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Color Perception and Neural Encoding: Does Metameric Matching Entail a Loss of Information?[1]

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It seems intuitively obvious that metameric matching of color samples entails a loss of information. Metamers are distributions of wavelength and intensity (or "spectral energy distributions") that perceivers cannot discriminate. Consider two color samples that are presented under ordinary white light and that appear to normal observers to be of the same color. It is well-established that such color samples can have quite different surface-reflective properties; e.g., two samples that appear to be the same shade of green may in fact reflect strikingly different patterns of wavelengths within the visible spectrum (see Figure 1). In this case, sameness of appearance under similar conditions of illumination does not entail sameness of surface reflectance. Spectrophotometrically diverse materials appear the same. It would seem then that information has been lost, that the visual system has failed in its task of chromatic discrimination.

This intuition implicitly relies on a conception of the function of color vision and on a related conception of how color samples should be individuated. It assumes that the function of color vision is to distinguish among spectral energy distributions, and that color samples should be individuated by their physical properties. I shall challenge these assumptions by articulating a different conception of the function of color vision, according to which color vision serves to partition visible objects into discrimination classes. From this perspective, objects are chromatically individuated by their membership in a particular equivalence class. Spectrophotometric diversity may in some cases (though not in all) be consistent with sameness of class membership. Metameric matching need not entail a loss of (pertinent) information.

My argument requires the articulation and adjudication of competing conceptions of the function of color vision. For my stalking horse I will examine the conception of color vision advanced by Barlow (1982c) and his followers (Buchsbaum & Gottschalk, 1983). I will contrast this conception with one derived from an approach to vision in the spirit of Marr's (1982), though it will turn out that it is not Marr's own analysis of color. My argument presents a function-based analysis of the content of color sensations (thereby extending Hatfield 1988, consistently with Matthen 1988); however, someone who accepted function-ascription in biology but was squeamish about content-ascription could reformulate the argument using only function-ascriptions.

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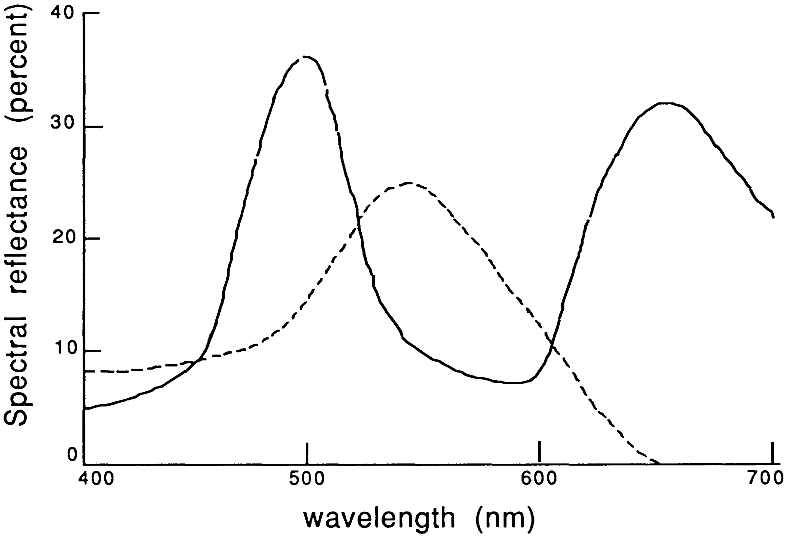

Figure 1. Two spectral reflectance distributions that produce matching greens in daylight for normal human observers. (After Hurvich 1981, 207.)

1. Task Analysis and Perceptual Content

In recent years there has been increasing attention to the role of task analysis in the investigation of psychological systems. A task analysis specifies what it is that a particular system does, where this "doing" cannot be captured through mere behavioral description; it is a specification of the function of a given system, or of its task within the economy of the organism. To take a non-psychological example, there are many things that the digestive system "does", including producing growling noises when inputs have been light. But its function, its contribution to the economy of the organism, is to break down nutrients for distribution in the body. In psychology, the task analysis approach seeks to determine the function of various psychological systems, or their contribution to the psychological or cognitive economy of the organism.

