginary" turtle with a retina whose photoreceptors have no oil droplets (Figure 5b).

To generate these kinds of color hyperspaces at the physiological and psychophysical levels, we need at least four channels. For teleost fish, these channels can be obtained in a manner similar to those for the pigeon – by maximally decorrelating the primary responses as known from microspectrophotometric and physiological data (Harosi & Hashimoto 1983; Neumeyer 1988). In this case, the transformation matrix from primary responses to channels is explicitly given in Appendix A. Here again the putative channels can correctly predict the known behavioral evidence for sensitivity, wavelength discrimination, and color mixture for the goldfish (Palacios 1991). It is interesting to note that Neumeyer and Arnold (1989) have recently shown that the goldfish switches from trichromatic to tetrachromatic modes depending on light conditions – an indication that the ecological embeddedness of the animal is quite pertinent even at this level of description.

This complex of issues can also be approached from a frequency analysis of color signals and responses that could provide a way to ascertain the dimensionality of color space directly. The basic idea was first proposed by Barlow (1982; see also Bowmaker 1983), but since it is rather novel, we have relegated our treatment to an appendix (see Appendix B).

In this section, we have presented an array of evidence for the existence of different kinds of color space among perceiving animals. The evidence includes the diversity of kinds of photopigments and sensitivity functions, wavelength discrimination and categorical perception, color mixture, physiological processes, and ethology. Although each form of evidence taken in isolation might be unconvincing, taken as a whole it makes a strong case for the existence of significant variations in the dimensionalities of color space among perceiving animals. We must now wonder what these differences might mean in experiential or phenomenal terms. What do these comparative variations in color space imply for our understanding of color experience?

2.3. Novel hues and diversity in color experience

Since some readers may be sceptical about attributing color experience to creatures other than ourselves (or our primate relatives), let us first attempt to distinguish more

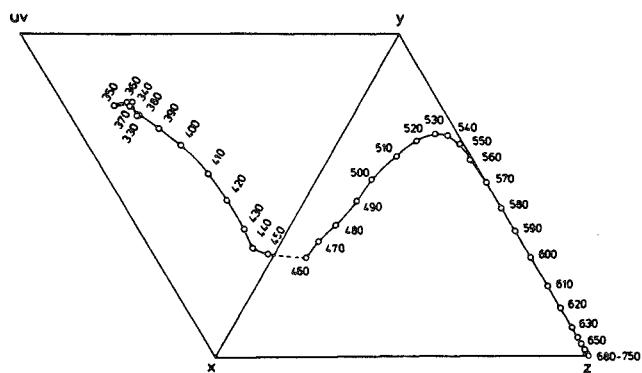
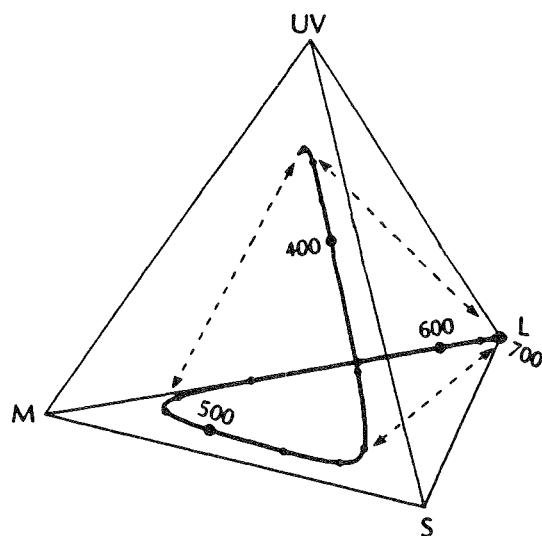
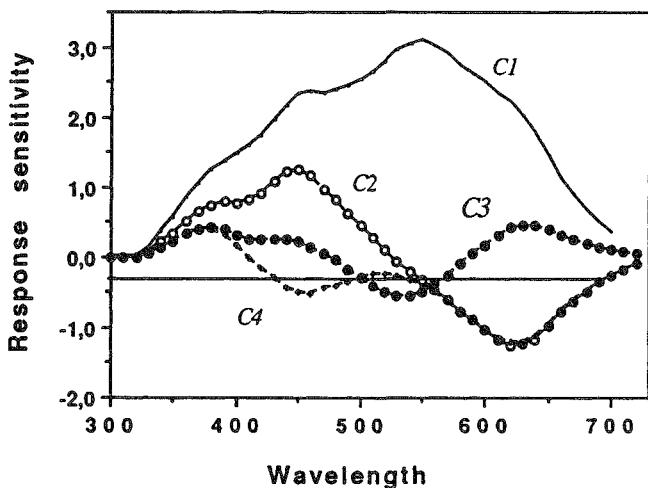
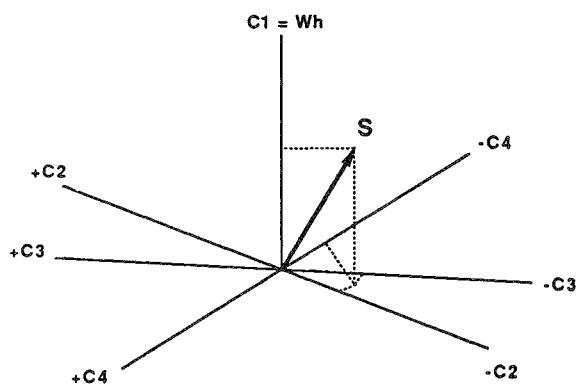
a**b****c**

Figure 5. Tetrachromatic color hyperspaces. (a) Pigment color space for the goldfish, requiring four relative values to span the entire space. In contrast to Figures 2 and 3, the representation demands an extra dimension, which is obtained by doubling the color triangle. The spectral loci thus obtained from pigment absorption data no longer fall on the boundaries of the space, but inside them. From Neumeyer (1988). (b) Pigment tetrahedron for an "imaginary" turtle with no oil droplets in its cones, with visual pigment maxima at 370nm, 450nm, 520nm, and 620nm. In this format it is easy to see that the animal is likely to have three nonspectral stimulus regions (see Figure 2) which would fall along the dashed lines. From Goldsmith (1990). (c) Proposed



chromatic opponent channels for the goldfish, by maximal decorrelation of the pigment data from Harosi and Hashimoto (1983). An achromatic channel and three opponent channels are found. These four channels adequately predict sensitivity, wavelength discrimination, and color-mixture data, as well as physiological data from the fish retina. From Palacios (1991). To the right, the putative channels are used as axes of a color hyperspace of four dimensions, with opponencies between three sets of dimensions (labelled here simply as $+C_1 - C_1$, $+C_2 - C_2$, etc.), plus the achromatic or brightness axis ($C_1 = Wh$). Compare with Figure 2c and 3c for the trichromatic spaces of humans and the bee respectively.

precisely between color vision and color experience. Although it is difficult to draw a principled distinction between mere wavelength-specific behavior and color vision (Menzel 1979), color vision is sometimes defined as the ability to discriminate wavelengths independent of their relative intensities. This ability would not seem to entail the enjoyment of color experience, however, for it seems possible to imagine the former without the latter. Unfortunately, it is also not clear how to draw a principled distinction between color vision as wavelength discrimi-

nation and the full-fledged perceptual experience of color.

A more satisfactory approach to this problem is to hold that color perception involves at least three important phenomena: additive color mixture (hue, saturation, and brightness matches for spectral stimuli), color contrast (simultaneous and successive) and color constancy. In particular, it seems reasonable to suppose that color contrast and color constancy are necessary for color experience.⁷ It is therefore interesting to note that these

chromatic phenomena have now been demonstrated for a variety of species. Color constancy and color induction have been found in bees (Neumeyer 1980; 1981), goldfish (Ingle 1985), and pigeons (Varela et al. 1991a). In the case of pigeons, we have also seen that these animals group adjacent wavelengths into categories, which though different from the groupings humans perform, nonetheless seem to be categories of hue (Wright & Cummings 1971). Given these psychophysical results, then, it does not seem unreasonable to suppose that these animals, especially birds and fishes, experience color.

Let us now consider color vision of higher dimensionality than our own. When they hear of the evidence for tetrachromacy or pentachromacy many people respond by asking: "Well, what are the extra colors that these perceivers see?" This question is understandable, but somewhat naive, for, as pointed out above, we should not suppose that tetrachromats or pentachromats are simply better at seeing the colors that we see. On the contrary, to see in four or five dimensions, as it were, is not to discriminate more finely in three dimensions. In other words, tetrachromats and pentachromats should not be conceived as perceivers who simply make finer hue-saturation-brightness discriminations among, say, blue and green or red and yellow (like perceivers who simply see finer shades of our colors). Such an ability would not amount to an increase in the *dimensionality* of color space; it would consist only in a relative increase in hue-saturation-brightness sensitivity within the dimensions of our trichromatic color space. If we wish to understand what tetrachromacy and pentachromacy imply for color experience, we must instead ask what the possession of additional dimensions to make chromatic distinctions could mean in experiential or phenomenal terms.

At this point, we can offer only imaginative speculation, for we still lack knowledge of the post-retinal neuronal processes involved in tetrachromatic and pentachromatic perception and we obviously do not know what such perception is *like* from the point of view of the goldfish or the pigeon.⁸ By returning to consider our color space, however, and by asking how this space would be transformed by the addition of a new dimension, we can perhaps achieve an indirect appreciation of what a tetrachromatic color hyperspace might be like. Recall, then, that because our visual system has two chromatically opponent channels, we are able to experience four unique hues (red, green, yellow, and blue) and their binary combinations (orange, purple, etc.). A tetravariant visual system, however, like that suggested for the goldfish (Figure 5), would contain three chromatically opponent channels. We are therefore entitled to speculate that these three channels (call them r-g, y-b, and p-q) would enable a tetrachromat to experience *six* basic hue components (r, g, y, b, p, q), binary combinations of these hues (e.g., r + y, y + p, etc.), and *ternary* combinations as well (e.g., r + y + p, g + y + p). Thus the color hyperspace of a tetrachromat might reflect a phenomenal structure composed not only of two new basic hue components, which would combine to form novel binaries, but also an entirely *new kind of hue* not found in the phenomenal structure of our color space, namely, ternary hues.⁹ These ternary hues would correspond to the additional kind of chromatic distinction available to a tetrachromat, but not to a trichromat.

This point about novel colors can be made more accessible with the help of the diagrams presented in Figures 2, 4, and 5. To represent tetrachromatic stimulus mixtures we found that we had to add an additional axis to the plane so that it became a volume (Figure 5). Therefore, as Burkhardt (1989) notes: "While in man's chromaticity diagram there is only one intermediate color which does not occur in the daylight spectrum, namely, purple, in tetrachromatic vision there would be three intermediate colors which are not present in the daylight spectrum, namely, mixtures of red and blue (purple), of green and UV, and of red and UV . . ." (pp. 794–95). Similar kinds of novel, nonspectral stimulus mixtures are indicated by the dashed lines in Goldsmith's (1990) pigment tetrahedron for an imaginary turtle (Figure 5b). If such novel, nonspectral stimulus mixtures can be shown to be treated as colors by the animal through its behavior, then the existence of color hyperspace as a domain of behaviorally significant distinctions would be strongly reinforced.

2.4. Computational objectivism revisited

We now pursue the implications of our comparative discussion, beginning with the view that we call "computational objectivism." Our first task is to determine whether some sufficient subset of the properties of color can be identified with such physical properties as surface spectral reflectance. If these properties of color cannot be so identified then we have reason to reject the objectivist's claim that color is simply surface spectral reflectance.

The obvious place to begin is color space. For something to be a color it must have a location in some color space; that is, it must be specifiable in terms of hue, saturation, and brightness. By taking these three properties as our reference point, we can construct an argument against the identification of color with surface spectral reflectance, which we will call the "argument from external irreducibility." (The main features of this argument were originally proposed by Hardin [1984; 1988, pp. 66–67].)

The argument from external irreducibility

1. For something to be a (chromatic) color it must be a hue.
2. For something to be a hue it must be either unique or binary (or ternary).
3. Therefore, if hues are to be reductively identified with physical properties, these physical properties must admit of corresponding unique, binary (or ternary) divisions.
4. Organism-independent, external properties such as light-waves and spectral reflectances do not admit of such divisions.
5. Therefore, color cannot be reductively identified with such organism-independent, external properties.

Although this argument has conceptual components, we do not intend it to be primarily conceptual. We are interested not in conceptual analysis, (i.e., in making claims about the essential features of the concept of color), but in determining what color is, given the concept of color as it figures in visual science, especially in psychophysical explanation. Thus (1) and (2) should be read as consequences that follow from how color is conceptually and empirically specified in visual science.

The main empirical claim in the argument is obviously (4). To put the point another way: Given only light wavelengths or the spectral reflectance profiles for surfaces, we cannot model or state generalizations about hue. Light waves or surface spectral reflectances do not stand in relations to each other that can be described as unique or binary, or for that matter opponent or nonopponent, balanced or unbalanced, saturated or desaturated, and so forth. There is simply no mapping from such physical properties to the properties of color that is sufficient to establish the objectivist identification.¹⁰

This argument obviously depends on considerations about what properties a mapping must have to be sufficient to establish objectivism. We are supposing that such a mapping must enable us to state generalizations about features of color such as the unique/binary structure of hue and the opponent relations. The objectivist might deny this point. Such a denial would be tantamount to claiming, contrary to (1)–(3) above, that we should replace our current understanding of color in visual science with a new concept of physical color as surface spectral reflectance. It is tempting to dismiss this conceptual replacement idea out of hand: It is one thing to argue for a distinction between physical color and perceived color, but it is quite another to uphold the distinction by divesting hue, and thereby color, of those properties used in its conceptual and empirical specification in visual science. If the properties of hue, such as being unique or binary, and the opponent relations, could be successfully identified with some set of physical properties such as surface spectral reflectances, then statements about these physical properties would provide us with an alternative theoretical access to the properties of color that figure in psychophysical explanation. We would then have reason for accepting a new notion of physical color. But because we have no physical model for these properties of color, what is to motivate such a notion?

The argument from external irreducibility could be and indeed has been advanced without taking into consideration comparative color spaces (Hardin 1984; 1988). We present the argument here because it becomes even stronger when we place it in the context of comparative color vision. Consider hue as it varies across dichromatic, trichromatic, and tetrachromatic (to say nothing of pentachromatic) color spaces. As we know from studies of human color blindness (see Hurvich, 1981, for an overview), a dichromat has only one opponent-hue pair (yellow-blue or more rarely red-green). Therefore, unlike a trichromatic color space, a purely dichromatic color space contains no binary hues. Similarly, a tetrachromatic color hyperspace would contain ternary hues not found in a trichromatic color space. There are thus different *kinds* of hue to be found in each of these color spaces. The unique, binary, and ternary structures that compose these different kinds of hue do not map onto properties of surface spectral reflectance. Neither the unity among the phenomena (color *qua* hue-saturation-brightness relations) nor the relevant diversity (different dimensionalities and hence kinds of hue) is to be found at the purely physical level of spectral reflectance.

At this point, the objectivist will no doubt appeal to the idea that the contents of (types) of perceptual states should be identified according to the distal properties they have the function to detect, that the function of color

vision is to detect surface spectral reflectance, and that this functionalist type-identification is sufficient to establish the claim that color is surface spectral reflectance (Matthen 1988).

Even if the function of color vision is to detect surface reflectance, it does not follow that color is surface reflectance. In fact, computational objectivists often simply beg the question about the status of color by building objectivism into their representationist theories of perception. But there is an even more fundamental problem we wish to stress: The claim that the function of color vision is to detect surface reflectance is at best considerably misleading and at worst seriously flawed. It is misleading because a comparative ecological examination of color vision reveals that color vision has many other biological functions besides those involved in the detection of surfaces. Most notably, color vision is concerned with illumination conditions in their own right and with the perceptual significance of color in guiding behavioral interactions (we provide examples shortly). It is flawed because it is not at all clear that surfaces are themselves perceiver-independent in the way the objectivist supposes. Let us begin with this point, because it is the more controversial.¹¹

In the top-down functional decomposition characteristic of the computational level of analysis (such as inverse optics), vision is decomposed into various more-or-less modular tasks. In the case of color vision, the task is to recover information about surface spectral reflectance given a collection of objects. This statement of the “problem” of color vision assumes that the visual scene has already been segmented into areas that correspond to distinct objects and their surfaces. But this assumption begs the question of the purposes that color vision may serve. As D’Zmura and Lennie (1986, p. 1666) note: “To find the loci of responses that correspond to different objects, one must already have segmented the scene to establish which lights come from which objects. This begs the question of the purpose of color vision, which we believe plays an important role in the discrimination among objects and in their identification.”

Consider the regularization constraints that we discussed above. Among these is the fact that naturally occurring illuminants and reflectances can be adequately modelled in a low-dimensional space. What, we might ask, constitutes a “naturally occurring reflectance”? If we examine these models, we see that so-called natural reflectances correspond to the surface reflectances of typical objects from our human environment (e.g., bricks, grass, buildings, etc.). Given a class of such objects, one measures their surface spectral reflectances and then determines which finite set of basis reflectance functions best models the variance in the class. The visual system, however, is never simply presented with such prespecified objects. On the contrary, the determination of what and where an object is, as well as its surface texture and orientation (hence the overall context in which color is perceived), is a complex process that the visual system must achieve.

In fact, we have already seen that color vision contributes to this process of spatial segmentation. For example, we reviewed Rubin & Richards’s (1982; 1988) idea that an early goal of biological color vision is to determine where material changes occur in a scene using spectral cross-points and opposite slope signs. Another example comes

from D'Zmura and Lennie (1986), who propose an algorithm for color constancy in which the geometric stability of hue contributes to segmenting a scene whereas variations in lightness and saturation contribute to establishing an object's shape and position. Finally, at the neurophysiological level, it is generally held that distinct retinal-geniculate-cortical pathways are involved in color, form, and movement perception (De Yoe & Van Essen 1988; Lennie 1984; Livingstone & Hubel 1988), but there is disagreement over the properties of these pathways and their relations (Lennie et al. 1990; Logothetis et al. 1990; Mollon 1990; Schiller et al. 1990). Nonetheless, it seems safe to say that not only the achromatic process involving the lightness dimension of surface color, but also the chromatically opponent processes play a role in spatial segmentation (e.g., color contrasts can be used to determine borders), to say nothing of how the specification of color and shape may be combined in, say, V4 (Heywood & Cowey 1987).

This interdependency between color vision and spatial segmentation is downplayed by computational objectivism. This view simply assumes that the surfaces of objects provide a perceiver-independent peg on which to hang objective color as spectral reflectance. The objectivist presumably thinks that the assumption needs no defence, since surface spectral reflectances can be specified in physical terms. But although the *reflectance* at any point in the scene can be specified in physical terms, what counts as a *surface* may in fact involve tacit reference to a type of perceiver. This point has not been evident for several reasons which we need to explore.

First, it is usually simply assumed that surfaces are properties of the world found at a purely physical level of description. At the level of description found in perceptual theory, however, surfaces also figure as properties of the *perceptual object*, that is, the object as construed in relation to the sensory-motor capacities of perceiving animals. Here surfaces are treated in relation to the body-scaling of the animal, and, in the case of vision, to properties like visual shape, texture, orientation, lightness, and color. How surfaces at this perceptual level are to be linked to the purely physical level is precisely the issue. Simply to assume that this link can be made without implicating the sensory-motor capacities of the animal is to beg the question. For example, the visual system responds to singularities at many scales that characterize apparent contours in edges, yet these scales are integrated into a unified behavioral designation. This integration, however, is not implicit in the singularities themselves: it depends on how the neuronal processes treat them (DeValois & DeValois 1988).¹²

Second, such issues often remain hidden because many theories of perception focus on tasks (e.g., recovering reflectance) in an already well-specified or easily segmented context (e.g., Mondrian displays). Uncritical attention to visual tasks in such artificially simplified contexts makes one forget the complexities involved in spatial segmentation itself.

Third, virtually all theories of perception focus on our familiar human environment rather than the considerably different environments of, say, birds, fishes, or insects. For example, the prespecified objects in low-dimensional models of reflectance are typically middle-sized, frontally viewed, "human" objects, such as bricks, grass, build-

ings, Munsell color chips, Mondrian displays, and so forth. They are not, for example, silhouettes against the background sky, as seen frontally and laterally by birds, ultraviolet reflectance patterns of flowers, as seen by birds and bees, aquatic objects that contrast with the volume colors of the downwelling or background space light as viewed by fishes, and so on. Because of this attention to prespecified human objects, the issue of how the world comes to be segmented into a given collection of surfaces by different perceiving animals is hardly ever empirically raised, or explored philosophically (but see Stroll 1986).

Finally, if, as Gouras and Zrenner (1981, p. 172) claim, "it is impossible to separate the object sensed from its color because it is the color contrast itself that forms the object," then what counts as the perceptual object may vary considerably depending on the type of color vision system involved.¹³ Gouras and Zrenner are referring here to the perceptual object. Nonetheless, the interdependency between color and surface perception is enough to show that at the level of description relevant to perception, it is not at all evident, as computational objectivism assumes, that the specification of surfaces is not relative to the perceiver. In other words, the kinds of surfaces that populate the world as visually perceived by a given animal may depend for their specification on the processes by which that animal segments its visual scene.

Let us summarize this line of argument, which we call the "argument from perceiver-relativity":

The argument from perceiver-relativity

1. Color vision contributes to the task of segmenting the visual scene into regions of distinct surfaces and/or objects.
2. Color vision varies considerably throughout the animal world.
3. We may accordingly expect spatial segmentation to vary as well.
4. What counts as the surface of an object (for perception theory) therefore has to be specified in relation to the perceiving animal.

We take this argument to be conditional, based on a reasoned hypothesis or conjecture that requires further empirical investigation in a comparative neurophysiological and ecological context. Nonetheless, we believe its plausibility undermines much of the computational objectivist's assumption that surfaces provide a perceiver-independent anchor for color.

The comparative ecology of color vision reveals several other points where computational objectivism is inadequate. The computational objectivist typically assumes that the sole or genuine function of color vision is object detection. Matthen (1988), for example, argues that the "biological function" of color vision is object detection via the recovery of surface reflectance. He claims that non-surface modes of color appearance, such as the blue of the sky, should be explained as the result of "normal misperception," that is, as cases of visual representation that are nonveridical, but do not result from the malfunction or maladaptation of the visual system. Thus Matthen tries to ground the philosophical claim that only surfaces are genuinely colored by relying on a notion of "biological function." The irony of this proposal is that Matthen's claim about the *biological* function of color vision is advanced on the basis of a rather controversial computa-

tional model (Land's retinex theory) and is undermined by the actual biological and ecological operation of color vision. Color vision is not limited to the perception of surfaces; it includes the perception of the ambient lighting conditions in their own right (not merely as "information to be discounted"), for these are relevant to a variety of environmental conditions, such as weather and time of day (Jameson & Hurvich 1989). Nonsurface modes of color vision also serve to heighten contrast between aerial or aquatic backgrounds (volume colors) and foreground objects (surface colors) (Levine & MacNichol 1982; Lythgoe 1979).

Although we still lack extensive knowledge of the ecological function of color vision in various animal species, the evidence we do have is sufficient to demonstrate that speculations about color vision should not be dictated by top-down computational models that rely on a considerably simplified human perceptual context. Instead, as the following examples will illustrate, color vision must be understood within the context of the quite different behavioral repertoires available to perceiving animals.

Consider first the link in chromatic ecology between visual pigments and animal niches. Studies of aquatic visual ecologies have shown that the retinas of deep sea fishes have been reduced to one rhodopsin pigment, with a sensitivity maxima around 470–490nm (Levine & MacNichol 1979; Loew & Lythgoe 1978; Partridge et al. 1989). According to one interpretation, this range would permit the maximum of contrast sensitivity for movement (Crescitelli et al. 1985; Muntz 1975). In contrast, for species that have a bioluminescent organ, a different pigment of the porphyropsin family, whose sensitivity maximum (513–539nm) coincides with the main luminous emission of the organ, has been described (Bowmaker et al. 1988; Partridge et al. 1989). As one moves upward toward more illuminated depths, all species have a larger diversity of photopigments and retinal arrangements, from which one may conclude that different visual objects are pertinent for each species (Lythgoe 1979). This ecological link between photopigments and environments becomes even more striking in migratory fishes, which go from river to sea: Here the relative amounts of rhodopsin and porphyropsin change according to the time of day and season (Beatty 1969, 1984; Bridges 1972; Muntz & McFarland 1977; Muntz & Mouat 1984; Whitmore & Bowmaker 1989). Such polymorphism is also present among other nonmigratory species (Archer & Lythgoe 1990; Archer et al. 1987; Whitmore & Bowmaker 1989). Neumeyer and Arnold (1989) have also recently shown, as we mentioned above, that the goldfish is tetrachromatic for an ambient illumination of 25lux, but trichromatic for a lower illumination around 1.5lux. They suggest that this capacity for a dimensional shift is likely to have an ecological interpretation. This evidence for aquatic ecologies is admittedly fragmentary, yet it serves to indicate the need to link chromatic performance to the ecological setting of the animal (Muntz 1975; Wheeler 1982).

Among birds, the retinal oil droplets vary considerably even for species with similar global living conditions (Budnik et al. 1984; Jane & Bowmaker 1988; Martin 1977; Martin & Lett 1985). For example, the common tern, a predator bird, has a significant amount of red and yellow

droplets in the dorsal retina, while the barn swallow, which catches insects, has a large quantity of translucent droplets (Goldsmith et al. 1984). In fact, Partridge (1989) has shown by means of cluster analysis that the ecological niche (herbivore, fishing, etc.) is more important in predicting the kinds and distribution of oil droplets than strict phylogenetic kinship. The presence of ultraviolet pigments in birds also provides an example. These pigments can be linked to bird-fruit coevolution, including the dissemination of kernels (Snow 1971; Burkhardt 1982), and to ethological factors involving animal recognition, for bird plumages have been shown to have high frequency content, and so might require higher-dimensional color spaces for their recognition (Brush 1990; Burkhardt 1989; Durrer 1986; Hudon & Brush 1989; Weedon 1963).

Ultraviolet sensitivity in birds may also be used in aerial navigation. As we have seen, pigeons have excellent short-wave and near-ultraviolet discrimination. It is possible that, in Nuboer's (1986, pp. 370–71) words, "the excellent spectral discrimination within this range . . . represents an adaptation to the coloration of an unclouded sky. This property enables the pigeon to evaluate short-wave gradients in the sky, ranging from white at the sun's locus to highly saturated (ultra) violet at angles of 90° to the axis between observer and sun." Furthermore, since pigeon navigation is based on orientation with respect to the sun's azimuth, "the perception of colour gradients in the sky may control navigation indirectly when the sun is hidden by clouds."

A different, but perhaps even more important feature of the ecological function of color vision is to yield a set of perceptual categories that have "cognitive significance" for perceiving animals in a variety of behavioral interactions (Jacobs 1981, pp. 170–71). A color category can guide behavior in various ways depending on the things which exemplify it: In the case of fruits, it guides feeding; in the case of animal coloration, it may guide various social interactions, such as mating. Pigeons have been shown to group spectral stimuli into hue categories, and the brightly colored feathers of birds must have cognitive significance for behavior, especially behavior involving sexual recognition. Finally, although object discrimination is obviously important for these kinds of behavior, the cognitive significance of color may have an affective dimension (perhaps related to the overall hormonal/motivational level of the animal) that cannot be explained simply as a function of object discrimination (Varela et al. 1983).

Much research remains to be done on the relations among color vision, perceptual color categories, and animal behavior (Burtt 1979; Hailman 1977). Although color as a perceptual category with cognitive significance obviously plays a great role in human life, there is still little evidence about this dimension of color perception in nonhuman animals, especially nonprimates. In the case of birds, however, it seems safe to conclude that this kind of color experience does exist, as we have been arguing here. In any case, the evidence that we have presented in the previous paragraphs serves to demonstrate our point that the functions of color vision should be understood in the context of the actual behavioral repertoires and visual ecologies of perceiving animals.

2.5. Neurophysiological subjectivism revisited

To emphasize the active role that color vision plays in tasks such as spatial segmentation and in guiding the interactions of perceiving animals implies an approach to color perception that is also different from neurophysiological subjectivism. To demonstrate this point, we need to consider Hardin's (1988; 1990) defense of neurophysiological subjectivism.

Hardin's strategy is to offer what we can call an "argument from internal reducibility" whose main claim is that the properties of hue (e.g., uniqueness, brightness) can be reductively identified with psychophysical and eventually neural properties of the visual system. This argument, coupled with the "argument from external irreducibility," leads Hardin to the position that there are no "extradermal" colored objects; there are only chromatic neural states. Hardin's defense of this idea is worth quoting:

We have no good reasons for thinking that such a replacement of the one [phenomenal] description by the other [neural] description would leave anything out, with a consequent loss of information. On the contrary, we have reason to expect that a proper neural description would be richer, more complete, and, in principle, more penetrable by the intellect. Problems that are intractable at the extradermal physical level or at the phenomenal level promise to yield analysis in neurological terms (1988, p. 111).

Two points appear to be contained in this remark, one ontological, the other methodological. The ontological claim is that color, or rather chromatic experience, is a type of neural state or process. The methodological claim is that color phenomena can be analyzed in neurological terms. These two claims obviously support each other: If colors are really neural states, then we have reason to pursue a neurological analysis of color phenomena; on the other hand, if we can give a neurological analysis of color phenomena (and we cannot give a comparable physical analysis), then we have reason to believe colors are neural states. We make this distinction not to be pedantic, but because it is primarily the methodological issue that we wish to address here, not the ontological one. In other words, we do not intend to evaluate Hardin's position by embarking upon a discussion of the mind-body problem for visual experience. It is, rather, the scope and limits of a purely neurological approach to color phenomena that interests us.

Our aim in this final section of the comparative argument will be to show that there are indeed phenomena that, intractable as they are at the extradermal and organism-independent physical level as well as the phenomenal level, nonetheless fail to yield to analysis in purely neurological terms. These phenomena are ecological in the broadest sense; that is, they encompass not only the extradermal world as an animal environment, but also perceiving animals as both assemblies of sensory-motor networks and as organismic unities that *shape the extradermal world into an environment in their interactions*.

Consider first the polymorphism in the color vision of the squirrel monkey and the spider monkey (Jacobs 1986). In these species, all males are dichromats, whereas

three-quarters of the females are trichromats. Several explanations have been proposed for this polymorphism (Mollon et al. 1984; Nuboer 1986). According to one, it has resulted from adaptation to the spatial heterogeneity of the environment: It is possible that different phenotypes inhabit regions of the jungle that differ in the spectral composition of their ambient light. A second proposal appeals to the hypothesis of group selection: It might be advantageous for the animal community to have members with several forms of color vision. A third proposal appeals to frequency dependent selection: There may be an ecological balance between the availability of certain fruits and the number of phenotypes that can detect them. Finally, another hypothesis holds that the colors of local fruits coevolved with the differences in color vision (Snodderly 1979).

Our second example comes from the color vision of bees. We have seen that bees have trichromatic vision that is shifted towards the ultraviolet. It has been argued that this distinctive form of trichromacy coevolved with the colors of flowers, which often have contrasting patterns in ultraviolet light (Barth 1985; Lythgoe 1979; Menzel 1989; Nuboer 1986). On the one hand, flowers attract pollinators by their food content, and so must be conspicuous and yet different from flowers of other species. On the other hand, bees gather food from flowers, and so need to recognize flowers from a distance. This mutual advantage seems to have determined a coevolution of plant features and sensory-neural capacities in the bee.

Finally, consider that the colored "objects" that animals discriminate are often (perhaps typically) other animals. Therefore, within an ecological framework our inquiry should be concerned just as much with animal coloration – indeed with the coloration of living things in general – as with animal color vision (see Burkhardt 1989; Burtt 1979; Hailman 1977; Lythgoe 1979). Coloration obviously affects an animal's visibility, both to conspecifics and to members of other species in its environment. It is therefore not surprising to find coloration involved in camouflage and in many kinds of visual recognition (e.g., species recognition, sexual recognition, individual recognition, recognition of motivational state, etc.; Baylis 1979; Rowland 1979). Indeed, the ecological entanglement of color vision and animal coloration is truly astounding. Consider, for example, the variations in color vision and coloration among fishes in a tropical coral reef, perhaps one of the richest of color environments.

These kinds of phenomena indicate that a purely neural explanation for color vision is incomplete. To explain the polymorphism in spider and squirrel monkey color vision, and hence the differences in the perceptual experiences of these animals, we must appeal not simply to the neurophysiological constitution of these animals, but also to the evolutionary histories of their environmental interactions, perhaps at several levels of selection.¹⁴ Similarly, to understand why bee color vision is shifted toward the ultraviolet, and hence why the color space of the bee might comprise novel hues, we must appeal to animal-environment coevolution. Finally, to understand the relations among color vision, animal coloration, visual recognition, and animal communication, we must appeal to a broad range of physiological, ecological, and evolu-

tionary considerations, ranging from the physiological functions of pigmentation, to coordinated inter- and intraspecific animal interactions, to the coevolution of the various behavioral partners (Burtt 1979).

We expect that Hardin would not deny any of these points. Indeed, Hardin has recently drawn on evolutionary – or more broadly, ecological – considerations to defend his view that although chromatic categories (red, green, yellow, and blue) have no counterparts in the extradermal world, such categories confer evolutionary advantages on perceiving organisms (Hardin 1990). Hardin argues that color vision does not represent the world as it really is, but rather “encodes information” about light, reflectance, and so forth, in a subjectively generated form that is salient, vivid, and of great practical value for the perceiver. The salience and vividness are to be explained neurophysiologically, whereas the practical value is to be explained ecologically.

We believe, however, that Hardin has not yet appreciated the moral that evolutionary and ecological considerations have for his neurophysiological subjectivism. Color vision does not merely provide practical knowledge of the environment; it also participates in the *codetermination* of perceiving animals and their environments. By codetermination we mean both (1) that animals select properties in the physical world relevant to their structure (body-scaling, sensory-motor capacities, etc.), shaping these properties into environments that have behavioral significance; and (2) that environments select sensory-motor capacities in the animal and thereby constrain animal activity (Levins & Lewontin 1983; 1985). Consider once again the coevolution of plant features and sensory-neural capacities in the bee (and other invertebrates). This coevolution implies not only that bee color vision is sensitive to ultraviolet because it is advantageous for bees to detect flowers that have ultraviolet reflectances, but also that flowers have ultraviolet reflectances because it is advantageous for them to be seen by bees. Thus, the evolution of bee color vision did not simply provide the bee with a practical knowledge of its environment; it also contributed to the very determination of that environment. As Barth (1985) says in his wonderful study of insects and flowers: “The colorful field of flowers is an insect environment that reflects the insects themselves (p. vii) . . . the plants and their pollinators are environment and reflection of one another” (p. 266). Such sensory-neural and environment coevolution provides, then, a particularly dramatic example of how the visual environment is not only relative to the animal, but also partly determined by the visually guided activity of the animal itself.

Such animal-environment codetermination is not limited to invertebrates. As Humphrey (1984) has observed, most of the world’s colors are organic colors carried by the pigments of plants and animals – for example, the colors of flowers and fruits, of plumages, of tropical fishes, and so on. Such organic colors have been selected because of their biological significance to those who can see them. It is interesting to note that some pigments, for example, carotenoids, play a key role both on the side of the discriminated object (plants, fruits, feathers), and on the side of the primary processes in the retina (visual pigments, oil droplets). Thus the presence of carotenoids is emblematic of the evolutionary codetermination of per-

ceiving animals and their environments (Rothschild 1975).

Hardin’s subjectivism neglects this role that visual perception plays in animal-environment codetermination. The neglect derives, we believe, from Hardin’s implicit acceptance of the subjectivist-objectivist framework for evaluating perception derived from Galileo, Newton, and Locke. Thus although Hardin has emphasized the role that color vision plays in generating chromatic categories that have intersubjective, cognitive significance for perceiving animals in their interactions, he nonetheless wishes to drive a principled wedge between, on the one hand, color construed as a subjective encoding of information about the world, and on the other hand, surface reflectances construed as objective properties of the world. He claims, for example, that colors are subjective because he supposes that if there were no perceiving animals in the world, there would be no colors; since objects and their surfaces would remain, however, these are objective (Hardin 1990). (This same argument was in fact given by Galileo in 1623: “. . . Colors and so on are no more than mere names so far as the object in which we place them is concerned, and . . . they reside only in the consciousness. Hence if the living creatures were removed, all these qualities would be wiped away and annihilated” [Drake 1957, p. 274].)

This line of argument not only overlooks but actually does violence to virtually every aspect of the ecologically entangled relations of perceiving animals and their environments. First, it overlooks the fact just mentioned that most of the world’s colors are organic colors. The evolution of color vision is inextricably linked to the evolution of organic coloration – so much so that “in a world without animals that possessed colour vision there would be very little colour” (Humphrey 1984, p. 146). It is therefore irrelevant – perhaps even somewhat perverse – to appeal to *metaphysical* intuitions about what the world would be like “if the living creatures were removed” when one’s concern is to provide a *naturalistic* explanation of perceiving animals and their environments.

Second, Hardin’s argument overlooks the role that color vision plays in spatial segmentation and hence the relational nature of the surfaces of perceptual objects, which we reviewed above. Elsewhere Hardin (1988, pp. 111–12) has himself drawn attention to a similar point: “Because perceptions of color differences and perceptions of boundaries are closely intertwined neural processes, we see colors and shapes together. Roughly speaking, as color goes, so goes visual shape.” For Hardin, however, there is an important difference between color and shape; thus he continues: “Consequently, there are no visual shapes in the ultimate sense, just as there are no colors. But visual shapes have their structural analogues in the physical world, namely, shapes *simpliciter*, and colors do not.”¹⁵ We find this point unclear, for Hardin does not tell us exactly what he means by “structurally analogous” and “shapes *simpliciter*.” We obviously agree with Hardin that colors do not have structural analogues in the physical world *in the way that objectivists have supposed* – that is, analogues that do not depend in any way upon the existence of perceivers. This point, however, does not prevent our specifying *context-dependent and interest-relative* structural analogues of

color, as the science of colorimetry and its associated color technologies clearly indicate (see Hurvich 1981, Chapters 20–21). This point might strike some as unfair, since Hardin's claim might be that there are no context-independent and non-interest-relative structural analogues for color, whereas there are for visual shape. But if this is Hardin's point, then we are not at all convinced it is true. Unlike Newton and Locke, we no longer take shape to be among the fundamental, microscopic properties of matter (cf. Priest 1989). And, as a macroscopic property, what gets picked out as a given shape may depend on the interests and capacities of those performing the specification. In this sense, surfaces as specified in terms of shapes and boundaries might be more properly thought to belong not to the physical world *per se* (the world at a purely physical level of description), but rather to what Gibson (1979) calls the "ecological environment," that is, the world as construed in relation to certain animal capacities (cf. Stroll 1986).

The moral of these considerations, we believe, is that the empirical study of color vision – indeed, of perception in general – should not be saddled with some *a priori* subjective/objective distinction. There is nothing wrong with drawing a distinction between subjective and objective, or internal and external, relative to the framework of a given neurophysiological, psychophysical, or behavioral experiment. The problems arise, rather, when we attempt to force perception theory as a whole into some absolute, subjective/objective straitjacket derived from the empiricist tradition. Hardin (1988) has already impressively demolished many of the dogmas about color in this tradition. He has rightly built his case from biological evidence, but this evidence demands a more sophisticated interactionist approach to color vision than neurophysiological subjectivism delivers. We now turn to the more constructive task of outlining such an approach.

3. Toward an enactive view of color vision

Although the shortcomings of computational objectivism and neurophysiological subjectivism are different, they are related. Computational objectivism conceives of color vision as the "recovery" of animal-independent, distal properties; neurophysiological subjectivism conceives of color vision as the "projection" of subjectively generated qualities onto a distal world of objects and their surfaces. In either case, the role that vision plays in the codetermination of animal and environment is neglected.

Consider the question: "Which came first, the world or the image?" The answer of inverse optics is given ambiguously by the names of the tasks investigated – to recover shape from shading, surface reflectance from varying illuminants, and so on. We call this stance the "chicken position":

Chicken position: The distal world can be specified independently of the animal; it casts images on the perceptual system whose task is to recover the world appropriately from them.

This position is so ingrained that we tend to think the only alternative is the "egg position":

Egg position: The perceptual system projects its own world and the apparent reality of this world is merely a reflection of internal laws of the system.

Our discussion of color vision, however, indicates that neither position is satisfactory. We have seen that colors are not already labelled properties in the world which the perceiving animal must simply recover (objectivism). On the other hand, we have seen that they are not internally generated qualities that the animal simply projects onto the world (subjectivism). Rather, colors are properties of the world that result from animal-environment codetermination. Our case study of color vision suggests that the world and the perceiving animal determine each other, like chicken and egg.

To situate our discussion of vision within the context of animal-environment codetermination, it is worth repeating the summary provided by Levins and Lewontin (1983; 1985) of how organisms "construct" their environments: (1) Organisms determine in and through their interactions what in the physical environment constitutes their relative environments; (2) organisms alter the world external to them as they interact with it; (3) organisms transduce the physical signals that reach them, and so the significance of these signals depends on the structure of the organism; (4) organisms transform the statistical pattern of environmental variation in the world external to them; and (5) the organism-environment relationship defines the "traits" selected for in evolution (cf. Oyama 1985). These five kinds of phenomena involve circular and reciprocal (though not symmetrical) processes of interaction in which the structure of the environment constrains the activity of the organism, but the activity of the organism shapes the environment, and so contributes to the constitution of the environmental constraints (cf. Odling-Smee 1988). It is on the basis of these interactive processes that Levins and Lewontin claim that "the environment and the organism actively co-determine each other" (1985, p. 89).

The implications of this codetermination of animals and their environments have been mostly neglected in perceptual theory, not only by the computational research program of inverse optics, but even by proponents of the so-called "ecological" approach to visual perception (Gibson 1979; Turvey et al. 1981). We will comment on the ecological approach presently; at the moment, we wish to delve further into the reasons for the neglect of animal-environment codetermination in the research program of inverse optics (Marr 1982; Poggio et al. 1985).

Simplifying for the purposes of brevity, inverse optics claims that the animal visually perceives by instantiating various functions that map from two-dimensional images on the receptor array (input) to perceptions of the three-dimensional world (output) via intermediate representations (and given various independent physical constraints). So stated, this account of perception has at least three important consequences that run counter to the idea that visual perception participates in animal-environment codetermination.

First, animal and environment are treated as fundamentally separate systems: The distal environment (objects, surfaces, etc.) is specified in advance; it provides a source of input that is independent of the animal. The perceiving animal, on the other hand, is treated as an input-output system whose function is to solve the ill-posed problem of recovering this prespecified environment. Second, perceptual and motor mechanisms are treated as fundamentally distinct subsystems of the ani-

mal. Since the "outputs" of perceptual systems are considered to be perceptual beliefs about the distal scene, perceptual systems form a mechanism for the fixation of belief. On the basis of its perceptual beliefs, the animal may adjust its activity, but the adjustment of activity *per se* is not treated as part of the perceptual process. Third, perception does not in any way shape the environment; it merely recovers the environment. It might be admitted that animal activity can perturb, select, or construct the environment, but since perception is considered to be fundamentally distinct from action, perception *per se* does not participate in animal-environment codetermination.

This account of perception is based in a well-established empirical research program and so should not be dismissed either on conceptual grounds or simply by adducing counterexamples. It can be challenged, however, by offering an alternative theoretical and empirical framework as a rival research program. At this point in our target article we obviously do not intend to embark on a detailed defense of such an alternative research program.¹⁶ Our intention here is simply to outline briefly a framework for understanding visual perception in which we take seriously the role of vision in the codetermination of animal and environment.