Teleology lingers in the background of task analyses (sometimes being brought into plain sight). Such teleology is underwritten by appeal to natural selection. In the popular Wrightian analysis of functions (and its descendants), a function is ascribed to a type of system through an etiological analysis: a system's function is whatever it does that explains (evolutionarily) its presence in organisms of a certain type (Wright 1973; Matthen 1988, Millikan 1984). To ascribe a function is to make a conjecture about the adaptive significance of a given structure, and hence about the characteristics of the structure that led to its fixation and subsequent maintenance in a (temporally persisting) species of organisms. Such conjectures are difficult to confirm or disconfirm, but they are not totally immune from empirical evidence (and science is in the business of venturing beyond the data). In any event, task analysis is central to physiology and psychology, and an appeal to adaptation and evolution currently offers the most promising means of legitimizing the latent teleology of such analyses.

When applied to representational systems such as the visual system, task analysis provides a means of ascribing representational content to states of the system.

Matthen makes this point in treating perceptual systems as systems that have the function of detecting the presence of certain environmental conditions; the "on" state of the detector mechanism is then ascribed representational content in accordance with the environmental condition it serves to detect. Thus, the "on" state of an edge detector has the content *edge* (Matthen 1988). More generally, various states of the visual system are assigned content in virtue of the environmental characteristics it is their function to represent: determinate shapes, sizes, motions, positions, and colors, to name a few (Hatfield 1988, 1991).

The notions of task analysis, etiological function ascription, and function-based content ascription have not received universal endorsement. But for present purposes I will take them as given. My aim is to show how competing task analyses have been given for the function of the visual system and in particular for the reception and post-retinal transmission of information about color. These competing analyses lead to different conceptions of the content of color perception, or of the function of color detecting mechanisms in the visual system.

2. Contrasting Task Analyses of the Visual System

Marr (1982) should be credited for drawing attention to the important role of task analysis in the investigation of perceptual systems. But he did not invent task analysis. Visual theorists have proposed (or presupposed) conceptions of the function of vision from earliest times (Aristotle 1984, 436b18- 437a9; Ptolemy 1989, bk. 2), and more recently Gibson (1966) made investigation of the natural functions of the senses central to his "perceptual systems" approach. Marr's own analysis, which assigns to human "early vision" the function of producing a representation of the spatial and chromatic properties of the distal scene, shares much with Gibson's (1950, 1966) analysis of the visual system. According to this conception, the perceptual apparatus is "distally focused", that is, it is tuned toward representing structures at a distance, and is not particularly tuned toward the representation of its own proximal states (e.g., the state of the retina).

Marr contrasts his approach with that of Barlow, and he criticizes the latter for merely describing the activity of single cells without addressing the question of the function of that activity (Marr 1982, 12-15, 19). In their work on space and color coding Barlow and his followers have emphasized the problem of the encoding and neural transmission of the physical characteristics of the retinal image, as opposed to the problem of representing distal scenes. This is not, as Marr charges, because Barlow failed to appreciate the importance of task analysis itself. Rather, it is because he (and his followers) gave a different task analysis than that favored by Marr. Examination of these contrasting task analyses will bring into relief the issues about metamers in color vision that I wish to address.

Far from failing to appreciate the notion of task analysis, Barlow explicitly proposes to analyze the functions of the sense organs. Thus, in an early paper he asserts that birds' wings are for flying, and asks, in effect, what sensory relays are for (1961b, 217). Indeed, his early work on fly detectors (Barlow 1953) led him to formulate the "password" hypothesis, according to which certain physical characteristics of stimuli act as "releasers" to initiate adaptively appropriate behavior, such as tongue-shooting (1961b, 219-220). But by and large, Barlow and his followers have emphasized the function of the senses as recorders of the physical properties of the image on the retina. Barlow described the function of the retina as follows: "The retina is a thin sheet of photoreceptors and nerve cells lining the back of the eye where the image is formed. It is obvious that its functional role is to encode the image falling on the retina as a pattern of nerve impulses in order to transmit the picture up the optic nerve to the brain"

(Barlow 1982b, 102). More recently, Sterling has written that "the retina's task is to convert th[e] optical image into a 'neural image' for transmission down the optic nerve to a multitude of centers for further analysis" (1990, 170). Although these authors are analyzing the function of the retina, not of the visual system as a whole, their conception of retinal functioning is part of a larger conception of how the visual system works. According to this conception, the retina records the physical image for efficient transmission to central visual centers (Barlow 1961a, Woodhouse and Barlow 1982), where subsequent processes "interpret" the neurally encoded image (Barlow 1982a, 31-32). Barlow in fact conceives of the senses as physical instruments designed to accurately encode the physical properties of the proximal stimulus; remarking on the familiar practice of labeling the external senses as "exteroceptors", he observes that "these so-called exteroceptors are really specialised interoceptors; they sense the outer world only by means of its physical and chemical influence on the special sense cells of the nose, the ears, or the eyes" (Barlow 1982a, 1). De facto, he has adopted what Gibson once labeled the conception of the senses as "channels of sensation" (1966, 3), by which he meant that one conceives the sense organs as recording their own state, rather than as components in a system that has the function of perceiving the distal environment. (Of course, all concerned agree that sensory transducers are affected by physical energy; the matter in question is the functional analysis of the detection and representational systems in which the transducers serve.)

Marr, by contrast, conceives vision—or at least early vision in primates—as having the function of generating a representation of the distal layout (1982, 41-42, 268-269). In connection with this conception of early vision, he considers the transduction process from the standpoint of the reception of stimulus characteristics that will allow recovery of distal properties. In considering the coding of spatial information on the retina, he focuses on the problem of detecting the aspects of the image that are informative of distal spatial structure. He thus looks for aspects of the image that "correspond to real physical changes on the viewed surface" (1982, 44). Hence, he emphasizes zero-crossings because of their correlation with physical edges in the world (pp. 49-50, 54). Similarly, in considering what encoding of the retinal image might best serve as input for stereopsis and detection of directional motion, he emphasizes that "by and large the primitives that the processes operate on should correspond to physical items that have identifiable physical properties and occupy a definite location on a surface in the world" (p. 105); again, Marr proposes that zero-crossings might be appropriate (p. 106). A Barlowist might object that detection of zero-crossings is not a good idea because it does not lead to an efficient encoding of the retinal image (Eckert, Derrico, and Buchsbaum, unpublished). But Marr would be nonplussed: he did not view the visual system as having the function of encoding the retinal image for transmission to higher centers. Rather, he saw the retina as detecting distally-relevant features of proximal stimulation. In Marr's analysis, the image is not conceived simply as a two-dimensional pattern that must be encoded with minimum loss of information about the image itself, as if the problem of retinal encoding were one in video engineering.