The first step for perceptual theory is to refuse to separate perception from action, or, more generally, from perceptually guided activity. This refusal is in fact common to a number of different research programs, such as the "ecological approach" of Gibson (1979) and his followers (Turvey et al. 1981), the biological approach to cognition of Maturana and Varela (1980; 1987), Freeman's view of brain processes (Freeman 1975; Freeman & Skarda 1985; Skarda & Freeman 1987), and the recent work in AI and robotics of Brooks (1986; 1987; 1989). All of these research programs take as central the fact that perception and action have evolved together – that perception is always *perceptually guided activity*. But whereas the first research program (Gibson's) chooses to focus on properties of the animal environment and optical properties of the ambient light, the others focus on the sensory-motor structure of the animal, either as neuronal networks that link sensory and motor surfaces or as "layers" of "activity producing systems" in artificial robotic "creatures."

We must encompass both the extradermal world conceived as the animal's environment and the sensory-motor structure of the animal in any adequate theory of perception. We believe that the original Gibsonian program exaggerated the role of invariances in the receptor array activity and their hypothesized specification of the environment. That program neglected not only the complex neural processes that are required to guide activity, but also how those processes contribute to shaping different environments depending on the animal. The original Gibsonian program remains unsatisfactory precisely because it does not take this further step, namely that of shifting the reference point for understanding perception from the environment to the structure of the perceiving animal, understood as the kinds of self-organizing neuronal networks that couple sensory and motor surfaces, which determine both how the animal can be modulated by environmental events and how sensory-motor activity participates in animal-environment codetermination.

[See also Ullman: "Against Direct Perception" *BBS* 3(3) 1980.] Elsewhere one of us has argued that a consistent application of this shift in perspective is tantamount to treating the animal as an autonomous self-organizing system rather than as a heteronomous input-output system (Varela 1979; 1984; 1989; see also Freeman & Skarda 1985; Skarda & Freeman 1987). We do not intend to repeat these arguments here; we mention the point because it is primarily this second step – emphasizing the autonomous organization of the animal – that marks the difference between our emphasis on perceptually guided activity and Gibson's. In contrast, many Gibsonians continue to treat perception in largely optical terms, and so attempt to build up the theory of perception almost entirely from the side of the environment. We believe this tendency is largely the result of Gibson's belief that the only alternative to the mistaken sense-data view of perception is direct realism (see Gibson 1967; Turvey 1977). Our approach, however, like that of some more recent Gibsonians (e.g., Kelso & Kay 1987), takes from Gibson the deep insight that perception must be understood within the ecological context of guided activity, but we develop this insight in two important ways: (1) by focusing on the self-organizing properties of neural networks as the proper substrate of animal activity; and (2) by treating the environment not simply as the ecological setting for animal activity, but also as something determined by that very activity. To label this concern with perceptually guided activity thus understood, we will use the term *enactive* as proposed by Varela (1989; 1991a), and as subsequently developed by Varela et al. (1991b).

The point of departure for an enactive approach to vision, then, is not the problem of recovering a pre-specified distal world. Rather, it is to specify the sensory-motor patterns that underlie the visual guidance of animal activity in its local situation. Our examination of differences in color vision led us to hypothesize that animals with different sensory-motor capacities would segment the world in different ways. As a corollary, we claim that the prespecified world we find in, say, low-dimensional models of surface reflectance is actually the world as described in relation to the sensory-motor capacities of the higher primates. It is perhaps a legitimate simplification to specify or label the world in advance when studying our own visual capacities (or those of animals very much like us). It is not legitimate, however, when studying perception in animals that differ considerably from us.

To make this point clearer, consider again the visual system of birds, which provides such a stark contrast to the visual systems of the more familiar mammals. As we mentioned above, the avian retina has two regions of high neuronal density (foveas), which give rise to distinct frontal and lateral visual fields that in turn correspond roughly to further anatomical projections in the brain – the parallel thalamo-fugal and tecto-fugal pathways. Experiments reveal interesting differences between these two visual fields: Frontal fixation is used for static and slow stimuli, and lateral fixation for fast-moving stimuli (Maldonado et al. 1988). There are also differences in accommodation, depth of focus (Bloch & Martinoya 1983), spectral sensitivity (Nuboer & Wortel 1987; Remy & Emmerton 1989), and probably chromatic vision (Varela et al. 1983). Thus, visual discrimination for birds is not a cyclopean image reconstruction but a con-

textualized specification according to avian sensory-motor activity – a visual world-to-the-front and a visual world-to-the-side are enacted by the animal. It is the visuomotor behavior that actually reveals what constitutes a relevant world for the animal, not a reconstruction of the world as it appears visually to us.

This emphasis on sensory-motor patterns of activity is not, of course, incompatible with abstract task-analyses for vision *per se*. Our objection, rather, is to the biologically implausible idea of a prespecified or already labelled world that the perceiving animal must recover appropriately. Although this assumption is built into Marr's conception of the computational level of analysis and of vision as inverse optics, it need not be accepted by those who wish to provide abstract task-analyses for vision and to build artificial visual systems. Indeed, there are models that considerably relax this assumption, such as Grossberg's (1984; Carpenter & Grossberg 1987) adaptive resonant neuronal networks and Edelman's selective recognition automata (Reeke & Edelman 1988). Similarly, in Brooks's (1986; 1987; 1989) recent works in robotics, the ongoing updating of sensory-motor activity is the key for successful design, rather than the representation of prespecified features of the world. By construing visual perception not as recovery or re-presentation, but as guided activity, these models implicitly embody the shift in perspective that we are calling "enaction."

This enactive orientation also implies an understanding of the relationship between the physical and the perceptual different from the usual one in the computational level of analysis. Inverse optics typically assumes that the task of perception is simply to recover properties of the physical world. The enactive approach suggests that perception is not about the physical world in this way. The world that a given animal perceives cannot be given a purely physical-level specification, for what an animal perceives depends on three kinds of factors: (1) physical-level constraints; (2) sensory-motor activity as constituted by neuronal processes and developmental constraints; and (3) evolutionary history. For example, such physical-level constraints as spectral reflectances and light signals are certainly ingredients of what the animal sees. They are not sufficient to determine the *perceptual object*, however, for, as we have seen, color spaces of different dimensionalities can be constructed on the basis of the same physical signals. To account for these differences and hence for the differences in color among the relevant perceptual objects, we must in addition appeal to sensory-motor activity and evolutionary history. Each of these three factors is necessary to determine the perceptual object; in the absence of any one of them, therefore, the perceptual object cannot be properly explained.

This claim about the status of the perceptual object also serves to mark the difference between enaction and subjectivism. Hardin's subjectivism implies that the perceptual object is simply "in the head," and so can be reconstructed in entirely neural terms. As he says: "The tactic that suggests itself is to show how phenomena of the visual field are represented in the visual cortex and then to show how descriptions of the visual field may be replaced by descriptions of neural processes" (Hardin 1988, p. 111). Our critique of neurophysiological subjectivism in the previous section implies that the perceptual object, though experiential, is also ineliminably ecolog-

ical, and so, contrary to Hardin, is not simply "in the head."

The enactive view of perceptual content is also different from both the "externalist" view that perceptual content is provided by distal physical properties and the "internalist" view that perceptual content is provided by subjective qualities (qualia). According to the enactive view, the contents of perceptual states are to be type-identified by way of the ecological properties perceived, and these ecological properties are to be type-identified by way of the states that perceive them. One should not be put off by this circularity, for it is informative. To specify perceptual content for a given animal we must investigate the relevant environmental properties, and to determine the relevant environmental properties we must investigate the sensory-motor patterns of activity that constitute the animal's perceptual states. This circularity is also empirically well-founded: Recall the discussion of how color vision and the ecological properties detected by color vision (e.g., plant and animal coloration) have in the course of evolution been selected for each other. The enactive view of perceptual content thus follows from animal-environment codetermination.

Now that we have provided an idea of the kind of conceptual space in which an enactive approach to vision could grow, let us return specifically to color vision. According to enactivism, color is neither a perceiver-independent property, as in objectivism nor is it merely a projection or property of the brain, as in subjectivism. Rather, it is a property of the enacted perceptual environments experienced by animals in their visually guided interactions. Unlike computational objectivism and neurophysiological subjectivism, this does not lead to an eliminativist position regarding color: color is not divested of its phenomenal or experiential structure in favor of spectral reflectance; nor is it divested of its extradermal locus in favor of neural states. Instead, color is a property of the extradermal world understood as an animal's environment, a world that is enacted by animal-environment codetermination. Thus we arrive at the view announced at the beginning of this paper, according to which color is both ecological and experiential.

Our view might in some respects recall Locke's (1690/1975) concept of color as a relational property, but there are significant differences. Locke held that color is relational because it is a "secondary quality," a disposition of objects to cause color sensations in a perceiver. According to the Lockean view, then, color is not merely *relational*, but also *dispositional* and *subjective* (see Bennett 1971). Ecological experientialism, however, does not imply that color is dispositional and subjective. We have not tried to explicate the relational nature of color by attempting to link dispositional properties of an organism-independent physical world, and private sensations, qualia, or sense-data. This is not feasible, we feel, despite repeated empiricist attempts (Westphal 1987; Thompson 1989). Nor does ecological experientialism rest on the distinction between primary and secondary qualities. On the contrary, our argument that not only color but also other high-level, spatial properties of the scene (object surfaces as determined by shapes and boundaries) are relational runs directly counter to the Lockean and Newtonian attempt to draw a principled distinction between color as a secondary quality, and size,

shape, and so forth, as primary qualities. Rather, we have emphasized the relational nature of the perceptual environment as a whole resulting from the enactive dimensions of visually guided activity.

Our intention in this target article has been to offer a broad, comparative framework for the ongoing, interdisciplinary effort to understand color vision and visual perception in cognitive science. This framework suggests specific directions for further research.

(i) The first concern of our comparative approach is to determine more precisely the kinds of color space there are in the animal world. For tetrachromacy, we need further evidence of four-way color mixture; to establish pentachromacy, we need evidence of five-way color mixture. Frequency modulation in the study of color vision (as described in Appendix B) might be useful in this area.

(ii) A related question concerns how the relevant color vision mechanisms and the dimensionalities of color space are related to perceptual phenomena such as constancy and segmentation of the visual scene. Of particular interest here is how color and other visual phenomena such as visual shape, texture, and space, interact to constitute different perceptual objects for various perceiving animals.

(iii) A third research objective is to determine (at least to a degree comparable to what is known of primates) the neuronal mechanisms underlying the variety of color spaces of different animal groups, especially fishes and birds. This is the key to understanding how color vision figures in the larger context of animal life and behavior.

(iv) Finally, the ecological aspects of the perceptual environment need to be investigated, for example, local illuminance and reflectance conditions, animal coloration, and animal communication. The task here is to develop further the means to describe the perceptual environment from a given animal's point of view, rather than imposing anthropocentric assumptions about such environments.

These questions have hardly begun to be addressed in detail in visual science, but we can expect their investigation to reveal even further the splendor of color as a naturalized aesthetic, or, in the words of Cézanne, "the place where our brain and the universe meet" (Merleau-Ponty 1964, p. 67).

APPENDIX A

Decorrelation procedure for calculating chromatic channels

(Buchsbaum & Gottschalk 1983; Palacios, in press)

Consider responses r_i to an arbitrary illuminant belonging to a set $\{I(\lambda)\}$,

$$r_i = \int d\lambda w_i R^i(\lambda) I(\lambda)$$

where the w_i are weighting factors for each primary response (as explained below). Next construct a covariance matrix Γ between the receptor response as follows:

$$\Gamma = \begin{matrix} \gamma_{11} & \dots & \gamma_{1n_{recep}} \\ \vdots & \ddots & \vdots \\ \gamma_{n_{recep}1} & \dots & \gamma_{n_{recep}n_{recep}} \end{matrix}$$

with

$$\gamma_{ij} = Ex\{r_i r_j\} - Ex\{r_i\} \cdot Ex\{r_j\} \quad [11]$$

where Ex is the expectation operator. To achieve optimal decorrelation the obvious step is to obtain the eigenvalues φ_i and eigenvectors for Γ , and the new matrix A constituted of the eigenvectors and their transpose A^T so that:

$$A^T \circ \Gamma \circ A = \begin{bmatrix} \varphi_1 & 0 & 0 \\ 0 & \ddots & 0 \\ 0 & 0 & \varphi_{n_{recep}} \end{bmatrix}$$

The eigenvector transformation is now well defined by:

$$\tilde{s}_r = A^T \cdot \tilde{s}_r \quad [12]$$

and the postulated chromatic channels ($C^1, \dots, C^{n_{recep}}$) thus calculated can be compared with the available experimental evidence. As Buchsbaum and Gottschalk (1983) emphasize, the covariance matrix depends not only on the shape of the primary responses, but also on the ensemble properties of the illuminants $\{I(\lambda)\}$. In fact, to arrive at an explicit expression for the correlations, we need to make some assumptions about the expectations $Ex\{I(\lambda)\}$ of the ensemble. A correlation $R(\lambda, \mu)$ and a covariance $K(\lambda, \mu)$ function can be defined as follows:

$$\begin{aligned} R(\lambda, \mu) &= Ex\{I(\lambda)I(\mu)\} \\ K(\lambda, \mu) &= R(\lambda, \mu) - Ex\{I(\lambda)\} Ex\{I(\mu)\}. \end{aligned} \quad [13]$$

If the choice is $K(\lambda, \mu) = \delta(\lambda - \mu)$ where δ is the Dirac delta function, this amounts to using monochromatic illuminants. Inserting [13] into [11] finally yields an explicit form for the entries in the covariance matrix [11]:

$$\gamma_{ij} = \int d\lambda R^i(\lambda) R^j(\lambda) \quad [14]$$

Thus the relative contributions from each class of retinal receptors need to be filled in by weighting factors previously mentioned. These are the only unknowns in our calculations; we have adjusted them so that the resulting channels have a good fit with experiments. These values should not be seen as ad hoc, however, but as proportions that should covary with neural characteristics.

For example, in the case of the goldfish this procedure yields:

$$\begin{matrix} C^1 & 0.11 & 0.37 & 0.72 & 0.58 & R^1 \\ C^2 & 0.83 & -0.5 & 0.23 & -0.12 & R^2 \\ C^3 & 0.26 & 0.68 & 0.15 & -0.67 & R^3 \\ C^4 & -0.48 & -0.4 & 0.64 & -0.44 & R^4 \end{matrix}$$

For the putative color channels of the pigeon, see Figure 4d.

APPENDIX B

Frequency analysis of color vision (Barlow 1982; Bonnardel & Varela 1989).

The basic strategy is to consider an illuminant (or a response capacity of the visual system) in the *frequency* domain, that is, to examine the spectral power distribution of the signal (or the response mechanism) in terms of cycles over "visible" window. For example, we can consider the frequency response of the three chromatic channels required for human vision. The channels proposed by Hurvich and Jameson, when studied under Fourier analysis, predict that beyond 2–3 cycles/300nm there should be little response, with a peak of sensitivity for signals around 1.7 cycles/300nm. These predictions correspond well with the first measurements of such a *modulation sensitivity function* (MSF) obtained with a specially built apparatus that can produce sinusoidally modulated illuminants with controlled contrast, frequency, and phase (Bonnardel & Varela 1989). The conclusion is that the signals for color vision are *band-limited*, that is, bounded in both the variable ("visible" window) and the frequency (cycles per "visible" window) domain. Now a nontrivial relationship exists between a collection of such band-limited signals and the number of significant independent samples required to reconstruct with sufficient accuracy any func-

tion in the collection (Buchsbaum & Gottschalk 1983; Dym & McKean 1975). Specifically, it can be shown that:

$$n_{\text{sample}} = \Phi[BT] + 1 \quad [15]$$

where $\Phi[x]$ stands for the highest integer smaller than x ; and n_{sample} is the number of independent channels required to sample the space of signals limited by B (in the frequency domain) and by T (in the wavelength domain).¹⁷ For example, if we take $n_{\text{sample}} = 3$, and $T = 300\text{nm}$, as in the human trichromatic system, a band-limitation $B = 1.5 \text{ cycle}/300\text{nm}$ is predicted. This limitation is within the range of the measured band-limitation of human natural scenes, which contain about 98% of all reflectances within the 1.5 cyc/300nm limit (Maloney 1985) but falls a little short of the observed MTF in humans which peaks at this value. In contrast, if $n_{\text{sample}} = 4$ and $T = 330\text{nm}$, as is the case in birds, one would predict a band-limit of $B = 0.001 \text{ cyc}/\text{nm}$. This result is due in part to the avian sensitivity window being large into 370nm, and on the other hand, to the pigment sensitivities being narrower: the combination of these two allows for less demodulation of the MSF at higher frequencies and corresponds to the higher frequency content directly visible in the putative channels discussed before.

Briefly stated, then, different chromatic dimensions will satisfy the sampling theorem with different combinations of the three quantities involved (n_{sample} , B and T), thus permitting quantitative comparisons of diverse color vision mechanisms. In particular, the measurements of MSF might represent a way to ascertain directly the dimensionality of a color space. On the basis of such a determination of color space, one could then undertake a comparison of the frequency-limitations of color vision mechanisms with the frequency-limitations of the reflectances of the relevant objects in the animal's environment. As we mentioned above, data have been collected concerning the frequency-limitations of human natural scenes (Maloney 1985); in the case of birds, some data have been collected about the reflectance properties of objects such as feathers, which, not surprisingly, have higher frequency contents than those of human natural objects (Burkhardt 1989). Obviously, work in this area is just beginning.

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NOTES

1. For further discussion, see Churchland and Sejnowski (1988), Sejnowski et al. (1988), and Boden (1988). Marr's optimality assumption has been criticized by Kitcher (1988); for some related points see Ramachandran (1985).

2. In visual science there is confusion and some disagreement over the use of the terms "brightness" and "lightness." According to Wyszecki and Stiles (1982, pp. 493–500), *brightness* is the "attribute of a visual sensation according to which a given visual stimulus appears to be more or less intense" (p. 493), whereas *lightness* is the "attribute of a visual sensation according to which the area in which the visual stimulus is

presented appears to emit more or less light in proportion to that emitted by a similarly illuminated area perceived as a 'white' stimulus" (p. 494). Strictly speaking, then, "brightness" refers to a dim-to-dazzling scale, whereas "lightness" refers to the gray scale of black and white. Nevertheless, many visual scientists, a large number of whom we cite in this paper, use "brightness" to refer to the white-black dimension. Furthermore, "lightness" has also been used in a related, but somewhat different sense by Land (1977; 1983), and by other researchers in computational color vision (Hurlbert 1986), to mean the psychophysical correlate of average relative reflectance (Land 1983) or scaled integrated reflectance (McCann et al. 1976). To avoid confusion, then, we use "brightness" for the achromatic dimension.

3. The material on which we are drawing here can be found in Boynton (1979), Hurvich (1981), Wyszecki and Stiles (1982), Mollon and Sharpe (1983), and Ottoson and Zeki (1985).

4. Our point in citing this passage is not that computational color vision commits one to objectivism about color – Land (1978; 1983), for example, holds distinctly nonobjectivist views. It is, rather, that the computational conception of color vision as concerned almost exclusively with the task of recovering surface reflectance suggests a form of objectivism.

5. For additional studies of near-ultraviolet sensitivity in bird vision, see Wright (1979), Delius and Emmerton (1979), Emmerton and Delius (1980), Emmerton (1983), Burkhardt (1982; 1989), and Burkhardt and Maier (1989). Cones with peak sensitivity in the near-ultraviolet have also been found in fishes: Harosi and Hashimoto (1983); Neumeyer (1985); Bowmaker and Kunz (1987).

6. Notice that channel C2 in Figure 4d has the appearance of an achromatic channel because of very small negative contributions from the long-wave primaries. This issue, as well as the general problem of the relative merits of a tetrachromatic or pentachromatic model for explaining the empirical data on pigeon color vision, require more elaborate discussion than we can provide here (see Palacios 1991).

7. This point is made clearly by Gouras (1985, p. 386), though it is a familiar theme in the history of color science. See Wasserman (1979) for a historical survey.

8. Some philosophers would no doubt go even further and argue that we cannot know what tetrachromatic or pentachromatic perception is like because the relevant facts (tetrachromatic or pentachromatic experience) are accessible only from the point of view of tetrachromatic and pentachromatic perceivers (cf. Nagel 1974). Although this claim is certainly relevant to our discussion, space constraints do not allow us to consider the various arguments here. We will therefore reserve discussion of this matter for another occasion (see Akins 1990; P. M. Churchland 1985; and Jackson 1982).

9. Hardin (1988, p. 146) notes this possibility of ternary hues by imagining a hypothetical tetrachromatic "visual superwoman," but does not extend his discussion to actual tetrachromacy among vertebrates such as birds and fishes.

10. Several objectivists (P. M. Churchland 1985; 1986; Hilbert 1987, pp. 111–18; Matthen 1988) have argued that such a mapping can be found in Edwin Land's (1977; 1983) retinex color space in which colors correspond to points in a three-dimensional space whose axes correspond to values of lightness calculated independently in each of three long-, middle-, and short-wave bands based on the sensitivities of the human (cone) photoreceptors. These arguments overlook two features of Land's model: (i) The axes of Land's color space are usually given as axes of lightness, not (average relative) reflectance. This is important because lightness is a sensation that can be measured only by a visual system, and problems arise for the straightforward identification of lightness with reflectance just as they do for color. (ii) Since the retinex color space attempts to specify colors purely in terms of lightness values it does not model the opponent relations and unique/binary structure of hue. In fact,

we cannot at present be said to understand how (chromatic) color could be generated purely from (achromatic) lightness comparisons.

11. It should also be noted that computational objectivist arguments such as Matthen's (1988) rely on a very strong notion of adaptive biological functions. We believe there are serious problems with this notion, but we will not pursue this point here. See Varela (1984); Maturana and Varela (1980).

12. We intend to investigate this issue in greater detail in another essay.

13. This claim is similar to one made by Berkeley (1710, Part I, para. 10). See also Wilson (1987).

14. A similar claim could be made for polymorphism in the evolution of human color vision, for example, red-green color blindness in human males.

15. This line of argument corresponds closely to one of Locke's (1690/1975) formulations of the primary/secondary quality distinction. Locke held that in the case of shape, our ideas (visual shapes) resemble (are structurally analogous to) their physical causes (shapes simpliciter), whereas in the case of color, they do not. Our criticism of this view as espoused by Hardin is similar to Berkeley's rejection of the view as espoused by Locke (see note 13).

16. For extensive elaboration of a research program for neuroscience in which the perceiving animal is treated not as an input-output system specified in terms of external mechanisms of control, but rather as an autonomous self-organizing system, see Maturana and Varela (1980; 1987), and Varela (1979; 1984; 1989; 1991a; 1991b), and Varela et al. (1991b).

17. This so-called sampling theorem requires, however, that the ensemble of band-limited functions have stringent averages (Brill & Benzschawel 1985).

wavelengths in the atmosphere, and so on. Then there are questions about the organism itself: Where does it live and what does it do? Exactly how you would draw on spectral information would depend on what visual tasks are appropriate to the organisms tempered by the spectral information locally available.

Consider an actual example – the visual/spectral problems confronting the fish (Levine & MacNichol 1979; Munz & MacFarland 1977). First, water absorbs light – the deeper the water the less light – but exactly which wavelengths are absorbed depends on the types of suspended organic particles. So, for example, clear water with little organic matter (such as in tropical oceans) will most easily absorb red and violet light. At depths below 25 meters, essentially all red and violet light has been filtered out, leaving only the intermediate “blue” wavelengths. Hence the “Mediterranean blue” appearance of such water to us. Marshes and swamps, but contrast, contain decomposing plants, tannins, lignins, and yellow-green plankton that effectively filter out almost all light at the depth of only three meters. The light that does survive, however, is in the red-orange region of the spectrum and gives the water its dark red-brown appearance. In addition, water molecules (and the suspended particles in water) scatter light – the medium of transport is itself “colored.” So, assuming that one visual task of the fish is to spot objects underwater, this detection must be done against a background of colored light.

One current hypothesis is that the rods and cones of some fish have evolved to function as *filters* that serve to highlight the contours of objects against the background space light. If the photopigment is “matched” (maximally sensitive) to the spectral range of the background light, then a dark object will be highlighted against the brighter background; if the photopigment is “offset” from the dominant wavelengths of the background light, then a bright object will be outlined against a poorly illuminated background. In fact, this scheme seems to be used in many species of fish. For example, the skipjack tuna, which spots its prey from below (dark object against a bright surface), has only one photopigment that is matched to the background light. The guppy's retina is divided into two regions. In the lower region, which looks upward and is used to spot prey, there is one photopigment that is matched to the background space light. The upper region, which looks down on the colorful mating display of the male guppy, has three spectrally diverse cone types. Finally, the walleye, bluegill, and piranha, which inhabit dark, particle-laden (hence, red-shifted) waters, are each dichromats, with one cone type matched to the near-infrared – a wavelength common to their “black” water habitat during the dusk and dawn hours of feeding.

What the above examples illustrate, we think, is that the use of spectral information could take many forms. It could be used to recover the invariant surface reflectances of opaque objects; then again, it might be used for the delineation of object from ground, to discern shape, monitor motion (Dobkins & Albright 1990), as a cue for eye movement (Ballard, forthcoming), and so on. There is, in other words, no *a priori* answer to the question, “What role does spectral information play in a visual system?”

What are the implications of this fact for color vision? Questions of consciousness aside, color vision, as defined behaviorally, is a certain *kind* of chromatic visual function – a selective response to light stimuli of different wavelengths regardless of intensity. (There seems no need to second guess the kinds of visual function that are necessary for our color experience insofar as questions of ontology hinge on the facts about function. If the ontological conclusions can be reached for any kind of color vision, then they will hold for conscious color experience as well.) Here, the form of such discriminations can vary immensely between species – the type of color vision a creature has will depend on the number of its color receptors, the response profiles of those receptors, and the additional “wiring” farther up the line. One can think of the initial “choice” of

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More than mere coloring: The art of spectral vision

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Suppose you were God, with a month of free Sundays, and you decided to design a visual system for a small creature. What would you do with the abundance of spectral information available from the world? How would you make use of the fact that sunlight ranges in wavelength from about 320 nm. in the ultraviolet out past 800 nm. in the infrared (NASA 1977), or of the fact that the refraction, absorption, and reflection of light by various media alters the composition of those spectral frequencies?

The right answer, we think (as Thompson et al. would agree), is just this – it all depends. First, you would (as a less than omnipotent god) be subject to the standard “materials” constraints. These are the various facts about the way the physical world is – the amount of energy it takes to break chemical bonds, what wavelengths of light would be absorbed by potential materials for the eye, the abundance or paucity of particular

receptors, the number and their response profiles, as providing a first filter on the spectral information available to the organism. For example, the kinds of receptors clearly restrict the range of spectral information that will be available (think of us and the bees). The wiring, on the other hand, is necessary to make accessible (or causally effective) certain kinds of information – to calculate hue (by disentangling intensity versus wavelength information for a monochromatic light source) or to disambiguate the spectral information from polychromatic sources. Wiring can also subserve computations that, although clearly useful, result in information *loss*, for example, by the categorization of spectral information (see Thompson et al.'s example of pigeon color categories) or by providing color constancy. Again, the “choices” made will depend on the uses to which that information is put.

Several points follow. First, what makes interspecies comparisons interesting is not their dimensionality, hence formal incommensurability, per se. (Consider that, in this sense, the color space of any tetrachromat would be “commensurate” with the gustatory space of man, or of any organism with four taste receptors). Rather, a comparison of color systems points to the “subjectivity” of color vision because each species represents a different informational “cut,” constrained only by utility and possibility, on the objective spectral world.

Second, as Thompson et al. claim, the scientific explanations of color vision (and other visual tasks that use spectral information) will advert to the environment of the organism, the organism's other visual functions, and its behavioral repertoire. It will include events both internal and external to the organism. For example, in explaining why one species of fish, the sea raven is a trichromat, Levine and MacNichol (1982) say:

Sea ravens possess three pigments . . . which cover a much broader spectral range than one would expect in a fish that spends most of its life at depths of more than 100 meters. . . . In the sea raven's breeding season, which is in late fall, the fish moves to shallow and thus to brighter and spectrally broader light. The bodies of reproductive individuals turn bright yellow, orange and scarlet, and after fertilizations the eggs are deposited on a species of sponge that is colored bright orange or yellow.

Note, however, that, contrary to Thompson et al.'s view of codetermination, such functional explanations rely on a certain fixed explanatory ontology – of light frequencies and intensities, and even of sponges and “bodies.” We explain the categories of fish color vision by first adopting a certain “scientific” vocabulary that will allow us to show how those categories came about. (In any explanation of a color system, we will use new terms and concepts as we discover and name new color categories and functions. But these terms will be part of what is to be explained, not part of the explanation itself.) This is so even in cases of coevolution – if, say, one were to explain the breeding coloration of the sea raven and the yellow color of the sponges in conjunction with the development of the sea raven color system. Of course, the trick in offering a legitimate explanation, we believe, will lie in not importing our own *a priori* biases, engendered by our conscious experience, into the initial vocabulary of explanation. But to say this is not to endorse the authors' view of ontological codetermination.

A limited objectivism defended

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Statements of natural laws (e.g., the Newtonian law of gravity) mention properties (e.g., mass) and relations (e.g., distance), and these laws govern objects in so far as objects have these properties and relations. A *physical property* of an object is any

property of the object in virtue of which it is governed by natural laws; or, as some prefer, in virtue of which the object can enter into causal interactions. (*Physical relation* is similarly defined.) Objectivism is the thesis that colors are either physical properties or logical constructions from physical properties (e.g., disjunctions or conjunctions of physical properties). One form of objectivism, call it “SR,” holds that the color of a nonradiating object is its surface spectral reflectance, and the color of a radiating object is its spectral radiance. (As Thompson et al. say, an objectivist must give an account of the color of radiating objects.)

Thompson et al. write: “Color is a property of the extradermal world understood as an animal's environment, a world that is enacted by animal-environment codetermination” (sect. 3). So colors (and surfaces) are *nonphysical* properties of objects. It follows that light striking an object is not effected by the object's color (or surface), although that color is a property of the object. This raises questions about color and light: Does light carry information about an object's color? If so, how does light do this? If not, how can one tell the color of an object by seeing it? (On a projectionist view, the light from an object does not carry information about the color of the object. This is all right, given projectionism, because the colors attributed to objects are not properties of those objects [contrary to what Thompson et al. hold].) If colors (and surfaces) are nonphysical properties, then these properties are causally disconnected from the rest of the world, and so the perception of color is causally disconnected from the interactions between light and objects, and light and the retina. Such a consequence makes the positive views of Thompson et al. implausible.

Just as the above criticism of Thompson et al. is a “mechanism of perception” criticism, so they make a mechanism of perception criticism of SR. They claim that, given SR, a surface must be perceived as opaque before it can be assigned a color by SR; but this is impossible, because part of perceiving a surface as an opaque surface involves identifying its color. Suppose that perceptual identification takes place in stages. In a preliminary stage an opaque surface is identified as having edges, corners, and some color features (such as being light, or being some color or other, or being somewhat reddish), although a determinate color is not attributed to it. This stage identifies an opaque surface as the sort of thing that can be colored, which it must be to be an opaque surface. (Presumably this is what seems impossible to Thompson et al., but I do not understand why this should be impossible.) At a later stage a more complete perceptual identification of the surface is made, as a surface having a determinate color, and this latter identification reconfirms the initial identification. So I see no problem for SR in all of this.

Consider two opaque nonradiating surfaces (which scatter all the light they reflect, i.e., they are not mirrors) that share the same lighting conditions. If the reflected light from the surfaces is different in wavelength composition, intensity, or polarization we would see this difference (if we could see it at all) as a difference in color. This would be true even if we saw the difference with the aid of special goggles designed, say, to react differently to some forms of polarized light. Furthermore, if the two surfaces looked different in color to anyone this would result from an objective difference in the surfaces (i.e., they reflect light differently), because to hold otherwise is to hold that in some cases the same cause can have different effects. So a perceived *color distinction*, under these conditions, is a perception of a physical difference between surfaces. (For more on this point see Averill 1985.) To capture this idea, let LO (limited objectivism) be the view that two opaque nonradiating surfaces (scattering all the light they reflect) are different in color if and only if, under some lighting condition, the surfaces reflect light differently. Given LO, there is more to color distinctions than SR allows, for example, differences in polarization – just as Thompson et al. claim. Furthermore, different animals can see different color distinctions – just as Thompson et al. claim. More

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 analytic 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

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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 "naïve" 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, 1988, 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 a first (naïve) glance to be located in objects; closer inspection shows that colors are produced in the brain (see Cormann, 1975, for remaining possible philosophical positions compatible with scientific results, pp. 217–46 for falsification of naïve 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) or on a combination of both. Whether a color vision system is 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 1969) an additional meaning ("colour, 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 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 14.6a–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-

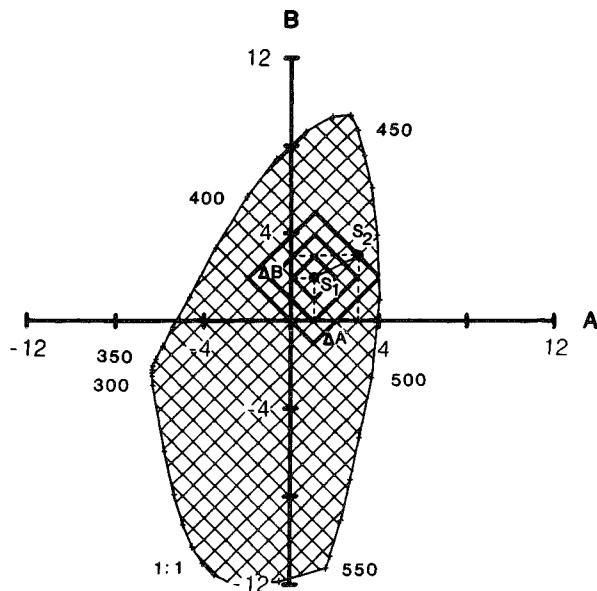


Figure 1 (Backhaus and Menzel). Geometry of the color opponent coding (COC) diagram presenting chromaticity (hue and saturation) of color stimuli (from Backhaus 1991). The excitations of the two opponent coding systems A, B caused by a color stimulus are linearly related to the respective cell excitations E in 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 10nm steps and the mixtures of the lights of the ends of the visible spectrum (300nm and 550nm), 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 dogmatic. 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

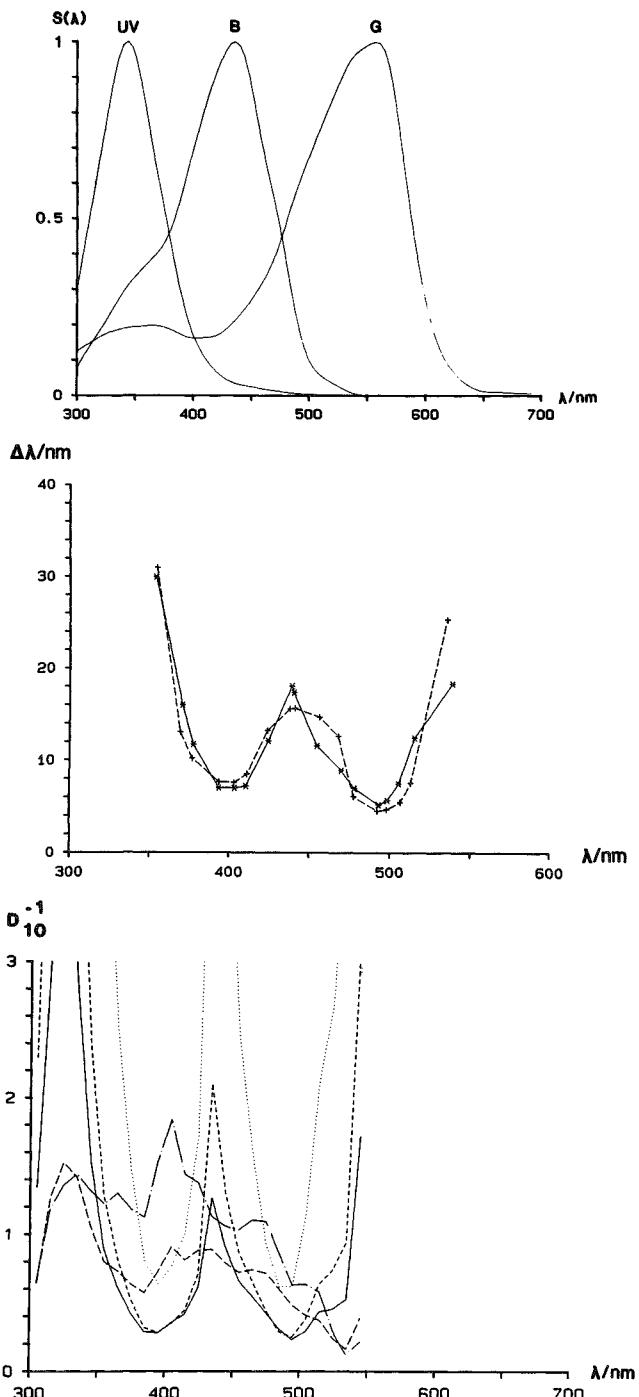


Figure 2 (Backhaus and Menzel). Relationship between photoreceptor spectral sensitivity and wavelength discrimination. (a) Spectral sensitivity functions of honeybee photoreceptors (best estimate functions, from Menzel & Backhaus 1989). (b) Comparison of the measured spectral discrimination curve (dashed, 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 10nm, 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. $Q = 0.1$: ···, $Q = 0.5$: -·-, $Q = 5$: —, $Q = 10$: -·-. The third minimum in the UV-region becomes dominant over the second around 400nm 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 rhodopsin 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 these 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

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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 elegant 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 subject, whereas objectivism conceives of them as the 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 – is 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 psychical, 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 activity 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*, 425b26). 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

this respect. Aristotle, for example, says that in actual perception the perceiver and the object are one and the same despite the difference between their modes of being. This difference is demonstrated in the fact that as potentialities one of them may exist without the other (see *On the soul*, III, 2). Gibson also considers the distinction between the physical and perceptual level of description to be crucial for understanding the perceptual environment. Although Thompson et al. begin by discussing this notion, they hardly make any use of it in their brief ontological discussion. Accordingly, one may doubt whether their approach consists of more than a few plausible pronouncements.

On another related issue the authors say that the perceptual environment cannot be given a purely physical-level specification, as it depends on three kinds of factors: (1) physical-level constraints; (2) sensory-motor activity; (3) evolutionary history. I would add another factor (which may be more dominant in human beings than in other animals): (4) personal history. This factor, which expresses a psychological-level specification, reflects the fact that perceptual content is shaped by the perceiver's personal background, anticipation, moods, emotions, and similar psychological variables. I do not know whether the authors' neglect of the psychological-level specification is accidental. I do know that admitting its presence would make the ontological status of the perceptual environment more subjective. Precisely because of this implication Gibson denies that this factor determines meaningful perceptual content. Thus, he argues that "the affordance of something does not change as the need of the observer changes"; the affordance "is always there to be perceived" (Gibson 1979, p. 139). This contention, however, contradicts the relational nature of the perceptual environment assumed by Gibson (see Ben-Ze'ev 1984; Heft 1989). Limiting the description of the perceiver to neurophysiological and biological factors is justified neither in Gibson's approach nor in Thompson et al.'s.

The authors also neglect some important epistemological issues. They rightly reject the assumption that the perceiving animal must recover a prespecified or already labelled world. They also say, however, that the prespecified world (or at least part of it) "is actually the world as described in relation to the sensory-motor capacities of the higher primates" (sect. 3). Assuming the existence of a prespecified world is natural if we do not wish to revert to idealism. There are difficulties in claiming that we know this world, however. If we assume that all of our cognitive capacities are shaped (as perception is) by the agent's structure and activity, then it will be hard (though perhaps not impossible) to know something about the prespecified world. Because the authors do not refer to such issues, I do not know whether their approach can cope with them.

In summary, Thompson et al. are on the right track and should be praised for explaining its necessity; the philosophical value of their view has yet to be demonstrated, however.

Nonreductionism, content and evolutionary explanation

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In their impressive target article, Thompson, Palacios & Varela argue for an "enactive view of content" and for an evolutionary "animal-environment codetermination," suggesting that the first "follows from" the second. (sect. 3, para. 19) I am attracted by the first; I am persuaded by the second; but I am unsure that the two issues connect as the authors claim. There is a form of codetermination in both domains, but it is different in the two cases, and I fear that the nonreductionism appropriate in the

theory of content would, if applied in evolutionary explanation, tie the hands of scientists with whom Thompson et al. would rather remain friends. Thompson et al. are arguing that computational objectivism and neurophysiological subjectivism lead not just to bad ontology but to bad science. For the most part, I agree; but I should like to suggest ways in which the explanation of colour-phenomena needs to make more use of noncolour notions, and even the notion of a "given" physical world, than they seem happy to allow.

The "enactive view of content" is that the content of perceptual states is to be identified by way of the ecological properties perceived, and these ecological properties are in turn to be identified by way of perceptual states. This seems attractive: A perception of red will be identified in terms of the property of redness, and redness will in turn be identified by way of perceptions of red.

The case of evolutionary "animal-environment codetermination" is rather different. The evolution of animal and environment are intertwined – the colouration of flowers and the colour vision of bees, for example, have evolved together. (sect. 2.5, para. 7) My first point is a simple one: Evolutional codetermination is a very different phenomenon from codetermination in the theory of content. The former is causal, the latter is constitutive. The former necessarily takes time; the latter need only involve one time. (The perception and the redness may, for example, be those present in a certain group of animals in a certain environment at a certain point in April 1991.) The "determination" in the theory of content is genuinely symmetrical – the content of experiences of red both (constitutively) determines and is determined by the nature of the property of redness. In evolutionary codetermination, on the other hand, the parties on each side change. The flowers of one time influence which genes survive into the *next* generation of bees; that generation of bees in turn influences the flowers of a *later* time. It isn't as though there is one state of the flowers that both (causally) determines and is (causally) determined by a single state of the bees. My second point is that evolutionary codetermination of this kind is not obviously a good reason to hold codetermination in the theory of content. If evolutionary theory told us that organisms "constituted" their environment, then this would be a reason – and sometimes it looks as though this is Thompson et al.'s claim. But I am not sure that evolutionary theory tells us any more than that organisms causally affect their environment and the environment causally affects organisms: The further claim would be plausible only for someone who already accepted the kind of theory of content that evolutionary theory was meant to be establishing here.

There is a more important general issue, although I am not sure whether it involves a real disagreement. Thompson et al. do not specify the appropriate terms in which to give a scientific explanation of colour phenomena, but their objections to the methods of computational optics might suggest that they would resist using "physical" terms in preference to colour terms. If they did, then they would rob themselves of many of the explanations they themselves cite: Fish have different kinds of colour vision because of the physically different character of light in their niche; pigeons may benefit from sensitivity to UV light because it enables them to "evaluate short-wave gradients in the sky," which aids navigation (sect. 2.4). It is the wavelength of the light that is cited, not the colour. In the case of the bees and flowers, it is the fact that the flowers show a contrast pattern in UV light and that some bees are sensitive to UV light that explains the survival of that type of bee. If, on the other hand, Thompson et al. do allow such physical evolutionary descriptions, then the points of the previous paragraph are strengthened: It becomes even harder to see how the existence of such evolutionary explanations serves as a ground for a nonreductive theory of content.

We need more empirical information on the evolution of colour vision and of coloration to know exactly in what areas the

claim of coevolution is correct. Thompson et al. resist the idea of a determinant physical world that poses for different species the single problem of how to become aware of its “given” physical properties. I am sure they are right to resist the idea in its full generality. But at each point in evolutionary history there are some features of the environment that are both (relatively) given and (relatively) physical, and these may serve to explain evolutionary changes that result in these features (or phenomenal counterparts of them) becoming part of the “life-world” of members of the species. There will no doubt be some features of the environment that have hardly changed at all with the evolution of sentient organisms (chlorophyll perhaps). There may be some features of the visual system that could hardly (for engineering reasons!) change, however great the evolutionary advantages. (The green of most animals absorbs more infrared light than does the chlorophyll green of plants; but vision, sensitive in the infrared, which would enable an animal easily to distinguish them, has not been found.) For a given species in a certain kind of environment there will be limits to how far the former can affect the latter and vice-versa; and to that extent, there will be features that are simply “given.” It would be good to know where exactly the limits have lain in the case of animals in their actual historical environment.

I say this not to question Thompson et al.’s nonreductive theory of content, which on the contrary I find extremely attractive, nor to disparage the evolutionary explanations that they actually cite. I say it to defend the view that there will be scientific explanations of the genesis of colour vision that use concepts from outside the life-world of the species. In some cases, it may be precisely because a feature lies outside the life-world of the species but correlates with, or has consequences for, features within the life-world, that there is pressure for the species after all to develop an awareness of it. On this view, there will be some evolutionary explanations that invoke relatively objective features of the environment – the kinds of features, either physical or physiological, which, when used exclusively, gave rise, as Thompson et al. rightly show, to the excesses of computational objectivism and physiological subjectivism. There is a place, I am sure, for nonreductive colour science (I give some examples myself in Broackes 1992); but there are other cases where explanations of colour phenomena, including evolutionary phenomena, will necessarily involve noncolour notions.

Surfaces and colour vision. In their critique of “computational objectivism,” Thompson et al. use an “argument from perceiver-relativity” to show that what counts as the surface of an object will vary with the perceiving animal’s colour vision. They present the argument as “conditional” on an empirical “conjecture,” that colour vision contributes to the individuation of surfaces. The conclusion seems rather implausible – colourblind humans do not in fact disagree with their coloursighted fellows on the existence of surfaces – and this in turn casts doubt on the conjecture the way the authors intend it. The surfaces that figure in the life-world of an animal are determined among other things by the needs, environment, and perceptual abilities of the animal. Colour vision certainly plays a part in *informing* the animal of these surfaces; but, in the context of the other ways an animal has of perceiving and thinking of surfaces, it hardly seems to *define* which surfaces exist. If one of the tasks of colour vision is the “recovery” of surfaces, then this is a task in which success is defined in terms independent of colour vision, although not independent of the broader life of the organism.

Color and science. The main claim of the target article is that computational objectivism and neurophysiological subjectivism lead not just to bad ontology but also to bad science. In both cases, the main objection is that there are generalizations that cannot be expressed in the language of the chosen approach. Computational objectivism can find no physicalist equivalent for, for example, “orange is a binary hue”; neurophysiological subjectivism has no place for explanations of colour vision in

evolutionary terms. In both cases I wonder if the arguments are too quick. Some physicalists would regard “orange is a binary hue” as attributing to a strictly physical property the higher-level property of “looking to ordinary perceivers to be composed of two hues.” The latter is an obviously psychological property (like “reminds me of Jack Nicholson”), which they will reduce later when they get round to it, but which can be applied to genuinely physical first-level properties. There is no question of saying that the colour is binary but the physical property is not; both are binary, and there is no objection to the physicalist identification. A reply to this might, I think, build on a distinction between colours and colour properties: Maybe the latter can be identified with physical properties, but the former are a different kind of thing. But developing that goes well beyond the present commentary.

On the subjectivist side: Thompson et al. actually recognize that Hardin (1990) himself wants to use evolutionary explanations. Their reply is that he has nonetheless not appreciated how colour vision “contributes to the very selection and constitution of animal environments.” But it is not clear that this is an objection to Hardin’s subjectivism: He could allow, for example, that bee vision has causally contributed to the selection of certain flowers without compromising his views if (1) he said that what was contributing was in fact a mechanism that produced mere *illusions* of colour, and (2) he didn’t in his own explanations attribute real colours to the flowers. There are other ways to put pressure on Hardin’s subjectivism, but I suspect that they need to consider more broadly either or both of the assumptions (a) that only what science tells us exists really does, and (b) that colour is not a scientifically respectable property.

Reductionism and subjectivism defined and defended

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As a reductionist and a subjectivist I find little to dispute, and much to cheer, in the use of the comparative argument against objectivism. The best available form of objectivism is anthropocentric realism, and at the very least the comparative argument dispels much of the *motivation* for that position. But I have qualms with the arguments arrayed against “neurophysiological subjectivism.” I do not think they demonstrate failures either in neurophysiological reductionism or in subjectivism.

Thompson, Palacios & Varela clearly deny neurophysiological reductionism. They write that chromatic experiences “do not yield to analysis purely in terms of the neurophysiological structure of the perceiver” (sect. 1.4, final para.); that “a purely neural explanation for color vision is incomplete” (sect. 2.5, para. 8); that color “experience can be understood only in the context of its ecological embodiment” (sect. 2.1, para. 2) and that any “adequate account” of color must be *ecological*. Furthermore, the embrace of the preferred ecological and “enactive” perspective is claimed in several places to be *contrary* to subjectivism, presumably meaning that they cannot both be true.

In outline the argument against neurophysiological subjectivism proceeds as follows:

(1) Animal capacities for color vision in many cases coevolved with the very colors that those capacities enable the animal to discriminate.

(2) Hence color vision contributes to the determination of the environment of an animal.

(3) Hence the qualities perceived in color vision are not purely internal and “in the head,” as subjectivism claims, but *ecological*.

A neurophysiological reductionist will happily agree to (1), dispute the terms in (2), and steadfastly deny the inference to (3). As examples of (1) the authors cite polymorphism in the color vision of squirrel monkeys, the coevolution of honey bee color vision and flower colors, and the evolution of animal coloration for camouflage and signal purposes. None are inconsistent with neurophysiological reductionism. The neurophysiological reductionist claims that the chromatic experiences a species has today can be explained without remainder in terms of the visual nervous system that species has today (Clark 1980; 1992). Curious humans can go on to ask: *Why* do these various species have the visual systems they have? One hopes evolutionary theory will someday provide an answer. But whatever the answer is, it will not contradict neurophysiological reductionism as described. The neurophysiological story is, admittedly, "incomplete," but only in the sense that it does not ask – and so does not answer – the question of the origins of the systems to which it refers. Presumably no one thinks that evolutionary history affected color vision *independently* of its effects on nervous systems!

In the second stage of the argument the authors shift from claims of animal-environment coevolution to what they call "codetermination." The term is paradoxical. At least in the ordinary sense of "environment," animals with distinct perceptual capacities can share the same environment. *Which* animals determined its features? Flowering plants are parts of the environment of many different animals. According to Thompson et al., some have incommensurable color spaces. If the color of flowers were determined by animal-environment coevolution with one of those species, it could not have been determined by the history of its interactions with other species. Contrary properties cannot *both* be determinative. If the bees did it, it cannot have been the pigeons.

At some points the authors use the words "environment" and "perceptual object" in ways that would lead them to deny that environments or perceptual objects are (or even *could* be) shared by species with different perceptual capacities. Such usages are salient in the third stage of the argument, where it is urged that we adopt an "ecological" and "enactive" approach to color vision. The gaps left in neurophysiological accounts are to be plugged by treating perception always as perceptually guided activity. Colors are "properties of the world that result from animal-environment codetermination" (sect. 3, para. 4). There is much in this talk that I do not understand or that seems open to immediate and devastating counterexamples. Try star gazing. On a moonless night, find a dark field, sit still, and you will see the colors of the stars. Although there are those who believe the stars determine the fate of humans, the stirring history of our species *could not* have affected any feature of the light entering one's eyes. It is also unclear what sort of "perceptually guided activity" is going on in our motionless star-gazer.

Perhaps the "ecological" perspective on the flower in my garden is as follows: That flower is part of my environment, and by hypothesis its colors are in part determined by the interactions its ancestors had with mine. That same flower is *not* part of the environment of honey bees; instead, they perceive a *different* object, with different colors, determined in part by the history of interactions between *that* object and the ancestors of the bee.

One problem with talking this way is that evolutionary theory could not corroborate any claims about *that* kind of "environment." For purposes of evolutionary theory we must be able to talk about the one flower out there in the garden, the one with genes, and so on, that can interact with many different species.

A subjectivist and reductionist description of the situation seems much more straightforward. The one flower out in the garden has various properties. When suitably illuminated it causes in me various kinds of chromatic experiences, and other kinds, perhaps incommensurable kinds, in the honey bees and local pigeons. The character of those experiences can in principle

be entirely explained by – reduced to – the neurophysiology of our various visual systems. We happily turn to evolution for hints as to why the species have the different systems that they do. The same account accommodates star-gazing most elegantly. Our visual system evolved, and we can admit it may have coevolved with a panoply of animal and plant colors in biological environments. Nevertheless, it now gives us certain capacities, and we can exercise those capacities even when confronted with stimuli (such as starlight) remote from biological environments and for which a codetermination story is completely implausible.

Finally, only straw-man versions of subjectivism are contrary to claims of animal-environment coevolution. Subjectivists need not define colors as "internally generated qualities that the animal simply projects onto the world," (sect. 3, para. 4) and they do not endorse the view that colors are simply "in the head." (sect. 3, para. 16) We can admit the existence of *stimuli*. The point is rather that the "collecting principles" – or that in virtue of which two stimuli are perceived to be the *same* color – cannot be framed in extradermal terms. The stimuli are indeed out there in the world – note that they *must* be, if genes can ever control them. But the principles that collect those stimuli into color classes can be found only in the innards of visual nervous systems. That different species operate in such radically different ways is just sauce for our (putatively pentachromatic) goose.

Color is as color does

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Thompson, Palacios & Varela object to computational models of color vision that emphasize the recovery of spectral reflectances of surfaces because these models do not capture the subjective experience of color. This is certainly true, and I think there is a very good reason for this omission in computational models. The kinds of tasks these computational models address do not require access to the kinds of information carried by an organism's subjective experience of color. Because color may do many things for us, and presumably for other animals, we should not be surprised if some tasks result in models that take into account the phenomenal structure of the animal's color experience while others do not. What you think color is (your model) depends on what you think color does for you (the task).

Computational models of color vision, or what Thompson et al. refer to as objectivist theories, generally address a very delimited task, that of computing descriptors of the spectral reflectance of a surface that are independent of the illumination under which the surface is encountered, of the surrounding spatial context, and of the viewing geometry of the situation. In other words, these are models of how a visual system in a particular environment with a particular complement of photoreceptors and postreceptoral elements could achieve some degree of invariance in its representation of the material properties of a surface in the face of varying viewing conditions. This is the classic problem of color constancy. The question of interest here concerns what kinds of mechanisms one must propose to achieve a desired degree of constancy. What kinds of procedures are necessary to perform this task?

We now know from numerous attempts to solve this problem computationally (Brill 1978; Buchsbaum 1980; Dannemiller 1989; Gershon & Jepson 1989; Land & McCann 1971; Maloney & Wandell 1986; Sällström 1973) that the kinds of algorithms that will solve this problem all involve very low-level processes in the visual system, such as adaptation (Helson 1938), spatial averaging (Hurlbert & Poggio 1988), and subtractive combinations across classes of photoreceptors (D'Zmura & Lennie 1986).

It is not necessary to know anything about the phenomenal structure of an animal's color space to achieve a reasonable degree of color constancy with these models. The low dimensionality constraints to which Thompson et al. refer capture statistical aspects of the environment; as such, they place boundary conditions on these algorithms. These constraints tell us that in some environments these procedures will accomplish this limited task reasonably well, whereas in others they will fail. The point of this example is that if the task calls for the computation of color constant surface descriptors then these models can perform this task reasonably well without postulating anything about the animal's subjective experience of color. It is at least reasonable to suppose that the visual systems of humans and animals could also accomplish this task using such low-level mechanisms. The absence of any mention of the experiential aspects of color vision in these computational models is a result of theoretical economy; such information is not necessary to solve the problem.

Consider another task – that of determining the shapes and material characteristics of various objects in a complex visual environment. The presence of illumination gradients, shadows and the shading produced by smooth changes in the orientation of a surface with respect to the direction of an illuminant all complicate this task. But color can play a potentially useful role in disambiguating the many factors that contribute to the local luminance of a point in the scene (Gershon et al. 1986; Rubin & Richards 1982). Why is it necessary to postulate anything about the phenomenal structure of an animal's color experience to understand the role that color plays in this task? It is certainly true that in this task and the previous one what constitutes a surface should be made sensitive to the animal's scale at some point in processing, as Thompson et al. point out. But this segmentation problem may initially depend more on the structure of the environment as captured at a particular station point in an optic array than on the scale of the animal. Gershon and Jepson (1989) have a computational model of color constancy that contains a regional segmentation algorithm that is driven by the chromatic structure of the image and some fairly simple merge and split rules.

Next consider a different task – searching for a particular object in a cluttered environment, for example. This object may be located visually by its shape, texture, relative size or color. Suppose that color is used to aid the search. Here it is reasonable to propose that if one were to model this task, one would almost certainly want to know something about the phenomenal structure of the animal's color experience. Are reds and greens opposed to one another? How does the animal partition the spectrum into color categories? Are there unique hues for this animal, and if so what are they? How good is the animal at discriminating saturation when hue is constant? The answers to these questions would be very useful if one were trying to model visual search using color as one of the variables over which the search could be executed. The efficiency with which this task could be performed probably depends on how salient certain chromatic distinctions are for the animal. This in turn probably depends on the categorical nature of the animal's color experience. In such a top-down task, prototypical colors function as particularly efficient symbolic descriptors with which to guide the search (Treisman & Gormican 1988). The prototypicality of a color depends on the structure of the animal's color space. So here is a task for which it would be useful to understand the animal's subjective experience of color. Color, when used as a descriptor in such a task, may be embedded in a symbolic structure subject to constraints very different from those governing computational models of color constancy (Kuehni 1989).

The way chromatic information participates in various tasks will determine whether or not it is necessary to include an animal's subjective experience of color in one's model. Some tasks can be performed without recourse to such information because they are determined by the optical properties and

statistics of environments. These statistics are in turn determined by the animal's ecological niche. Such tasks require fairly simple mechanisms. Other tasks are more complex, requiring color to be used to guide attention, modulate activity or make judgments. The procedures involved in these tasks may require the theoretician or model builder to be cognizant of the ways colors are experienced by the animal. When viewed in this way, the distinction between objectivist and subjectivist approaches may be more amenable to a theoretical rapprochement than Thompson et al. believe is possible.

What is a colour space?

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Thompson et al. have tried to resolve the mind-body problem for colour by resorting to their new principle of ecological enactment. The extent to which their study of comparative colour vision will resolve time-honoured conceptual difficulties is left to other commentators. They will need to understand how, apart from the effects of Darwinian selection, one can conclude that "colors are properties of the world that result from animal-environment codetermination" (sect. 3). Nor do I consider here the alternative roles proposed for colour, although its use in object discrimination (sect. 2.4) certainly requires qualification (Davidoff 1991). The issue my commentary addresses is different; it concerns Thompson et al.'s version of subjective colour space. The question asked (sect. 1.2) is, "Why does (our) color space have this phenomenal structure and not some other?"

We might first consider whether colour space really exists in the modular (Fodor 1983) form traditionally proposed for it. The independent processing procedures required for a colour module are denied, to a limited extent, because colour matching is marginally affected by the shape (Egeland & Pachella 1969; Overmyer & Simon 1985; Williams 1974) and meaning (Menaud-Buteau & Cavanagh 1984) of the boundaries that contain the colours. Although these effects are small, they reveal an important aspect of colour. To be modular, colour needs to be dissociated from its containing boundary; generally, it is not. Thus, we do not usually talk of seeing a green but of seeing green (objects). Colour is therefore a concrete property of an object that is made abstract by locating it within a colour space. The concrete and abstract aspects are easily confused because when seeing an apple (or any other object) we apply the same term (e.g., red) to the (concrete) recovery of distal information as to the part of our internal colour space at which the term applies to an infinity (or a very large number) of different locations.

Whatever the limitations on the modularity of colour space, it has regularities that result from the output of neurophysiologically defined channels. These regularities can be derived from wavelength discrimination functions without the need for the emphasis (sect. 1.3) on colour constancy mechanisms. Mullen and Kulikowski (1990) showed that at threshold detection, wavelength discrimination was not continuous but categorical, with four, or perhaps five, colour regions. If, as is reasonable to suppose, these regions result from opponent-process output, species with different numbers of cone types might well show different numbers of colour regions in their colour space (sect. 2.3). There is no one-to-one mapping of cone types to the division of colour space, however. In particular, it is not necessary for the colour space of humans to be tripartite, as in the Munsell system. Although aspects of surface appearance related to hue, lightness, and saturation may be highly correlated with the output of cells in the visual system, the efficient use of these three categories is not achieved without consider-

able experience. The Munsell components of colour interact in categorisation tasks (Felfoldy & Garner 1971; Garner & Felfoldy 1970) and, for that reason, Garner (1974) calls them integral. To the observer it would seem that a coloured surface is first seen as a whole or, as Lockhead (1972) puts it, a blob. Thus, even though it is possible to break down colours into subcomponents, they resist separation. The separation of surface colour into its components (hue, saturation, and lightness) can be achieved, with more or less success, according to task demands (Garner 1988), individual differences (Stalmeier & De Weert 1988; Ward et al. 1986) and training (Foard & Kemler-Nelson 1984), but it is difficult even for colour experts (Burns & Shepp 1988). Amateurs, in particular, often confuse brightness with saturation (Davidoff 1974).

The organisation of colour space does not correspond directly to the output from opponent-process mechanisms even though it is, in part, derived from them: In the internal colour space, red is not necessarily paired with green, or yellow with blue; Dixon (1960) also argues this for the unconscious use of colour. Individual items (locations) in the colour space represent *combinations* of wavelength and intensity differences. These locations could be compared (see Davidoff 1991) to stored descriptions of objects that are viewer-centred (Marr 1982). The individual items are organised into regions (categories) of colour (red, green, etc.); these could correspond to stored descriptions of objects that are object-centred. Neuropsychological evidence shows that an impaired ability to categorise colours may coexist with intact "viewer-centred" mechanisms (De Renzi et al. 1972; Sittig 1921).

Hitting the nail on the head

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This target article is a valuable antidote to several different ill-examined preconceptions, but I don't think it has quite succeeded in unmasking and neutralizing the bogey that motivates them all. This commentary attempts to do this by reinforcing, with minor caveats, some of the authors' main points.

In defense of their "enactive" account, Thompson et al. occasionally protest too much. For example, the trouble with (external) objectivism is *not* that it makes the mistake of holding the external environment constant, setting a problem for the organism. Following Lewontin (1983; 1985), Thompson et al. insist on the role of the organism in creating its visual environment, but this is a process that occurs almost entirely on an evolutionary time scale. It is true, as Lewontin has often pointed out, that the chemical composition of the atmosphere, for instance, is as much a product of the activity of living organisms as a precondition of their life, but it is also true that it can be safely treated as a constant, because its changes in response to local organismic activity are usually insignificant as variables in interaction with the variables under scrutiny. The same is true of the colors of objects: They have indeed coevolved with the color-vision systems of the organisms, but, except on an evolutionary time scale, they are in the main imperturbable by organisms' perceptual activity.

The fact of their coevolution is as important as the authors insist, however, when it comes to answering the *why* questions of color vision (and we do want scientific answers to *why* questions). One of the flaws in (external) objectivism is that it discourages the exploration of a large class of empirically promising hypotheses. For example, why does a certain fruit turn a particular shade of red when it ripens? It *might* be that the availability of a certain photopigment for exploitation in the eyes of the target fructivores had a larger role to play in the answer than, say, the constraints on byproducts of sugar formation in

the fruit. The work cited on coevolution of organism coloration and color vision strongly suggests that color-coding (to reduce the cognitive load on the target perceiver) is at the basis of at least much if not all color vision (Dennett 1991). Things are the colors they are *because* we (or other creatures) have the sorts of color-vision systems we have, and we have the systems we have because they enable us to see the colors things are.

But still the traditional appeal of the idea that colors must be objective, independently existing properties of surfaces asserts itself. Consider the chameleon. We accept that the chameleon actually changes color (as opposed to merely seeming to change color) because we understand that it has a way of changing the relevant microphysical structure of its surface, the structure that determined "surface spectral reflectance." In contrast, we would be more disinclined to say that some other organism changed color (as opposed to merely seeming to change color) if it accomplished this by merely moving into different illumination without changing its surface microstructure. But this might be just as valuable a countermeasure, and hence should be viewed as just as sturdy a candidate to anchor the biological category of color.

Consider the well-known mimicry by nonpoisonous species of brightly colored poisonous species in the vicinity. I do not know if there are any actual cases, but it could be that a mimic species had discovered a microphysically different "way of being bright red" – at least in the normal illumination environments of the relevant predators. Would we say that these mimics were *the same color* as the poisonous species? They might not be seen to be the same color by us, or even by their predators under abnormal conditions, and yet such a case should count as different ways of being the same color. The two species would "match," for instance, in the same way the color of the drapes matches the color of the woodwork – the way that matters (to us) – even if they don't match under all conditions.

But what, then, *are* colors? Doesn't this imply that only a circular definition of color is possible? Yes, but as the authors say, "one should not be put off by the circularity" (sect. 3, para. 16). The real bogey is the fear that if we cannot give a foundational, objective definition – either in the form of an external objective definition (e.g., Hilbert 1987) or in the form of an equally objective internal or neurophysiological definition – we will be stuck with "intrinsic, ineffable, unknowable" qualia. The true value of the enactive view is that it explains why neither of these sorts of objective account is necessary to avoid the extreme subjectivism of Nagel (1974). Both these varieties of reduction are embarrassed by the specter of having to deal with all the counterexamples by brute force enumeration of exceptions – a telltale sign, presumably, that they have failed to capture the "essence" of color. An enactive account, however, can explain, objectively and scientifically, everything that needs explaining – including the fact that no compact, noncircular definition of color is possible – with no leftovers conceded to mystery.

Enactivist vision

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Thompson et al. attempt to establish that an animal's capabilities and goals are the fundamental determiners of how it perceives the world. They certainly convince us that this holds for their own treatment of the vision literature. Computational vision has a reconstructionist branch, but also an older and equally productive group of researchers studying active vision. And the reconstructionists are keenly aware of segmentation issues and have never considered inverse optics as the end product. More generally, the target article includes a (very nice) detailed

review of some aspects of vision research but totally ignores several others – for example, attention (Posner & Hubel 1990), adaptation and priming (Livingstone & Hubel 1988) – that bear on the relation between internal and external aspects of color.

It is hard to believe that visual scientists will find much to quarrel with in the conclusions that vision is interactive and ecologically determined. What does need to be challenged is the appeal late in the paper (sect. 3) to the “self-organizing properties of neural networks.” Having refuted pure reconstruction, Thompson et al. gratuitously identify this with all forms of internal representation and promote pure sensory-motor activity as the basis for vision. There are mechanisms of this sort even in primates (the subcortical mechanisms such as the vestibular-ocular and other reflexes) but these elaborate innate neural structures could hardly be called self-organizing. More important, denying the existence of representation in the vision of higher animals flies in the face of everything that has been learned about cortical maps, spatial cognition, and, in fact, all but the simplest behavior (Livingstone & Hubel 1988). Like the Gibsonian perspective, enactivism can provide a useful corrective to excessively mechanistic views of perception, but to actually believe it would be crippling for visual and other cognitive scientists.

Psychophysical modeling: The link between objectivism and subjectivism

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To the extent that they develop computational models that are physiologically plausible, psychophysicists bridge the gap between objectivism and subjectivism. One weakness of the objective position is the implication that if we conducted enough experiments, varying enough stimulus parameters, we would eventually explain color vision. Models are inevitably oversimplified, often suggesting that an experiment isolates specific psychophysical channels (e.g., long-wavelength cone pathway) or cell types (e.g., red/green opponent cells). In reality, a model that describes one set of data will fail to account for other findings.

In any case, the goal is not only to find a series of equations that describe some data; the theory should be consistent with visual physiology. Yet as Thompson et al. note (sect. 1.2), comparing psychophysics and physiology is precarious, even when the connections seem obvious (Hood 1981; Teller & Pugh 1983). The need to specify explicitly one's psychophysical assumptions, physiological assumptions, and linking hypotheses was demonstrated by a series of experiments examining the detection of small, brief lights (Finkelstein 1988a; b; Finkelstein & Hood 1981; 1982; Hood & Finkelstein 1983). The studies measured, not color appearance per se, but relative sensitivity to lights of different wavelengths.

The open circles in Figure 1 show a spectral sensitivity for a large, long-duration foveal flash (49 minute diameter, 500 msec duration). The peaks in the data are narrower than receptor absorption spectra, and they are shifted relative to the cone sensitivities. The solid and dashed curves are the red/green and yellow/blue functions, respectively (from Ingling & Tsou 1977). The data are well fit by an envelope of the opponent spectral sensitivities. The results suggest that large foveal flashes are detected by pathways consisting of spectrally opponent cells (e.g., Finkelstein & Hood 1984; King-Smith & Carden 1976; Sperling & Harwerth 1971). This conclusion was supported by cancellation experiments in which bichromatic test mixtures were found to be less detectable than either component presented alone (e.g., Guth & Lodge 1973; Stromeyer et al. 1978).

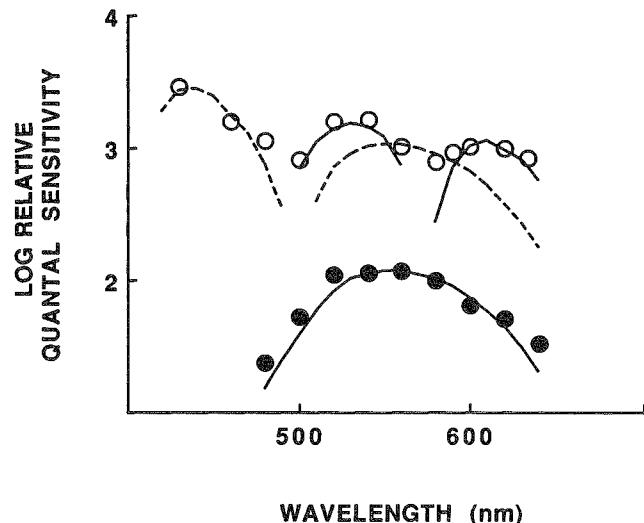


Figure 1 (Finkelstein). Spectral sensitivities for foveal test lights 49 minutes in diameter and 500 msec in duration (open circles) or 10 minutes in diameter and 40 msec in duration (filled circles). Stimuli were presented on a 4.0 log td unfiltered tungsten steady background. The log reciprocal intensity required for detection is plotted. The solid and dashed curves through the large-test data are the relative spectral sensitivities of the red/green and yellow/blue systems, respectively (from Ingling & Tsou 1977). The curve through the small-spot results is the CIE photopic luminosity function. [Reprinted from *Vision Research* (1984) 24: 175–81, Figure 1.]

Color naming experiments showed further that the hues of these lights are discriminable at detection threshold (e.g., Ingling et al. 1977; Krauskopf 1978). The consensus in the color literature was that large, long-duration lights are detected by spectrally opponent cells or opponent channels.

Complications arose when the same assumptions about the properties of neurons and psychophysical channels were applied to measurements made with small, brief lights. The filled circles in Figure 1 are spectral sensitivity data for a 10 minute, 40 msec target. The curve through these data is the photopic luminosity function. The broadband luminosity function is attributed to the activity of nonopponent cells (e.g., DeVelois et al. 1966). Its fit to the small-spot data suggested that these lights are detected via a nonopponent pathway consisting of spectrally nonopponent cells (e.g., King-Smith & Carden 1976).

Subsequent field sensitivity, test mixture, and color naming data, however, implicated red/green cells in the detection of small, brief lights (Finkelstein & Hood 1982; 1984). Figure 2 shows the field sensitivity for 49 minute, 500 msec fields of monochromatic light. The procedure measures the relative ability of fields of different wavelengths to reduce sensitivity to a 10 minute, 40 msec, 580nm test (see figure caption for details). Note the narrow peaks in sensitivity around 540nm and 600nm and the notch at 580nm; the data resemble the red/green spectral sensitivity.

The prevailing assumptions about the properties of opponent and nonopponent cells and psychophysical pathways made reconciling the small-spot test and field sensitivity data difficult. A partial solution was provided by physiological data showing that opponent cells can become nonopponent with decreased stimulus size or duration (e.g., Gouras & Zrenner 1979; Wiesel & Hubel, 1966). The changes in spectral tuning are a consequence of the spatial opponency of the cells' receptive fields. The physiology suggested a “variable tuning” model in which small foveal flashes are detected by a red/green channel with a nonopponent spectral sensitivity (cf. Finkelstein et al. 1990; Finkelstein & Hood 1982; 1984; Ingling 1978; Wandell & Pugh

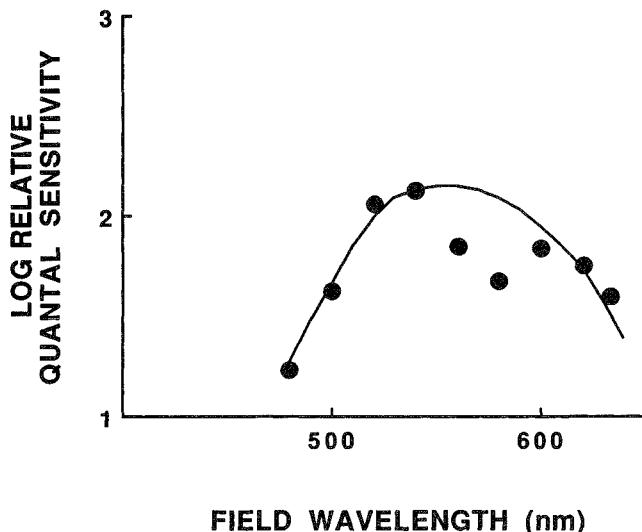


Figure 2 (Finkelstein). Field sensitivity for 49 minute, 500 msec monochromatic fields. The test was a 10-minute diameter, 40 msec, 580nm light. Test and field were presented on a 4.0 log td "white" (unfiltered tungsten) adapting background. The figure shows the log reciprocal field intensities required to raise threshold for the test 0.3 log units above the threshold obtained on the adapting background alone. The solid curve is the CIE photopic luminosity function pinned to the field sensitivity at 540nm. [Data reprinted from *Vision Research* (1982) 22: 89-95, Figure 3A.]

1980). In this model, the differences between large- and small-spot test sensitivities do not imply a change either in the type of cell involved or in its properties. Rather, the data reflect variability in the way individual receptive fields are stimulated.

Yet the "variable tuning" solution itself produces new questions. How do we explain our ability to discriminate the hues of small spots? Answering this requires revising the traditional view that hue is signaled in the response polarity of two classes of opponent cells (red/green and yellow/blue). One alternative is a model in which hue is coded in the pattern of activity across cell types (Finkelstein & Hood 1984). This approach, if developed, will undoubtedly produce other problems for traditional models of opponent pathways.

Despite the obvious limitations of the computational approach, quantitative models have led to significant advances in our understanding of color vision. One contribution of Thompson et al.'s target article is the recognition that computational and neurophysiological approaches are both integral to the development of a unified theory of color vision.

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Multivariant color vision

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Ways of coloring is an interesting essay that attempts to emphasize the importance of the integration of motor and sensory modalities in visual perception. The authors contend that this idea can have significant heuristic value in advancing our understanding of color vision. I tend to agree with this hypothesis. They call this approach an "enactive" one, a somewhat dysphemistic neologism, which may impede rather than further their cause.

There are several levels at which this "enactive" approach can work. The most obvious involves visual interactions between cooperative organisms, especially interactions influencing reproduction, such as those between bees and flowers and monkeys and fruit trees. Here visuomotor interaction actually alters the physical environment.

A second level involves a fixed physical environment which is perceived differently by organisms with different visuomotor systems. Color vision is a good example because color is the most illusory of visual perceptions. Thompson et al. emphasize different effects that the dimensionality of color vision can have on visual perception. As humans we have good insights into what these changes can be. We can compare monovariant nocturnal rod vision or better black and white TV vision with trivariant daylight vision. We can also communicate with divariant human subjects who have lost one dimension. The overall changes in our visual universe are not great, however, because it is so structured by form. Form vision must be significantly altered to have a major impact on our perception of the external world. The authors raise a good point in using comparative biology to implement their hypothesis. Organisms that fly or swim and consequently are very active in three rather than two dimensions encounter many different perspectives of the external world. When this motor activity is coupled to tetra- or penta- variant color vision, views of the external world other than those encountered by horizon-oriented species are possible.

A point not made in this target article concerns the limitations of multivariant color vision in high resolution achromatic contrast. The greater the variety of spectrally different photoreceptors, the greater is the problem of chromatic aberration. Photoreceptors of different spectral selectivity respond best to different image planes. Such a factor must be responsible for making our foveolas di- and not tri-varient. Multivariant color vision compromises high resolution achromatic vision.

The most intriguing problem about imagining the visual universe of organisms with smaller brains is knowing whether the high degree of chromatic contrast detection they have leads to a greater palette of perceived colors. The visual universe we experience depends on the memory of multiple changing views that our oculomotor system generates in our visual system. Determining how movement-generated visual signals are assembled in the brains of flying or swimming organisms is an intriguing and important challenge for scientists of vision, even those most mobile in color vision. In highlighting this idea, Thompson et al. should be complimented.

Color for pigeons and philosophers

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To study color is, in a narrower sense of the word, to study black, white, red, yellow, green, and blue. But in a broader sense of that term, it is to study the qualitative visual states of animals, human and nonhuman alike, as well as the environmental intensity and wavelength modulations of a certain band of electromagnetic radiation. There is everything to be said for taking the proper domain of scientific investigation to include color in the broader sense. Indeed, we will gain a full understanding of red, green, and the like only by locating them in this wider context, although in so doing we must avoid such practices as identifying hues with spectral reflectances or uncritically assigning hue labels to the qualitative visual states of nonprimates.

In *Color for philosophers* (Hardin 1988) I chose to focus on color in the narrower sense because this is what I took to be one

locus of philosophical perplexities about the relationship between mind and body. I did not intend to advance a more sweeping "methodological claim" that, in the broader sense of color, "color phenomena can be analyzed in neurological terms." Instead, I applaud the efforts of Thompson, Varela & Palacios to draw us into worlds of alien color (or, perhaps, "color") vision, worlds that I find much more stimulating to the imagination than the fantasies about Martian experiences beloved of some philosophers. When the authors wish to characterize the manner in which their views differ from mine, however, they sometimes state their views misleadingly, and this makes it seem that we disagree more than we really do.

For example, Thompson et al. assert (sect. 2.5) that "Hardin neglects [the] role that visual perception plays in animal-environment codetermination." My neglect is said to consist in my overlooking (1) "the fact . . . that most of the world's colors are organic colors" and (2) "the role that color vision plays in spatial segmentation and hence the relational nature of the surface of perceptual objects." But all that (1) comes to is the uncontroversial claim that the activities of perceiving animals (e.g., bees) have selected many of the *reflectances* of plants (e.g., flowers) and of other animals in their environments. The reflectances of flowers are "colors" in one of the broader senses, but – as the authors themselves are at pains to argue – certainly *not* colors in that narrower sense of the term in which one can contrast the color space of one species with that of another.

Furthermore, the selection of environmental reflectances is the work of populations of animals interacting with populations of plants and other animals. It would be misleading to urge that we have here a case of individual animals *making* the colors in their surroundings. By contrast, in case (2), which I am also said to have overlooked, the individual animal is using its color perception to segment its visual scene into visual surfaces. Here the colors of surfaces are the product of the animal's perceptual activity, and those colors are not, in Thompson et al.'s opinion or mine, reflectances. But then the object in question isn't a physical object either, but a "perceptual object," an object as experienced by the animal (to the extent that we are entitled to speak of the animal as having perceptual experiences). The upshot is that populations of animals generate colors (spectral reflectances) as constituents of their physical environments, whereas individual animals generate colors (visual states) as constituents of their perceptual environments. The "enactivist" view of perception, insofar as it is supposed to represent an alternative distinct from "subjectivism," thus seems to involve equivocating between perceivers as individuals and perceivers as species, as well as between representations and physical objects. Once the equivocations are removed, I can find little in enactivism with which to disagree.

Thompson et al. seem to find problematic my distinction between visual shape, which is always bound up with color (narrowly construed) and dependent on the animal, and shape simpliciter, which is not. Perhaps the following words will be of some help in positioning my view with respect to theirs: I use the term "shape simpliciter" to refer to the physical structure that is, in the first instance, picked out by both visual and tactal-kinesthetic sensing, and is capable of being studied by various physical instruments. *Visual* shape is a certain projective transformation of physical shape simpliciter that is entangled, as shape simpliciter is not, with color qualities. Although physical shape thus described is not organism-relative, it is certainly relative to our scale and level of resolution. It may then in turn be assimilated to a more general, and physically basic, notion, that of spatial configuration (or, if one wishes to generalize still further, spatiotemporal configuration).

The vocabulary of spatial configuration surely gives us a species-neutral way to describe the characteristics of any animal we like, as well as the environment that it inhabits. This basic vocabulary – think of it as the terminology of analytic geometry – is indifferent to scale and resolution, although the effective

description of a phenomenon at a particular scale and level of resolution for a particular purpose typically demands a spatial-configuration vocabulary appropriate to that scale, level, and purpose. (The planetary astronomer, for example, will consider Saturn's oblately spherical shape rather than the spatial arrangement of its constituent atoms.) Because we human beings are doing the investigating of other species, we are inevitably the ones who must abstract those configurations that we find explanatorily valuable for the purpose at hand, but they need not be the same configurations to which we would have attended had the object of our investigation been some other animal. To examine the life-world of an animal we must attend to what is significant to that animal. The important point, however, is that whatever spatial configuration is attended to, and for whatever reason, attending to it only selects it from a background but does not generate it. The same can be said of spectral reflectances. But in the sense of "color" that Thompson, Varela, Palacios, and I use to speak of the dimensionality of the color spaces of pigeons and people, the animal nervous system does not select color, but rather generates it.

Comparative color vision and the objectivity of color

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To be an objectivist about color is to hold that color is a property that objects can have independently of whether or not they are perceived by human beings or other sentient creatures. If we are to restrict ourselves to physical properties then there are compelling reasons for supposing that color must be somehow connected to the reflecting properties of surfaces. Within this rather minimal framework, objectivist views of color can take a variety of different forms and be supported using a number of different arguments. To establish the untenability of objectivism it is not enough to show that some variants within this framework are inadequate; the framework itself must be challenged. Although the target article establishes the untenability of some versions of objectivism, the framework itself remains untouched and in fact much of the evidence Thompson et al. offer in favor of their enactivist point of view can be comfortably accommodated within the objectivist framework.

One way the authors attempt to use the considerable variation in color vision among different kinds of animals relies on the role color vision may play in the visual segmentation of a scene into distinct surfaces. Thus variation in color vision may lead to variation in scene segmentation. The strategy of the argument is to attempt to undermine objectivism about color by undermining objectivism about surfaces, leaving the objectivist with nothing to which objective colors can be attached. This argument can be taken two different ways. As a refutation of color objectivism the argument is clearly question-begging. The mere fact that color vision plays a role in the segmentation of scenes into distinct surfaces shows nothing directly about the objectivity or relational character of either surfaces or colors. The argument merely establishes that the processes that contribute to the perception of color also contribute to the perception of form. Objectivists distinguish between perceptual states and objective states, and establishing a dependence between two perceptual states does not establish a similar dependence between the objective properties with which the perceptions are associated.

Although the argument from perceiver-relativity does not constitute a direct refutation of color objectivism, it does point out an important fact that any objectivism has to take into

account. The properties of the physical world that an organism has perceptual access to may not be the same ones that human beings are able to perceive, and which properties these are depends importantly on the perceptual apparatus (and ecological needs) of the organism in question. Any view of color that entails that the physical facts completely determine what color is perceived, even in ideal conditions, is clearly inadequate. Thompson et al.'s discussion of comparative color vision drives this point home quite forcefully, although it can also be made simply by considering the variability in human color perception.

To address this variety of perceiver-relativity an objectivist must give up any commitment to there being exactly one correct description of the world of colored objects (although there may be a unique *complete* description). Suppose that color is surface spectral reflectance. What perception gives access to for a given kind of organism is not the determinate reflectances themselves but rather that a given surface has a reflectance of a particular kind. Which kinds the organism has perceptual access to will depend in part on the characteristics of its perceptual system. Different organisms may perceptually use different categorizations, but they will all be classifications of the same reality. The fundamental point is that perception gives us only partial information about the color properties of objects and that once this is recognized many of the facts drawn from comparative studies of color vision can be seen to be compatible with color objectivism. A similar account can be given of variations in the way different organisms segment the visual world into scenes. We need to acknowledge a relativity to the characteristics of the organism in the kind of information it is able to obtain about the spatial properties of the world but this does not imply that these characteristics determine the character of the world the organism occupies.

If the comparative study of color vision is to pose difficulties for objectivist views of color then it will be for different reasons from those given in the argument from perceiver-relativity. Computational objectivism, as characterized by Thompson et al., has at its heart the claim that color is whatever physical property it is the biological function of the color vision system to detect. It may be plausible to think that in the case of human beings and our near relatives this property is reflectance. But there is no *a priori* reason to rule out, and according to the authors some empirical reason to rule in, the possibility that for some organisms color vision serves to detect quite different properties. If this possibility is realized then there is no single physical property that it is the function of color vision to detect. This would seem to preclude any objectivist theory of color. (The argument also raises difficulties for any non-subjectivist theory of color, including the authors' enactivist theory, for the very same reasons.)

There is at least one response to this argument open to the objectivist, however, and that is to make a virtue out of what the authors paint as objectivism's greatest sin, its parochialism. Discussions of the ontology of color, as well as a large part of color science, are, after all, primarily concerned with a property that human beings perceive, reflect on, and talk about. If it turns out that this property is not perceived by some other kinds of organisms that is neither surprising nor a challenge to the adequacy of our accounts of this property of particularly human interest. Seen in this light the comparative considerations merely show that not all organisms are capable of perceiving color; and given the diversity in ecological circumstances and needs found in the animal world it is scarcely surprising that a property that is perceptually important for one kind of organism plays no role in the perceptual life of some other kinds of organisms.

Although I am inclined to think this response is along the right lines, there is one glaring difficulty with upholding such a human-centered defense of the objectivity of color. The original problem was raised by the possibility of there being organisms in which color vision has a function different from the one it has in human beings, but the point of view just sketched implies that

there is no literal sense in which such organisms possess color vision at all. They do not, by hypothesis, perceive color, although they may use somewhat similar visual machinery to perceive a different property. Attributions of color vision to nonhuman organisms have traditionally not been made on the basis of the function their visual processes play in detecting distal properties (those functions are usually not known) but rather on the basis of other less teleological characteristics, such as the ability to distinguish wavelengths independent of relative intensity. Thus, there is a mismatch between the objectivist account of the nature of color and the kinds of considerations that are involved in attributing the presence or absence of color vision to nonhuman organisms.