An important moral of this brief comparison is that depending on one's conception of the function of vision, one will have differing conceptions of the properties that are encoded and hence represented in the process of neural transmission. Barlow, reflecting the inspiration of his approach in engineering and communication theory, emphasizes the reliable coding of generic physical properties present at a sender (such as spatial frequencies on the retina) so that the physical properties could be reconstructed at the receiver (in the visual cortex). Ultimately, he suggests, a completely reversible code, in which one could fully specify the causes of sensation, would depend upon a completed scientific (read: physical) description of sensory energy (1961a, 354-359). Detection of physical properties is primary; information about such properties subsequently enters into inferential reasoning about distal causes, and only through such "interpretation" does it yield representations of the distal (behaviorally relevant) world. Marr, by contrast, reflecting the inspiration of his approach in biology and psychology, looks to the biological significance of sensory systems and hence conceives of them as systems for representing organismically significant properties of the distal environment. These properties are described in a biological vocabulary: Marr (1982, 32) describes the functional organization of spider vision to detect mates by detecting a pattern of light characteristic of a conspecific of opposite sex; in early human vision, he emphasizes the representation of distal spatial structures of human scale. These biological properties of course have a physical realization; indeed, the physical properties of light, distal objects, and optical media place constraints on the mechanisms of visual representation and detection. Nonetheless, in Marr's conception, as in Gibson's, the senses are taken to be detectors of biologically relevant properties. And the regularities upon which sensory systems depend for their functioning—Marr's "physical assumptions" (1982, 44-51) and Gibson's ecological regularities (1966, ch. 1)—are not laws of physics, but local (earthly, or even niche-specific) regularities in the relations between organism and environment. The difference between the "physical instruments" and "perceptual systems" approaches can be articulated more fully by returning to the case of color.

3. Competing Task Analyses of Color Vision[2]

What is the function of color vision? No single answer can be given for all organisms. Even if the question is narrowed to the function of color vision in vertebrates, it still admits a variety of answers, depending on how widely one construes "function". Here I intend to leave aside various functions that color vision has assumed in complex human societies, and to focus on conceptions of the function of color vision explicit or implicit in the literature associated with the Barlow and Gibson/Marr approaches. These competing conceptions of the function of color vision lead to differing task analyses and hence to differing conceptions of the content of color perception, and in particular of the properties in the world that perceived colors represent.

Barlow and his followers ascribe to the color receptors in the retina, and to color vision itself, the function of encoding accurately (and hence discriminating among) spectral energy distributions in the visible range of the spectrum. As Barlow puts it, "For colour vision, the task of the eye is to discriminate different distributions of energy over the spectrum" (1982c, 635). Buchsbaum and Gottschalk echo the same point: "The visual system is concerned with estimating the spectral functional shape of the incoming colour stimulus" (1983, 92). A spectral energy distribution is a well-defined physical magnitude mapping wavelength against intensity within a given sample of light, and thereby producing a particular "spectral functional shape". According to Barlow's conception, an optimal color system would encode each spectral energy distribution differently. Our trichromatic system is good, but not perfect, at encoding various distributions. It discriminates many distributions, but for some physically distinct combinations of wavelengths it gives the same response. This is the phenomenon of metamerism, illustrated in Figure 1.[3] According to Barlow (1982c) and Buchsbaum and Gottschalk (1983), metameric matching (same response to distinct energy distributions) is a failure of the visual system, a loss of information. It counts as a failure in the context of a specific conception of the function of the color system: to discriminate among spectral energy distributions. This approach to color vision is consonant with Barlow's conception of the visual system as a physical instrument. It treats the problem of color encoding much as a video engineer might treat the problem of building a good television camera: as the problem of accurately encoding the physical characteristics of a signal within given dimensions of variation. It may not be the happiest conception of the task of vertebrate color vision.

Marr's (1982, 250-264) brief treatment of color is an extension of his general program: he ascribes to the color system the function of determining the color of a distal surface, where "color" is defined as the spectral distribution of the surface reflectance. Although he differs from Barlow and his followers in emphasizing the distal focus of color vision, he nonetheless adopts the common attitude that color is to be understood as a physically-defined property of the distal stimulus, in this case, its surface-reflective characteristics. As far as can be told from Marr's analysis, he considered it the function of color vision to represent each physically distinct surface reflectance differently. Hence, he too might consider surface metamerism to reveal a deficiency in color vision.