If this argument is correct then something has to give. Space considerations preclude a more extended discussion of these points, and it may be that this argument establishes nothing more than the fact that although the interests of philosophers and visual scientists may overlap at places, they also diverge at others. Those interested in ontology and those interested in the uniformities of visual systems may be led to cross-clarify the same phenomena in the pursuit of the best theory in their respective domains.

The view of a computational animal

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Thompson et al. argue that the computational approach to color vision is both limited and conceptually wrong in assuming that color vision's goal is to recover surface spectral reflectance: limited, because color vision serves diverse purposes across the animal kingdom, not just to discern the reflectance properties of surfaces, and wrong, because "recovery" implies that the thing exists before it is recovered, yet neither surfaces nor colors exist except in that animals perceive them.

First, the statement of computational vision's view of color is misleading. A more accurate statement would be that computational vision assumes one goal of color vision to be to label surfaces (I justify the use of this blighted word below) with invariant descriptors that thereby aid in object recognition (see, e.g., the introductory comments in Lee, 1986, and Hurlbert 1989). The ideal candidate for such a descriptor is an estimate of surface reflectance.

Although it would be limiting to state that the only goal of color vision is to recover invariant surface descriptors, Thompson et al. must agree that this is at least one goal of human color vision: They argue that an essential ingredient in the experience of color vision is color constancy. Yet color constancy means surface color constancy. In their definition (sect. 1.3), Thompson et al. leave "color appearance" dangling, evidently refusing to tie it to an anthropocentrically defined surface. Their point seems to be that we must talk about color constancy in animals and that surfaces are not the same to different animals. Yet for an animal to have color constancy it must perceive surfaces whose colors tend to remain constant, even if the surfaces are themselves partly or wholly defined by their color, and even if one animal's surface is another's volume. Among humans, we have a clear notion of what we mean by a surface and what surface color constancy is. Trying to agree with a bee on where a surface begins and ends might be more difficult.

Still, Thompson et al. would seem to object to the notion that color vision might serve to recover invariant surface descriptors because "recover" implies that the thing is "out there," whereas color is not. Thompson et al. admit that it is logically possible to recover spectral reflectance at a location in the scene because reflectance can be physically measured. The illogical leap is in

equating color with spectral reflectance. This is what the computational objectivist does, but this man seems to have been created from straw the better to be burned, and his view of color probably has as much in common with that of a computational-vision scientist as the latter's does with a bee's. Most investigators of computational vision heed the distinction between the physical stimulus (light, of which reflectance is a determinant) and the perception (color) to which it gives rise.

To say that computational vision limits its view of color to the recovery of invariant surface descriptors grossly downplays the significant work done on segmentation algorithms using color (see Brill, 1990, for an analytical review). Far from ignoring the role that color plays in segmenting the world, computational theories assume that a central goal of color vision is to aid in discriminating object boundaries. It is also wrong that computational models of color constancy discard information about the illuminant: All algorithms implicitly or explicitly recover an estimate of the illuminant together with reflectance.

The question of how color interacts with other percepts to define surfaces is, as Thompson et al. conclude, a fascinating one, calling for hard scrutiny in the study of both human and machine vision. Several machine vision algorithms incorporate interaction between visual modules to segment the image – for example, color, motion, texture, depth – explicitly assuming that distinct modules working in isolation may segment the image in distinct ways (see, e.g., Poggio et al. 1988). Investigators of computational vision who evaluate the success of these segmentation algorithms typically use their own perception of objects as the criterion, in effect assuming that the robots equipped with these algorithms should be “animals very much like us” (sect. 3). This too contradicts the notion that computational vision is concerned only with the recovery of “animal-independent” properties of the world.

To say that “colors are properties of the world that result from animal-environment codetermination” (sect. 3) raises tricky questions. Thompson et al. suggest that “animal-environment codetermination” acts on the time-scale of evolution. A mutation occurs in a fruit color. A mutation occurs in a bird’s visual pigment. This enables the bird to pick out the fruit; he eats it, and he, his visual pigment, and the fruit seed survive. But when the bird picks out the fruit he apprehends some property of the way it reflects light – and perceives this as color. That evolution plays a role in determining perception is not inconsistent with the idea that at any given moment perception involves recovering the environment, if the environment is considered to consist of such physical properties as reflectance; indeed, it seems to require it. Or do Thompson et al., in suggesting that “organisms alter the world external to them as they interact with it” (sect. 3), mean that organisms continuously change the very nature of light, rewriting the physics of reflection?

Computational models founded on inverse optics do not prespecify the environment, nor do they imply that perception cannot shape the environment, if the environment is defined as something created by the animal in the act of perceiving. Rather, they are attempts to discover what can be perceived, given such physical constraints as the nature of light, and such sensorymotor constraints as photoreceptor spectral sensitivities. The claim that computational vision treats “perceptual and motor mechanisms . . . as fundamentally distinct” (sect. 3) downplays not only the more recent work mentioned as counterexamples but also such earlier, seminal work as the Reichardt-Poggio theory (1976) of how visual stimuli make flies fly.

The intriguing possibility Thompson et al. raise is that our approximate color constancy is the result not of a failed attempt to recover surface reflectance but of a successful attempt to apprehend another feature of the physical environment. This computational-vision scientist welcomes the views of other animals on that possibility.

Data and interpretation in comparative color vision

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In their engaging target article, Thompson, Palacios & Varela profess no small ambition. Their goal (para. 2) is no less than “to offer . . . a new empirical . . . perspective on color vision, one which is based on recent experimental research in comparative color vision.” Why is this new perspective required, and what are its proscriptions with respect to comparative color vision?

The authors portray the contemporary study of color vision as preoccupied with the debate (principally promulgated by professional philosophers) as to whether colors are perceivere-independent physical properties (the objectivist view) or internal sensory qualities (the subjectivist view). The current resurrection of this ancient argument is characterized as representing alternative viewpoints drawn from the respective wisdoms of computational vision and neurophysiology/psychophysics. Although they come down on the subjectivist side of this debate, Thompson et al. find this position wanting because it does not sufficiently credit the interactive role between the visual environment and the perceiving animal. They propose what they term an “enactive” view of color vision based on the notion that there is animal/environment codetermination. Trotted out as support for this position are the familiar (but, startlingly undocumented) examples of the coevolution of organic pigmentation and animal color vision. Although the arguments are eventually allowed to go off in several directions, this view seems best encapsulated in section 2.5 where it is argued that an understanding of color vision requires, in addition to data from neurophysiology and psychophysics, (a) attention to the evolutionary histories of the animal’s environmental interactions, (b) an understanding of animal/environment coevolution, and (c) appeal to a broad range of other physiological, evolutionary, and ecological considerations. I think the authors are mistaken if they imagine that anyone with concern for the problems of comparative color vision would find this viewpoint heretical or generally objectionable.

It is suggested that the enactive view of vision provides a framework for understanding color vision. With respect to comparative color vision, four specific research directions are encouraged (sect. 3). Although these hardly represent a novel call to arms (e.g., readers are urged to study neuronal mechanisms for color vision in other species and to explore the ecological aspects of the relevant viewing environments), they clearly represent worthwhile research directions. What is less clear is whether it will be sufficiently appreciated just how difficult it often is to reasonably interpret the data from studies of color vision and its mechanisms. Because this problem is central to much of Thompson et al.’s target article, and seems particularly acute in the study of comparative color vision, it is worth illustrating.

It is argued that the “first concern” of the enactive view of color vision is to determine more precisely the dimensionality of the color vision of different animals because variations in dimensionality hold cues as to the color world of the animal. But in doing so the authors show an eager readiness to accept all kinds of indicators that can be far less than compelling. For example, it is concluded (sect. 2.2) that the shape of the wavelength discrimination function can be taken to indicate the type of color vision system – trichromatic systems have two minima, tetrachromatic systems have four minima, and so on. Yet, many wavelength discrimination functions reported for trichromatic humans (including Figure 2a, target article) show three minima. What implication does this hold for dimensionality? And probably the classical collection of wavelength discrimination functions for

known human anomalous trichromats show either one or two minima (Wright 1946). On this ground are some to be judged dichromatic, others trichromatic? Whereas we can probably explain these differences on the basis of other facts about human color vision, such results could be completely misleading if they constituted the sole data base for some nonhuman subject from which one was forced to infer the dimensionality of color vision. To draw an example from comparative color vision, what are we to make of the wavelength discrimination functions obtained for the pigeon, a putative tetrachromat? Some of these functions show three minima in the visible spectrum (Figure 4c), others (e.g., Jacobs 1981, p. 114) show only two.

Similar ambiguity surrounds the common practice of deriving color vision dimensionality from a count of the number of spectrally distinct, first-stage filters (e.g., Figure 4). Various combinations of screening and cone pigments provide multiple filter possibilities in various avian (e.g., six in the pigeon – Bowmaker 1977) and reptilian (e.g., five in a freshwater turtle – Liebman 1972) retinas. Whereas these provide the intriguing possibility of color vision dimensionality that greatly exceeds trichromacy, there is in most cases still a lack of consistently compelling evidence that the visual systems of these animals fully exploit this first-stage potential. For example, the pigeon retina contains (at least) a total of four spectrally distinct receptor types operative in the 580–640 nm portion of the spectrum (Figure 4b); despite this, direct discrimination tests (Palacios et al. 1990b) were unable to exclude the possibility that the pigeon behaves dichromatically in this region of the spectrum (to be fair, this experiment was also unable to exclude pigeon trichromacy in this part of the spectrum). If all that is required to determine color vision dimensionality is to count the number of first-stage spectral filters, then we should stop lauding bird color vision and award the title for the “most complex color vision space” to the mantis shrimp whose 10 spectrally distinct types of photoreceptors (Cronin & Marshall 1989) make it the first-known decachromat.

It can probably be granted that counting spectral filters and examining some aspects of visual discrimination that principally reflect postreceptor processing (wavelength discrimination, spectral sensitivity) may provide only uncertain clues as to color dimensionality. A more direct way (urged by the authors – sect. 3) is to carry out color mixture experiments. Whereas these clearly get closer to the root of the problem, they need not be the panacea the authors appear to believe them to be. For one thing, with nonhuman subjects the outcome often has multiple interpretations (as in the example of pigeon color mixing data noted in the previous paragraph). Even in cases where we believe we fully understand the issue of dimensionality, color matching data may, by itself, prove ambiguous. No more clear cut case of this exists than for classically defined human dichromats – protanopes and deutanopes. Over a certain range of test light intensities and for some spatial test configurations, many of these subjects make color matches that must formally classify them as having trichromatic color vision (Nagy 1980; Smith & Pokorny 1977). In my view the moral is clear – although it may be pleasant and satisfying to draw fanciful diagrams of color space based on fragmentary evidence, one should not be deluded into believing that these necessarily provide insight into color experience.

Color enactivism: A return to Kant?

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As a psychologist with a background in physics I am torn between what Thompson et al. call computational objectivism

and neurophysiological subjectivism when I wear my physics hat, but I am most attracted by their view of color vision as an enactive process when I wear my psychology hat. A typical physicist's position is the one described by Wright (1988), who supposed that there is a subjective color palette in the brain waiting to be stimulated by the incredibly complex pattern of neural signals. He acknowledged that these signals are not the colours themselves. But the problem with this position is: How does the palette develop in the first place?

Having spent many years studying normal and deficient color vision in humans and speculating about the sensory mechanisms, I was intrigued to read Thompson et al.'s target article linking color vision with cognitive science. Their contrast between computational objectivism and neurophysiological subjectivism, their assessment that neither provides a satisfactory explanation of how we perceive color, and their proposal for the enactive view of perceptual content gave me a *déjà-vu* experience and sent me rummaging through my files for the British Psychological Society's Presidential Address of 1961 given by James Drever II.

The address was entitled “Perception and Action” and examined a much broader area than color vision, namely, how we perceive objects in space. Drever (1961) reviewed Kant's *Critique of pure reason* and noted that Kant stressed the conative nature of the self. Organisms do not behave *in vacuo* but act on and in the environment. Brunswik (1956), too, viewed perception as an achievement made possible by the use of cues that acquire ecological validity with time. The distal stimulus is what is in the environment, the proximal stimulus is what is present on the surface of the organism (e.g., the retinal image in the case of vision), and the achievement of perception according to Brunswik is being able to sense the distal stimulus despite all the vagaries of the proximal stimulus. Piaget (1969) also cannot accept that we are able to derive the spatial world from a consideration of the proximal stimuli alone. He proposed that awareness of space is based on action in space; a child learns to perceive space by motor activity in space. So back to the present authors.

Thompson et al. (sect. 3, para. 9) also state that “the first step for perception is to refuse to separate perception from action, or more generally from perceptually guided activity.” They cite Gibson's (1979) ecological approach in partial support, although they share my worry that Gibson went too far in hypothesizing that our ability to sense the environment is by being able to detect affordances from the ongoing stimulation independent of memory or any other cognitive function. They have reviewed old ideas about the nature of perception and dressed them in new clothes. They have specifically addressed the problem of how we perceive color rather than the more general question of how we perceive visual space. Their fascinating speculations about tetrachromacy remind us to keep the other extreme in mind, the limited colour world of the colour-vision defective observer. This helps to confirm in my mind their thesis of an animal and environment codetermination.

I still have an inner urge to posit an external physical world existing independently from any living creature and to view perception as the process of becoming aware of that external world. But when one remembers that, physically, colour can be measured only in spectrophotometric terms, and that our perception is based on the nature of our sensory equipment as well as more subtle mechanisms such as colour constancy, one is forced to conclude that Kant, and now Thompson et al. are right: Perception (and color) have to be achieved through action (enaction) with the environment. The authors have rediscovered the wheel, and in the process have provided a useful summary of the state of the art in color vision research, as well as some intriguing speculations regarding the color vision of other animals.

Ethological and ecological aspects of color vision

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Behavioral studies can be useful in testing hypotheses about mechanisms of color discrimination derived from data on photosensitive retinal elements or aspects of the dimensions of color space. Alternatively color discrimination, expressed as a behavioral response, cannot always be convincingly attributed to any biological feature of a species. For example, in the breeding season, male common toads, *Bufo bufo*, prefer blue "female dummies" and other blue objects, exhibiting color discrimination and constancy of color perception (Gnjubkin et al. 1975). In contrast, male common frogs, *Rana temporaria*, prefer red objects and reject blue ones, exhibiting a real color choice (Kondrashev et al. 1976). The mating response in frogs can be accounted for by very marked sexual dimorphism in color (males have a blue throat and a bluish-grey body, whereas females have a reddish-orange throat and belly). This explanation is not valid for toads, however, as they have no such dimorphism and, moreover, female toads are reddish-brown.

It should be emphasized that behavioral responses can differ even when the same peripheral sensory mechanisms of the retina are involved (they are very similar in frog and in toad; Reuter & Virtanen 1976). Besides, such color preferences are only displayed during mating and are not characteristic of other types of amphibian behavior. This is evidence for an important role for central nervous system mechanisms that modulate messages from peripheral inputs.

Determining the dimensionality of color space can prove to be complicated. The target article gives an example of a change in dimension when, with a decrease in illumination, the goldfish turns into a trichromat from a tetrachromat. In contrast, a decrease in dimensionality with an increase in illumination can be expected in more than 100 fish species possessing a unique corneal light filter system: Within 40 to 60 minutes the cornea becomes intense yellow-orange in light and colorless again in darkness. Such a change in the color of the cornea is caused by special chromatophores with carotenoid pigments that in daylight produce a filter with an optical density of 3–4 log. units for a spectrum with $\lambda_{\max} < 520$ nm. Evidently, with such cut-off filters, characteristics of the color space change reversibly and depend on the ambient illumination within a broad range (10–3000 lux; Gnjubkin 1989; Heinerman 1984; Kondrashev et al. 1986; Orlov & Gamburtzeva 1976).

In connection with the presence of colored light filters a question arises about color constancy mechanisms in fish (Dimentman et al. 1972). Changeable corneal light filters cause, along with the change in the absolute amount of light reaching the retina, a change in its spectral composition. The appearance of yellow or red pigment in the cornea leads to changes in the image color on the retina. From the physical point of view, this is analogous to the transition from one overall illumination to another, for example, from white to more yellow.

Could constancy of color perception be realized in the presence of colored light filters? Calculations indicate (Gnjubkin 1989) that in fish with yellow filters of medium density (1–1.5 log. units) changes in the excitation of cones are comparable to those observed in the absence of filters when there is distortion of color temperature from natural light sources, for example, at the transition from twilight to midday sunlight. It appears that color constancy can be still maintained under these conditions. In some species from families *Hexagrammidae* and *Tetraodontidae*, very densely colored filters should probably interfere with normal color discrimination in bright light, unless some stronger mechanisms of color constancy are involved. Thus, the case is fairly unusual, when at the transition to bright daylight

color discrimination worsens and other biological goals prevail (e.g., improvement of apparent contrast and protection of photoreceptors against the excess light in shallow waters where these fishes are predominantly found).

The situation with color filters of the cornea, together with other examples of narrow-band spectrum light conditions for deep-sea fishes show that findings on ecological aspects of the perceptual environment outlined in Thompson et al.'s conclusions do not necessarily lead to an adequate description of mechanisms of color discrimination. There are real situations in which particular characteristics of color space and illumination conditions may be such that a particular biological task (selection of prey or shelter, protection of young, etc.) is accomplished with the aid of vision but excluding color as a key stimulus or significant feature.

Objectivism-subjectivism: A false dilemma?

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The authors of the target article argue that the objectivist/subjectivist dichotomy on the question of color must be rejected in favor of what they call an "enactive" approach to color vision. Although I am not prepared to take a stand here on the objectivist/subjectivist controversy itself (though I lean toward subjectivism), I am not convinced by the arguments for abandoning the framework of that debate or adopting the positive alternative the authors propose. In general, my complaint is that whereas the authors provide us with a wealth of empirical data to bolster their case, they fail to demonstrate adequately the bearing of this data on the central questions at issue.

Thompson et al.'s principal argument against objectivism derives from the comparative study of color vision, which reveals wide variation in the nature of this capacity across the animal kingdom. Species differ in their sensitivities to various wave lengths, in the dimensionality of their color spaces, in the neurophysiological processes subserving color vision, and even in the ways they segment the visual field into surfaces and objects. According to the authors, this variation shows that the properties with which color experiences are correlated can only be characterized relative to the perceiver, and are therefore not objective properties of external objects. Where the objectivist attempts to identify color with the spectral reflectance of a surface, the authors respond that even the notion of a surface itself must be relativized to the perceiving subject.

The nonobjectivity of color, however, does not follow from the variability of color experience across the animal kingdom. There are many different ways of carving the world into objects and properties, but that does not make any one way nonobjective. So long as a certain perceptual state in humans is found to track some external property, the objectivity of that property is not impugned by the fact that bees or fish track a different property. A genuine problem for the objectivist position can indeed be raised (as it is by Hardin) by calling into doubt the claim that chromatic perceptual states in fact track an objective physical property, such as spectral reflectance. But comparative studies of color vision do no work for this argument.

Thompson et al. also criticize Hardin's "neurophysiological subjectivism." Their argument is that Hardin does not pay sufficient attention to the extent to which color vision and coloration in the environment are "codetermined," and that he is therefore wrong to identify colors with properties of the internal states of organisms. Again, the authors' conclusion doesn't follow. It may indeed be true that flowers, for example,

have the coloration they have partly as a consequence of the visual properties of the bees that aid the flowers' reproductive capacities. But that does not mean that the properties of the flower are thereby ontologically determined in part by the visual capacities of the bees. The authors seem to be confusing causal or genetic determination with ontological determination.

In general, Thompson et al.'s conception of the goal of a theory of color seems to be infected with an equivocation between causal and ontological determination. In presenting their argument against Hardin's subjectivist position, they say: "To explain the polymorphism in spider and squirrel monkey color vision . . . we must appeal not simply to the neurophysiological constitution of these animals, but also to the evolutionary histories of their environmental interactions . . ." (sect. 2.5, para. 8), and again: "It is therefore irrelevant . . . to appeal to *metaphysical* intuitions about what the world would be like 'if the living creatures were removed' when one's concern is to provide a *naturalistic* explanation of perceiving animals and their environments." (sect. 2.5, para. 13)

If the object of inquiry is to explain how it is that organisms came to have the type of color vision they have, then an appeal to their evolutionary histories is necessary. But if the object of inquiry is to explain what color is, then it takes additional argument – more than merely citing the phenomenon of co-evolution – to establish the relevance of evolutionary history. Using the phrase "explaining color vision" to cover both sorts of inquiry only muddies the waters.

As for the authors' alternative "enactive" approach to color vision, I find it difficult to get a clear sense of what this means. For example, take the following claim: "In any case, the evidence that we have presented in the previous paragraphs serves to demonstrate our point that the operation of color vision should be understood in the context of the actual behavioral repertoires and visual ecologies of perceiving animals." (sect. 2.4, para. 25) What is it to "understand in the context of"? It might mean that the context in question plays a causal role, in which case there is little to argue about. Or it might mean that the context in question plays an ontologically determinative role, in which case the concerns raised above apply. But if it is neither of these, then I fail to grasp what it does mean.

Finally, a word about color constancy. The authors point out that objectivists tend to lean on the phenomenon of color constancy, as this lends support to the view that the visual system is computing the value of an external property on the basis of proximal inputs. Deviations from perfect color constancy, from changes in illumination and the like, are then treated as illusions. Subjectivists, on the other hand, lean heavily on these deviations to support the claim that there is no objective property of the distal stimulus that the visual system is tracking. This is an interesting case study for theories of content, given that the question of what counts as error is crucial to the debate. In essence, we have the disjunction problem here. One might try applying Fodor's (1987) asymmetric dependency condition here to determine whether, with the subjectivists, we should assign the "disjunctive content," or with the objectivists, we should assign the spectral reflectance as the content. It would be interesting to see whether his theory, or any other theory of content, could shed light on this problem.

Ontogeny and ontology: Ontophyletics and enactive focal vision

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Wär' nicht das Auge sonnenhaft,
Wie könnten wir das Licht erblicken?

[Were not the eye akin to the sun,
How could we behold the light?]

– Goethe, *Zur Farbenlehre* (1810)

Casting new light on ecological optics (Gibson 1961; 1979) and the adaptive radiation of the vertebrate eye (Polyak 1957; Walls 1942), this target article reminds us once again that the sun has brought forth a variety of eyes other than our own, a multitude of other ways of beholding the world. The central ideas in this treatise, the "codetermination" of the perceiving animal and its environment and the "enactive" nature of perception, are reminiscent of the "Umwelt" concept of von Uexküll (1926; 1957) and the notion of perception as "implicit preparation to respond" (Sperry 1952, p. 302).

These central themes should not be taken as arcane departures from the common paradigms of perception critiqued in the target article. Rather, eschewing the usual theoretical focus on "our familiar human environment," (sect. 2.4) this comparative view of perception is somewhat like a biological "theory of relativity" for cognitive science. As with Einstein's theories, we are once again called on to abandon our familiar notion of The Physical World, this time to conceive of a multitude of biological perceiver-relative worlds, a multitude of "enacted perceptual environments experienced by animals in their visually guided interactions." (sect. 3) In this way each species has its own metaphysics, its own ontology.

Departing from the usual reliance on our familiar concepts of the physical world, Thompson et al. point out that, "the world that a given animal perceives cannot be given a purely physical-level specification, for what an animal perceives depends on three kinds of factors: (i) physical-level constraints; (ii) sensorimotor activity as constituted by neuronal processes and developmental constraints; and (iii) evolutionary history." (sect. 3, para. 14) These developmental constraints and the evolutionary history whereby an organism attains its sensory-motor constitution are intimately related (Gould 1977; Katz 1983; Northcutt 1990). Ontophyletic processes ultimately give form to an animal's ontology.

Although it is easier perhaps to make the departure from our usual conceptions advocated here in the consideration of more exotic perceptual worlds, I aim to maintain the perspectives thus gained in reconsidering "the world as described in relation to the sensory-motor capacities of the higher primates" (sect. 3), and to point to what may represent an ontophyletic development instrumental to the evolution of enactive focal vision.

Focal vision is an exemplary enactive process (Lia 1989). Surveying mammals, it is apparent that focal visual behavior, and concomitant focal retinal topography, frontal position of the eyes, and wide binocular field, is correlated with visually guided use of the forelimbs in the exploitation of what has been termed "praxic space" (Hughes 1977; Trevarthen 1968). The raccoon may surpass the cat in manipulatory behavior, but the felidae surpass all other nonprimate mammals in visually guided deployment of the forelimbs in praxic visual space. Through convergent evolution of focal vision, both the felidae and the primates are animals that reach with their eyes as well as with their hands. In an enactive sense, it may be argued that we move our eyes not so much because of the focal sensitivity of our retina, but rather that we have focal retinal topography in order better to move our eyes (Lia 1989; Walls 1962). "Or, putting it in

another way, perhaps we cannot understand how the retina works unless we understand how the eye works" (Gibson 1961, p. 259). Regarding Thompson et al.'s contention that "animals with different sensorimotor capacities would segment the world in different ways" (sect. 3), focal vision has long been associated with a superior cognitive "grasp" of the visual world (Elliot Smith 1932).

This parallel development of visually guided manipulative praxis and focal vision is apparent in comparing prosimian and simian primates. One may wonder then why focal vision has not developed as least among the diurnal felidae to the degree it has among the primates? The area centralis of the feline retina seems to fall just short of the development of a fovea centralis (Rowe & Dreher 1982). Of course, a variety of contingencies can be imagined, among them somato-motor developments limited by the specialized retractable feline claw. I would like to point out, however, a possible ontogenetic constraint related to the partial decussation of the visual system that may have limited the evolution of binocular vision in nonprimate mammals generally. The nasotemporal division is another feature of retinal specialization accompanying focal topography that is also fundamental to enactive binocular focal vision.

The strict hemiretinal nasotemporal division of the primate retina is unique among mammals (Allman 1977; Pettigrew 1986). Specialized for frontal, binocular vision, the retinogeniculostriate pathway obeys a more straightforward nasotemporal division in relation to the frontality of the eyes even among nonprimate mammals. In nonprimates, however, crossed projections arise from the temporal as well as the nasal hemiretina, so that there is a panoramic representation of the entire contralateral retina in the superior colliculus. The presence of such a complex of decussation patterns in the nonprimate may be related to their capacity for two modes of vision, frontal and panoramic (Lia 1989). This is exemplified by the two discrete eye postures of the rabbit and the "two-state" organization of its cortical system for forward vision (Hughes & Vaney 1982). It may also be evident in the ungulate's tolerance for disjunctive eye movement (Pettigrew 1986), and in the differing habits of vergence behavior observed between laboratory and barnyard cats (Hughes 1972). Primates exhibit obligate frontal vision.

We have recently shown that the unique primate nasotemporal division is not sculpted during development by selective ganglion cell death from a decussation pattern characteristic of other mammals (Chalupa & Lia 1991). In nonprimate mammals, on the other hand, even the retinogeniculate decussation pattern arises as such a secondary refinement of the original projection pattern, as has been shown in the cat (Leventhal et al. 1988) and ferret (Jeffery 1990). Moreover, the extremely precise specification of both the crossed and uncrossed projections in the macaque may result from the lack of intermingling projections from the developing temporal hemiretina, so that positional determinants operate more effectively (Chalupa & Lia 1991).

I suggest here that the complexities of the developing nonprimate decussation pattern may present an ontogenetic constraint on the evolution of binocular vision. The straightforward ontogenetic pattern of the primate nasotemporal division may in some way simplify the development of a binocular visual system and set the stage for the expression of the high degree of precision evident in developing retinogeniculostriate projections in the macaque monkey (Chalupa & Dreher 1991; Chalupa & Lia 1991; Lia et al. 1989). A highly specified visual substrate seems to be required for precise, praxic eye movement given highly focal topography. The primate plan for nasotemporal ontogenesis may represent a key exaptation (Gould & Vrba 1982) for the further adaptive evolution of enactive focal vision.

We have found that both of these regional specializations for enactive focal vision, focal topography (Lia & Chalupa 1988; Lia et al. 1987) and the primate nasotemporal division (Chalupa & Lia 1991), arise in the course of retinal morphogenesis. Unlike

in nonprimate mammals, they are virtually independent of regressive developmental events governed by interactions of optic projections within central structures. Thus, as in other sensory modalities, peripheral changes may remodel the central nervous system (Killackey 1990; Van der Loos 1979; Volman 1990). Indeed, we have proposed that the lack of exuberance of the uniquely defined pattern of striate callosal development in the macaque (Chalupa et al. 1989; Dehay et al. 1988) may have underpinnings in the ontogenesis of its nasotemporal division (Chalupa & Lia 1991). Similarly, more information about ontophyletic processes may even help us some day to understand the differing plans among various mammals for the further connectivity of the visual cortical areas (Killackey 1990; O'Leary 1989; Rakic 1988; Sereno & Allman 1991).

Clearly, comparative studies of visual system ontogenesis with appropriate out-group comparisons will be needed to support such speculations (Northcutt 1990; Sereno & Allman 1991). As a first step, it may prove instructive to compare the ontogenetic specificity of the diurnal macaque with that of the nocturnal simian owl monkey, whose visual capacities match those of the domestic cat. In any event, the perspectives outlined in this target article serve to enhance not only the understanding of our own ontology, of our own niche, but also its evolution. Cognition is not merely "in the head," but is a "codetermined" process with a long ontophyletic history behind it.

In search of common features of animals' color vision systems and the constraints of environment

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In their elaborate target article Thompson et al. offer a broad overview on the two main approaches, objectivism and subjectivism, to explain the ontology of color. Their suggestion of a new approach, the enactive view of comparative color vision, is developed on a spectrum of relevant examples of the color vision of various animals. Their approach seems most striking and fertile for examining and discussing an animal's color vision only in the context of the animal's environment. Nevertheless, there are some problems implicitly addressed in their paper but not cited enough in their importance for an understanding of color vision.

First, color vision is but one of the various tasks a visual sensory organ has to fulfill. Depending on this multifunctional organization, color vision may play a more or less dominant role, depending on the relative importance of other essential perceptual tasks for an animal (e.g., nocturnal vision; specialization of certain retinal regions for movement detection, etc.). Hence color vision should always be examined and discussed as one facet of the whole visual sensory organ.

Second, it is definitely necessary to examine and explain the color vision of a given animal in the context of its environment. The color vision of various animals should be tested this way. But then the comparative argument should be emphasized more strongly. Where are there differences in color vision? What are the reasons for those differences? And most of all, are there common features of color vision among different animals?

To our mind, Thompson et al. concentrate too much on searching for and pointing out differences (sect. 3) in the color vision of various animals, whereas the search for common features seems especially to offer the possibility of a better understanding of the ontology of color. Where could such common features be found?

Using recent results, we present some possible target do-

mains for examining and comparing color vision. Despite different levels of chromaticity (di-, tri- and tetrachromacy) and different phylogenetic classifications (such insects as honeybees; such vertebrates as fishes, birds or mammals), there seems to be a clustering of spectral regions of best wavelength discrimination in different animals (at about 400 nm, 500 nm, 600 nm; Neumeyer 1988). This could be a hint that in the respective spectral regions acute hue discrimination is necessary for various animals; the question of the biological significance of this accordingly arises.

Another target domain for further investigation could be the fact that so far only partially known ecological factors seem to cause similar adaptations of color vision among various animals. The spectral properties of the cone types of a penguin (*Spheniscus humboldti*) resemble those of certain fishes more than those of many other birds (Bowmaker & Martin 1985). Another example seems to occur in animals active at twilight; these all tend to be dichromats. This tendency even holds in such phylogenetic classes with highly evolved color vision as the birds: The tawny owl, *Strix aluco*, possesses a dichromatic color vision (Martin & Gordon 1974).

Evolutionary constraints must be strong to build up such analogous features. What are the forces in animals and in the environment that give rise to the evolution of common features of color vision? Searching for such convergent characteristics seems to be more promising than concentrating on the many differences of color vision systems, necessary as this is (Maier 1990).

Another problem arises in the comparison of recent forms of color vision of various animals: How is one to compare different levels of evolutionary adaptation? There is no "steady state" of color vision, but a permanent adaptation to environmental conditions. Perhaps this problem can be best explained in mammals. Why do mammals, including man, have such restricted color vision compared to those of many fishes, reptiles, and especially birds? Most mammals are dichromats. Even the trichromacy in primates is relatively poor, compared to those of other animals. The following hypothesis has been offered by way of explanation: During early states of evolution mammals may have been nocturnal. An elaborate color vision system was unnecessary, compared with other needs the visual system had to fulfill (e.g., a good scotopic system). Their color vision could therefore be reduced (Bowmaker 1980a). From an evolutionary viewpoint, only recently have various mammals become diurnal, with their color vision re-evolving. Contemporary mammalian color vision, even that of the primates, hence still seems to be limited compared to its possible culmination in birds. Comparing "just evolving" and highly evolved color vision systems under their natural conditions seems to be another rather fertile way of examining the evolution and adaptation of color vision, thus clarifying the ontology of color.

The fact that color vision has evolved (independently) throughout the animal kingdom, combined with the knowledge of the animals' colored environment, points to the importance of this form of perceptual experience. Thompson et al.'s comparative approach, combined with the above suggestions, could present a new and promising way to emphasize some new aspects of the biological ontology of color.

A mathematical framework for biological color vision

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Thompson et al. propose an explanation of color vision intended as an alternative to what they term computational vi-

sion. Summarized here is what I perceive to be the relation between one computational vision approach, the *linear models framework*, and the experimental study of comparative color vision. It is intended to be the "alternative theoretical and empirical framework" and "rival research program" that the authors invite.

The linear models framework serves two functions: to provide a mathematical framework for the careful analysis of biological and computational color vision, and to generate hypotheses to guide experimentation. It assigns a special role in color vision to surface spectral reflectance (SSR) as defined in Wyszecki & Stiles (1982, p. 234). It provides a clear hypothesis about the nature of the physical properties corresponding to intrinsic colors. It is intended to describe color vision systems that can assign approximately constant intrinsic colors to objects despite changes in illumination.

The associated algorithms by Brill (1978; 1979), Buchsbaum (1980), Maloney and Wandell (1986), and others do not simply predict "approximate color constancy" when the assumptions of the algorithms are not satisfied. They provide explicit predictions of the direction and degree of color nonconstancy for a given choice of linear models of light and surface and of algorithm. On the other hand, if any of the algorithms of Brill, Buchsbaum, or Maloney and Wandell are used across a range where their assumptions are satisfied, then they provide perfectly stable estimates of surface properties despite changes in the illuminant. The existence of such *privileged spaces* of lights and surfaces where color constancy is essentially perfect is perhaps the most significant prediction of the linear models for the study of human color vision or any color vision system that exhibits some degree of color constancy. The lights and surfaces across such a range, described by linear models, may be markedly different in their physical properties and still permit perfect color constancy. Large changes in the physical light are consistent with perfect color constancy for these models. Brainard and Wandell (1991; Brainard 1989) measured chromatic adaptation in response to illuminant changes simulated on a CRT display. Their results were consistent with hypotheses concerning chromatic adaptation and "privileged spaces" predicted by the linear models framework.

The framework and associated algorithms are not dependent on the choice of a particular visible spectrum or choice of photoreceptor spectral sensitivities. They are general. For any specified portion of the electromagnetic spectrum, it is possible to estimate linear models of SSR across that portion of the spectrum and to determine how many different classes of photoreceptors are needed to achieve a desired level of constancy. Thompson et al. comment that "color-spaces of different dimensionalities can be constructed on the basis of the same physical signals." The linear-models framework allows an analysis of the consequences for visual performance of choice of dimensionality. Similarly, it is possible to estimate certain consequences of extending the visible spectrum for human color vision or other biological vision systems.

It is also possible to estimate the best choice of photoreceptor for the purpose of estimating intrinsic colors anywhere in the visible spectrum (Brainard et al. 1989; Maloney 1984; 1986; 1990). These analyses are potentially valuable for comparing color vision across species.

The framework lends itself to analyses of the circumstances under which it is and is not possible to reliably assign intrinsic colors to objects and to the analysis of models of visual processing not based on linear models. Brainard and Wandell (1986), for example, using the linear model, have analyzed the conditions under which variants of Land's retinex theory (Land 1983; Land & McCann 1971) can assign colors to objects that are approximately independent of changes in the illuminant. West and Brill (1982) analyze the circumstances under which other *lightness algorithms* (reviewed in Hurlbert 1986) can be color constant. The net outcome of these analyses is that lightness

algorithms, including Land's retinex theory, do not reliably assign constant colors to surfaces. The deviations from color constancy are large, predictable, and characteristic of lightness algorithms. Hence, any attempt to assess the validity of such algorithms for color vision in other species should consider these analyses.

The linear-models framework is *precise*. It permits careful analyses of the relationship between color vision performance and associated environmental factors. It is extendable, notably to a consideration of surface specularity (D'Zmura & Lennie 1986; Lee 1986) and nonuniform illumination (Funt & Drew 1988).

The linear-models approach is falsifiable. To falsify it in favor of Thompson et al.'s central concern ("perceptually-guided activity"), we need only find a species that represents as color some component of its environment not associated with SSR. We could imagine a species, *Homo aviator*, that encodes the threat-index of any object as a large, additive color shift in normal vision. Dangerous objects are coded by shifts in a particular direction in color space. So long as the threat is associated with the interior and not the surface of the object, linear models could be rejected by color matching experiments involving objects more or less threatening. A less dramatic but equally compelling rejection of the linear approach could come from any of several lines of research, notably failure to find a "privileged subspace."

Thompson et al., in contrast, formulate a description of biological color vision that is at once imprecise and scarcely falsifiable. I cannot bring myself to disagree with the notion that an organism is specialized to a particular ecological niche or to read more than this claim into the authors' presentation. I therefore suggest that the linear-models framework is the more useful tool for modeling and analyzing the interplay of species and environment. Maloney (1992) provides a brief review of the framework and related work.

Color vision: Content versus experience

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The distinction between (a) the perceiver-centered, conscious, or phenomenal, dimension of perception, and (b) its representational, content-bearing, or intentional role with respect to distal properties is conceptually clear, but hard to apply empirically. Following Hardin (1988), Thompson et al. argue that certain perceiver-centered aspects of color vision show color vision to have no objective content. The presuppositions of this bridging inference are not entirely obvious.

I have argued (Matthen 1988) that perception is useless to cognition without *epistemic access* to its output. [See also Searle: "Consciousness, Explanatory Inversion, and Cognitive Science" *BBS* 13(4) 1990] Suppose that phenomenal states of perceptual awareness constitute this access – suppose, in other words, that perceptual consciousness is a mechanism that makes the content of perceptual states available to the perceiver for the purposes of constructing a rational picture of the world. Then there will be two quite distinct quality spaces relevant to such a perceptual module as color vision – phenomenal space and the quality space that constitutes the content of color vision.

Obviously there will be considerable correlation between awareness and content. On the other hand, we have no reason to expect the correlation to be perfect: A need for awareness of content is not sufficient to ensure the evolution of a perfect correlation between these two aspects of perception. This makes it difficult to know whether certain features of phe-

nomenal color space carry over into the property space that constitutes its content. For example, Berlin and Kay (1969) showed a certain universality in color terms across languages and cultures. This shows, presumably, that phenomenal color space is nonhomogeneous, the metric becoming more dense around certain focal points. But does it follow that the content space is similarly lumpy? Not necessarily. In an exactly analogous way, it is hard to know to what extent the features of phenomenal color space referred to in the target article entitle us to draw conclusions about the content of color vision.

The functional view of content is not committed to the kind of smooth mapping from experience to distal property space that Thompson et al. envisage. Phenomenal space might contain structure that totally fails to correlate with anything in the structure of content. Consequently, the objectivist need not recommend that "we should replace our conception of color as understood in visual science with a new concept of physical color." Rather the objectivist would be well-advised to give visual science its conception of color (especially given that most color concepts are founded on the phenomenal structure of color vision, which is what is directly available to us), and to maintain, paradoxically perhaps, that it is not color that is the content of color vision, but some other physical quantity. For that is the clear consequence of distinguishing between content and experience and allowing each a role of its own. (This cleavage was not clear in Matthen, 1988, I confess, especially in section 8, the source of most of the views to which Thompson et al. object.)

In Matthen (1988) I was reasonably explicit about what I took perceptual content to be: It is a presentation of some object external to the state itself as possessing some feature – for example, a presentation of some individual as moving along a certain path in three-dimensional space. Such content is expressible by means of a linguistic description attributed to the object of perception. The attribution of content explains (a) the relationship of perception to the external world, (b) its computational aspects, and (c) perceptual error, particularly *normal misperception*, which is what occurs when a probabilistic algorithm is applied to an unusual situation – as in visual illusions, for example. (It is compatible with this description of content that some perceptions, color perceptions for example, should fail to possess content.) It is certainly true that this notion of content is considerably more restricted than the one to which many contemporary philosophers subscribe. Nevertheless, its role would be clear if one could pin it down in particular cases.

This way of understanding the work of a theory of content implies that content cannot be individuated by correlation. It may be that color experience does not fit very well with any objective property space. However, suppose that the Horn-Land type of algorithm embodied assumptions that were largely true in a two-dimensional world of "Mondrian" type scenes, but failed in the three-dimensional, multidirectionally illuminated, real world. In these circumstances, color vision would correlate poorly with such real properties as reflectances, and we should constantly see surfaces and colors that simply have no objective correlates. But it might still be true that reflectances and the like are the content of such misperceptions. For suppose that the Horn-Land algorithm gave us good predictions of what errors we should make under real three-dimensional conditions. This is just the sort of case in which I should want to say that color vision has reflectance as its objective content, but because it is full of error it fails to correlate well with reflectance or with real surfaces. Now I no longer want to assert that reflectances do in fact behave the way I have just outlined. But it is still possible, despite the authors' protestations, that a task-oriented, algorithmic analysis of color vision will ultimately provide objectivists with some reasonable substitute for reflectances (see Dannemiller 1989).

Having said this, I must now acknowledge the strength of Thompson et al.'s "enactive" approach. Many realists treat perceptual properties as if they were features of the world that

existed before organisms got there, and of perceptual systems as if they were plopped into the environment to detect such features, like a space probe sent to Venus. But this sort of conception makes no evolutionary sense – an organism is likely to record task-relevant aspects of its interaction with the environment, and these aspects might well be defined relative to the organism. The enactive perspective encourages us not to look always for discrete external correlates for our perceptual states, but to allow them instead to assume a much more complex relationship with environmental conditions – any relationship that would allow the organism to function would be sufficient.

So it is important for the objectivist to understand that although perceptual *content* always makes reference to something outside the perceptual state itself, distality is a matter of degree. Perceptions of three-dimensional motion might be distal to a maximal degree, for they purport to inform us of perceiver-independent states of external objects. Acoustic and olfactory perceptions have less distal content: They deal with something independent of the perceiver, perhaps, but something in the medium rather than in the object. (This was indeed how color perception was thought of by Newton, before color-constancy was discovered, namely, as informing us only of light-color, a property of the medium rather than the object.) Many tactile perceptions are less distal still, telling us of interactions between the perceiver and other objects. Finally, the sensations of pleasure and pain that Berkeley characterized as *tertiary* inform us of states of our own bodies, and of nothing outside, even where these private states are clearly caused by something external, such as a sound or sight.

The idea that distality comes in degrees allows the objectivist to respond constructively to the challenge posed by the target article. Color vision might not detect something “out there” – it might just record a complex situation with several external variables and some internal to the perceiver. This does not necessarily show that it has no content. The objectivist is not defeated merely by showing that color is not maximally distal. Even if it is true that color vision is concerned with things other than the detection of properties of surfaces, this might entail only that color content will be demoted in the scale of distality. (Incidentally, the observation that “color vision is concerned with illumination conditions in their own right” does not suffice for such a demotion, since detecting surface reflectance does tend to leave illumination conditions as a residuum.)

Finally, a comment on the use of biological functions to anchor objectivism. The authors treat this as if it were a commitment to some small set of distal properties so that all perceptual systems converge on their detection. Not at all. One could imagine a plethora of closely related features of the world or of the interactive perceiver-world complex, so that even neurophysiologically similar systems might not converge on the very same feature. Such an ontology, a natural basis for something like “anthropocentric realism” (Hilbert 1987), makes it quite plausible that human color vision should have a very different content from that of birds. Indeed, the “comparative argument” could be taken as suggesting just such a picture. Biological theories of content, then, need not be adaptationist in an objectionable way. Once the degrees of distality have been noted, such theories can appropriate many of the interesting features of the “enactive” theory.

On possible perceptual worlds and how they shape their environments

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We are very sympathetic both to the broad perspective conveyed by Thompson, Palacios & Varela and to the many specific ideas that counteract various constrictions found in research on color perception. Regrettably, the exposition is often careless and incoherent in detail and conflates conceptual and methodological levels of analysis. We therefore believe that the metaphor of a holistic “enactive approach” falls short of serving the purposes claimed by the authors.

The inherent Janus-facedness of the concept of color. Un-disputedly, the concept of human color vision involves both a subjective component, as it refers to a perceptual phenomenon and an objective one (imagine, by contrast, color experiences where perceived objects were “colored” subjectively according to emotional or intentional states). We take this subtle tension to be the essential ingredient of research on color perception, which cannot be disposed of by an essentialist definition of the kind “color is . . .,” be it subjectivist, objectivist, or enactivist.

Although an indispensable moderate objectivism tacitly pervades the arguments, Thompson et al. attempt to underpin their position by attacking a (straw man?) version of computational objectivism that simply reduces color to, for example, spectral reflectance. The “ultraobjectivist” correspondence requirements involved in Hardin’s argument from external irreducibility (sect. 2.4), which Thompson et al. adopt as a key argument, is not necessarily implied by computational objectivism. Furthermore, it is difficult to justify or even clearly state such a demand, as it refers implicitly to (the problematic concept of) “natural kinds,” rather than to perceptual and physical properties as such. (Notice in passing that it would already apply to the notion of two lights or surfaces having the “same color,” i.e., to equivalence classes with respect to metamerism). We do not deny, though, that the untenability of this demand is in tune with a comparative perspective focusing on variations across species which may be hypothesized to “imply different phenomenal color spaces” (sect. 2.1).

Is “phenomenal color space” a clear notion at all? Thompson et al. introduce “phenomenal color space” (whatever this means exactly in animals) in terms of hue, saturation, and brightness. However, already in the context of human color vision, this very concept amounts to “downplaying the phenomenal structure of color,” which even seems to give rise to higher-dimensional concepts of color space; witness the corresponding discussions by, for example, Hering (1920), Katz (1911) or Evans (1974), and the remarks on brightness/lightness in Thompson et al.’s Note 2. The orthodoxy of this view is in surprising contrast with the complexity rightly assumed otherwise, for example, in taking color perception to serve not only reflectance-related functions and to be intertwined intrinsically with spatial features of perception (and thus with the emergence of perceived objects as such).

Thompson et al. place phenomenal color space at the top of a hierarchy of color spaces (sect. 1.2), which are vaguely related to levels of neural organization. The concept of level involved here remains ambiguous, if not obscure, all the more so as – ironically enough – human phenomenal color space is identified with the color space as defined by the Comission Internationale de l’Eclairage (CIE) and the corresponding tristimulus values (not to mention some confusion in detail). These are actually based on color-matching experiments with respect to small spots of light (aperture colors) and that have for practical reasons been chosen from a family of linearly-related color codes, among

which are those (e.g., Smith-Pokorny's r', g', b', cf. Wyszecki & Stiles 1982) that are commonly interpreted as receptor-level ones. Thus, at the top of the hierarchy we find ourselves back at level (i), as it were.

The concept of color space is devoid of any (empirical) meaning if it is not associated with that of a color code, a color code being understood here as a vector-valued mapping defined on suitable stimuli (parametrized by physical indices) that represents specific perceptual or neural features/relations on the appearances of signals evoked respectively in a specified context.¹ Although Thompson et al. allude to corresponding distinctions, they tend to jump to conclusions by neglecting the methodological and conceptual distinctions necessary at this point. Only a precise notion of a code allows a proper treatment of the concept of dimensionality, let alone of "incommensurability." For example, what sense does it make to assert that a "bee color space and human color space can be said to be commensurable, for the dimensionalities of the spaces are the same" (sect. 2.2), if the equivalence classes for metamerism already fall apart?

Evolving environments. We endorse the importance of an evolutionary and ecological perspective and acknowledge the limitations of the usual computational approaches based on the idea of isolating static single functions. In this connection, two units of analysis need to be carefully distinguished, namely, the evolving species and the individual (in a specific context). In view of this distinction, as well as from an evolutionary point of view, we consider the role attributed by Thompson et al. to codetermination (important though it is) and the dichotomy of an "autonomous self-organizing system" versus a "heteronomous input-output system" (sect. 3) to be, at best, overstated.

It remains unclear to us whether the "enactive view" based thereon is simply to express the well-known dialectical relationship between the notion of a stimulus and "the structure of the perceiver" or whether it attempts to achieve a synthesis by introducing a new ontological specification of "environment" transcending the objective-subjective distinction. It seems barely possible to accommodate the above-mentioned issues and to develop a theory of perception – regardless of whether or not it is evolutionary in spirit – without carefully distinguishing the following ontological/epistemological levels of analysis: (i) the physical environment (be it organic or anorganic), (ii) the "perceptual environment from a given animal's point of view" (sect. 3) (be it conceived phenomenally or neurally), and (iii) the theory that a scientist constructs regarding (ii) and its relation to (i). Although Thompson et al.'s arguments referring to experimental results necessarily rely on this distinction, the notion of environment seems to escape any precise specification in their programmatic considerations and philosophical claims. Notwithstanding the target article's many stimulating aspects, Thompson et al.'s enactive view, somehow being reminiscent of Goethean holism, leaves us with the feeling that it encompasses visions of vision that aim at more than science can be expected to provide.

NOTE

1. A measurement-theoretic approach along the lines of Suppes et al. (1989, Chapter 15) might be useful at this point.

Colors really are only in the head

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Thompson, Palacios & Varela, "ecological enactivists" all, tell us that subjectivists are wrong – that colors aren't in the head.

They also tell us that the objectivists are wrong – that colors (identified by the objectivist with surface spectral reflectance properties of physical objects) aren't out there in the world. Where are they? The enactivist begins an answer to this question by saying that colors can be identified and mapped only by attaching them to pairs consisting of organisms (of some evolved type) and *their* environments. The subjectivist also says something like this: A particular organism's colors in the head are "projected" onto things out there. But the enactivist does not want to speak of projection. The enactivist wants to make colors into properties of "enacted perceptual environments experienced by animals in their visually guided interactions." (sect. 3) Colors, attached to objects in an organism's environment, are properties of things "out there" after all. This is not, we are told, a Gibsonian realism – it is not a noncomputationalist color objectivism. Nor is it some arcane form of subjectivism. But if it is neither, what is it? I confess that after my efforts to understand the enactivist answer I am still mystified. And I find no reason to abandon subjectivism, a subjectivism that is reinforced by the data Thompson et al. provide.

It is clear from what Thompson et al. claim that it is essential for the enactivist to establish that a particular color is inconceivable apart from a particular ecological niche – that is, from classes of organisms and *their* (external) visual perceptual objects ("a relevant world for the animal," section 3). To attempt to establish this, the enactivist begins by pointing to the close association between action and perception. Perceptual properties are used in the identification and reidentification of objects; they subserve, then, the purposes of visual identification and reidentification – the survival and thriving of a class of organisms. This is uncontroversial. The enactivist then argues that these objects are identified and reidentified by means of properties that are in principle unique to members of the relevant class (typically, species) of organism. Establishing uniqueness is the focus of most of the target article. I grant that different species have different color spaces. Certainly having different color spaces in certain cases confers advantages on a species – particularly if tetra- and pentachromicity (as in birds) affords them advantages in the frequency domain. (Appendix B) If relevantly different species do have different color spaces, although it does not follow directly that the objects of a niche are identified by properties that are in principle unique to the species, it is certainly plausible that they are. So this too can be granted. Another point enactivists must establish is that these unique properties are properties of the perceptual objects of the class of organism in question. Let us grant this. Think of it as a definitional matter: A visual perceptual object should be the sort of object that has the properties – including colors – that it is seen to have (in this case, by a class of organisms). But to place these things in an environment, the enactivist must also establish that these perceptual objects are identical with objects "out there." I do not think that this can be granted.

The enactivist cannot claim that the perceptual object with its color properties is identical with a physical object with certain surface spectral reflectance properties, for the enactivist agrees with the subjectivist that it cannot be. If the perceptual object is not identical with the physical object out there, however, it is not obvious that we should trade a subjectivist position that holds that, strictly speaking, colors are located in the head and only "projected" out there, for a view that holds that colors are out there, but that does not explain how they are or can be. With some qualifications, subjectivists can accept everything I said enactivists claim except that colors are out there. And they can, unlike enactivists, explain how colors appear to be out there. They are projected.

Projection may seem mysterious in this domain. Where projection is articulated, it is often explained in terms of truth or assertibility. Contemporary constructivists follow this route, but it is no help. In explaining the projection of colors we must

deal with pigeons as well as ourselves, and pigeons notoriously lack the high-level cognitive states that figure in truth. To explain the relevant sort of projection, we must begin by saying that the object out there is the object about which the visual system needs to have information, including information concerning its surface spectral reflectances. (These are very useful for identification and reidentification, for they are relatively invariant.) Call this physical object the "intended object." It typically has surface spectral reflectance properties (unless it is an emitter of light), but it is not colored. Now we must locate colors inside the head. Make them properties of "phenomenal objects," which can be identified with neural events. These objects are ways external objects are perceived, and colors on this view become event properties, making them (strictly speaking) colorings. So an object with such-and-such a surface spectral reflectance curve is presented greenly by and in a phenomenal object that is not *seen*, but undergone. Green-colored objects that are seen – the enactivist's perceptual objects – are illusions. But they are natural illusions, the results of a visual system's effectively and efficiently (for the organism) gauging physical objects in certain positions in an environment.

This is not the occasion to elaborate and defend this realist-subjectivist view of colors. My aim is to suggest that the evidence the enactivists have given so far does not provide a plausible case against the subjectivist unless they explain how, given that surface spectral reflectance objectivism is wrong, there is nevertheless something that has colors and is, strictly speaking, outside the brain. They must convince us that these things are not illusions (albeit natural illusions).

On perceived colors

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The theory that each animal lives in its own "subjective" world that is determined by the properties of its sensory organs and its brain was stated for the first time by Jakob von Uexküll (1928). Each animal creates its own "Umwelt," which is not only determined by its senses but also by its motor responses, its behavior. Thompson, Palacios & Varela have worked out this point nicely in the context of color vision where the comparison of different color vision systems makes it entirely clear how much care is needed not to get trapped in an anthropocentric view. In the question of how "colors" are perceived by an animal, or how its world is composed with respect to color, the authors come to some important conclusions that I would like to emphasize and expand.

(1) In human trichromatic color vision there are four "unique" colors, with "yellow" as a color that can be understood only on the basis of neuronal interactions between different "photoreceptor channels." It is tempting to explain unique yellow with the properties of certain "color-opponent" neurons. But, as the authors point out, this is so far only an analogy, and it is not at all demonstrated that these neurons are the physiological basis for "unique" colors and "opponent" colors. In the honeybee, for example, which has a color vision very similar to that of humans (except for the shift into the ultraviolet range), it is not known whether the number of unique hues is higher than three. Even in the ingenious experiment on the pigeon by Wright and Cummings (1971) cited by the authors it is not clear whether the "transition points" correspond to the locations of unique colors. To get insight into this problem, very refined behavioral experiments are required. On the other hand, I would like to add that tetraphasic (opponent) neurons proposed by the authors for theoretical reasons for tetrachromatic color vision were indeed

found in the Japanese dace (*Tribolodon hakonensis*) by Hashimoto et al. (1988). This fish has an ultraviolet (UV) cone type, and most probably a tetrachromatic color vision, but one that has not been investigated behaviorally.

(2) The statement that tetrachromatic color vision systems possess "ternary" colors cannot be overemphasized. It means that there are colors that are perceived as "red-green-blue" at the same time! This is impossible for us to imagine. For the goldfish or the turtle *Pseudemys* (Arnold & Neumeyer 1987) we must expect four classes of such colors that are located in the four planes of the tetrahedron: "red-green-blue," "red-UV-green," "green-UV-blue," and "blue-UV-red."

(3) From our introspection we know that an additive mixture of "red," "green," and "blue" results in the perception of "white," which has a specific quality that we describe as "neutral" or "uncolored." So far – and here we go one step further than the authors, who do not touch this point – it is an entirely open question whether an animal perceives "white" as "neutral" as we do. Only in the honeybee does there seem to be an indication of this (Menzel 1981). For a tetrachromatic animal we would expect that "UV-blue-green-red" is perceived as white, but it is also possible that an additive mixture of the appropriate wavelengths would result in a simultaneous percept of all four colors. (Here it has to be noted that, at least in cyprinid fishes, the existence of so-called nonopponent or monophasic neurons has nothing to do with the perception of achromatic colors). Furthermore, I think that one must be careful to treat the three qualities of human color vision – hue, brightness, and saturation – as universals common to all color vision systems, as the authors do.

Areas of ignorance and confusion in color science

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Thompson et al.'s target article presents an elegant dissection of computational, psychophysical, and comparative views of color vision. Although the authors present valuable arguments for the comparative view, perhaps their greatest accomplishment is in clarifying the distinctions among the three views, thereby helping scientists engaged in color vision to be more aware of their presuppositions.

In making a case for the comparative approach, the target article speaks volumes concerning what is *not* known about color vision. I comment on one area of ignorance and one area of confusion. We are incredibly ignorant concerning the spectra of natural objects and the spectral composition of real illuminants (especially when multiply reflected). Our ignorance makes ecological arguments often impossible to decide, for both our own and other species. For example, do photopigment action spectra covary with the regions of the spectrum containing most information for the particular species? We cannot answer without knowing what the typical spectra are. The extraordinary proposition that nature is (almost) trichromatic, in that natural reflectances can be (almost entirely) composed from three basis functions, could explain the evolution of trichromacy in animals; but the proposition is based on little more than an analysis of the pigments used by the Munsell company. Is the purpose of color vision to improve discrimination or not? With clever lighting, a black/white movie can look like the real thing, so, at least for humans, color is not essential for recognition (or even aesthetics). Perhaps natural lighting is not so clever, however, and important distinctions require color; we do not know. Do human or monkey rod monochromats labor under a handicap,

other than the obvious one of bleaching in direct sunlight? Do pigeons gain significant information from their additional receptors? Again, we do not know. It is not enough to argue from the existence of a thing directly to its utility, however plausible.

The area of confusion is color constancy. Although the authors take this to provide an important case against which the various ontological views of color vision can be tested, the evidence here is contradictory. The current view is that color constancy exists, meaning that human observers can perceive the reflectance of an object and discount the illuminant. Constancy can indeed be near-perfect for lightness (white-gray-black), but this is far from the case for color (hue and saturation). Because our data contradict the standard view, the research is summarized in some detail:

Arend and Reeves (1986) and Arend et al. (1991) showed that color constancy is at best only moderately good, and at worst almost absent. Moreover, color constancy, far from being automatic, is strongly task dependent. The extent of color constancy in a Mondrian display varied from near 60% of perfect constancy to less than 20%, depending on whether the task required judgments in what Evans (1974) termed "surface mode" or "light mode." Our observers adjusted the chromaticity of a patch in a test display presented under one phase of daylight to match the same patch in standard display presented under another phase of daylight. Under surface mode instructions, they matched the patches as if they "were cut from the same piece of paper." Under light mode instructions, or what we also call "unasserted" mode, subjects matched the saturation and hue of the test patch disregarding other areas of the display. Note that our methods improved on those in earlier work, which had claimed more consistent color constancy. We used natural, not haploscopic, viewing (the latter produces differential adaptation of the two eyes, which is grossly unecological); we used the same displays for test and comparison stimuli, with only the illuminant varying; we controlled light adaptation; and we specified the matching task in detail.

It did not surprise us that mode should have a large effect on constancy, as this is typical in perception. For example, observers can judge both real size ("size constancy") and retinal size, and do so remarkably well, as Thouless (1931) showed long ago. Observers can match the same test patches using lightness (perceived reflectance) or brightness (apparent intensity), as Arend and Goldstein (1987) showed using an achromatic version of the Mondrian configuration just described. Their lightness matches followed reflectance nearly perfectly ("lightness constancy"), whereas brightness matches followed intensity according to the power law. Thus, in surface mode, observers show near perfect achromatic (lightness) constancy and up to 60% of color constancy. In light mode, constancy does not hold; judgments follow a power of the intensity of the stimulation (the product of illumination and reflection) in the case of brightness, not just reflectance; and in the case of color, matches show 20% or less color constancy.

We were surprised to find that the context of stimulation had virtually no effect on color matches. We found very little effect of stimulus complexity (comparing many-element Mondrians to simple center-surround configurations), luminance variations (comparing near equiluminant displays with displays in which brightness varied), cues to the illuminant, or presentation method (simultaneous or successive presentations of test and standard displays). Lightness constancy was slightly inferior when simple rather than complex displays were used.

How do our data affect theories of color ontology? Computational models such as Land's retinex, which discount the illuminant in complex (but not simple) scenes are contradicted by our finding almost no effect of stimulus complexity and virtually no constancy in the light mode. A model is needed in which the observer is permitted access to the visual system's best guesses about both the illuminant and the objects viewed. This contradicts the surface-fixated computational viewpoint described in

the target article, but it does not contradict the computational viewpoint in general. There are good reasons why the organism should attempt to compute, and represent, the pattern of illumination as well as the nature of the objects in the field of view. The finding that observers have partial access to both surface chromaticity and light at the eye, like the discovery that observers can report both actual and retinal size, does not bear on whether a "computational" or "ecological" explanatory perspective is to be preferred, only on what needs to be explained.

What in the world determines the structure of color space?

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True, the physical reflectances in a field of flowers have been shaped by the eye and brain of the bee (target article: sect. 2.5, para. 11 – following Barth 1985). At the same time, all eyes and brains have been shaped by enduring regularities of the physical world (Shepard 1987). Whatever emerges from the coevolution of an organism and its environment, including the dimensionality of the organism's representation of colors, may reflect (a) invariant properties of the physical world, (b) entrenched properties of the resident organisms, and (c) random accidents or symmetry breakings over evolutionary history. These alternatives are not equally fundamental, however. An animal's color space is undeniably a direct manifestation of its biological makeup (alternative b). But any explanation of that biological makeup beyond one that simply posits a history of accidents not deducible from general principles (alternative c) must be grounded in some enduring properties of the world (alternative a). Only this way can we explain how the color of a flower, however different it may appear to a person or a bee, appears constant to each despite wide variations in the light that the flower scatters back, under various conditions of illumination, to our various eyes. In this commentary, I use color constancy to draw attention to a possible environmental determinant of the dimensionality of a species' color space.

Three distinctions are helpful: The first is between the problems posed by the world and the neurophysiological mechanisms that have evolved because they provide solutions to those problems – even though those problems may have changed along with the coevolving environment. An indiscriminate aducing of environmental constraints and neurophysiological findings, as if the two were on equal footing, blurs this distinction and obscures what must ultimately count as an explanation. The second distinction is between ecological features of our world that have prevailed for evolutionarily significant periods and such recent additions as "bricks," "buildings," and "Mondrian displays" (target article, sect. 2.4, para 11; 16), which cannot have played a role in the phylogenetic shaping of our perceptual systems. Likewise, the cited departures from color constancy under artificial illuminants (sect. 1.4, para. 1) are irrelevant to the question of our degree of color constancy under natural conditions. The third distinction is between the aspects of surface reflectances that determine our perceptual representations and the degree of color constancy of those representations. These are lumped together by a definition of color constancy as "the recovery of the invariant surface spectral reflectances in a scene" (sect. 1.4, para. 4). Yet, under natural conditions, constancy can be achieved without fully capturing spectral reflectances.

In fact, the mapping from reflectances to perceived colors is generally many-to-one. The dimensionality of the color spaces of most species fall short of the number of degrees of freedom of surface reflectances (which may be somewhere between five

and seven – Maloney 1986). Moreover, the dimensionality of color space evidently varies between species. The conclusion drawn in the target article (sect. 1.4, para. 12) is that color cannot “be found in the (distal or proximal) physical stimuli.” Instead, we are urged to give “more attention to the local, context-dependent features of perception than to the high-level, physically invariant properties of the environment” emphasized in “the original Gibsonian program” (sect. 1.4, para. 7; sect. 3, para. 9).

Taking the opposite tack, I have proposed that we search for invariances at still more general and abstract levels (Shepard 1987; 1990; 1991). For highly visual diurnal species, the single most important factor determining the dimensionality of its color space may not be the ill defined five to seven degrees of freedom of surface reflectances in its present local niche. Instead, it may be the more sharply delimited number of degrees of freedom that has long constrained natural illumination in the terrestrial environment as a whole. These three degrees of freedom correspond to (1) a *light-dark variation* between direct illumination from midday sun and clear sky versus reduced but spectrally similar illumination reaching an object only by scattering from achromatic clouds, cliffs, or moon, (2) a *red-green variation* between the long-wavelength-rich illumination direct from a low sun versus the long-wavelength-rich illumination penetrating an atmosphere loaded with water vapor, and (3) a *blue-yellow variation* between mostly short-wavelength-rich illumination scattered to an object from clear sky versus mostly short-wavelength-poor illumination reaching that object directly from the sun (see Judd et al. 1964; Dixon 1978; Shepard 1990; 1991). It may be no accident that these three degrees of freedom of terrestrial illumination also correspond to the light-dark, red-green, and blue-yellow opponent processes proposed for the human visual system, on quite different (psychophysical and neurophysiological) grounds, by Hering (1878) and Hurvich and Jameson (1957).

The target article does speak of the “perception” of conditions of illumination (sect. 1.4, para. 6; sect. 2.1, para. 4[iii]). But what is most important, I suggest, is not the *perception* of conditions of illumination, as such, but the perceptual *compensation* for variations in that illumination in order to recognize significant objects. On the basis of Maloney & Wandell’s (1986) general linear model for color vision, I have argued that regardless of how much of the spectral reflectances of surfaces our visual systems represent, our systems must analyze visual input into three chromatic channels to correct for the illumination and, thereby, to achieve constancy of color (including lightness) under terrestrial conditions (Shepard 1990; 1991). Indeed, even if the chromatic colors of the objects themselves were irrelevant for us, even if we required a representation that (like a “black-and-white” photograph) was merely achromatic, we would still need an initial analysis into three chromatic channels for the resulting shades-of-gray representation to achieve lightness constancy.

Of course, the chromatic aspects of objects are not irrelevant for us. Like our ancestors, we benefit from the ability to detect red berries against green leaves even when these are of similar achromatic lightnesses. For the same reason, the need for constancy is almost certainly not the only factor influencing the dimensionalities of color representations. Species that are active only in nocturnal, deep sea, murky, or subterranean environments, for example, may manage with fewer than three dimensions of color representation because limitations on the quantity or quality of available light (or on the varieties of visible surfaces) either permits sufficient constancy with fewer than three dimensions or precludes analysis into as many as three chromatically distinct channels. For other species, dimensions of representation of spectral reflectances beyond the three needed for constancy may have become a significant factor in the identification of foods, mates, offspring, competitors, predators, or the like. In some species, more than three chromatic channels may

also have been favored to compensate for additional, subtle degrees of freedom of lighting that are peculiar to their niches – for example, variations in illumination transmitted through media or scattered from surfaces (such as leafy canopies) having special, spectrally selective properties.

The structure of color space for each species may thus be shaped, in part, by “local, context-dependent features” of that species’ niche. But such shaping must be understood in the context of an evolutionary explanation of color perception in terms of general constraints on objects, surfaces, and illumination in the world. In particular, the possibility should not be neglected that the three-dimensionality of the color spaces of such diverse and highly visual species as the human and the bee may most fundamentally reflect a long enduring abstract invariant of that world, namely, the prevailing three-dimensionality of variations in terrestrial illumination.

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Ecological subjectivism?

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Thompson et al. promise a new model of color vision that departs from two approaches: One (objectivism) is that color is a property of objects and that perception consists in the internalization of these physical properties; the other (subjectivism) is that colors are produced by and explainable in terms of neurophysiological functioning. The data cited are intriguing, the emphasis on a more biologically realistic, less anthropocentric approach to vision is important, and the discussion of the limitations of the two views is instructive, especially in scientific circles where theoretical presuppositions of this type go unnoticed but influence the direction taken by research. Unfortunately, however, the promised new model never materializes.

Thompson et al. argue convincingly against the objectivist view with data that show, for example, that what is perceived is determined by the sensory-motor properties of the animal. The view that vision is about “recovering” properties of objects ignores the fact that what counts as an object is determined in part by the structure and behavior of the animal. I have argued elsewhere (Skarda 1989) that if perception were about recovering the features of objects then whenever the same object impinges on receptors it should lead to neural processing that remains identical for that object over time. This does not happen. Perception is different from what the objectivist model would have us believe.

Against subjectivism, the authors point out that the facts about color vision do not all yield to a neurophysiological analysis. What are these facts? They include the observation that animals are adaptive as their organic environment is, and that they have coevolved: The animal’s activity changes the environment and tells us about what it perceives and how it perceives it. Thus, to understand the perceptual object for any given animal, we must take this ecological information into account.

But the fact that we need this information to explain the perceptual *object*, does not automatically result in a new model of color vision. It is consistent with objectivism, for example, that the animal’s neurophysiological structure affects what is perceived, that receptors act as “filters” for objective properties. Subjectivists, like Hardin, accept this point already. All

researchers determine what is perceived on the basis of animal behavior, and no one I know of quarrels with the fact that animals and their environments coevolve. So what is new about Thompson et al.'s model of perception? How does it differ from the tradition they criticize?

In section 2.4 (para. 11) Thompson et al. claim that "the visual system must achieve" segmentation of the visual world and later (para. 14) they tell us that surfaces are properties of the world but "also figure as properties of the perceptual object." Underlying these claims is the traditional model of perception: Perception occurs when an object causally impinges on the organism, producing an internal counterpart ("perceptual object") of the world. Clearly, this perceptual object is animal-relative and hence evolutionarily determined; furthermore, if we want to know about *what the animal perceives*, then a "purely neurophysiological" account is unsatisfactory because it is pitched at the wrong level of description (I urge the authors to pay closer attention to this issue). None of this ensures that the authors' model represents a departure from the tradition, however.

The problem is a very difficult one. Thompson et al.'s "ecological subjectivism" is not a solution, even if it represents a move in the right direction. The problem is to find a new model of perception rather than to reject one "ism" in favor of its alternative. Significantly, most of the authors' arguments are directed against objectivism, and the subjectivism they criticize is a very weak and muddled version indeed, if their account is accurate. But there is nothing "new" about the authors' model of vision. They accept the traditional problem: The perceptual object is not identical with the physical object, so how does vision succeed? The tradition offers two options, subjectivism and objectivism. Thompson et al. opt for the subjectivist approach, but rather than reject the world outright, they attempt to "modify" it using evolution and interaction to get a better fit, to eliminate the gap or to make it less noticeable. The world, they tell us, has the form it has because it has been shaped by animal activity; it bears the imprint of this interaction. In effect, the authors have discovered a less subjective-appearing solution by transforming the world into a sensory-motor experience. This, however, is not a new solution to the problem of perception. It is an optical illusion.

Confusing structure and function

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Thompson, Palacios & Varela lay out a case for the importance of comparative date in cognitive science. Using color vision, they contrast objectivism (presented as a computational variant of realism) and neurological subjectivism (a modern version of Muller's law of specific nerve energies). They conclude that an updated version of subjectivism, one that attends to ecological niche and evolutionary history, is most preferable. In this commentary, I make the point that Thompson et al. appear headed into a subjectivist swamp by too much emphasis on structural differences between the visual systems of pigeons and people. I suggest that the problem comes from the following two mistakes: They equate structure with function and explanation with intersubjective intercourse. I then discuss work on form/categorical perception by pigeons that underscores the importance of the distinction between structure and function, concluding that this line of work provides more support for objectivism than Thompson et al. would anticipate.

Structure and function are related, but they are not isomorphic. A new species was not created anew. It was cobbled together from old parts, now used in new situations. Those old

parts were themselves cobbled. The path of speciation is a twisty little maze, and reproductive success does not follow necessarily from design principles taught in the better engineering schools (Gould & Lewontin 1979). But there is a common factor, a world in which all designs must work satisfactorily. Vertebrate or invertebrate, all types of bodies reflect different mechanisms of adaptation to the common constant of gravity.

Thompson et al. document the differences in retinal physiology between people and pigeons, which suggest that there are fundamental differences in their color spaces. Although there will be arguments about the particular values of the minima, the potential of a pentachromatic system in the pigeon seems likely. It is also true that this produces a problem of commensurability, a pentachromatic (or even tetrachromatic) space could not be completely mapped onto a trichromatic space without remainder. What concerns me is the meaning of the problem for Thompson et al. They do not seem to be so worried about accounting for what pigeons do, but what they "experience" (their discussion in section 2.3 is a clear example). On this point I suggest that they have fallen into the classical mire of solipsism in their speculative concern over the unbridgeable gaps between species. Their mistake is to attend too much to differences and to miss the common function. Their mistake is akin to worrying about the different number-worlds of slide rules and electronic calculators. The mechanisms of the two are very different; the errors each mechanism is liable to produce are different; and the types of problems for which each mechanism is most accurate are different. Examined very closely, slide rules and electronic calculators produce the fundamental problems of commensurability that exist between analog and digital systems. But the emphasis on differences misses the great commonality in function. It misses the important similarity over specified scales of problems. There may be several satisfactory paths to a common goal.

The alternative of multiple mechanisms for a common function is seen in operant conditioning research on form/categorical perception in pigeons. Operant research on form perception by pigeons has been historically *unconcerned* with the structural differences between pigeons' and people's visual systems. Initially the question was whether pigeons could be trained to form perceptual categories that people used, such as the distinction between the presence and absence of a person in a photographic slide (Herrnstein & Loveland 1964). It has turned out that pigeons can be trained successfully with such discriminations – more easily than often assumed. The field quickly moved on to the question of mapping the borders of such categories. What were the domains of perceptual categories in pigeons that were exposed to such procedures? These turned out to be remarkably humanlike across many tasks. A pigeon's segmentation of categories with natural variation (such as fish or the leaves of trees) turned out to be quite similar to distinctions used by people (Cerella 1979; Herrnstein & de Villiers 1980). Multidimensional scaling and cluster analysis of discrimination performance with human-specific categories, like the American alphabet or geometric forms, also looked very similar to data from people (Blough 1982; 1990). More abstractly, the production of integral or configural stimulus effects in pigeons was driven by the factors of proximity and similarity in a manner similar to people (Steele 1990).

The similarities in performance between pigeons and people were close enough to justify the initial suggestion that the means underlying the performance were the same (Herrnstein et al. 1976). Pigeons see the way we see. That interpretation is now strongly in doubt. Pigeons do not seem to use information in the scene that we normally use (Cerella 1982; 1990). And pigeons use information in scenes that typically escapes our attention or is even hard for us to use when informed (Green 1983; Vaughn & Green 1983). Thus you have the following combination. On the one hand, similarity of categorization performance; on the other hand, dissimilarity of mechanisms underlying this performance.

This suggests that you have different visual mechanisms that produce common effects because they have a common function or goal: visually guided activity in an objective world. The results are like the differences and similarities between a slide rule and a calculator.

The problem for Thompson et al., in their preference for neurophysiological subjectivism is to explain *similarity* in performance between pigeons and people given such different retinal and neural structures. Their last section on the enactive view makes it clear that they plan a behavioral approach. I think that if they pursue their enactive approach then some type of objectivist assumption will be seen to have more pragmatic value than neurological subjectivism.

Wavelength processing and colour experience

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The history of epistemological theory encompasses positions that range from extreme subjectivism (everything is in the mind of the perceiver) to critical realism (things exist independent of the perceiver and affect him, but he has no way of knowing to what extent his perceptions reflect their nature) to naive realism where it is simply assumed that what we perceive is the reality (our perceptions and reality are congruent). The revolution caused by evolutionary theory not only removed man from his cherished position as the epitome of divine creation, it also had an enduring impact on epistemology, giving critical realism a biological foundation. Like the animals themselves, their perceptual and cognitive repertoire has evolved in constant interaction with the environment and, depending on the needs of the organism and the properties of its ecological niche, will be tuned to different aspects of reality. This implies that there is a real world outside, independent of the mind, and that a part, tiny though it may be, of its properties are perceivable in a way that enables the perceiver to act successfully within this world – successfully enough to survive. It also implies that within-species differences in perceptual and cognitive abilities may exist if the species has adapted to very different environments.

Colour vision is one of those many abilities that help to differentiate the components of the visual world. Without actually using the term “evolutionary epistemology,” as introduced by Spencer (1890), Lorenz (1943), and a variety of contemporaries (e.g., Taylor 1979), Thompson et al. use this approach to elaborate aspects of comparative colour vision that demonstrate that other species with more than three types of colour receptor, such as ducks and pigeons, see “a quality that is neither bluish, nor reddish, nor greenish, nor yellowish, but resembles blue, red, green, and yellow as much as they resemble one another” (Hardin 1988), rendering their colour vision unimaginable to beings with a more limited colour space such as ourselves.

In the course of their arguments, Thompson et al. adopt a commonly used definition of colour vision, that is, the ability to discriminate wavelength independent of relative intensity; they go on to say that this ability “would not seem to entail the enjoyment of colour experience, for it seems possible to imagine the former without the latter.” Indeed, it is not only possible to imagine this dissociation, but we know of examples of wavelength discrimination unaccompanied by colour experience. The first example is wavelength discrimination in blindsight. Blindsight is a term coined by Weiskrantz et al. (1974) to describe the phenomenon of residual visual functions that persist after the patient has suffered damage to striate cortex, producing a homonymous visual field defect within which the

patient is experientially blind. [See also Campion et al. “Blindsight” *BBS* 6(3) 1983.] Despite the blindness, he may be able to respond to stimuli confined to the blind field when he can be persuaded to “guess.” Using conditions meant to favour the colour-opponent system, and two-alternative forced-choice guessing, we have recently demonstrated that patients may not only have a normal, if reduced, spectral sensitivity (Stoerig & Cowey 1989), but that they may also be able to discriminate wavelength stimuli matched for luminous efficiency on the basis of their own spectral sensitivity curves (Stoerig & Cowey, submitted). As the blindsight patients do not experience any visual sensation when their blind field is stimulated, these results demonstrate discrimination of wavelength independent of their relative intensities that does not entail the experience of colour, or indeed of seeing.

In contrast, in the second example it is only the experience of colour that is lacking, but again wavelengths may nevertheless be discriminated. This is the example of acquired cortical colour-blindness or cerebral achromatopsia. In the extreme form of this condition, caused by destruction of cortex in the lingual and fusiform gyri, the patient perceives the world in grey shades, like a black and white TV. Nevertheless he can detect the border between adjacent colour fields, such as red and green, irrespective of their luminance (i.e., there is no null point at which the border disappears) and despite the fact that the two colours look “the same shade of grey.” Even more impressive, he may look at a display of colours and pick the odd one out, even though they all look the same shade of grey. The patient still possesses neurons whose job it is to signal chromatic or achromatic edges or changes, no matter how they arise, and he can make crude wavelength discriminations, although his experience of colour is lost.

A dissociation of colour experience and wavelength discrimination is therefore more than just a possibility, although it is pathological. The loss of colour experience robs the visual world of emotional and aesthetic delights. To take just one example, an achromatopsic patient described his surroundings as “being darkly coloured, as in an unlit room at twilight, even when they were bathed in sunlight” (Heywood et al. 1987, p. 25). We do not wish to suggest that animals who have developed the experimentally demonstrable ability to discriminate wavelengths do not experience the colours they see. Indeed, the much more elaborate systems that some species have developed may enable them to perceive beauty we cannot even dream of because with our physiological system we cannot imagine a colour that “is neither bluish, nor reddish, nor greenish, nor yellowish.” Colour and beauty are in the eye and brain of the beholder, and whatever colour and beauty are perceived must depend on both, and on the species-specific world in which they evolved.

The ethnocentricity of colour

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I agree with most of Thompson, Palacios & Varela’s criticism of the limitations of objectivist and subjectivist approaches to colour, but I think their “enactive” research program doesn’t go far enough in eradicating anthropomorphism and ethnocentrism.

I believe that “the world” underdetermines physical level specifications. This sort of conceptual relativity need not concern us here. Hence I proceed as if our best theories were reasonably successful in describing the physical world as it is. Many objects reflect UV-light; species may take advantage of

that, the more so in “animal-environment codetermination” (sect. 2.5). This does not change the physical fact that UV-related information is retrieved from the physical environment. Hence, there can be no doubt that when Thompson et al. write that “animals with different sensory-motor capacities would segment the world in different ways” (sect. 3, para. 11), this refers to segmenting something like the *phenomenal* world differently, not the physical world. On the one hand, this isn’t going far enough, on the other, it’s going too far.

In saying “that the phenomenal structure of color and the structure of the visual system covary” (sect. 1.2, para. 9) Thompson et al. don’t go far enough. Adding the structure of the organism to the incoming light-rays still underdetermines the phenomenal structure of colour, at least for humans. It’s not just a matter of “perceiver relativity” (sect. 2.4) for different species. Such variation already occurs among humans, for whom perception is conceptually loaded and action-oriented in different ways. This has two consequences. First, the “phenomenal structure of color” (sect. 1.2) is not a fact of nature but an ethnocentric artifact. (How is a “metallic” appearance to be explained in terms of hue, saturation, and brightness? How do we account for people who insist that there are two unique hues of blue or who cannot be convinced that yellow and green are really different things?)

Second, it is not the case that psychophysical colour channels correspond to neuronal pathways. Knowledge of neuronal pathways, at least for a long time to come, severely underdetermines possible psychophysical channels. (Actually, I believe that “linking propositions” (sect. 1.2) can at best be only locally valid, context-dependent statistical generalizations.)

There is no room here to argue for all of this (see van Brakel 1991). I limit myself to showing that nothing is lost and perhaps something is gained by accepting these points of view. That nothing is lost can be seen, for example, from the fact that the research program Thompson et al. advocate (sect. 3) can easily be reformulated in nonphenomenal language. Or, to take a concrete example, consider a feather-sorting contest for pigeons who allegedly live in a four- or five-dimensional “colour” world. The pigeons divide a pile of indistinguishable white feathers into two (or more) piles. What can be said about this? Physically we can establish that some whites reflect UV-light, which the pigeon is apparently able to “see.” What does it add to say that it sees extra hues? How do we know that the “non-UV” white looks *white* to the pigeon? Why would the sensitivity to UV-light show up phenomenally as an extra unique hue? Why not as an extra type of brightness, or as a metallic look, or as if vibrating slowly? We could try to design experiments to exclude such possibilities, but what could such experiments show over and above the pigeon’s sensitivity to UV-light?

Dropping the ethnocentric color space models opens up the possibility of finding species-independent regularities or species-specific characteristics independent of the constraint that whatever might be discovered must fit the terminology of hue/brightness/saturation and unique and nonunique hues, if not cold and warm colors. After all, if the pigeon is ascribed ternary color experiences, there’s no reason why it shouldn’t be ascribed mysterious X-experiences that fit the third dimension of the triad: cool, warm, X. This brings me to Thompson et al.’s anthropomorphizing about pigeons (and other animals), in which they are going too far.

They suggest that there are “different phenomenal color spaces, some of which are incommensurable” (sect. 2.1, para. 1), but this still assumes that the pigeon has *color* experiences. On the one hand, the way of life (and neurophysiology) of pigeons and humans are so different that any assumption about *experiential* similarities is tendentious, even if both were to have the same number of identical cone absorption curves. On the other hand, the fact that some people are dichromats or blind doesn’t imply that their phenomenal worlds are *incommensurable* to other humans. There’s a sense in which a blind

person lives in a world of different perceptual objects, but there’s a stronger sense in which a blind person lives in the same *experiential* world as other humans.

Moreover, *physically*, it’s not at all clear at what point incommensurability would hold. Think, for example, of rod assisted color vision in dichromats, of trade-off between dimensionality and sensitivity, and of the effect on “dimensionality” of large variations in cross-over points of ganglion cells.

Hence I suggest that we drop anthropomorphic color talk, give up the assumption that color “must be specifiable in terms of hue, saturation, and brightness” and forget that “to be a hue it must be either unique or binary (or ternary)” (sect. 2.4, para. 2). This is not a plea for austere objectivism. Thompson et al. are right in stressing that perception is “context-dependent and interest-relative” (sect. 2.5). The comparative study of “color” vision should be governed by the interest-relativeness of categories, thereby replacing the mistaken interest in pure perception. What a physically specified category means to a human or other animal should be apparent from what the human or animal does with it and how it helps guide activities, not by how it is (thought to be) experienced phenomenally.

Ways of coloring the ecological approach

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Thompson et al. analyze current approaches to color perception, computational vision on the one hand and neurophysiology and psychophysics on the other, and find that their implicit ontologies are either objectivistic (color is spectral reflectance “in the world”) or subjectivistic (color is “in the head”), respectively. Based on a review of comparative studies of color vision, the authors conclude that neither position is satisfactory because colors result from animal-environment codetermination. In this commentary we indicate that their so-called “enactive view” is not fundamentally different from the much more widely known “ecological approach” instigated by Gibson (1979) and that Thompson et al. attempt to increase the contrast by coloring the ecological approach in a particular way, that is, by neglecting a fundamental body of research within this tradition. In addition, we present some unpublished results on human perception and the use of color mixture (together with color contrast and constancy among the three basic phenomena of color perception), which raise some questions about the pervasiveness of ecological laws. Whereas our first comment is rather critical, the second is more like an open question with respect to another way of introducing color in the ecological tradition.

1. A criticism. When taken through the discussion of objectivism versus subjectivism to the dilemma of the chicken versus egg position, the reader familiar with perceptual approaches immediately thinks of Gibson’s (1979) treatment of these issues and his plea for the study of perception as an activity of a perceptual system in its environment. Thompson et al. seem to realize this link and begin to refer to Gibson and other adherents of the ecological approach at this point in the target article. Although they admit some affinity between their own enactive view and Gibson’s ecological position, they prefer to stress the differences. We have the feeling, however, that the way the authors color the ecological approach does it some injustice. [See also Ullman: “Against Direct Perception” *BBS* (3)3 1980]

To start with, Thompson et al. applaud the ecological refusal to separate perception from action and Gibson’s deep insight that perception must be understood within the ecological context of guided activity. To show that these are not mere slogans,

it would have been useful to refer to some interesting empirical work based on these assumptions, such as Lee's paradigmatic study of plummeting gannets (Lee & Reddish 1981) and research by Warren and his group on optic flow (Warren et al. 1991; Warren et al. 1988). Instead, Thompson et al. criticize the original Gibsonian program for the exaggerated role of invariances, the neglect of the complex neural processes, and the way these processes contribute to shaping different environments depending on the animal.