In this case Marr has not been true to the spirit of his approach, which enjoins the investigator to reflect upon empirically given regularities of the visual environment (as extant during the evolution of the visual system) in seeking to understand the functioning of the visual system. That is, he does not provide a set of "physical assumptions"—ecological regularities pertaining to the earthly environment—for color vision, corresponding to those he provided for the recovery of the spatial structure of distal surfaces (1982, 44-51). His analysis of color vision does not analyze the characteristics of the distal stimulus as fully as it might; rather, it simply accepts the usual spectrophotometric description.

What would correspond, in the case of color, to the "physical assumptions" of Marr's analysis of spatial perception? Consider the spatial case more fully. Marr's analysis sought to discover regularities of reflective surfaces in earthly environments that a visual system might be built to exploit in reducing the informational equivocation of the retinal image. Marr conjectured that the visual system might have evolved to make use of certain surface regularities, such as evenness of grain, which allow it implicitly to restrict the domain of permissible perceptual outcomes, thereby allowing the system, in environments for which the regularities hold, to recover successfully surfaces that it otherwise could not. In the case of color, a similar restriction would occur if it were supposed that the function of the color system is not to discriminate all possible spectral energy distributions, or surface reflectance characteristics, within the range of the visible spectrum, but rather is to permit useful discriminations among determinate, environmentally given classes of surface reflectances. Adjudication of the functional adequacy of color discrimination would require consideration of the actual distribution of surface reflectances and of the organismic significance of differences among objects with differing surface reflectances for a token species kind in its characteristic environment; it could not be carried out by an abstract analysis of spectral resolving power alone. (This is not to deny the usefulness of analyzing the system's abilities in this regard, on which see section 4.)

Assume that one function of color vision is to enhance the discriminability of objects and surface features, and that a particular color system serves to promote the discrimination of healthy green plants from soil and rocks. Such a color system must be able to discriminate the surface reflectances of green plants from other reflectances. In evaluating the proficiency of the system, it would be of no consequence if there were physically possible but not actual (nonplant) metameric matches to green plants that the system could not discriminate. As long as such potentially equivocal stimuli were not extant in the environment, the fact that the color system could not discriminate them would not imply a functional deficiency. Similarly, for the purpose of enhancing the discriminability of foliage, it would be of no consequence if various types of soil and rocks possessed metameric surface reflectances. Indeed, it might well be an advantage if classes of surfaces that were biologically equivalent in relation to a given organism appeared to be of the same color to that organism, despite spectrophotometric variations in surface-reflective properties (an advantage consisting in fewer irrelevant differences among sensory representations). Under this analysis, an adaptively better color system would be one that allowed the organism to do a better job of discriminating environmentally-significant objects or surface characteristics than could a conspecific with less sensitive or no color vision.

An approach to color vision of the sort just canvassed has in fact been taken by investigators who adopt a comparative and evolutionary approach. Jacobs (1981) is one such investigator. He approaches color vision with the working hypothesis that its primary function is to enhance object discrimination, and ultimately, object recognition, by providing an additional source of information, beyond achromatic differences in surface reflectances, for discriminating objects with characteristic surface compositions. He reports that achromatic luminance discrimination is very good in vertebrates, but that performance is enhanced by as much as one third when color is added (1981, 168-169). He repeats the familiar conjecture, harking back to Polyak (1957), that one function of color vision might be to aid in the discrimination of ripened fruit (taking on a red, orange, or yellow color) from the surrounding green foliage (Jacobs 1981, 160, 179). He concludes that "it is hard to believe that color visual systems did not evolve in concert with the particular spectral energy distributions that are critical that each species be able to discriminate", though he adds that firm evidence for this view has yet to be found (p. 174). In any event, the implied conception of the function of color vision is clear: its function is to facilitate discrimination among biologically relevant, environmentally given classes of object surfaces.