We agree that it would be interesting to develop additional theories and models of the self-organizing properties of neural networks as the proper substrate of perceptual and other activity (Humphreys & Riddoch 1986; Wagemans 1990), but we think one cannot be blamed for not doing everything at the same time. If ecological optics – which differs from classical, physical optics, by the way, because it studies light with respect to the perceiver – shows that a certain invariant is picked up from the light, the story is indeed not a full-fledged perceptual theory (Ramachandran 1985; Wagemans 1988), but perhaps it is enough if the psychophysical findings and their interpretations in terms of perceptual mechanisms are not incompatible with basic properties of known possible means of implementation.

The second way Thompson et al.'s enactive view is supposed to extend Gibson's ecological approach is by treating the environment not simply as the ecological setting for animal activity, but also as something determined by that very activity. Here, we think, the authors neglect a fundamental part of Gibson's theorizing, which results in an apparent enhancement of their own contribution. Although Gibson has always struggled with the ancient dualisms discussed in the target article, even in the context of color perception (see Gibson 1967), it was only in his last writings that he coined the notion of "affordances" to indicate the properties of things with respect to the perceiver's behavior.

He explicitly states that "affordances are not simply phenomenal qualities of subjective experience nor physical properties of things as now conceived by science, but ecological in the sense that they are properties of the environment *relative to an animal*" (Gibson 1982, p. 404; stress in the original). Gibson also indicates that "affordances, and the stimulus information to specify affordances, are neither subjective nor objective but transcend this dichotomy; the actor/perceiver and the environment are *complementary*" (Gibson 1982, p. 411; stress in the original). So, it is not only the distinction between actor and perceiver that is given up, as Thompson et al. want us to believe, but also the dualism between organism and environment. An affordance is typically determined by the organism's activity and hence dependent on the perceiver's characteristics. The climb-on-ability of stairs is not the same for a basketball player and a crawling infant, nor is the walk-through-ability of different apertures. Again, empirical research is inspired by these ideas (Mark 1987; Warren 1984; Warren & Whang 1987). We agree that the notion of "affordances" seems odd and somewhat mystical, but the same flavor is present in some of Thompson et al.'s remarks, such as the one about the role of carotenoids in colored objects and the retina. This seems like the "similis similibus curantur" of medieval medicine.

In conclusion, although we are very much in sympathy with the approach to color perception proposed by Thompson et al., it must be admitted that the contrast between their own enactive view and Gibson's ecological approach is less sharp than suggested. Perhaps this results from their coloring of other approaches. In fact, a similar black-and-white picture is given of the computational approach. In light of some very recent developments, the implicit philosophy of this approach is far from being a narrow minded and onesided objectivism. Not only is Brooks's (1991) recent work in robotics heavily dependent on the direct interfacing of parallel activity-producing units to the world through perception and action, as admitted by the authors; Watt's most recent monograph (1991) is also full of

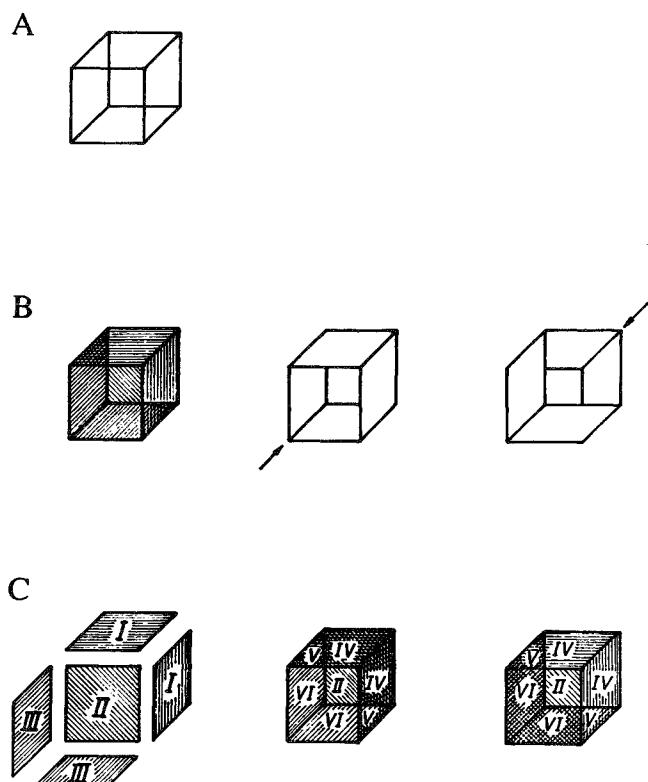


Figure 1 (Wagemans & De Weert). Necker cube (A) and colored variants (B-C) used in experiments on color mixture. B is a black-and-white representation of one of the stimuli used, together with two possible 3-D interpretations. In C the color relations are indicated (each number represents a color). The leftmost item is the first part of the display presented to the subjects, always followed by one of the two possible "boxes," corresponding to the 3-D interpretations in B (see text).

examples of why and how computational theories of vision have to take the perceiver's actions into account.

2. An open question. We are currently investigating human perception and the use of color mixture by means of colored variants of the Necker cube (see Figure 1). The stimulus displays are two-dimensional (2-D) patterns that can be interpreted as three-dimensional (3-D) boxes. In the original Necker cube (see Figure 1A), the 3-D interpretation is ambiguous. In our experiments we attempt to disambiguate the displays by coloring them in a specific way so that the overlapping patches are colored as the additive mixture of the constituting colors (see Figure 1B and C). For example, when the patches indicated by number IV are colored as the additive mixture of the colors of the patches indicated by numbers I and II, a box as in Bii is seen. Alternatively, when patches VI are colored as the additive mixture of II and III, then a box with a different 3-D orientation is perceived (Biii).

Although we must still run some essential control conditions, preliminary results indicate that human perceivers indeed select the 3-D orientation that corresponds with the additive mixture rules (on 65% or 75% of the trials, averaged across different color conditions; for a more detailed description, see Wagemans 1990). This seems to suggest that the rules of additive color mixture are used, although these are only valid for mixed lights, not for the transparent surfaces that seem to be implied by the box-like interpretation. Does this mean that our color perception does not incorporate the appropriate laws of color mixture? In normal ecological settings we are only seldom confronted with additive color mixture, yet we have the right

machinery to compute the result (e.g., opponent chromatic channels with summative properties). Considering the way our color vision system is equipped, it is very unlikely that we are able to use subtractive rules of color mixture in experimental tasks such as these, yet subtractive color mixture occurs much more often in our natural habitat. How does the enactive view of color perception explain this apparent dilemma?

Authors' Response

On the ways to color

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In *Ways of coloring*, our aim was to develop a novel theoretical framework for the study of color vision in cognitive science based on recent research in comparative color vision. By making the ecologically embedded, perceptually guided activities of color-seeing animals the Archimedean point for understanding color vision, we intended to move beyond the subjectivist/objectivist framework that characterizes much current visual research. We argued that this framework, specifically in its up-to-date form of “neurophysiological subjectivism” versus “computational objectivism,” is not only philosophically unsatisfactory, but also scientifically inadequate. In contrast, our “enactive” approach is intended to provide an ecological framework that can encompass specific research in neurophysiology, psychophysics, computational vision, and ecological optics without the conceptual and methodological shortcomings of subjectivism and objectivism.

Our Response falls into three sections. In the first, we address the more empirical and scientific issues raised in the commentaries. In the second, we address the relation between our comparative argument and the philosophical positions of computational objectivism and neurophysiological subjectivism. Finally, we address issues that center on animal-environment codetermination and our enactive approach.

1. Visual science

1.1. Open experimental questions. Several commentators raise a number of issues that can be substantively addressed only by further experimental research. Several subtle but important aspects of behavioral experiments in comparative color vision are elaborated upon by Neumeyer. One pertinent example that we used in our target article is the relation between hue opponency and the structure of chromatic channels. Neumeyer draws attention to evidence that we neglected for tetrachromatic color channels in the Japanese dace (Hashimoto et al. 1988). She also raises an important point about what

might count as white in a tetrachromatic color space, because it is possible that an additive mixture of all colors in such a space would not be perceived as a unified “neutral.” This question clearly needs further experimental attention. Kondrashev cites several studies on anuran sexual discrimination and fish physiological optics that provide good examples of the relations between ecological aspects of the perceptual environment and mechanisms of color discrimination. Gouras raises another issue that requires further experimental investigation: How does an increase in photoreceptors of different spectral sensitivity avoid chromatic aberration since the receptors will respond to different image planes? We know of no work addressing this question.

The relation between hue opponency and opponent coding is also discussed by Backhaus & Menzel for the visual system of the bee. We certainly agree that a linear relation between these two cannot be assumed a priori; our qualifications about color space and linking propositions (sect. 1.2) should indicate that we made no such assumption. Rather, our intention was simply to show that there is empirical evidence to support this relation as a hypothesis, as Backhaus & Menzel themselves indicate for the bee. There are clearly technical difficulties, however, and further issues that need to be explored. Finkelstein provides a nice example from psychophysical studies of human color vision for small and large spots of light. Her results seem to imply that a color channel must be seen as a “variable tuning,” which increases and decreases its degree of opponency.

Jacobs is rather skeptical about the evidence that we invoke to draw conclusions about color space. For example, he discusses how the number of minima in the wavelength discrimination curve or the number of spectrally distinct photoreceptors can be misleading as indications of color space dimensionality. (The same point is raised by Backhaus & Menzel for the bee.) We agree with Jacobs that a dose of skepticism here is healthful, but such a skepticism does not imply that we must treat the evidence in a piecemeal fashion, foregoing a broader and more inclusive perspective like the one we attempt to develop. For example, although there is clearly no one-to-one logical correlation between wavelength discrimination minima or number of photoreceptor types and color space dimensionality, their covariance is clearly supported by convergent evidence from retinal organization, physiological channels, and behavioral color mixture in primates, insects, birds, and fishes. It is this kind of multilevel analysis that can integrate the otherwise “fragmentary” evidence, and that makes the notion of comparative color spaces empirically defensible (a notion that is missing in Jacobs’s important pioneering monograph [Jacobs 1981]).

The multilevel analysis we advocate is misconstrued by Mausfeld et al. when they claim that we have created a “hierarchy of color spaces, which are vaguely related to neural structures” in which phenomenal color space is at the top. On the contrary, we have proposed only various levels of analysis that need stand in no (noninterest-relative) hierarchy and that together constitute a color space with various attributes. As for the relation to neural structures, we agree that the links here are problematic, as we explicitly indicated in relation to the problem of linking propositions. Furthermore, we not only outline

what is known about color space at various levels, but also provide some new ideas (e.g., the decorrelation procedure for calculating chromatic channels and the frequency analysis of color vision; see Appendixes A and B) that are admittedly only partial but certainly not vague.

Wagemans & de Weert contribute unpublished experimental results with additive coloration on Necker cube faces (see their Figure 1). In their eyes, this experiment raises the question of why additive rules are used for transparent-like surfaces in Necker boxes. Because the exposition and interpretation of their results is so brief, we do not understand what "challenge" their results pose for our view. We must therefore postpone any discussion of these experiments until their paper is published.

1.2. Coevolution and physical constraints. Agreement is expressed by **Shepard** with our view (stated in sect. 3) that perceptual theory must simultaneously consider (i) physical-level constraints; (ii) sensori-motor activity as constituted by neuronal processes and developmental constraints; and (iii) evolutionary history. In his eyes, however, these three are not equally fundamental; rather, (i) takes priority. From this position, he suggests that trichromacy in primates and bees can be explained (via a linear models framework: see **Maloney**) by the limited three degrees of freedom in terrestrial illumination. In response, we have two points to make. First, the preeminence that Shepard wishes to accord to physical-level constraints and invariants is certainly possible as a hypothesis, but contrary to what Shepard appears to suggest, it cannot be taken as either logically necessary or empirically demonstrated. Indeed, one goal of comparative research is to determine more precisely the various roles played by (i), (ii), and (iii). We return to this point in more detail in section 3. Second, even if Shepard's hypothesis about the three degrees of variance in terrestrial illumination is right, it hardly provides an explanatory framework for the color vision of "highly visual diurnal species" for it takes primate trichromacy as the norm when in fact this kind of color vision is most likely degenerate from an evolutionary perspective (Goldsmith 1980; 1990). Furthermore, tetrachromacy and pentachromacy appear to be common not only among diurnal birds, but also among vertebrate lineages in general (Goldsmith 1990). Surprisingly, Shepard does not address (either in his commentary or his 1990 paper) this considerable challenge to his view.

Maier & Burkhardt appear to agree with **Shepard** about the importance of physical-level constraints when they claim that we make too much of the differences in color spaces and ignore the commonalities. In particular, they point to the interesting cluster of regions of best wavelength discrimination in different animals and argue that evolutionary constraints must be quite strong to build up such a convergence. We certainly agree that such convergences must be explained, and hence that item (i) above could eventually turn out to be the one that carries the most explanatory weight here. But it is also possible that such clustering could be explained by the constraints involved in biochemical synthesis – witness for example the protein sequence similarity between avian and primate pigments (Goldsmith 1990). Furthermore, there are quite dramatic differences in neural channel implementation that these areas of best discrimi-

nation afford and these would seem to be more significant in determining the animal's color experience. In general, our plea is for a more parsimonious two-way determination between properties of organisms and their environmental constraints. How much invariant physical constraints per se – that is, as not mediated through the structure of organisms – can explain remains to be seen. Until all the evidence is in, it seems to us that the room for diversity is far larger than that for convergence. Indeed, the mere fact that, as **Maier & Burkhardt** note, color ontology continues to evolve and change, is a strong indication that arguments from adaptive optimality might be short of the mark.

Akins & Lamping also address this issue. In their view, comparative research indicates that the color vision of each species constitutes a "different informational 'cut' . . . on the objective spectral world." They support this claim by citing data from studies of fishes (which we also cite: sect. 2.4) that reveal the covariance between pigment sensitivities and ambient illumination. Again, such broad physical-level constraints as properties of the ambient illumination are clearly important, but (as with the data cited by **Maier & Burkhardt**) how these constraints are shaped by the animal into a color space is another matter. **Akins & Lamping**'s data are limited to the peripheral receptor level, but from this level to the constitution of a behavioral color space there are numerous layers of neuronal structure and activity. To describe these layers as merely generating different informational "cuts" on some objective list of parameters strikes us as "importing an a priori bias into . . . the initial vocabulary of explanation" contrary to **Akins & Lamping**'s own agenda. We therefore prefer to describe these layers as generating emergent behavioral domains or emergent domains of ecologically situated animal activity.

Backhaus & Menzel add a number of important details about the color systems of insects, including a clearer account of the geometry of color opponency, receptor sensitivity, and wavelength discrimination. We thank them for greatly improving the evidence we cited in the target article by contributing their two figures and for reminding us (personal communication) that von Helversen (1972) measured the honeybee's discrimination curve and that Werner et al. (1988) provide evidence for color constancy. They agree with us about the importance of coadaptive mechanisms for understanding the evolution of color vision, and they add to this point their fascinating not yet published studies of the ecology of 500 insect-pollinated plant species in Israel (Menzel & Shmida, in preparation). As they summarize this evidence, there is an amazing covariance between floral spectral reflectances and the photoreceptor maxima of the visiting insects. Because we do not yet have access to these results we cannot comment further, but we certainly agree that these kinds of studies provide a major advance for research on the coevolution of color vision and animal environments. We are puzzled, however, by Backhaus & Menzel's view that maximal decorrelation (Appendix A) and frequency analysis (Appendix B) do not allow specific predictions in this area. On the contrary, it is by using the decorrelation transformation that we are able to predict using no other ad hoc results the discrimination minima and color channel geometry of the goldfish as discussed in the text; we have also used this procedure to generate

predictions that match the known data for the honeybee (numerical details in Palacios 1991). In the case of frequency analysis, although work in this area is only beginning, measurements of the modulation sensitivity function (MSF) are a first step toward a comparison of the frequency limitations of color vision mechanisms with the frequency limitations of the relevant objects in the animal's environment.

1.3. Color space and diversity of perceptual experience. Various authors take issue with our use of phenomenal color space as described in terms of hue, saturation, and brightness (Davidoff; Mausfeld et al.; Neumeyer; van Brakel). The main criticisms are that this specification is oversimplified, hopelessly bound to human experience, and problematic when extended to other animals.

Davidoff argues that phenomenal color space is a questionable concept if we consider it an independent module. He considers a whole array of evidence that shows that at every stage color perception is interdependent with concurrent perceptual phenomena. For example, color is inseparable from shape and boundary, categories, and various modifications of chromatic channels. We entirely agree on this point and are grateful to Davidoff for adding this clarification. To speak of color space as a unit of perception and behavior is a mere convenience to isolate a center of attention; we in no way wish to assume that it is modular in the traditional sense. Indeed, our attempt to integrate color perception into the framework of perceptually guided activity is consonant with this point.

Mausfeld et al. rightly note that many complexities are involved in the phenomenal dimensions of color space, complexities that go beyond just the three dimensions of hue, saturation, and brightness. These commentators are mistaken, however, when they claim that we identify phenomenal color space with the CIE space. On the contrary, we explicitly indicate that the CIE tristimulus values are only one useful way of mapping one aspect of phenomenal color space, namely, its extent.

Van Brakel offers several incisive comments about phenomenal color, particularly when he imagines a hypothetical "feather sorting contest" among tetrachromatic pigeons. He rightly wonders why sensitivity to UV light should show up phenomenally as an extra hue and not as, say, an extra type of brightness, a metallic look, or slow vibrations. Van Brakel's point is well taken. What we should have said is that the phenomenal structure of any color space can be assumed to have some fundamental dimensions that specify it (these can be allowed to vary for interest-relative purposes). In the psychophysical studies of human color perception, these are hue, saturation, and brightness, although there are certainly other phenomenologically significant dimensions, such as the focal/nonfocal categorical organization studied by Rosch (1973). The dimensions appropriate for chromatic experience in other creatures could well be different, however, – with the one proviso that there be a hue dimension, which would seem to be a minimal conceptually necessary condition for something to count as a chromatic space.¹

Stoerig & Cowey summarize the evidence from human patients where wavelength discrimination and color ex-

perience can be dissociated, for example, in the phenomena of blindsight and cerebral achromatopsia. As they indicate, these phenomena provide evidence for our claim that mere wavelength discrimination does not entail color experience. But this evidence might also be thought to challenge one of the central claims in our target article, namely, that wherever a color discrimination apparatus (i.e., one involved in additive color mixture, color contrast, and color constancy) is in place, a color experience proper to the color space in question exists. Furthermore, it is this claim that supports our attribution of color experience to nonhuman animals. Thus the phenomena that Stoerig & Cowey review bring into focus from a different angle the complex issue just discussed of what color experience can mean in the context of other species. Our position has been a parsimonious one: If there are the color discrimination behaviors and apparati to define a color space, then we assume that such chromatic abilities are experiential in the sense that Griffen (1984) has discussed for various animal capacities. It certainly does not follow that animal experience so understood implies self-consciousness or self-awareness as in human experience, which is constituted by language and self-reflection. The phenomena that Stoerig & Cowey cite, however, do invite us in a comparative context to wonder what might correspond to achromatopsia in animals and how this could be revealed experimentally. Just as a lesion can collapse individuals' experience so they no longer experience color, we might imagine experimental demonstrations in animals where the full presence of a color space and its associated experience (say, in color discrimination associated with sexual recognition) are collapsed by a disconnection syndrome leaving intact only residual chromatic discriminatory abilities. This intriguing idea must remain speculative for the time being.

Can different color experiences in the sense of "experience" just indicated be commensurable? Let us offer a clarification. In our article, we followed a venerable tradition in color science and referred to the "dimensionality" of color space in the strict technical sense of the number of independent variables needed to specify it as a vector space. Accordingly, when we say that two color spaces are "incommensurable" we mean that there is no mapping between the dimensions of the two spaces without some remainder. (It should be noted here that the dimensions are not specified purely at the receptor level, hence Akins & Lamping are mistaken when they say that the color space of any tetrachromat would be commensurable with the gustatory space of any animal with four taste receptors.) Both Mausfeld et al. and van Brakel appear to have been led astray because they took "incommensurable" in a much broader sense than we intended. How color experiences can be said to be commensurable or incommensurable in a broader sense is a complex issue that we do not have the space to discuss here (see Thompson 1992).

Steele raises a different point about our discussion of diversity in color experience. He thinks that by emphasizing the differences between people and pigeons we are sliding into solipsism. He argues that these are merely differences in how the same function is implemented, a function that ultimately consists in a solution to a problem

posed by the physical world. His analogy is that of slide rules and calculators. We find this analogy quite mystifying, for it begs precisely the question we pose; the comparative evidence suggests that for color vision there is no such "same problem" to be solved by different implementations. Steele fails to give any account of what would count as the "common function" in the case at hand. There is surely a family resemblance among the various color spaces, but to assume that this resemblance is based in a common function, as slide rules and arithmetical calculators share the same arithmetical function, is to go round in circles by assuming what needs to be proven. Steele does give an interesting account of the history of form perception in pigeons, however, showing how recent research has come to the conclusion (not surprisingly from our point of view) that pigeons have a quite different sense of what counts as a visually relevant scene, though it is not difficult to get pigeons to mimic the same shape and form categorizations that humans perform. Steele suggests that the "common function or goal" is nonetheless "visually-guided activity in an objective world." We agree that both humans and pigeons have visually guided activity in their respective environments and that these share common basic physical constraints. As the comparative evidence indicates, however, there is a great deal of mediation among physical constraints, organismic processes, and evolutionary history; for this reason, we do not believe that broad physical constraints automatically specify universal problems to be solved. We take up this point in detail in section 3.

1.4. Computational color vision. Several researchers in computational vision address our target article from that point of view (Dannemiller; Feldman; Hurlbert; Maloney; Reeves). Their commentaries are considerably helpful in sharpening the differences between computational vision as inverse optics and our enactive approach.

1.4.1. Are we talking to a straw-man? According to Hurlbert, our depiction of computational vision is a "straw man." (Wagemans & de Weert also accuse us of presenting a "black-and-white" picture of the computational approach). In Hurlbert's view, the point of inverse optics is to recover invariant surface descriptors in general, of which reflectance is a good candidate. She also claims that computational visual scientists do not equate color with such surface descriptors as reflectance, but rather "heed the distinction between physical stimulus . . . and the perception (color) to which it gives rise." Our complaint, however, is not that computational visual scientists confuse stimulus and perception, which of course they do not, but rather that they assume that once reflectance is recovered color specifications can be constructed from such descriptors without remainder. Indeed, Hurlbert herself has written: "The computation of color is a prime example of the difficult problem of inverse optics . . . The computational goal underlying color constancy seems to be the extraction of invariant surface spectral reflectance properties from the image intensity signal, in which reflectance and illumination are mixed." And then, discussing lightness algorithms, she writes: "Computing color is thereby reduced to extract-

ing surface reflectance from the intensity signal in a single chromatic channel" (Hurlbert & Poggio 1988, p. 482). This is precisely the objectivist position (exemplified also in the passage from Maloney [1985, p. 119] we cited) that we take to task in our article.

In her commentary, however, Hurlbert offers a more moderate and eclectic approach, one that is similar to that advocated by Dannemiller. Both hold that determining constant color descriptors is primarily a matter of extracting reflectance, but they admit that this task is insufficient to characterize the full range of chromatic phenomena. In Dannemiller's words, "chromatic information participates in various tasks" and these tasks "determine whether or not it is necessary to include an animal's subjective experience of color in one's model." Similarly, Hurlbert welcomes the "views of other animals" on various chromatic tasks. We are quite sympathetic to this multitask approach, but would give it a somewhat different interpretation. There are surely some discrimination tasks where the nature of an animal's color space can be safely bracketed out of the picture. When we need to account for the full-fledged behavior of the animal, however, we must take into account its specific color space, for this will guide and constrain the lower-level mechanisms closer to optical properties. In contrast to Dannemiller's language, we would not say that this amounts simply to "taking into account the animal's subjective experience of color"; rather, it amounts to taking into account the entire range of phenomena that determine what color is. It does not suffice to assume that one can move back-and-forth between "objective color" and "subjective experience," for this merely perpetuates a bad duality in an unstable compromise. Instead, what we have tried to do is to move beyond the forced choice of objectivism versus subjectivism by taking into account the entire range of color phenomena in an integrated ecological framework.

1.4.2. Spatial segmentation, representation, and related issues. The objection is made by Hurlbert that we "grossly downplay" the research on segmentation algorithms using color. This criticism is surprising, because we introduce these algorithms as one of the three components of computational color vision theory (sect. 1.3). We explicitly state that one goal of computational vision is to link surface and color, as reflectance is a property of surfaces, not of unspecified boundaries. Our complaint was rather that the implications of this work are ignored or downplayed by those who assume that surfaces are prespecified properties of the environment that the animal must simply recover via the appropriate representations.

Hurlbert appears to agree with us that spatial segmentation for other species depends on their sensorimotor abilities, but she states that "computational models founded on inverse optics do not prespecify the environment, nor do they deny that perception can shape the environment, if the environment is defined as something created by the animal in the act of perceiving it." Once again, we find Hurlbert's stance on this matter far more open-minded than most of the literature on inverse optics, which certainly does assume that prespecified physical properties provide the primary data from which to

recover invariants. Consider, for example, Marr's (1982, p. 42) statement that "[t]he purpose of these representations is to provide useful descriptions of aspects of the real world. The structure of the real world therefore plays an important role in determining both the nature of the representations that are used and the nature of the processes that derive and maintain them." Or consider this description from Poggio et al.'s now classic description of regularization theory as applied to vision: "Early vision consists of a set of processes that recover physical properties of the visible three-dimensional surfaces from the two-dimensional intensity arrays" (1985, p. 314). Against this approach we do not deny the importance of physical constraints; what we deny is that they play the primary role such that their recovery via representations is the central feature of color perception.

Hurlbert rightly reminds us that there is research on sensorimotor processes and visually guided activity in computational vision, such as Reichardt & Poggio's (1976) study of visual orientation in the fly. This more biologically inspired approach has yet to affect the main direction of research in computational color vision, however. Similarly, Feldman criticizes us for ignoring research on "adaptation, attention, and priming that bear on the relation between internal and external aspects of color," but he provides no references to substantiate his claim, nor does he indicate how this supposed literature is related to the mainstream of computational color vision research. He also takes issue with our characterization of such sensorimotor processes, claiming that these cannot simply be described as self-organizing. He is right that such a characterization is insufficient, and we do provide a number of examples of specific neural circuits akin to the ones he cites (vistibulo-ocular reflexes). Our point in the article was not to eliminate the distinctive properties of specific networks but simply to highlight the fact that neural processes involve emergent properties that must be taken into account. We do not think Feldman would disagree with this point (and a more careful reading of our target article might have avoided the misunderstanding).

Feldman thinks that our critique of representations contradicts what has been learned about "cortical maps, spatial cognition, and in fact, all but the simplest behavior." We certainly do not deny that there are always internal states of organisms (or machines) that covary with perceptual and cognitive behaviors. Feldman misses the point of our critique, which is aimed at representation in a stronger sense, namely, the idea that the basic function of perceptual and cognitive processes is to recover independent physical descriptors that instruct animal (or machine) behavior. Here internal states are treated as the instantiation of some semantic domain or world model. Contrary to Feldman's suggestion, representation in this sense is not a fact, but a hypothesis, theory, or research program, one which is being increasingly criticized throughout cognitive science. One of the most striking examples is the trend in robotics pioneered by Brooks (1986; 1987; 1989; see also Maes 1990) at the very heart of artificial intelligence. Indeed, far from being "crippling for visual and other cognitive scientists," an enactive approach has proven to be quite fertile in the pragmatic task of attempting to build autonomous robotic devices. The debate over representations and the enactive cri-

que are therefore entirely legitimate and cannot be dismissed with a wave of one's hand.

1.4.3. Can the linear models framework suffice? It is rightly pointed out by Maloney that the linear models framework (LMF), of which he is one of the main architects, has provided fundamental insights into the phenomena of color constancy. It predicts both the direction and degree of nonconstancy for various models and algorithms, as well as the existence of privileged spaces of lights and surfaces where constancy is near perfect. And because LMF is stated in general terms, it can be transposed to various signal spaces, photoreceptor families, and dimensionalities. We fully agree with these important contributions of LMF and have discussed some of them in section 1.3.

Our differences with Maloney center on whether LMF is sufficient as an explanatory framework for color vision. With respect to color constancy, the commentary by Reeves is quite interesting, for it calls into question the supposedly central role of constancy and surface invariants in color perception. His data appear to contradict the "surface-fixated computational viewpoint" that emphasizes constancy at the expense of sensitivity to the pattern of illumination (cf. Jameson & Hurvich 1989), but they do not contradict the "computational viewpoint in general." They might reveal LMF to be a more narrow perspective than is needed for the entirety of color phenomenology in humans, however.

In relation to the comparative data, Maloney holds that the only reason to seek tools other than LMF at this time would be to falsify LMF. We do not claim in the target article that the comparative data falsify LMF in any strong sense. Our view is not contradictory to the LMF framework; we merely find this framework is limited. What need to be considered along with computational models that focus on extracting surface invariants are all the other neurological, ethological, and ecological dimensions of animal color spaces. LMF and computational vision in general have not addressed this large body of evidence, which, until proven otherwise, must enter into the explanation of color vision in natural systems. The issues therefore do not center on the falsification of LMF, but rather on how it proposes to address the larger set of issues revealed by the comparative data. Consider, for example, the possible role that color vision may play in aerial navigation among birds or in generating perceptual categories that have behavioral significance for animals in their interactions. Maloney does not indicate how these phenomena are to be integrated into a framework that relies exclusively on physical constraints and invariant descriptors. Instead, he chides us for advocating an approach that "is at once imprecise and scarcely falsifiable." The range of ecological phenomena to which we point has barely begun to be studied, however, and so accusations of unfalsifiability are hardly appropriate at this stage. We welcome any contributions that LMF has to make, but to suppose that LMF provides a sufficient theoretical framework for the ecological diversity of natural color spaces and therefore that we need no new tools is reminiscent of the well-known story of the man who continued to look for his lost key under the lamppost because only there was there enough light.

2. The comparative argument

2.1. Objectivism. Among the commentators who discuss objectivism, there appears to be some disagreement over how this position is to be understood. We take objectivism to be the position articulated by **Hilbert** (1987) and **Matthen** (1988), and defended in their commentaries: Color is a property that objects have independently of perceivers. This statement of the objectivist thesis differs from that offered by **Averill**, who holds that objectivism is the view that colors are either physical properties or logical constructions from physical properties, where a physical property of an object is one in virtue of which it is governed by natural laws (or in virtue of which it can enter into causal interactions). Because this sense of "physical" does not rule out properties of perceivers (e.g., physiological properties), objectivism in Averill's sense could include an account of color that refers to such (physical) properties (cf. **Dennett** who describes **Hardin**'s subjectivist view as internal objectivism). But because any such account would be perceiver-relative, it would contradict the basic objectivist thesis of the perceiver-independence of color as advocated by Hilbert (1987) and Matthen (1988). (We return to discuss Averill's position at the end of this section.) It should also be noted that it follows from this thesis that colors objectively understood need not correspond in any one-to-one manner with colors as perceived (as Hilbert, 1987, extensively discusses). Therefore, contrary to the contention of **Backhaus & Menzel**, objectivism about color is not at all "naïve realism," which typically holds that things are objectively as they are perceived.

We offered two main arguments against objectivism – the "argument from perceiver-relativity" and the "argument from external irreducibility" (sect. 2.4). **Hilbert**, **Matthen**, and **Levine** claim that the basic objectivist framework is untouched by these arguments and that our comparative evidence can be accommodated within this framework. A number of other commentators make specific points about the argument from perceiver-relativity (**Averill**; **Dannemiller**; **Hardin**) and the argument from external irreducibility (**Mausfeld et al.**). We address these specific points first and then proceed to a more general discussion of the objectivist framework.

2.1.1. The argument from perceiver relativity. Several misinterpretations of this argument are apparent in the commentaries. **Hilbert** supposes that the argument is meant as a refutation of color objectivism and argues in reply that it is question-begging. **Averill** supposes that the point of the argument is to establish the impossibility of perceiving a surface as an opaque one without perceiving it as colored. These are both misconstruals of the argument. First, as we explicitly indicated, the argument is intended to be conditional, based on a reasonable hypothesis about the interdependence of color and spatial segmentation, and so it does not have the status of a conceptual or logical refutation. Second, the argument does not purport to establish that it is *impossible* to perceive an opaque surface as a surface before perceiving it as colored. Instead, it simply purports to establish that what is actually perceived as a surface involves color vision. The point is to draw attention to the variations in

spatial segmentation among perceiving animals in relation to their color perception (see the commentaries by **Gouras**, **Hardin**, and **Hurlbert**, which appreciate this point). These variations certainly do not establish the impossibility of objectivism about perceptual content for color and surface perception, but they do challenge its *plausibility*. Objectivists cannot simply assume without argument that what counts as a surface can be specified independently of the perceiving animal. On the contrary, because objectivism about color depends on objectivism about surfaces, objectivists owe us an account of the latter. And just as objectivism about color must be defended not simply as conceptually possible but as empirically plausible in the face of wide variations in color vision throughout the animal world, so objectivism about surfaces must be defended as empirically plausible in the face of wide variations in spatial segmentation throughout the animal world.

It is the subjectivist **Hardin** who addresses this issue. In his commentary, he explains that his notion of "shape simpliciter" can be assimilated to a physically basic notion of spatial configuration, which provides a species-neutral way of describing characteristics of animals and their environments. This distinction between physical spatial configuration and visual shape is obviously the kind of distinction that is needed to ground an objectivist account of surfaces. Our view (which can only be indicated programmatically here) is that surfaces are not transparent entities in perception. Recent results on signal analysis for example (Mallat & Zhong 1989) prove rigorously that shape descriptions can be obtained by considering just the sharp discontinuities in a signal measured at various scales (what Marr called multiscale edges). This condensation of salience in discrete signal points is nontrivial as the mathematical tools brought to bear show and undermines the notion of shape as some neutral "spatial configuration." Furthermore, both the nature of the discontinuities and the relevant scales provide a range of physically significant anchor points that the neuronal mechanisms of each animal will treat in different ways. Thus although based on the same physical singularities, diverse shapes and contours are stabilized depending on animal behavior.

In a somewhat different vein, **Dannemiller** denies that we need to postulate anything about the phenomenal structure of an animal's color experience to understand the role that color vision plays in spatial segmentation. The link we attempted to establish between color vision and spatial segmentation in other animals, however, did not depend on hypothetical speculations about, say, ternary hues in pigeon color space, but on the kinds of segmentation algorithms that would be involved in tetra- or pentachromatic color vision. Our point is simply that such algorithms would most likely segment the world in ways different from, say, the algorithms developed by Rubin and Richards (1982; 1988), which correspond to the color-opponent channels in trichromatic humans.

2.1.2. The argument from external irreducibility. Computational objectivism does not necessarily imply that the unique/binary structure of hue must reduce to spectral reflectance, **Mausfeld et al.** claim, and therefore the "correspondence requirements" involved in this argu-

ment (premise 3) are too strong. Similarly, Matthen claims that computational objectivism is not committed to any “smooth mapping” from color experience to distal properties. The argument from external irreducibility was not intended to meet this kind of point; rather, it was meant to bring out the gap between the phenomenal structure of color and animal-independent distal properties like spectral reflectance. Our view is that given this gap, computational objectivism becomes a considerably implausible position. To defend this view, let us turn to the arguments offered by Matthen and Hilbert in their commentaries.

Matthen’s reply to the argument from external irreducibility is to distinguish between two distinct quality spaces for color vision – phenomenal quality space and a distal quality space. The former corresponds to our notion of phenomenal color space (sect. 1.2); the latter corresponds to the distal properties that, Matthen supposes, it is the biological function of chromatic perceptual states to detect, and that, in his view, determine perceptual content. Whereas we argued that for objectivism to be plausible some mapping between these two quality spaces must be provided that enables us to capture generalizations about hue, Matthen is willing to allow that phenomenal space might contain structure that completely fails to match anything in the structure of the distal property space. This possibility, however, leads Matthen to suggest that “it is not color that is the content of color vision, but some other physical quantity.”

Matthen admits that this consequence may seem paradoxical. To us, however, it seems like a *reductio* of the objectivist view. That color should be the content of chromatic perceptual states is a criterion of adequacy for any theory of perceptual content. If one’s theory of content or one’s theory of color leads to a contrary conclusion then one must revise or abandon it. Contrary to Matthen’s view, the claim that color is not the content of color vision is not a “clear consequence of distinguishing between content and experience, and allowing each a scientific role of its own.” It is, rather, a consequence of combining the distinction between content and experience with the view that it is the biological function of perception to “recover” animal-independent distal properties. When the distinction between content and experience is combined with an enactive account of perception, however, Matthen’s consequence does not follow. The enactive account of perceptual content incorporates a distal component but holds that the relevant distal properties are *ecological*: They are properties of the world understood as an animal environment and so must be identified in relation to the perceptually guided activities of animals. This does not imply, as Matthen seems to think, that color vision has no content, nor does it lead to the counterintuitive view that color is not the content of color vision. Rather, it implies, in Broackes’s elegant formulation, that perceptions of red will be identified by way of the property of redness, and redness in turn will be identified by way of perceptions of red. The informative circularity of this account exemplifies what Mausfeld et al. call “the inherent Janus-facedness of the concept of color.” Mausfeld et al. are therefore wrong to suppose that our enactive view implies an “essentialist” definition of color; on the contrary, the enactive account shows how,

in Dennett’s words, “no compact, noncircular definition of color is possible.”

2.1.3. Anthropocentric objectivism and the comparative argument. The main challenge to objectivism made by the comparative argument does not consist merely in the variability of color experience across the animal kingdom. Rather, it consists in the fact, revealed by comparative research, that there is no single distal property that is the biological function of color vision to detect. To repeat: Both across and within animal species, color vision plays many roles in the perceptual guidance of activity – surface perception, perception of ambient lighting conditions, and the generation of perceptual categories that have cognitive and behavioral significance.²

Hilbert, Matthen, and Levine respond to this challenge in the same way, namely, by claiming that it is a virtue of objectivism that it is “anthropocentric.” In their view, the ontology of color is concerned with a property that human beings perceive, and the objectivity of this property is not impugned by other species perceiving different properties. First, it should be noted that this reply simply ignores one of the central points we make, namely, that even in the case of primates and within the human species, color vision plays many roles besides those involved in the perception of surfaces (Burtt 1979; Hailman 1977; Jacobs 1981; Jameson & Hurvich 1989; and the commentary by Reeves). Although this point can be made without the comparative argument, it is nevertheless the comparative perspective that brings this fact most readily and quickly to light. For this reason, Levine is mistaken when he says that “comparative studies of color vision do no work for this argument.”

Second, as Hilbert recognizes, anthropocentric objectivism has a “glaring difficulty” – if color is identified with that distal property perceived by humans, and if other organisms, despite having similar visual machinery, do not perceive this property, then it follows that those organisms do not possess color vision (though they would in Hardin’s sense perhaps possess “color” vision). This difficulty is indeed glaring, perhaps even disastrous. Because the objectivist claims that color is that property perceived by the human visual system, the ultimate reference point for determining the nature of color must, even for the objectivist, be the structure and performance of the human visual system. As the comparative research indicates, however, other animals possess appropriately similar visual systems. It is therefore far more plausible and parsimonious to say that these animals possess color vision than to deny that they do because of a prior commitment to an objectivist theory of perceptual content. Suppose, for example, that our speculations about ternary hues in a tetrachromatic color space are right. Tetrachromats would then perceive a quality, which, as it would bear a resemblance relation to red, green, yellow, and blue – that is, resemble red, green, yellow, and blue as much as they resemble each other and yet not be reddish, greenish, yellowish, or blueish (see Hardin, 1988, and the commentaries by Neumeyer and Stoerig & Cowey) – would count as a *hue* (despite what other features it might have: see van Brakel). This possibility drives home from a rather different angle the point admitted by Hilbert that there is a mismatch between the

objectivist's account of the nature of color and the considerations involved in attributing color vision to nonhuman animals. Something does indeed have to give here, and it is the objectivist theory of color. By abandoning objectivism, the interests of philosophers and those of visual scientists need not part company as Hilbert envisions at the end of his commentary. The comparative argument shows not just what is wrong with the objectivist framework as a whole, but also how better theories can be developed from the cooperation of philosophers and visual scientists.

2.1.4. Averill's "limited objectivism". It is claimed by Averill that our view of colors as properties of the extradermal world understood as an animal environment implies that colors are nonphysical in his sense (i.e., they are not properties in virtue of which objects are governed by laws or enter into causal interactions). We certainly do not believe that color properties figure in the laws of *physics*, and so we are not perturbed that colors are nonphysical in this sense. Whether there are *natural* laws at some level in which color properties figure strikes us as an open question, however, one that is not decided by our enactive approach. Suppose, for example, that colors are, as we claim, ecological properties, and furthermore that Gibsonians are right that there are lawlike regularities to be stated at a distinctly ecological level. Then color properties might figure in the statement of these laws and so be physical properties in Averill's sense. (In a somewhat different vein, Broackes, 1991, has argued that there are nonreductive forms of scientific explanation that appeal to color properties.) We do not have the space to discuss these issues here. In any case, Averill's inference that colors cannot figure in natural laws if they are ecological properties does not follow.

Averill's own position has some intriguing features, however, ones that actually overlap with our ecological position. He argues that the proper question is not, "Are colors physical properties," but rather, "What features of colors are physical properties?" In his view, those features of color that are physical are differences in reflectance, transmittance, polarization, and so on – in short, the properties of physical optics. Those features that are perceptual, on the other hand, are hue properties, that is, redness, greenness, blueness, and yellowness. We like Averill's question, but we would answer it in a somewhat different way. Because we claim that colors are relational properties of animal-environment ecosystems, we are happy to say that colors have physical properties in Averill's sense as long as it is remembered that these do not exhaust the features of color and that they must be individuated in relation to the animal. In answer to Averill's question, then, we would say that the physical components of color actually correspond to those studied in ecological optics (see Wagemans & de Weert), that is, they are properties of the ambient optic array or surface layout as taken in relation to the sensory-motor capacities of animals.

2.2. Subjectivism. In our target article, we considered subjectivism to be the view that colors are internal sensory qualities. Neurophysiological subjectivism is the view that arises when one claims in addition that internal

sensory qualities are to be reductively identified with neural states (Hardin 1988, pp. 111–12). Thus this philosophical view has both a subjectivist and a reductionist component.

A number of commentators defend neurophysiological subjectivism against our ecologically based criticisms (Backhaus & Menzel; Clark; Hardin; McGilvray). Backhaus & Menzel endorse both the subjectivist and reductionist components when they claim that although "we experience our sensations . . . as located at the positions of the objects outside . . . 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 . . ." This statement seems both confused and question-begging. First, we experience objects as intrinsically colored; we do not experience them as being painted over, as it were, with a coating of our sensations. Second, neurophysiology and psychophysics show us that chromatic visual experiences depend on the visual system, but the dependence is surely distributed and nonlocalized. Finally, the straightforward identification of neuronal processes with color simply begs the (conceptual and empirical) question of whether the term "color" is better applied to spectral reflectances as objectivists claim, to neuronal processes as subjectivists claim, or to relational properties of animal-environment ecosystems as we enactivists claim.

Clark claims that our characterization of subjectivism as the view that colors are "internally generated qualities that the animal simply projects onto the world" is a straw man, despite the fact that Hardin (1988) explicitly defends this view, as does McGilvray in his commentary. In Clark's view, the real point of subjectivism is that the principles that collect stimuli into perceptual equivalence classes cannot be framed in extradermal terms. But objectivists need not disagree with this claim; indeed, in Hilbert's (1987) view, the color classes "red," "green," "yellow," and "blue" are anthropocentric whereas objective color is spectral reflectance. Subjectivism becomes a substantive philosophical position, then, when it claims that colors are qualities that are generated by internal states.

Clark argues that none of the evolutionary and ecological phenomena we cite in support of our enactive approach is inconsistent with neurophysiological subjectivism. In his view, neurophysiology explains without remainder the chromatic visual experiences that species have today, whereas evolutionary theory explains why species have the visual systems they do. Our point in citing the evolutionary and ecological phenomena, however, was to provide evidence for the claim that a *narrow*, that is, entirely intradermal, account of chromatic visual experience is unsatisfactory. (We admit that this point was not made clear enough in the target article.) The problem with neurophysiological subjectivism, in our view, is that it gives only a *proximal* account of chromatic perceptual content, and so neglects how visual experience is ecologically constituted. (Computational objectivism errs at the other extreme by having an animal-independent distal account of perceptual content.) If chromatic experience is construed narrowly, then it is at least a defensible research program to attempt to explain such experience exhaustively in neural terms. (It should

be noted, however, that there are severe problems even here. Consider human color categories, for example, which involve linguistic and cultural dimensions; see Lakoff 1987; MacLaury 1987; and the commentary by van Brakel.) If, on the other hand, chromatic experience is construed *widely*, that is, in the extradermal context of its ecological embeddedness, then it is quite implausible to suppose that it can be explained entirely in neural terms. Finally, when chromatic experience is thus construed, the plausibility of identifying colors with neural states as Clark, Hardin, and McGilvray advocate, is undermined in favor of the view that treats them as relational properties of animals and their environments.

McGilvray challenges us to explain how, given that computational objectivism is wrong, there is nevertheless something that has colors and is outside the brain. McGilvray appears to believe that the only way for perceptual objects to be outside the brain is for them to be identical with physical objects, that is, with objects as described in the organism-independent vocabulary of (macroscopic) physics. Our claim that colors are properties of the extradermal world understood as an animal environment, however, means that they are properties of the world at an ecological level of description in Gibson's (1979) sense, that is, of the world as described in relation to the perceptually guided activities of animals. As we indicate toward the end of the target article, this view implies that colors are strictly speaking *relational properties* of animal-environment ecosystems. We do not understand why McGilvray is "mystified" by this view. There is, after all, considerable precedent in the philosophical tradition for treating colors relationally: Locke had a relational account and, as Ben-Ze'ev rightly reminds us, so did Aristotle. (Our view is actually closer to Aristotle's than Locke's, for as we indicate in the target article, we reject Locke's sense-data account for visual experience and hold that the relevant extradermal properties are ecological rather than purely physical.) The conviction, which appears to underly McGilvray's discussion, that colors must be either entirely "out there" or entirely "in the head" provides an example of the subjective/objective straightjacket into which perception theory should not be forced (see the commentary by Ben-Ze'ev for an insightful extension and critical discussion of this point).

McGilvray also challenges us to explain why the perceptual object is not a "natural illusion." This term is also used by Hardin (1988, pp. 111–12) and refers presumably to illusions that nonetheless confer evolutionary and ecological benefits on perceivers. It would appear, however, that the standpoint from which the perceptual object is judged to be illusory in this case is that of physics. But why should the criteria for what is real and what is illusory be purely physical when our concerns are biological, ecological, and psychological? To suppose that they must implies a strong physicalist metaphysics that cognitive scientists need not accept.

Despite our view that the perceptual object is a relational feature of the ecosystems of perceiving animals, a number of commentators believe that ours is a modified "ecological subjectivism" (Jacobs; Kinnear; Skarda; Steele). Skarda in particular claims that we simply accept the "traditional model of perception" according to which perceptual objects are internally produced entities that

result from external objects causally affecting the visual system. Our rejection of this model is explicit, however, and is discussed by a number of commentators (Ben-Ze'ev; Broackes; Dennett; Lia; Wagemans & de Weert). Indeed, one of the central points of our discussion, which we develop explicitly in section 3, is that perception must be understood not as "recovery" (objectivism) or "projection" (subjectivism), but as a form of action, that is, as perceptually guided activity.

Skarda appears to have ignored much of our article in writing that we "accept the traditional problem: The perceptual object is not identical with the physical object, so how does vision succeed?" We distinguish between the physical object and the perceptual object to highlight the ecological status of the latter, not to locate it in the head. And, again as we say in section 3, to ask how vision succeeds in an enactive context is not to ask the "traditional" question of how a prespecified distal world is recovered from proximal images, but rather how sensorimotor patterns underlie the visual guidance of animal activity in its ecological context. Finally, Skarda seems to think that because our enactive approach claims that the world an animal perceives cannot be given a purely physical-level specification, it follows that we are "transforming the world into a sensorimotor experience." Skarda does not supply the missing premises that supposedly led her to this conclusion. In any case, the claim certainly does not follow, nor did we argue for it; on the contrary, we list physical-level constraints as ingredients of the perceptual environment toward the end of our article.

In conclusion, then, it is a mistake to think of our enactive approach as simply an updated, ecologically modified version of subjectivism. We develop this point further as we address issues concerning animal-environment codetermination and the enactive approach.

3. Enaction and the perceptual environment

3.1. Gibson's ecological approach. In section 3 of our target article, we briefly discussed the relation between our enactive approach and the ecological approach to visual perception pioneered by Gibson (1979). [See also Ullman: "Against Direct Perception" *BBS* 3(1) 1980.] We stressed what we saw as the differences largely because we wished to elicit commentary. As Wagemans & de Weert and Ben Ze'ev quite rightly point out, however, there are some fundamental similarities between enaction and the ecological approach. The main similarity consists in our agreement with Gibson that perception should be understood as guided activity in an ecological context. On this point, we agree with Wagemans & de Weert that we should have referred to such studies as Lee & Reddish's (1981) on ecological optics and visually guided activity in gannets, and Warren's (1984) on the perception of affordances in the visual guidance of activity in stair climbing. We also agree that Gibson struggled to become free of the "ancient dualisms," such as subjectivism/objectivism, but we do not think he was entirely successful. As Ben-Ze'ev notes and as others have discussed (Heft 1989; Thompson 1992), Gibson often ignores his own insight into the relational nature of the perceptual environment by describing the affordances of the environment and the invariances in the ambient optic

array as if they were independent of the animal (Gibson 1979, pp. 138–39; 1972, p. 293). We believe that this tendency derives from a (healthy) desire to eschew idealism in the theory of perception. It is the single-minded concern with this issue, however, that leads Gibsonians to neglect the basic insights implicit in their own approach – for example, that invariances in the ambient optic array depend not simply on how the distal layout sculpts the light, but also on how sensorimotor activity shapes the light in ways relevant to the animal's needs. Of course, we do not wish to blame Gibsonians for “not doing everything at the same time.” Our point, rather, is that if Gibsonians rigorously followed through the consequences of their own insights, they would be led to embrace the kind of approach we are calling enactive. For example, as Wagemans & de Weert note, ecological optics differs from physical optics because it studies light with respect to the perceiver. What exactly does this mean? Despite Gibson's remarks about invariances existing in the ambient optic array independently of the animal (Gibson 1972, p. 293), if one actually looks at the details of studies in ecological optics one finds that the sensorimotor capacities of the perceiver (which, let us remember, depend on the interneuronal networks that couple sensory and motor surfaces) specify (enact) patterns in the light that inform the perceiver about both the distal layout and his own ongoing activity (see Warren, 1984, for stair climbing; Kelso & Kay, 1987, for a general treatment). It is precisely this idea, implicit in ecological optics but not done justice by Gibsonian realism that is made explicit in the enactive approach. Because space precludes further discussion of this point (see Thompson 1992), we turn now to the central idea of our enactive approach, namely, the codetermination of animal and environment.

3.2. Animal-environment codetermination. A number of commentators address this idea from both philosophical and empirical perspectives (Akins & Lamping; Backhaus & Menzel; Ben-Ze'ev; Broackes; Clark; Dennett; Hardin; Hurlbert; Levine; Mausfeld et al.; Shepard). Their criticisms center on two points: (1) We do not clearly distinguish between the time scales of evolution and of individual behavior (Backhaus & Menzel; Broackes; Dennett; Hardin; Hulbert; Mausfeld et al.); and (2) we do not clearly distinguish between “causal” and “constitutive” or “ontological” codetermination (Akins & Lamping; Broackes; Clark; Levine). We agree that we did not state our position clearly enough with respect to these distinctions and we accordingly wish to restate our view in their light.

As we stated in our target article and discussed above, to encompass the entire range of phenomena involved in comparative color vision in particular and perceptually guided activity in general we need an explanatory framework that combines (i) physical-level constraints; (ii) sensorimotor activity as constituted by neuronal processes and developmental constraints; and (iii) evolutionary history. (Or in Shepard's terms: (i) invariant properties of the physical world; (ii) entrenched properties of resident organisms; and (iii) random accidents or symmetry breakings over evolutionary history.) What are the relations among these three items in the explanation of perception?

This question is best addressed at two different time scales – that of evolution and that of individual behavior. An evolutionary time scale is needed for the structural constitution of animals and environments (e.g., body patterns, perceptual apparatus, neural circuits, patterns of environmental variation, etc.). The time scale of individual behavior, on the other hand, is needed to encompass the current physiology, psychology, ecology, and social life of perceiving animals.

At either of these two time scales, the basic issue that divides us from our critics is the role played by category (i). The traditional view, which is espoused in somewhat different ways by Akins & Lamping, Clark, Hurlbert, and Shepard, is that the physical parameters in category (i) are the preeminent explanatory items in both evolutionary history and individual activity. In contrast, our view is that at both time scales the items in all three categories are of equal explanatory importance. We wish to use the phrase “animal-environment codetermination” as shorthand for the view that physical parameters, sensorimotor activity, and evolutionary history are so entangled with one another that none can be accorded any (context-independent and noninterest-relative) preeminence in the explanation of perceptually guided activity and the ontological status of the perceptual environment.³

An analogy can clarify the difference between these two views. In the traditional view, such physical parameters as illuminants and reflectances play a role like that of the notes in a score faithfully followed by a classical musician, however much individual interpretation he allows himself to exercise. In our view, however, physical parameters are more like the notes the jazz musician picks up for his improvisation. In the former case, the notes comprising the score do have a certain preeminence in relation to the performance: They are indeed given or prespecified and instruct the performance in the sense that they must be faithfully rendered. In the latter case, the notes play the role of fragmentary boundary conditions and do not instruct or specify the improvisation. Rather, the improvisation emerges from how the melody, the capacities of the particular instrument, the style and temperament of the individual player, and the group in which the musician is playing come together in a given performance.

It is an empirical issue whether the physical parameters involved in perception are more like the notes in a classical score or more like the notes in a jazz improvisation. Our claim is that because of the enormous layering of evolutionary pathways, sensorimotor structures, and individual behavioral repertoires, physical parameters play only the latter role rather than the former. Comparative color vision provides a particularly dramatic example. At the evolutionary time scale, color-seeing animals actually modify their physical environments: They contribute to determining the availability of certain fruit-bearing plants (frequency-dependent selection); they help to determine the evolution of plant pigmentation; and they even change the patterns of illumination in the environment by constructing dwellings, nesting, and so forth.⁴ This kind of codetermination is clearly the most literal and dramatic, and it is the one typically emphasized by critics of adaptationism in evolutionary theory (Levins & Lewontin 1983; 1985; Odling-Smee 1988). We

certainly do not believe, however, that every physical constraint entering the evolutionary story is so modified – as **Hurlbert** notes, animals do not rewrite the laws of reflection every time a new zoological group or class occurs in evolution. Nonetheless, it does not follow, as some appear to suppose (**Dennett**), that codetermination holds only in these evolutionary contexts. In the sense outlined above, codetermination applies not simply to the evolutionary modification of the environment, but also to individual behavior. At this time scale, the sensorimotor patterns that underlie perceptually guided activity endow the purely physical level with ecological significance. Here perceptual color space provides the best example. It is the chromatic capacities of the animal that determine how reflectance and illuminant values are combined to engender a color space of a given dimensionality; these capacities also determine the hue categories that have perceptual significance for animals in their ecological interactions. For other examples, we can consider the likely diversity in spatial segmentation among perceiving animals and the fascinating enactive approach to focal vision outlined by **Lia** in his commentary.

Now that we have restated our view in relation to the two time scales of evolution and individual behavior let us turn to the difference we have supposedly neglected between “causal” and “constitutive” or “ontological” codetermination. According to **Akins & Lamping, Broackes, Clark, and Levine**, the evolutionary and ecological phenomena we cite show only that animals causally affect the environment but not that they determine what it is. This issue depends greatly on how the term “environment” is understood. If the environment is taken to be merely the physical constraints of category (i) above, then it is indeed true that although animals causally affect (some of) these constraints, they do not determine what they are. But if the environment is taken to be the world at a level of description that *implicates relationally* the evolutionary history and sensorimotor capacities of perceiving animals, then animals do determine its ontology, i.e., they determine what the environment is and the kinds of properties it contains. In fact, within such a conceptual framework there are strictly speaking only animal-environment ecosystems and hence no animal without an environment and no environment without an animal. On this point, we are indebted both to **Gibson** (1979) who pioneered such a conceptual framework for the perceptual environment and to the critique of adaptationism in evolutionary theory (Levins & Lewontin 1983; 1985) – which, contrary to the views of **Broackes and Clark**, does indeed imply that animals constitute their environments (in the relevant non-physicalist and ecological sense of “environment”).⁵

In reply to **Mausfeld et al.**, then, we do indeed wish to introduce “a new ontological specification of ‘environment’ transcending the subjective/objective distinction.” We would say that the perceptual environment is distinctively ecological in the sense that it emerges from the interactions among physical constraints, sensorimotor activity, and evolutionary history. **Mausfeld et al.** chide us for not having a ready-made set of categories for making this ecological specification of the environment more precise. Further precision is indeed needed, but to demand that we have a set of categories already available when the ecological study of color vision and perception

in general is in its infancy is inappropriate. It is precisely for this reason that at the end of our article we call for studies that, rather than imposing anthropocentric assumptions, describe the perceptual environment from the relevant animal’s point of view.

A few points about the perceptual environment and perceptual content remain to be discussed. First, it is the ecological specification of the perceptual environment that provides a framework beyond the problem-space of subjectivism/objectivism. **Hardin** neglects this point when he claims that inssofar as our enactive approach is supposed to differ from subjectivism it involves an equivocation “between perceivers as individuals and perceivers as species as well as between representations and physical objects.” We have already addressed the supposed equivocation between individuals and species. As for the second, Hardin assimilates our notion of the perceptual object to a perceptual representation. But as we have just discussed and as we indicated in our article, we hold that the perceptual object is ecological – it is a relational feature of animals and their environments or a property of animal-environment ecosystems. It is therefore precisely not a representation, at least where “representation” is understood in the strong sense as an intradermal (subjective) entity that provides a map or model of the world. In Hardin’s view, colors are such intradermal entities (chromatic neural states); in our view, they are relational properties of perceiving animals and their environments. Although Hardin’s view in his commentary strikes us as less extreme than the view he outlined in his book (Hardin 1988), he does not address the relational ecological treatment of color in contrast to neurophysiological subjectivism and so we are not sure where he stands on this issue.

Second, in response to **Broackes**, we agree that we were mistaken to suggest that ecological codetermination logically implies codetermination in the theory of content. In the sense of “codetermination” that we have outlined in this section, animals and environments are reciprocally constitutive in an ecological sense. As **Broackes** notes, however, codetermination in the theory of content is based on a relation that is genuinely *symmetrical*: Color and the content of color experience determine what each is. Nevertheless, we think that there is a rather close relation between the two kinds of codetermination. In our view, ecological codetermination provides a naturalistic basis for holding codetermination in the theory of content, despite the absence of a strict logical relation of implication between them.⁶

Finally, **Ben-Ze’ev** raises a number of important points about the perceptual environment and perceptual content. He wishes to add to our three categories above a fourth that he calls “personal history,” which is meant to be a “psychological-level specification” encompassing the perceiver’s personal background, anticipations, moods, emotions, and so forth. We agree that in the case of humans (and perhaps other animals) this fourth category should be added. In the case of color perception, this category might encompass research on the relation between color and mood, emotion, and affective perception in general. We agree with Ben-Ze’ev that admitting this category would make the perceptual environment more subjective – where “subjective” is understood as “experiential” – but not more *subjectivist*. In other words, the

affective and personal dimensions of the perceptual environment can be admitted without being analyzed in the subjectivist/objectivist framework of internal sensory qualities versus objective physical properties (see Merleau-Ponty 1945/1962). Indeed, in the case of human perception, a fifth category that is experiential but certainly not subjective must be added to encompass the distinctively cultural aspects of the human perceptual environment.⁷ [See also Deregowski: "Real Space and Represented Space; Cross-cultural Perspectives" *BBS* 12(1) 1989.]

NOTES

1. It should also be noted that any nonhue dimension must be appropriately connected to that of hue. On the other hand, if hue, saturation, and brightness are internally related (as it is reasonable to suppose) then it would be conceptually impossible for something to be counted as a color space unless it comprised these dimensions (although it could also comprise others). This point raises philosophical issues that we cannot pursue here. For further discussion see Thompson (1992).

2. It is for this reason that we said "color vision should be understood in the context of the actual behavioral repertoires and visual ecologies of perceiving animals," a remark that puzzles Levine. Our point is simply that the operation of color vision should be understood in a theoretical context that is defined by its concern for the role that it plays in ecologically embedded, perceptually guided activity, rather than in a theoretical context that imposes engineering considerations that are insensitive to the behavioral life of the animal.

3. This statement of the meaning of "animal-environment codetermination" differs from that offered in the article in section 2.5, which misleadingly suggests that codetermination occurs only on an evolutionary time scale. We are here offering a more general framework within which to address the points raised by the commentators.

4. Clark is therefore mistaken when he claims that "the stirring history of our species couldn't have affected any feature of the light entering one's eyes." On the contrary, the history of a species can and indeed has affected the features of the light entering its members' eyes: Consider any primate species the evolution of whose eyes may have been affected by migration from, say, a forest environment to the environment of an open savannah. Clark also supposes that star-gazing provides a counterexample to our enactive theory that colors are properties of the world that result from animal-environment codetermination. But star-gazing hardly provides a paradigm of perception in the relevant sense of perceptually guided activity (as Clark notes) and so is unlikely to provide much insight into ecologically situated perception.

5. Clark is right that evolutionary theory must be able to refer to the environment that is shared by animals, but it must also refer to animal-specific environments – or better specific animal-environment ecosystems – and can indeed corroborate claims about them. This task is presumably the province of ecology in evolutionary theory.

6. Broackes also wonders whether we would resist using physical terms in the explanation of color perception. As the above threefold framework makes apparent, we think physical terms are an essential ingredient in explaining color, but we do not see why this undermines the ability of ecological codetermination to ground codetermination in the theory of content.

7. Brusatin (1986) provides a fascinating discussion of these cultural dimensions for human color experience.

References

- Akins, K. (1990) Science and our inner lives: Birds of prey, bats, and the common (featherless) bi-ped. In: Interpretation and explanation in the

- study of animal behavior, ed. M. Bekoff & D. Jamieson. Westview. [aET]
- Allman, J. (1977) Evolution of the visual system in the early primates. *Progress in Psychobiology and Physiological Psychology* 7:1–53. [BL]
- Archer, S. N. & Lythgoe, J. N. (1990) The visual pigment basis for cone polymorphism in the guppy (*Poecilia reticulata*). *Vision Research* 30:225–33. [aET]
- Archer, S. N., Endler, J. A., Lythgoe, J. N. & Partridge, J. C. (1987) Visual pigment polymorphism in the guppy (*Poecilia reticulata*). *Vision Research* 27:1243–52. [aET]
- Arend, L. E. & Goldstein, R. (1987) Simultaneous constancy, lightness and brightness. *Journal of the Optical Society of America A* 4:2281–85. [AR]
- Arend, L. E. & Reeves, A. (1986) Simultaneous color constancy. *Journal of the Optical Society of America A* 3:1743–51. [AR]
- Arend, L. E., Reeves, A., Schirillo, J. & Goldstein, R. (1991) Simultaneous color constancy: Papers with diverse Munsell values. *Journal of the Optical Society of America A* 8:661–72. [AR]
- Arnold, K. & Neumeyer, C. (1987) Wavelength discrimination in the turtle *Pseudemys scripta elegans*. *Vision Research* 27:1501–11. [CN]
- Averill, E. (1985) Color and the anthropocentric problem. *The Journal of Philosophy* 82:281–304. [EWA]
- Backhaus, W. (1988) Color difference and color opponency in bees. In: *Sense organs. Interfaces between environment and behaviour*, ed. N. Elsner & F. G. Barth. *Proceedings of the 16th Göttingen Neurobiology Conference*. Thieme. [WB]
- (1991) Color opponent coding in the visual system of the bee. *Vision Research* 31:1381–97. [WB]
- (in press) The theory of colour vision and colour choice behaviour in honeybees (Die Theorie des Farbensehens und des Farbwahlverhaltens der Honigbiene). *Verhandlungen der Deutschen Zoologischen Gesellschaft* 84. [WB]
- (submitted) Graphical representations of tetrachromatic color vision. *Journal of the Optical Society of America A*. [WB]
- Backhaus, W. & Menzel, R. (1987) Color distance derived from a receptor model for color vision in the honeybee. *Biological Cybernetics* 55:32–31. [WB]
- Backhaus, W., Werner, A. & Menzel, R. (1987) Color vision in honeybees: Metric, dimensions, constancy, and ecological aspects. In: *Neurobiology and behavior of honeybees*, ed. R. Menzel & A. Mercer. Springer. [WB]
- Ballard, D. H. (forthcoming) Animate vision. *Artificial Intelligence*. [KAA]
- Barlow, H. B. (1982) What causes trichromacy? A theoretical analysis using comb-filtered spectra. *Vision Research* 22:635–43. [aET, WB]
- Barth, F. G. (1985) *Insects and flowers: The biology of a partnership*. Translated from the German by M. A. Biederman-Thorson. Princeton University Press. [aET, RNS]
- Baylis, J. R. (1979) Optical signals and interspecific communication. In: *The behavioral significance of color*, ed. E. H. Burtt. Garland STPM Press. [aET]
- Beatty, D. D. (1969) Visual pigments of the burbot (*Lota lota*) and seasonal changes in their relative proportions. *Vision Research* 9:1173–83. [aET]
- (1984) Visual pigments and the labile scotopic visual system of fish. *Vision Research* 24:1563–73. [aET]
- Bennett, J. (1971) *Locke, Berkeley, Hume: Central themes*. Oxford University Press (Oxford). [aET]
- Ben-Ze'ev, A. (1984) The Kantian revolution in perception. *Journal for the Theory of Social Behavior* 14:69–84. [AB-Z]
- (1988) The schema paradigm in perception. *Journal of Mind and Behavior* 9:487–513. [AB-Z]
- (1989) Explaining the subject-object relation in perception. *Social Research* 56:511–43. [AB-Z]
- (1991) Cognitive development: Two paradigms. In: *Cognition, information processing and psychophysics: Basic issues*, ed. H. G. Geissler, S. W. Link & J. T. Townsend. Erlbaum. [AB-Z]
- (1992) *The perceptual system*. (in press) [AB-Z]
- Bergson, H. (1982) Materie und Gedächtnis. Eine Abhandlung über die Beziehungen zwischen Körper und Geist. Ullstein. [WB]
- Berkeley, G. (1710/1965) The principles of human knowledge. In: *Berkeley's philosophical writings*, ed. D. M. Armstrong. Macmillan. [aET]
- Berlin, B. & Kay, P. (1969) *Basic color terms: Their universality and evolution*. University of California Press. [aET, MM]
- Bloch, S. & Martinoya, C. (1983) Specialization of visual functions for the different retinal areas in the pigeon. In: *Advances in behavioral neuroethology*, ed. P. Ewert, R. Capranica & D. Ingle. Plenum Press. [aET]
- Blough, D. S. (1982) Pigeon perception of letters of the alphabet. *Science* 218:397–398. [KMS]
- (1990) Form similarity and categorization in pigeon visual research. In:

References/Thompson et al.: Ways of coloring

- Quantitative analyses of behavior*, vol. 8, ed. M. L. Commons, R. J. Herrnstein, S. M. Kosslyn & D. M. Mumford. Erlbaum. [KMS]
- Boden, M. (1988) *Computer models of mind*. Cambridge University Press. [aET]
- Bonnardel, V. & Varela, F. J. (1989) Response of the human color vision system to sinusoidal power distributions. *Neuroscience Abstracts* 15(1):625. [aET]
- Bowmaker, J. K. (1977) The visual pigments, oil droplets and spectral sensitivity of the pigeon. *Vision Research* 17:1129–38. [aET, GHJ]
- (1980a) Birds see ultraviolet light. *Nature* 284:306. [EM]
- (1980b) Colour vision in birds and the role of oil droplets. *Trends in Neurosciences* 3:196–99. [aET]
- (1983) Trichromatic colour vision: Why only three receptor types? *Trends in Neurosciences* 6:41–43. [aET]
- Bowmaker, J. K. & Martin, G. R. (1985) Visual pigments and oil droplets in the penguin, *Spheniscus humboldti*. *Journal of Comparative Physiology A* 156:71–77. [EM]
- Bowmaker, J. K. & Kunz, Y. W. (1987) Ultraviolet receptors, tetrachromatic colour vision and retinal mosaics in the brown trout (*Salmo trutta*): Age-dependent changes. *Vision Research* 27:2101–08. [aET]
- Bowmaker, J. K., Dartnall, H. J. & Herring, P. J. (1988) Longwave-sensitive visual pigments in some deep-sea fishes: Segregation of “paired” rhodopsine and porphyropsins. *Journal of Comparative Psychology A* 163:685–98. [aET]
- Boynton, R. M. (1979) *Human color vision*. Holt, Rinehart & Winston. [aET]
- (1988) Color vision. *Annual Review of Psychology* 39:69–100. [aET]
- Brainard, D. H. (1989) Understanding the illuminant's effect on color appearance. Unpublished doctoral dissertation, Stanford University. [LTM]
- Brainard, D. H. & Wandell, B. A. (1986) An analysis of the retinex theory of color. *Journal of the Optical Society of America A* 3:1651–61. [LTM]
- (1991) A bilinear model of the illuminant's effect on color appearance. In: *Computational models of visual processing*, ed. J. A. Movshon & M. S. Landy. MIT Press (in press). [LTM]
- Brainard, D. H., Wandell, B. A. & Cowan, W. B. (1989) Black light: How sensors filter spectral variation of the illuminant. *IEEE Transactions on Biomedical Engineering*, T-BME 36:140–49. [LTM]
- Bridges, C. D. (1972) The rhodopsin-porphyrin visual system. In: *Handbook of sensory physiology*, VII/1, ed. H. J. Darnall. Springer-Verlag. [aET]
- Brill, M. H. (1978) A device performing illuminant-invariant assessment of chromatic relations. *Journal of Theoretical Biology* 71:473–78. [JLD, LTM]
- (1979) Further features of the illuminant-invariant trichromatic photosensor. *Journal of Theoretical Biology* 78:305. [LTM]
- (1990) Image segmentation by object color: A unifying framework and connection to color constancy. *Journal of the Optical Society of America* 7:2041–47. [AH]
- Brill, M. & Benzschawel, T. (1985) Remarks on signal-processing explanations of the trichromacy of vision. *Journal of the Optical Society of America A* 2:1794–96. [aET]
- Broackes, J. (1992) The autonomy of color. In: *Reduction, explanation and realism*, ed. D. Charles & K. Lennon. Clarendon Press (in press). [rET, JB]
- Brooks, R. (1986) Achieving artificial intelligence through building robots. *AI Memo* 899, MIT Artificial Intelligence Laboratory. [arET]
- (1987) Autonomous mobile robots. In: *AI in the 1980s and beyond*, ed. W. E. L. Grimson & R. S. Patil. MIT Press. [arET]
- (1989) A robot that walks: Emergent behaviors from a carefully evolved network. *AI Memo* 1091, MIT Artificial Intelligence Laboratory. [arET]
- (1991) Intelligence without representation. *Artificial Intelligence* 47:139–59. [JW]
- Brown, P. K. & Wald, G. (1964) Visual pigments in single rods and cones of the human retina. *Science* 144:45–52. [aET]
- Brunswik, E. (1956) *Perception and the representative design of psychological experiments*. University of California Press. [PHK]
- Brusatin, M. (1986) *Histoires des couleurs*. Flammarion. (Translated from Italian edition of 1983.) [rET]
- Brush, A. H. (1990) Metabolism of carotenoid pigments in birds. *FASEB* 4:2969–77. [aET]
- Buchsbaum, G. (1980) A spatial processor model for object colour perception. *Journal of The Franklin Institute* 310:1–26. [aET, JLD, LTM]
- Buchsbaum, G. & Gottschalk, A. (1983) Trichromacy, opponent colours coding, and optimum colour information transmission in the retina. *Proceedings of the Royal Society of London B* 220:89–113. [aET, WB]
- Budnik, V., Mpodozis, J., Varela, F. J. & Maturana, H. R. (1984) Regional specialization of the quail retina: Ganglion cell density and oil droplet distribution. *Neurosciences Letters* 51:145–50. [aET]
- Burkhardt, D. (1982) Birds, berries and UV: A note on some consequences of UV vision in birds. *Naturwissenschaften* 69:153–57. [aET]
- (1989) UV vision: A bird's eye view of feathers. *Journal of Comparative Physiology A* 164:787–96. [aET]
- Burkhardt, D. & Maier, E. (1989) The spectral sensitivity of a passerine bird is highest in the UV. *Naturwissenschaften* 76:82–83. [aET]
- Burns, B. & Shepp, B. E. (1988) Dimensional interactions and the structure of psychological space: The representation of hue, saturation and brightness. *Perception and Psychophysics* 43:494–507. [JBD]
- Burtt, E. H. Jr., ed. (1979) *The behavioral significance of color*. Garland STPM Press. [arET]
- Carpenter, G. & Grossberg, S. (1987) A massively parallel architecture for a self-organizing neural pattern recognition machine. *Computer Vision, Graphics, and Image Processing* 37:54–115. [aET]
- Cerella, J. (1979) Visual classes and natural categories in the pigeon. *Journal of Experimental Psychology: Human Perception and Performance* 5:68–77. [KMS]
- (1982) Mechanisms of concept formation in the pigeon. In: *Analysis of visual behavior*, ed. D. J. Ingle, M. A. Goodale & R. J. W. Mansfield. MIT Press. [KMS]
- (1990) Shape constancy in the pigeon: The perspective transformations decomposed. In: *Quantitative analyses of behavior* vol. 8, ed. M. L. Commons, R. J. Herrnstein, S. M. Kosslyn & D. M. Mumford. Erlbaum. [KMS]
- Chalupa, L. M. & Dreher, B. (1991) High precision systems require high precision “blueprints”: A new view regarding the formation of connections in the mammalian visual system. *The Journal of Cognitive Neuroscience* 3(3):209–19. [BL]
- Chalupa, L. M. & Lia, B. (1991) The nasotemporal division of retinal ganglion cells with crossed and uncrossed projections in the fetal rhesus monkey. *The Journal of Neuroscience* 11:191–202. [BL]
- Chalupa, L. M., Killackey, H. P., Snider, C. J. & Lia, B. (1989) Callosal projection neurons in area 17 of the fetal rhesus monkey. *Developmental Brain Research* 46:303–08. [BL]
- Chen, D. M. & Goldsmith, T. H. (1986) Four spectral classes of cones in the retinas of birds. *Journal of Comparative Physiology A* 159:473–79. [aET]
- Chen, D. M., Collins, J. S. & Goldsmith, T. H. (1984) The ultraviolet receptor of bird retinas. *Science* 225:337–40. [aET]
- Chittka, L. & Menzel, R. (in preparation) Optimal sets of spectral inputs to the color vision system of trichromatic, flower-visiting insects. *Journal of Comparative Physiology*. [WB]
- Chittka, L., Menzel, R. & Shmida, A. (1990) Optimal sets of spectral inputs and opponent processes for coding of natural colors in insect color vision. In: *Sense organs. Interfaces between environment and behaviour*, ed. N. Elsner & F. G. Barth. *Proceedings of the 16th Göttingen Neurobiology Conference*. Thieme. [WB]
- Churchland, P. M. (1985) Reduction, qualia, and the direct introspection of brain states. *Journal of Philosophy* 82:8–28. [aET]
- (1986) Some reductive strategies in cognitive neurobiology. *Mind* 95:279–309. [aET]
- Churchland, P. S. & Sejnowski, T. J. (1988) Perspectives on cognitive neuroscience. *Science* 242:741–45. [aET]
- Clark, A. G. (1980) *Psychological models and neural mechanisms: An examination of reductionism in psychology*. Oxford University Press. [AGC]
- (1992) *Sensory qualities*. Oxford University Press (in press). [AGC]
- Cornman, J. W. (1975) *Perception, common sense, and science*. Yale University Press. [WB]
- Crawford, M. L. J., Anderson, R. A., Blake, R., Jacobs, G. H. & Neumeyer, C. (1990) Interspecies comparisons in the understanding of human visual perception. In: *Visual perception. The neurophysiological foundations*, ed. L. Spillman & J. S. Werner. Academic Press. [aET]
- Crescitelli, F., McFall-Ngai, M. & Horwitz, J. (1985) The visual pigment sensitivity hypothesis: Further evidence from fishes of varying habitats. *Journal of Comparative Physiology A* 157:323–33. [aET]
- Cronin, T. W. & Marshall, N. J. (1989) A retina with at least ten spectral types of photoreceptors in a mantis shrimp. *Nature* 339:137–40. [GHJ]
- Dannemiller, J. L. (1989) Computational approaches to color constancy: Adaptive and ontogenetic considerations. *Psychological Review* 96:255–66. [JLD, MM]
- Dartnall, H. J. A., Bowmaker, J. K. & Mollon, J. D. (1983) Human visual pigments: Microspectrophotometric results from the eyes of seven persons. *Proceedings of the Royal Society of London B* 220:115–30. [aET]

- Davidoff, J. B. (1974) The psychological relationship between lightness and saturation. *Perception and Psychophysics* 16:79–83. [JBD]
- (1991) Cognition through color. MIT Press. [JBD]
- Dehay, C., Kennedy, H., Bullier, J. & Berland, M. (1988) Absence of interhemispheric connections of area 17 during development in the monkey. *Nature* 331:348–50. [BL]
- Delius, J. D. & Emmerton, J. (1979) Visual performance of pigeons. In: *Neural mechanisms of behavior in the pigeon*, ed. A. M. Granda & J. H. Maxwell. Plenum Press. [aET]
- Dennett, D. C. (1991) *Consciousness explained*. Little Brown (forthcoming). [DCD]
- DeRenzi, E., Faglioni, P., Scotti, G. & Spinnler, H. (1972) Impairment of color sorting behavior after hemispheric damage: An experimental study with the Holmgren skein test. *Cortex* 8:147–63. [JBD]
- DeValois, R. & DeValois, K. (1975) Neural coding of color. In: *Handbook of perception*, vol. V: *Seeing*, ed. E. C. Carterette & M. P. Friedman. Academic Press. [aET]
- (1988) *Spatial vision*. Oxford University Press. [aET]
- DeValois, R. L., Abramov, I. & Jacobs, G. H. (1966) Analysis of response patterns of LGN cells. *Journal of the Optical Society of America* 56:966–77. [MAF]
- DeYoe, E. A. & Van Essen, D. C. (1988) Concurrent processing streams in monkey visual cortex. *Trends in Neuroscience* 11:219–26. [aET]
- Dimentman, A. M., Karas, A. Ya., Maksimov, V. V. & Orlov, O. Yu. (1972) On the constancy of color perception in carp. *Pavlov Journal of Higher Nervous Activity* 22:772–79. [SLK]
- Dixon, E. R. (1978) Spectral distribution of Australian daylight. *Journal of the Optical Society of America* 68:437–50. [RNS]
- Dixon, N. F. (1960) Apparent changes in the visual threshold: Central or peripheral? *British Journal of Psychology* 51:297–309. [JBD]
- Dobkins, K. R. & Albright, T. D. (1990) Color facilitates motion correspondence in visual area MT. *Society of Neuroscience 1990 Annual Meeting Abstracts* 16(2):1220. [KAA]
- Drake, S. (1957) *Discoveries and opinions of Galileo*. Doubleday. [aET]
- Drever, J. (1961) Perception and action. *Bulletin of the British Psychological Society* 45:1–9. [PHK]
- Durrer, H. (1986) Colouration. In: *Biology of the integument, the skin of birds*, ed. J. Bereiter-Hahn, A. G. Matoltsy & K. S. Richards. Springer. [aET]
- Dym, P. & McKean, S. (1975) *Fourier signals and integrals*. Academic Press. [aET]
- D'Zmura, M. & Lennie, P. (1986) Mechanisms of color constancy. *Journal of the Optical Society of America A* 3:1662–72. [aET, JLD, LTM]
- Egert, H. E. & Pachella, R. (1969) Multidimensional stimulus identification. *Perception and Psychophysics* 5:341–46. [JBD]
- Elliot Smith, G. (1932) The evolution of the instruments of vision. *Transactions of the Ophthalmological Society of the United Kingdom* 51:399–411. [BL]
- Emmerton, J. (1983) Pattern discrimination in the near-ultraviolet by pigeons. *Perception and Psychophysics* 34:555–59. [aET]
- Emmerton, J. & Delius, J. D. (1980) Wavelength discrimination in the “visible” and ultraviolet spectrum by pigeons. *Journal of Comparative Physiology A* 141:47–52. [aET]
- Erber, J., Menzel, R., Pflüger, H.-J. & Todt, D., eds. (1989) *Neural mechanisms of behavior*. Proceedings of the 2nd International Congress of Neuroethology, September 10–16. Thieme. [WB]
- Evans, R. M. (1974) *The perception of color*. Wiley. [RJM, AR]
- Felfoldy, G. L. & Garner, W. R. (1971) The effects on speeded classification of implicit and explicit instructions regarding stimulus dimensions. *Perception and Psychophysics* 9:289–92. [JBD]
- Finkelstein, M. A. (1988a) Spectral tuning of opponent channels is spatially dependent. *Color Research and Application* 13:106–12. [MAF]
- (1988b) Spectral tuning of opponent pathways is temporally dependent. *Color Research and Application* 13:369–75. [MAF]
- Finkelstein, M. A. & Hood, D. C. (1981) Cone system saturation: More than one stage of sensitivity loss. *Vision Research* 21:319–28. [MAF]
- (1982) Opponent-color cells can influence detection of small brief lights. *Vision Research* 22:89–95. [MAF]
- (1984) Detection and discrimination of small, brief lights: Variable tuning of opponent channels. *Vision Research* 24:175–81. [MAF]
- Finkelstein, M. A., Harrison, M. & Hood, D. C. (1990) Sites of sensitivity control within a long-wavelength cone pathway. *Vision Research* 30:1145–58. [MAF]
- Flew, A. (1984) *A Dictionary of Philosophy*. Macmillan. [WB]
- Foard, C. F. & Kemler-Nelson, D. G. (1984) Holistic and analytic modes of processing: The multiple determinants of perceptual analysis. *Journal of Experimental Psychology: General* 113:94–111. [JBD]
- Fodor, J. A. (1983) *The modularity of mind*. Bradford Books, MIT Press. [JBD]
- (1987) *Psychosemantics: The problem of meaning in the philosophy of mind*. MIT Press. [JL]
- Freeman, W. (1975) *Mass action in the nervous system*. Academic Press. [aET]
- Freeman, W. & Skarda, C. (1985) Spatial EEG patterns, nonlinear dynamics, and perception: The neo-Sherringtonian view. *Brain Research Reviews* 10:145–75. [aET]
- Funt, B. V. & Drew, M. S. (1988) Color constancy computation in near-Mondrian scenes using a finite dimensional linear model. *IEEE Conference on Computer Vision and Pattern Recognition*, Ann Arbor, Michigan, June 5–9. [LTM]
- Garner, W. R. (1974) *The Processing of information and structure*. Wiley. [JBD]
- (1988) Facilitation and interference with a separable redundant dimension in stimulus comparison. *Perception and Psychophysics* 44:321–30. [JBD]
- Garner, W. R. & Felfoldy, G. L. (1970) Integrality of stimulus dimensions in various types of information processing. *Cognitive Psychology* 1:225–41. [JBD]
- Gershon, R. (1987) The use of color in computational vision. *Technical Reports on Research in Biological and Computational Vision: RBCV-TV-87-15*. Department of Computer Science, University of Toronto. [aET]
- Gershon, R. & Jepson, A. D. (1989) The computation of color constant descriptors in chromatic images. *Color Research and Application* 14:325–34. [JLD]
- Gershon, R., Jepson, A. D. & Tsotsos, J. K. (1986) Ambient illumination and the determination of material changes. *Journal of the Optical Society of America* 3:1700–07. [JLD]
- Gibson, J. J. (1961) Ecological optics. *Vision Research* 1:253–62. [BL]
- (1967) New reasons for realism. *Synthese* 17:162–72. [aET, JW]
- (1979) *The ecological approach to visual perception*. Houghton Mifflin Co. [aET, PHK, BL, JW, AB-Z]
- (1982) Notes on affordances. In: *Reasons for realism: Selected essays of James J. Gibson*, ed. E. Reed & R. Jones. Erlbaum.
- (1972) A theory of direct visual perception. In: *The psychology of knowing*, ed. J. R. Royce & W. W. Rozboom. Gordon & Breach. [rET]
- Gnjubkin, V. F. (1989) Response of pigmented corneas of whitespotted greenling to changes in light. *Biologiya Morya* 1:25–32. (English translation - *The Soviet Journal of Marine Biology* 15:21–28) [SLK]
- Gnjubkin, V. F., Kondrashev, S. L. & Orlov, O. Yu. (1975) On constant color perception of common toad. *Biofizika* 20:725–30. [SLK]
- Goldsmith, T. H. (1980) Hummingbirds see near ultraviolet light. *Science* 207:786–88. [arET]
- (1990) Optimization, constraint, and history in the evolution of eyes. *Quarterly Review of Biology* 65:281–322. [arET]
- Goldsmith, T. H., Collins, J. S. & Licht, S. (1984) The cone oil droplets of avian retinas. *Vision Research* 24:1661–71. [aET]
- Gould, S. J. (1977) *Ontogeny and phylogeny*. Belknap Press/Harvard University Press. [BL]
- Gould, S. J. & Lewontin, R. C. (1979) The spandrels of San Marco and the Panglossian Paradigm: A critique of the adaptionist programme. *Proceedings of the Royal Society B* 205:591–98. [KMS]
- Gould, S. J. & Vrba, E. S. (1982) Exaptation – a missing term in the science of form. *Paleobiology* 8:4–15. [BL]
- Gouras, P. (1985) Color vision. In: *Principles of neural science*, ed. E. R. Kandel & J. H. Schwartz. Elsevier.
- Gouras, P. & Zrenner, E. (1979) Enhancement of luminance flicker by color-opponent mechanisms. *Science* 205:587–89. [MAF]
- (1981) Color vision: A review from a neurophysiological perspective. *Progress in Sensory Physiology* 1:139–79. [aET]
- Granda, A. M. & Maxwell, J. H. eds. (1979) *Neural mechanisms of behavior in the pigeon*. Plenum Press. [aET]
- Greene, S. L. (1983) Feature memorization of pigeon concept formation. In: *Quantitative analyses of behavior*, vol. 4, ed. M. L. Commons, R. J. Herrnstein & A. R. Wagner. Ballinger. [KMS]
- Griffen, D. (1984) *Animal thinking*. Harvard University Press. [rET]
- Grossberg, S. (1984) *Studies in mind and brain*. D. Reidel. [aET]
- Guth, S. L. & Lodge, H. R. (1973) Heterochromatic additivity, foveal spectral sensitivity, and a new color model. *Journal of the Optical Society of America* 63:450–62. [MAF]
- Hailman, J. P. (1977) *Optical signals: Animal communication and light*. Indiana University Press. [arET]
- Halsey, W. E., ed. (1969) *Collier's encyclopedia*, vol. 7. USA: Crowell-Collier. [WB]
- Hardin, C. L. (1984) Are “scientific” objects coloured? *Mind* 93:491–500. [aET, DCD]