Jacobs (1981, 160) distinguishes three uses of color perception in the cognition of objects: 1) object detection, by which he means the discrimination of separate objects (say, a red object from its green surroundings), 2) object recognition, or the recognition of an object as being of a certain kind (say, an apple), and 3) signal properties of color, or the use of color to discover further properties of a kind of object (that the apple is almost ripe). Each of these uses goes beyond the bare perceptual representation of color itself; each involves further representational or cognitive capacities, from the simple cognition of something as an object, to its cognition as an object of a certain kind, or as an object of that kind possessing one variable property rather than another. These are all cases in which the perception of color aids in a further cognitive achievement, involving additional representational content beyond that of mere color perception. I wish to ask about the representational content of perceived colors (or of color sensations) themselves.

The preceding analysis of the function of color vision suggests that the various color perceptions have as their content groups of surface reflectances. Focusing on the case of the perception of the colors of surfaces of objects, let us say that the content of our color perceptions is various object surface-colors. "Surface colors" themselves are determined in relation to a particular kind of visual system: to have the same surface color is to appear the same to normal observers under prevailing conditions of natural illumination. As metamerism reveals, surface color cannot be equated with a physical property such as spectral reflectance, because, under the present definition, two objects can have the same surface color but different reflectances. Color, as a property of the surfaces of objects, is that group of (often physically disjunctive) surface reflectances that form an equivalence class in relation to a given visual system in its characteristic photic environment.[4] It is a relational property, which must be defined in relation to a specific type of visual system, and it does not constitute a well-formed physical kind. Indeed, from the point of view of physics various equivalence classes are heterogeneous; they are only grouped together as color kinds because of their effects on a token kind of visual system. Color shares this relational aspect with other biologically constituted properties, such as *nutrient*.

On this conception, color sensations have their own representational content, prior to the subsequent cognitive categorization of objects into kinds. Color vision functions to enhance the discriminability of surfaces of objects of different kinds, but it falls to higher cognitive processes to recognize those objects for the kinds of objects they are, and hence to perceive their utility or lack thereof. For surface-perceiving visual systems such as those of primates, presumably this is so even if in a given environment the only reason to discriminate red from green is in order to be able to discern ripe fruit amidst foliage. Differences of surface color are represented in the processes of early vision, which are processes for representing the surface layout of the environment. The content of the representations produced by such processes is limited to surface properties. Color adds a new dimension of discriminability, or a new class of represented surface differences. But even if only ripe fruit is red, the bare perception of *red* doesn't mean *ripe fruit* unless the system it is part of is itself specialized for fruit detection. But presumably, if detection of ripe fruit was a selective pressure on the development of color vision, the animals in question could already discriminate fruit on the basis of other surface-reflective properties (shape, texture, achromatic luminance). Adding color gave them an added surface feature to use in discrimination. The content assigned to perceived colors in this case pertains to the surface feature, not to the more sophisticated cognitive achievement of recognizing an object as food of a certain sort.

As this sketch makes clear, content assignment to color sensations relies on a task analysis of the color system, and this analysis itself implicitly contains and is guided by evolutionary conjectures. The disparate tendencies of Barlow's physical instruments approach and of the perceptual systems approach as developed in this paper are rendered explicit in their respective analyses of the evolution of trichromacy.

4. Evolution, Optimization, and Trichromacy

The physical instruments and perceptual systems approaches adopt quite different analyses of the shift from dichromacy to trichromacy during the course of mammalian evolution. Barlow and his followers address this topic by asking how well trichromatic systems discriminate among all possible spectral energy distributions within the visible spectrum. Trichromatic systems do well, though not perfectly, as metamerism shows. On the ecological conception adopted by the perceptual systems approach, the relevant query is not how good trichromacy is at covering the spectrum; rather, one should ask what new (or improved) discriminations of environmentally-significant object surfaces trichromacy allows. Both approaches appeal to evolution, for Barlow couches his analysis of trichromacy in terms of optimality, and he assumes that evolving systems are driven toward optimal performance (within resource constraints). Comparing Barlow's appeal to evolution with other evolutionary accounts of color vision will allow us to see both the usefulness and the limitations of his physical instruments approach.