References/Thompson et al.: Ways of coloring

- (1988) *Color for philosophers: Unweaving the rainbow*. Hackett. [aET, WB, DCD, MM, PS]
- (1990) Why color? In: *Perceiving, measuring, and using color*, ed. M. Brill. *Proceedings of SPIE* 1250:293–300. [aET, JB, DCD]
- Harosi, F. I. & Hashimoto, Y. (1983) Ultraviolet visual pigment in a vertebrate: A tetrachromatic cone system in the dace. *Science* 222:1021–23. [aET]
- Hashimoto, Y., Harosi, F. I., Ueki, K. & Fukurotani, K. K. (1988) Ultra-violet-sensitive cones in the color-coding systems of cyprinid retinas. *Neuroscience Research Suppl.* 8:81–95. [rET, CN]
- Heft, H. (1989) Affordances and the body: An intentional analysis of Gibson's ecological approach to visual perception. *Journal for the Theory of Social Behavior* 19:1–30. [rET, AB-Z]
- Heider (Rosch), E. R. (1972) Universals in color naming and memory. *Journal of Experimental Psychology* 93:10–20. [aET]
- Heinerman, P. H. (1984) Yellow intraocular filters in fishes. *Experimental Biology* 43:127–47. [SLK]
- Helson, H. (1938) Fundamental problems in color vision. I. The principles governing changes in hue, saturation, and lightness of nonselective samples in chromatic illumination. *Journal of Experimental Psychology* 23:439–76. [aET, JLD]
- Helson, H. & Jeffers, V. B. (1940) Fundamental problems in color vision. II. Hue, lightness, and saturation of selective samples in chromatic illumination. *Journal of Experimental Psychology* 26:1–27. [aET]
- Helverson, O. v. (1972) Zur spektralen Unterschiedsempfindlichkeit der Honigbiene. *Journal of Comparative Physiology* 80:439–72. [rET, WB]
- Hering, E. (1878) *Zur Lehre vom Lichtsinn*. Berlin. (Republished in English translation as *Outlines of a theory of the light sense*. Harvard University Press, 1964.) [RNS]
- (1920) *Grundzüge der Lehre vom Lichtsinn*. Springer. [RJH]
- Herrnstein, R. J. & de Villiers, P. A. (1980) Fish as a natural category for people and pigeons. In: *The psychology of learning and behavior*, vol. 14, ed. G. H. Bower. Academic Press. [KMS]
- Herrnstein, R. J. & Loveland, D. H. (1964) Complex visual concept in the pigeon. *Science* 146:549–51. [KMS]
- Herrnstein, R. J., Loveland, D. H. & Cable, C. (1976) Natural concepts in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes* 2:285–302. [KMS]
- Heywood, C. A. & Cowey, A. (1987) On the role of cortical area V4 in the discrimination of hue and pattern in macaque monkeys. *Journal of Neuroscience* 7:2601–16. [aET]
- Heywood, C. A., Wilson, B. & Cowey, A. (1987) A case study of cortical colour "blindness" with relatively intact achromatic discrimination. *Journal of Neurology, Neurosurgery and Psychiatry* 50:22–29. [PS]
- Hilbert, D. R. (1987) *Color and color perception. A study in anthropocentric realism*. Stanford University: Center for the Study of Language and Information. [arET, WB, DCD, MM]
- Hood, D. C. (1981) Comments on linking the psychophysics of color vision to current physiology. In: *Relating physiology to psychophysics: Current problems and approaches*. Twelfth symposium, Center for Visual Science. [MAF]
- Hood, D. C. & Finkelstein, M. A. (1983) A case for the revision of textbook models of color vision: The detection and appearance of small brief lights. In: *Colour vision: Physiology and psychophysics*, ed. J. D. Mollon & L. T. Sharpe. Academic Press. [aET, MAF]
- Horn, B. K. P. (1974) Determining lightness from an image. *Computer Graphics and Image Processing* 3:227–99. [aET]
- Hudon, J. & Brush, H. A. (1989) Probable dietary basis of a color variant of the cedar waxwing. *Journal of Field Ornithology* 60(3):361–68. [aET]
- Hughes, A. (1972) Vergence in the cat. *Vision Research* 12:1961–94. [BL]
- (1977) The topography of vision in mammals of contrasting life style: Comparative optics and retinal organization. In: *The visual system in vertebrates*, ed. F. Crescitelli. Springer-Verlag. [BL]
- Hughes, A. & Vaney, D. L. (1982) The organization of binocular cortex in the primary visual area of the rabbit. *The Journal of Comparative Neurology* 204:151–64. [BL]
- Humphrey, N. (1984) *Consciousness regained. Chapters in the development of mind*. Oxford University Press. [aET]
- Humphreys, G. W. & Riddoch, M. J. (1986) Information processing systems which embody computational rules: The connectionist approach. *Mind & Language* 1:201–12. [JW]
- Hurlbert, A. (1986) Formal connections between lightness algorithms. *Journal of the Optical Society of America A* 3:1684–93. [aET, LTM]
- (1989) *The computation of color*. MIT AI Lab Technical Report 1154, Cambridge, MA. [aET, AH]
- Hurlbert, A. C. & Poggio, T. A. (1988) Synthesizing a color algorithm from examples. *Science* 239:482–85. [rET, JLD]
- Hurvich, L. M. (1981) *Color vision*. Sinnauer Associates, Inc. [aET]
- (1985) Opponent-colours theory. In: *Central and peripheral mechanisms of color vision*, ed. D. Ottoson & S. Zeki. Macmillan. [aET]
- Hurvich, L. M. & Jameson, D. (1957) An opponent process theory of color vision. *Psychological Review* 64:384–404. [aET, RNS]
- Ingle, D. J. (1985) The goldfish as a retinex animal. *Science* 235:651–53. [aET]
- Ingling, C. R. Jr. (1978) Luminance and opponent color contributions to visual detection and to temporal and spatial integration: Comment. *Journal of the Optical Society of America* 68:1143–46. [MAF]
- Ingling, C. R. Jr. & Tsou, B. H.-P. (1977) Orthogonal combination of the three visual channels. *Vision Research* 17:1075–82. [aET, MAF]
- Ingling, C. R. Jr., Scheibner, H. M. O. & Boynton, R. M. (1977) Color naming of small foveal fields. *Vision Research* 17:1075–82. [MAF]
- Jackson, F. (1982) Epiphenomenal qualia. *Philosophical Quarterly* 32:127–36. [aET]
- Jacobs, G. H. (1981) *Comparative color vision*. Academic Press. [arET, GHJ]
- (1986) Color vision variations in non-human primates. *Trends in Neuroscience* 12:320–23. [aET]
- Jameson, D. (1985) Opponent-colours theory in the light of physiological findings. In: *Central and peripheral mechanisms of colour vision*, ed. D. Ottoson & S. Zeki. Macmillan. [aET]
- Jameson, D. & Hurvich, L. M. (1989) Essay concerning color constancy. *Annual Review of Psychology* 40:1–22. [arET]
- Jane, S. D. & Bowmaker, J. K. (1988) Tetrachromatic colour vision in the duck (*Anas platyrhynchos L.*): Microspectrophotometry of visual pigments and oil droplets. *Journal of Comparative Physiology A* 162:225–35. [aET]
- Jeffery, G. (1990) The topographic relationship between shifting binocular maps in the developing dorsal lateral geniculate nucleus. *Experimental Brain Research* 82:408–16. [BL]
- Judd, D. B. (1940) Hue, saturation, and lightness of surface colors with chromatic illumination. *Journal of the Optical Society of America* 30:2–32. [aET]
- Judd, D. B., McAdam, D. L. & Wyszecki, G. (1964) Spectral distribution of typical daylight as a function of correlated color temperature. *Journal of the Optical Society of America* 54:1031–40. [RNS]
- Kandel, E. R. & Schwartz, J. H. (1985) *Principles of neural science*, 2nd ed. Elsevier North Holland. [aET]
- Kant, I. (1929) *Critique of pure reason*. Macmillan. [PHK]
- Katz, D. (1911) *Die Erscheinungsweise der Farben und ihre Beeinflussung durch die individuelle Erfahrung*. Barth. [RJM]
- Katz, M. J. (1983) Ontophyletics: Studying evolution beyond the genome. *Perspectives in Biology and Medicine* 26:323–32. [BL]
- Kay, P. & McDaniel, C. K. (1978) The linguistic significance of the meaning of basic color terms. *Language* 54:610–46. [aET]
- Kelso, J. A. S. & Kay, B. A. (1987) Information and control: A macroscopic analysis of perception-action coupling. In: *Perceptives on perception and action*, ed. H. Heuer & A. F. Sanders. Erlbaum. [arET]
- Killackey, H. P. (1990) Neocortical expansion: An attempt toward relating phylogeny and ontogeny. *The Journal of Cognitive Neuroscience* 2:1–17. [BL]
- King-Smith, P. E. & Carden, D. (1976) Luminance and opponent-color contributions to visual detection and adaptation and to temporal and spatial integration. *Journal of the Optical Society of America* 66:709–17. [MAF]
- Kitcher, P. (1988) Marr's computational theory of vision. *Philosophy of Science* 55:1–25. [aET]
- Kondrashev, S. L., Gamburtzeva, A. G., Gnjbukina, V. P., Orlov, O. Yu. & Pham Thi My (1986) Coloration of corneas in fish. A list of species. *Vision Research* 26:287–90. [SLK]
- Kondrashev, S. L., Gnjbukin, V. F., Dimentman, A. M. & Orlov, O. Yu. (1976) Role of visual stimuli in the breeding behavior of *Rana temporaria*, *Bufo bufo* and *Bufo viridis*. *Zoologicheskij Zhurnal* 55:1027–37. [SLK]
- Krauskopf, J. (1978) On identifying detectors. In: *Visual psychophysics and physiology*, ed. J. C. Armington, J. Krauskopf & B. R. Wooten. Academic Press. [MAF]
- Kuehni, R. G. (1989) What is color? A speculative essay. *Color Research and Application* 14:207–10. [JLD]
- Lakoff, G. (1987) *Women, fire, and dangerous things: What categories reveal about the mind*. University of Chicago Press. [rET]
- Land, E. H. (1977) The retinex theory of color vision. *Scientific American* 237:108–28. [aET]
- (1978) Our "polar partnership" with the world around us. *Harvard Magazine* 80:23–26. [aET]
- (1983) Recent advances in retinex theory and some implications for cortical computations: Color vision and the natural image. *Proceedings of the National Academy of Sciences U.S.A.* 80:5163–69. [aET, LTM]

- (1986) An alternative technique for the computation of the designator in the retinex theory of color vision. *Proceedings of the National Academy of Sciences U.S.A.* 83:3078–80. [aET]
- Land, E. H. & McCann, J. J. (1971) Lightness and retinex theory. *Journal of the Optical Society of America* 61:1–11. [JLD, LTM]
- Lee, D. N. & Reddish, P. E. (1981) Plummeting gannets: A paradigm for ecological optics. *Nature* 293:293–94. [rET, JW]
- Lee, H.-C. (1986) Method for computing the scene-illuminant chromaticity from specular highlights. *Journal of the Optical Society of America* 3:1694–99. [AH, LTM]
- Lennie, P. (1984) Recent developments in the physiology of color vision. *Trends in Neuroscience* 7:243–48. [aET]
- Lennie, P., Trevarthen, C., Van Essen, D. & Wässel, H. (1990) Parallel processing of visual information. In: *Visual perception. The neurophysiological foundations*, ed. L. Spillman & J. S. Werner. Academic Press. [aET]
- Leventhal, A. G., Schall, J. D., Ault, S. J., Provis, J. M. & Vitek, D. J. (1988) Class-specific cell death shapes the distribution and pattern of central projection of cat retinal ganglion cells. *The Journal of Neuroscience* 8:2011–27. [BL]
- Levine, J. S. & MacNichol, E. F. Jr. (1979) Visual pigments in teleost fishes: Effect of habitat, microhabitat and behavior on visual system evolution. *Sensory Processes* 3:95–131. [aET, KAA]
- (1982) Color vision in fishes. *Scientific American* 246:140–49. [aET, KAA]
- Levins, R. & Lewontin, R. (1983) The organism as the subject and object of evolution. *Scientia* 118:63–82. Reprinted In: Levins, R. & Lewontin, R. (1985) *The dialectical biologist*. Harvard University Press. [arET, DCD]
- (1985) *The dialectical biologist*. Harvard University Press. [arET, DCD]
- Lia, B. (1989) Prenatal development of regional specialization in the ganglion cell layer of the retina: The topography of focal vision (doctoral dissertation, University of California, Davis). *Dissertation Abstracts International* 50:332B. [BL]
- Lia, B. & Chalupa, L. M. (1988) Prenatal development of regional specialization in the primate retina. *Investigative Ophthalmology and Visual Science* 29 (Suppl.):378. [BL]
- Lia, B., Snider, C. J. & Chalupa, L. M. (1989) Topography and specificity of visual thalamocortical projections in the fetal rhesus monkey. *Society for Neuroscience Abstracts* 15:1210. [BL]
- Lia, B., Williams, R. W. & Chalupa, L. M. (1987) Formation of retinal ganglion cell topography during prenatal development. *Science* 236:848–51. [BL]
- Liebmam, P. A. (1972) Microspectrophotometry of photoreceptors. In: *Handbook of sensory physiology, vol. VII/1*, ed. H. J. A. Dartnall. Springer-Verlag. [GHJ]
- Livingstone, M. S. & Hubel, D. H. (1984) Anatomy and physiology of a color system in the primate visual cortex. *Journal of Neuroscience* 4:309–56. [aET]
- (1988) Segregation of color, movement, and depth: Anatomy, physiology, and perception. *Science* 240:740–49. [aET, JAF]
- Locke, J. (1690/1975) *An essay concerning human understanding*, ed. P. H. Nidditch. Oxford University Press. [aET]
- Lockhead, G. R. (1972) Processing dimensional stimuli: A note. *Psychological Review* 79:410–19. [JBD]
- Loew, E. R. & Lythgoe, J. N. (1978) The ecology of cone pigments in teleost fishes. *Vision Research* 18:715–22. [aET]
- Logothetis, N. K., Schiller, P. H., Charles, E. R. & Hurlbert, A. C. (1990) Perceptual deficits and the activity of the color-opponent and broad-band pathways at isoluminance. *Science* 247:214–17. [aET]
- Lorenz, K. (1943) Die angeborenen Formen möglicher Erfahrung. *Zeitschrift für Tierpsychologie* 5:235–409. [PS]
- Lythgoe, J. N. (1979). *The ecology of vision*. Oxford University Press. [aET, WB]
- MacLauray, R. E. (1987) Color-category evolution and Shuswap yellow-with-green. *American Anthropologist* 89:107–24. [rET]
- Maes, P. (1990) *Designing autonomous agents*. MIT Press. [rET]
- Maier, E. (1990) Verhaltensphysiologische Untersuchungen zum Farbensehen des Sonnenvogels (*Leiothrix lutea*, *Timalidae*, *Passeriformes*). Doctoral thesis, University of Regensburg. [EM]
- Maldonado, P. E., Maturana, H. & Varela, F. J. (1988) Frontal and lateral visual system in birds. *Brain, Behavior and Evolution* 32:57–62. [aET]
- Mallat, S. G. & Zhong, S. (1989) Complete signal representation with multiscale edges. *Technical Report No. 483*, Courant Institute, New York University. [rET]
- Maloney, L. T. (1984) *Computational approaches to color constancy*. Stanford University: Dissertation. Reprinted as (1985) *Stanford Applied Psychology Laboratory Report* 1985-01. [LTM]
- (1985) Computational approaches to color constancy. *Technical Report 1985-01*, Stanford University, Applied Psychological Laboratory. [arET]
- (1986) Evaluation of linear models of surface spectral reflectance with small numbers of parameters. *Journal of the Optical Society of America A* 3:1673–83. [LTM, RNS]
- (1990) Photoreceptor spectral sensitivities and color correction. In: *Perceiving, measuring, and using color*, ed. Michael H. Brill. Proceedings of the SPIE 1250. [LTM]
- (1992) Color constancy and color perception: The linear models framework. In: *Attention & performance XIV: A silver jubilee*, ed. D. E. Meyer & S. Kornblum. Erlbaum (in press) [LTM]
- Maloney, L. T. & Wandell, B. A. (1986) Color constancy: A method for recovering surface spectral reflectance. *Journal of the Optical Society of America A* 3(1):29–33. [aET, JLD, LTM, RNS]
- Mark, L. S. (1987) Eyeheight-scaled information about affordances: A study of sitting and stair climbing. *Journal of Experimental Psychology: Human Perception and Performance* 13:361–70. [JW]
- Marr, D. (1982) *Vision. A computational investigation into the human representation and processing of visual information*. W. H. Freeman. [arET, JBD]
- Marr, D. & Poggio, T. (1977) From understanding neural computation to understanding neural circuitry. *Neuroscience Research Program Bulletin* 15:470–88. [aET]
- Martin, G. R. (1977) Absolute visual threshold and scotopic spectral sensitivity in the tawny owl (*Strix aluco*). *Nature* 268:636–38. [aET]
- (1986) The eye of a passeriform bird, the European starling (*Strunus vulgaris*): Eye movement amplitude, visual fields and schematic optics. *Journal of Comparative Physiology A* 159:545–557. [aET]
- Martin, G. R. & Gordon, I. E. (1974) Increment-threshold spectral sensitivity in the tawny owl (*Strix aluco*). *Vision Research* 14:615–21. [EM]
- Martin, G. R. & Lett, B. T. (1985) Formation of associations of coloured and flavoured food with induced sickness in five avian species. *Behavioral Neural Biology* 43:223–37. [aET]
- Matthen, M. (1988) Biological functions and perceptual content. *Journal of Philosophy* 85:5–27. [arET, MM]
- Maturana, H. R. & Varela, F. J. (1980) *Autopoiesis and cognition: The realization of the living*. Boston Studies in the Philosophy of Science, vol. 42. D. Reidel. [aET]
- (1982) Colour-opponent responses in the avian lateral geniculate: A case study in the quail. *Brain Research* 247:227–41. [aET]
- (1987) *The tree of knowledge. The biological roots of human understanding*. New Science Library. [aET]
- McCann, J. J., McKee, S. P. & Taylor, T. H. (1976) Quantitative studies in retinex theory. *Vision Research* 16:445–58. [aET]
- Menaud-Buteau, C. & Cavanagh, P. (1984) Localisation de l'interférence forme/couleur au niveau perceptuel dans une tache de type Stroop avec des stimuli-dessins. *Canadian Journal of Psychology* 38:421–39. [JBD]
- Menzel, R. (1979) Spectral sensitivity and color vision in invertebrates. In: *Comparative physiology and evolution of vision in invertebrates, handbook of sensory physiology*, vol. VII/6A, ed. H. Autrum. Springer Verlag. [aET, WB]
- (1981) Achromatic vision in the honeybee at low light intensities. *Journal of Comparative Physiology A* 158:165–77. [CN]
- (1989) Bienen sehen vieles anderes. *Natürliches Farbsehsystem beschrieben. Forschung, Mitteilungen der DFG* 2/89:20–22. [aET, WB]
- Menzel, R. & Backhaus, W. (1989) Color vision in honeybees: Phenomena and physiological mechanisms. In: *Facets of vision*, ed. D. G. Stavenga & R. C. Hardie. Springer. [WB]
- (1991) Color vision in insects. In: *Vision and visual dysfunction*, vol. VII, ed. P. Gouras. Macmillan. [WB]
- Menzel, R. & Shmida, A. (in preparation) The ecology of flower colors in the insect pollinated plants of Israel. *Evolutionary Biology*. [rET, WB]
- Merleau-Ponty, M. (1945/1962) *The phenomenology of perception*. Translated by Colin Smith. Routledge & Kegan Paul. [rET]
- Merleau-Ponty, M. (1964) *L'Oeil et l'esprit*. Gallimard. [aET]
- Mollon, J. D. (1990) Neurobiology: The club-sandwich mystery. *Nature* 343:16–17. [aET]
- Mollon, J. D. & Sharpe, L. T. eds. (1983) *Color vision*. Academic Press. [aET]
- Mollon, J. D., Bowmaker, J. K. & Jacobs, G. H. (1984) Variations of colour vision in a New World primate can be explained by polymorphism of retinal photopigments. *Proceedings of the Royal Society B* 222:373–99. [aET]
- Mullen, K. T. & Kulikowski, J. J. (1990) Wavelength discrimination at detection threshold. *Journal of the Optical Society of America A* 7:733–42. [JBD]
- Muntz, W. R. (1975) Behavioral studies of vision in a fish and possible relationships to the environment. In: *Vision in fish*, ed. M. A. Ali. Plenum. [aET]
- Muntz, W. R. & Mouat, G. S. (1984) Annual variation in the visual pigments

References/Thompson et al.: Ways of coloring

- of brown trout inhabiting lochs providing different light environments. *Vision Research* 24:1575–80. [aET]
- Munz, F. W. & McFarland, W. N. (1977) Evolutionary adaptations of fishes to the photopic environment. In: *Handbook of sensory physiology*, vol. VII, ed. F. Crescitelli. Springer-Verlag. [aET, KAA]
- Nagel, T. (1974/1980) What is it like to be a bat? In: *Readings in the philosophy of psychology*, vol. 1, ed. Ned Block. Harvard University Press. [aET]
- Nagy, A. L. (1980) Large-field substitution Rayleigh matches of dichromats. *Journal of the Optical Society of America* 70:778–84. [GHJ]
- NASA (1977) Terrestrial photovoltaic measurement procedures. ERDA/NASA/1022–77/16; NASA TM 73702. [KAA]
- Nathans, J., Thomas, D. & Hogness, D. S. (1986) Molecular genetics of human color vision: The genes encoding blue, green, and red pigments. *Science* 232:193–202. [aET]
- Neitz, J. & Jacobs, G. H. (1986) Polymorphism of the long-wavelength cone in normal human color vision. *Nature* 323:623–25. [aET]
- Neumeyer, C. (1980) Simultaneous color contrast in the honeybee. *Journal of Comparative Physiology A* 139:165–76. [aET]
- (1981) Chromatic adaptation in the honeybee: Successive color contrast and color constancy. *Journal of Comparative Physiology A* 144:543–53. [aET]
- (1985) An ultraviolet receptor as a fourth receptor type in goldfish color vision. *Naturwissenschaften* 72:162–63. [aET]
- (1986) Wavelength discrimination in the goldfish. *Journal of Comparative Physiology A* 158:203–13. [aET]
- (1988) *Das Farbensehen des Goldfisches. Eine verhaltensphysiologische Analyse*. Thieme. [aET, EM]
- Neumeyer, C. & Arnold, K. (1989) Tetrachromatic color vision in the goldfish becomes trichromatic under white adaptation light of moderate intensity. *Vision Research* 29:1719–27. [aET]
- Northcutt, R. G. (1990) Ontogeny and phylogeny: A re-evaluation of conceptual relationships and some applications. *Brain, Behavior and Evolution* 36:116–40. [BL]
- Nuboer, J. F. W. (1986) A comparative view on colour vision. *Netherlands Journal of Zoology* 36:344–80. [aET]
- Nuboer, J. F. W. & Wortel, J. (1987) Colour vision via the pigeon's red and yellow retinal fields. In: *Seeing contour and colour*, ed. J. J. Kullkowshi. Cambridge University Press. [aET]
- Odling-Smee, F. J. (1988) Niche-constructing phenotypes. In: *The role of behavior in evolution*, ed. H. C. Plotkin. MIT Press/Bradford Books. [arET]
- O'Leary, D. D. M. (1989) Do cortical areas emerge from a protocortex? *Trends in Neurosciences* 12:400–06. [BL]
- Orlov, O. Yu. & Gamburtzeva, A. G. (1976) Changeable coloration of cornea in the fish *Hexagrammos octogrammus*. *Nature* 263:405–06. [SLK]
- Ottoson, D. & Zeki, S. eds. (1985) *Central and peripheral mechanisms of colour vision*. Macmillan. [aET]
- Overmyer, S. P. & Simon, J. R. (1985) The effect of irrelevant cues on "same-different" judgments in a sequential information processing task. *Acta Psychologica* 58:237–49. [JBD]
- Oyama, S. (1985) *The ontogeny of information: Developmental systems and evolution*. Cambridge University Press. [aET]
- Palacios, A. (1991) La vision chromatique chez l'oiseau: Etude comparantale. These de Doctorat. Université de Paris VI. [arET]
- Palacios, A. & Varela, F. J. (1991) Color mixing in the pigeon. II. A psychophysical determination in the medium and shortwave spectral range. *Vision Research* (in press). [aET]
- Palacios, A., Bonnardel, V. & Varela, F. (1990a) Autosizing as a method for the chromatic discrimination of the pigeon. *Comptes Rendues la Académie des Sciences (Paris), Sciences de la Vie* 331:213–18. [aET]
- Palacios, A. C., Martinoya, S., Bloch, S. & Varela, F. J. (1990b) Color mixing in the pigeon: A psychophysical determination in the longwave spectral range. *Vision Research* 30:587–96. [aET, GHJ]
- Partridge, J. C. (1989) The visual ecology of avian cone oil droplets. *Journal of Comparative Physiology A* 165:415–26. [aET]
- Partridge, C., Shand, J., Archer, S. N., Lythgoe, J. N. & Groningen-Luyben, W. A. (1989) Interspecific variation in the visual pigments of the deep-sea fishes. *Journal of Comparative Physiology A* 164:513–29. [aET]
- Peitsch, D., Backhaus, W. & Menzel, R. (1989) Colour vision systems in hymenopterans: A comparative study. In: *Neural mechanisms of behavior*, ed. J. Erber, R. Menzel, H.-J. Pflueger & D. Todt. Proceedings of the 2nd International Congress of Neuroethology, September 10–16. Thieme. [WB]
- Pettigrew, J. D. (1986) The evolution of binocular vision. In: *Visual neuroscience*, ed. J. D. Pettigrew, K. J. Sanderson & W. R. Levick. Cambridge University Press. [BL]
- Piaget, J. (1969) *The mechanisms of perception*. Routledge & Kegan Paul. [PHK]
- Poggio, T. and staff (1988) *The vision machine*. Proceedings of the IU Workshop, Cambridge, MA. [AH]
- Poggio, T., Torre, V. & Koch, C. (1985) Computational vision and regularization theory. *Nature* 317:314–19. [arET]
- Polyak, S. L. (1957) *The vertebrate visual system*. University of Chicago Press. [BL]
- Posner, M. I. & Petersen, S. E. (1990) The attention system of the human brain. *Annual Review of Neuroscience* 13:25–42. [JAF]
- Priest, G. (1989) Primary qualities are secondary qualities, too. *British Journal for the Philosophy of Science* 40:29–37. [aET]
- Rakic, P. (1988) Specification of cerebral cortical areas. *Science* 241:170–76. [BL]
- Ramachandran, V. S. (1985) The neurobiology of perception. *Perception* 14:97–103. [aET, JW]
- Reeke, G. N. & Edelman, G. M. (1988) Real brains and artificial intelligence. *Daedalus* 117(1):143–73. [aET]
- Reichardt, W. & Poggio, T. (1976) Visual control of orientation behaviour in the fly. *Quarterly Review of Biophysics* 9:311–438. [rET, AH]
- Remy, M. & Emmerton, J. (1989) Behavioral spectral sensitivities of different retinal areas in pigeons. *Behavioral Neuroscience* 103:170–77. [aET]
- Reuter, T. & Virtanen, K. (1976) Color discrimination mechanism in the retina of the toad (*Bufo bufo*). *Journal of Comparative Physiology* 109:337–43. [SLK]
- Robson, J. (1983) The morphology of cortico-fugal axons to the dorsal lateral geniculate nucleus. *Journal of Comparative Neurology* 216:89–103. [aET]
- Rodieck, R. W. (1973) The vertebrate retina. Freeman. [WB]
- Rosch, E. (1973) Natural categories. *Cognitive Psychology* 4:328–50. [arET]
- Rothschild, M. F. (1979) Remarks on carotenoids in the evolution of signals. *Coevolution of animals and plants*, ed. L. E. Gilbert & P. H. Raven. University of Texas. [aET]
- Rowe, M. H. & Dreher, B. (1982) Functional morphology of beta cells in the area centralis of the cat's retina: A model for the evolution of central retinal specializations. *Brain, Behavior and Evolution* 21:1–23. [BL]
- Rowland, W. J. (1979) The use of color in intraspecific communication. In: *The behavioral significance of color*, ed. E. H. Burtt Jr. [aET]
- Rubin, J. M. & Richards, W. A. (1982) Color vision and image intensities: When are changes material? *Biological Cybernetics* 45:215–26. [arET, JLD]
- (1988) Color vision: Representing material categories. In: *Natural computation*, ed. W. Richards. MIT Press/Bradford Books. [arET]
- Sällström, P. (1973) Colour and physics: Some remarks concerning the physical aspects of human colour vision. *Technical Report 73-09*, Institute of Physics, University of Stockholm, Sweden. [JLD]
- Schiller, P. H., Logothetis, N. K. & Charles, E. R. (1990) Functions of the colour-opponent and broad-band channels of the visual system. *Nature* 343:68–70. [aET]
- Sejnowski, T. J., Koch, C. & Churchland, P. S. (1988) Computational neuroscience. *Science* 241:1299–1306. [aET]
- Sereno, M. I. & Allman, J. M. (1991) Cortical visual areas in mammals: In: *The Neural Basis of Visual Function*, ed. A. G. Leventhal. Macmillan. [BL]
- Shepard, R. N. (1987) Evolution of a mesh between principles of the mind and regularities of the world. In: *The latest on the best: Essays on evolution and optimality*, ed. J. Dupre. MIT Press/Bradford Books. [RNS]
- (1990) A possible evolutionary basis for trichromacy. In: *Perceiving, measuring, and using color*, ed. M. Brill. Proceedings of the SPIE/SPSE Symposium on Electronic Imaging: Science and Technology 301–09. [rET, RNS]
- (1991) The perceptual organization of colors: An adaptation to regularities of the terrestrial world? In: *The adapted mind: Evolutionary psychology and the generation of culture*, ed. J. Barkow, L. Cosmides & J. Tooby. Oxford University Press (Oxford) (in press). [RNS]
- Sittig, O. (1921) Störungen im Verhalten gegenüber Farben bei Aphasiens. *Monatsschrift für Psychiatrie und Neurologie* 49:63–68; 169–87. [JBD]
- Skarda, C. (1989) Understanding perception: Self-organizing neural dynamics. *La Nuova Critica* 9/10:49–60. [CAS]
- Skarda, C. & Freeman, W. (1987) How brains make chaos in order to make sense of the world. *Behavioral and Brain Sciences* 10:161–95. [aET]
- Smith, V. C. & Pokorny, J. (1977) Large-field trichromacy in protanopes and deutanopes. *Journal of the Optical Society of America* 67:213–20. [GHJ]
- Snodderly, D. M. (1979) Visual discrimination encountered in food foraging

- by a neotropical primate: Implications for the evolution of color vision. In: *The behavioral significance of color*, ed. E. H. Burtt, Jr. Garland STPM Press. [aET]
- Snow, D. W. (1971) Evolutionary aspects of fruit eating by birds. *Ibis* 113:194–202. [aET]
- Spencer, H. (1890) *Principles of Psychology* (3rd ed.) Williams & Norgate. [PS]
- Sperling, H. G. & Harwerth, R. S. (1971) Red/green cone interactions in the increment-threshold spectral sensitivity of primates. *Science* 172:180–84. [MAF]
- Sperry, R. W. (1952) Neurology and the mind-brain problem. *American Scientist* 40:291–311. [BL]
- Spillman, L. & Werner, J. S. eds. (1990) *Visual perception. The neurophysiological foundations*. Academic Press. [aET]
- Stalmeier, P. F. M. & DeWeert, C. M. M. (1988) Large colour differences measured by spontaneous Gestalt formation. *Color Research and Application* 13:209–18. [JBD]
- Steele, K. M. (1990) Configural processes in pigeon perception. In: *Quantitative analyses of behavior*, vol. 8, ed. M. L. Commons, R. J. Herrnstein, S. M. Kosslyn & D. M. Mumford. Erlbaum. [KMS]
- Steriade, M. & Deschenes, M. (1985) The thalamus as a neuronal oscillator. *Brain Research Reviews* 18:165–70. [aET]
- Stoerig, P. & Cowey A. (1989) Wavelength sensitivity in blindsight. *Nature* 342:916–18. [PS]
- (submitted) Wavelength discrimination in visual field defects. *Brain*. [PS]
- Stroll, A. (1986) The role of surfaces in an ecological theory of perception. *Philosophy and Phenomenological Research* 46:437–53. [aET]
- Stromeyer, C. F. III, Khoo, M. C. K., Muggeridge, D. & Young, R. A. (1978) Detection of red and green flashes: Evidence for cancellation and facilitation. *Sensory Processes* 2:248–71. [MAF]
- Suppes, P., Krantz, D. H., Luce, R. D. & Tversky, A. (1989) *Foundations of measurement*. vol. II. *Geometrical, threshold, and probabilistic representations*. Academic Press. [RJM]
- Svaetichin, G. & MacNichol, E. F. (1958) Retinal mechanisms for chromatic and achromatic vision. *Annals of the New York Academy of Sciences* 74:385–404. [aET]
- Taylor, G. R. (1979) *The natural history of the mind*. Secker and Warburg, London. [PS]
- Teller, D. Y. (1984) Linking propositions. *Vision Research* 24:1233–46. [aET]
- (1990) The domain of visual science. In: *Visual perception. The neurophysiological foundations*, ed. L. Spillman & J. S. Werner. (eds) Academic Press. [aET]
- Teller, D. Y. & Pugh, E. N. Jr. (1983) Linking propositions in color vision. In: *Colour vision: Physiology and Psychophysics*, ed. J. D. Mollon & L. T. Sharpe. Academic Press. [aET, MAF]
- Thompson, E. (1989) Colour vision and the comparative argument: A case study in cognitive science and the philosophy of perception. Doctoral dissertation, Department of Philosophy, University of Toronto. [aET]
- (1992) *Colour vision: A study in cognitive science and the philosophy of perception*. Routledge Press. (in press) [rET]
- Thouless, R. H. (1931) Phenomenal regression to the “real” object. I and II. *British Journal of Psychology* 21:339–59; 22:1–30. [AR]
- Treisman, A. & Gormican, S. (1988) Feature analysis in early vision: Evidence from search asymmetries. *Psychological Review* 95:15–48. [JLD]
- Trevarthen, C. (1968) Two mechanisms of vision in primates. *Psychologische Forschung* 31:299–337. [BL]
- Turvey, M. T. (1977) Contrasting orientations to the theory of visual information processing. *Psychological Review* 84:67–88. [aET]
- Turvey, M. T., Shaw, R. E., Reed, E. S. & Mace, W. M. (1981) Ecological laws of perceiving and acting: In reply to Fodor and Pylyshyn. *Cognition* 9:237–304. [aET]
- Valberg, A., Seim, T., Lee, B. B. & Tryti, J. (1986) Reconstruction of equidistant color space from responses of visual neurons of macaques. *Journal of the Optical Society of America A* 3:1726–34. [WB]
- Van Brakel, J. (1991) The plasticity of categories: The case of colour. *British Journal for the Philosophy of Science* (in press). [JVB]
- Van der Loos, H. (1979) The development of topological equivalences in the brain. In: *Neural growth and differentiation*, ed. E. Meisami & M. A. B. Brazier. Raven Press. [BL]
- Varela, F. J. (1979) *Principles of Biological Autonomy*. Elsevier North Holland. [aET]
- (1984) Living ways of sense-making: A middle path for neuroscience. In: *Disorder and order: Proceedings of the Stanford International Symposium*, ed. P. Livingston. Anima Libris. [aET]
- (1989) *Connaitre: Les sciences cognitives, tendances et perspectives*. Editions du Seuil. [aET]
- (1991a) Perception and the origin of cognition: A cartography of current ideas. In: *Understanding origins: contemporary ideas on the origin of life, mind and society. Boston studies in the philosophy of science*, ed. F. Varela & J. P. Dupuy. Kluwer Associates. [aET]
- (1991b) Organisms: A meshwork of selfless selves. In: *Organism and the origin of self*, ed. A. Tauber. Kluwer Associates. [aET]
- Varela, F. & Singer, W. (1987) Neuronal dynamics in the visual cortico-thalamic pathway as revealed through binocular rivalry. *Experimental Brain Research* 66:10–20. [aET]
- Varela, F. J., Palacios, A. & Goldsmith, T. H. (1991a) Color vision. In: *Bird vision and cognition*, ed. H. J. Bischof & H. P. Zeigler. MIT Press. [aET]
- Varela, F. J., Thompson, E. & Rosch, E. (1991b) *The embodied mind: Cognitive science and human experience*. MIT Press. [aET]
- Varela, F. J., Letelier, J. C., Marin, G. & Maturana, H. R. (1983) The neurophysiology of avian color vision. *Archivos de Biología y Medicina Experimental* 16:291–303. [aET]
- Vaughn, W. Jr. & Greene, S. L. (1983) Acquisition of absolute discriminations in pigeons. In: *Quantitative analyses of behavior*, vol. 4, ed. M. L. Commons, R. J. Herrnstein & A. R. Wagner. Ballinger. [KMS]
- Volman, S. F. (1990) Neuroethological approaches to the evaluation of neural systems. *Brain, Behavior and Evolution* 36:154–65. [BL]
- Von Uexküll, J. (1926) *Theoretical biology*. Kegan Paul, Trench, Trubner & Co., Ltd. [BL]
- (1928/1973) *Theoretische Biologie*. Springer; Suhrkamp, (1973). [CN]
- (1957) A stroll through the worlds of animals and men. In: *Instinctive behavior*, ed. C. H. Schiller. International University Press. [BL]
- Wagemans, J. (1988) Modules in vision: A case study of interdisciplinarity in cognitive science. *Acta Psychologica* 67:59–93. [JW]
- (1990) “Smart” mechanisms emerging from cooperation and competition between modules. *Psychological Research* 52:181–96. [JW]
- Walls, G. L. (1942) *The vertebrate eye and its adaptive radiation*. Hafner Publishing Co. [BL]
- (1962) The evolutionary history of eye movements. *Vision Research* 2:60–80. [BL]
- Wandell, B. A. & Pugh, E. N. Jr. (1980) Detection of long-duration, long-wavelength incremental flashes by a chromatically coded pathway. *Vision Research* 20:625–36. [MAF]
- Ward, T. B., Foley, C. M. & Cole, J. (1986) Classifying multidimensional stimuli: Stimulus, task and observer factors. *Journal of Experimental Psychology: Human Perception and Performance* 12:211–25. [JBD]
- Warren, W. H. (1984) Perceiving affordances: Visual guidance of stair climbing. *Journal of Experimental Psychology: Human Perception and Performance* 10:683–703. [rET, JW]
- Warren, W. H. & Whang, S. (1987) Visual guidance of walking through apertures: Body-scaled information for affordances. *Journal of Experimental Psychology: Human Perception and Performance* 13:371–83. [JW]
- Warren, W. H., Mestre, D. R., Blackwell, A. W. & Morris, M. W. (1991) Perception of circular heading from optical flow. *Journal of Experimental Psychology: Human Perception and Performance* 17:28–43. [JW]
- Warren, W. H., Morris, M. W. & Kalish, M. (1988) Perception of translational heading from optical flow. *Journal of Experimental Psychology: Human Perception and Performance* 14:646–60. [JW]
- Wasserman, G. (1979) *Color vision: An historical introduction*. Academic Press. [aET]
- Watt, R. (1991) *Understanding vision*. Academic Press. [JW]
- Weedon, B. C. (1963) Occurrence. In: *Carotenoids*, ed. O. Isler. Birkhauser Verlag. [aET]
- Weiskrantz, L., Warrington, E. K., Sanders, M. D. & Marshall, J. (1974) Visual capacity in the hemianopic field following a restricted cortical ablation. *Brain* 97:709–728. [PS]
- Werner, A., Menzel, R. & Wherhan, C. (1988) Color constancy in the honeybee. *Journal of Neuroscience* 8:156–59. [rET, WB]
- West, G. & Brill, M. H. (1982) Necessary and sufficient conditions for von Kries chromatic adaptation to give color constancy. *Journal of Mathematical Biology* 15:49–58. [LTM]
- Westphal, J. (1987) *Colour: Some philosophical problems from Wittgenstein*. Basil Blackwell. [aET]
- Wheeler, T. G. (1982) Color vision and retinal chromatic information processing in teleost: A review. *Brain Research Reviews* 4:177–235. [aET]
- Whitmore, A. V. & Bowmaker, J. K. (1989) Seasonal variation in cone sensitivity and short-wave absorbing visual pigments in the rudd *Scardinius erythrophthalmus*. *Journal of Comparative Physiology A* 166:103–15. [aET]

- Wiesel, T. N. & Hubel, D. H. (1966) Spatial and chromatic interactions in the lateral geniculate body of the rhesus monkey. *Journal of Neurophysiology* 29:1115-56. [MAF]
- Williams, C. (1974) The effect of an irrelevant dimension on "same-different" judgments of multi-dimensional stimuli. *Quarterly Journal of Experimental Psychology* 26:26-31. [JBD]
- Wilson, M. (1987) Berkeley on the mind-dependence of colors. *Pacific Philosophical Quarterly* 68:249-64. [aET]
- Wright, A. (1972) The influence of ultraviolet radiation on the pigeon's color discrimination. *Journal of the Experimental Analysis of Behavior* 17:325-37. [aET]
- (1979) Color-vision psychophysics: A comparison of pigeon and human. In: *Neural mechanisms of behavior in the pigeon*, ed. A. M. Granda & J. H. Maxwell. Plenum. [aET]
- Wright, A. & Cummings, W. W. (1971) Color naming functions for the pigeon. *Journal of the Experimental Analysis of Behavior* 15:7-17. [aET]
- Wright, W. D. (1946) *Researches on normal and defective colour vision*. Henry Kimpton. [GHJ]
- (1988) A color palette in the brain? *Color research and application* 13(3):138-39. [PHK]
- Wright, W. D. & Pitt, F. H. G. (1934) Hue discrimination in normal colour vision. *Proceedings of the Physical Society of London* 46:459. [WB]
- Wyszecki, G. & Stiles, W. S. (1982) *Color science: Concepts and methods, quantitative data and formulae*, 2nd ed. Wiley. [aET, LTM, RJM]
- Yuille, A. (1984) A method for computing spectral reflectance. *AI Memo* 752. MIT AI Lab. [aET]
- Zeki, S. (1980) The representation of colours in the cerebral cortex. *Nature* 284:412-18. [aET]
- (1983) Colour coding in the cerebral cortex: The reaction of cells in monkey visual cortex to wavelengths and colours. *Neuroscience* 9:741-65. [aET]
- (1985) Colour pathways and hierarchies in the cerebral cortex. In: *Central and peripheral mechanisms of colour vision*, ed. D. Ottoson & S. Zeki. Macmillan. [aET]

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