Barlow and his followers evaluate trichromatic systems for their efficiency in coding color information. They ask, in effect, what the optimal coding for discriminating among spectral energy distributions might be, and then they test various assortments of receptors—mainly, trichromatic and tetrachromatic—for their sensitivity, concluding that a trichromatic system does remarkably well (Barlow 1982c, Buchsbaum and Gottschalk, 1983). The analysis is rigorous and ingenious. Thus, Barlow considers various ways in which distinct sinusoidal functions of wavelength and intensity ("comb-filtered" spectral energy distributions) can be resolved by color systems with various receptor properties. He concludes that, given the broad receptivity of human cones, little or no advantage in resolving such functions would be gained by having four types of cone rather than three. He offers this finding as an explanation for why trichromacy might have evolved in mammals (1982c, 641).

Barlow's argument appeals to the controversial notion that evolution optimizes. Recent work cautiously endorses the claim that optimizing selection has played a role in evolution (Travis 1989). Careful statements of the optimization approach, such as that of Maynard Smith (1978), avoid the assumption that organisms are in some general sense optimally designed. Maynard Smith characterizes optimization theories as attempts to formulate concrete hypotheses about the selective forces at work in shaping the diversity of living things. He contends that, when properly formulated, such hypotheses make specific assumptions of three kinds: 1) about the kinds of phenotypes that are possible given present species characteristics, 2) about what is optimized, and 3) about the mode of inheritance of the trait in question. As Maynard Smith (1978, 33-34) stresses, point 2) is a conjecture about the selection forces that have been at work in fixing a trait. He argues that candidate optimizing explanations must include as part of the hypothesis under test a specification of the trait that is being optimized and of the selection forces that operate upon it.

Optimization arguments have been applied to the evolution of the visual system with apparent success. Thus, Woodhouse and Barlow (1982, 136) have found that the spacing of receptors in the fovea is very near the theoretical limit set by the physical optics of the eye; they offer evolutionary optimization as the explanation. Others have found that photoreceptors in deep-sea fish have absorption properties that maximize photic sensitivity in a light-starved environment (Lythgoe 1979, 82-83). It is important that optimization arguments be constrained by assumptions of type 1), pertaining to possible phenotypes. Barlow (1982c) explains the lack of optimal spacing among the three types of cones in mammalian trichromats by appealing to the tradeoff between optimizing color sensitivity and spatial resolution. For the purpose of sampling spectral energy distributions, even spacing among the peak sensitivities would be desirable. As it happens, the "red" and "green" cones cluster at 535 and 570 nm while the "blue" cone is at 440 nm. Barlow speculates that the close similarity between red and green cones allows them to be pooled for the purposes of spatial resolution, thereby effectively doubling the number of foveal receptors (1982c, 642). Goldsmith (1991), in an extensive review of the interplay between optimization and constraints on phenotypic possibilities, offers a quite different explanation. The distinction between red and green cones is relatively recent (65 million years), and presumably stems from a mutation in the gene for an ancestral green cone. In some dichromatic species of New World monkeys, a related gene for the green cone regularly produces variants with a spread of 30-35 nm. Goldsmith conjectures that molecular genetic constraints fix the possible red and green cone variation in the range of 535-570 nm, and that this variation set the phenotypic boundaries within which selection for trichromacy could act. He concludes that "the capricious course of mammalian evolutionary history, rather than adaptation by natural selection, is probably primarily responsible for the spectral positions of the long- and mid-wavelength cone pigments" (1991, 317). (The blue cone, which has long been fixed in the genome, is not present foveally and hence doesn't enter the argument.) While further work may be needed to determine the relative roles of genetic constraint and selection pressures in this case, it is clear that optimization arguments should seek to specify the domain of phenotypic possibilities.

As section 3 has shown, characterization of what is being optimized may be even more fundamental. The optimization arguments of Barlow and his followers suggest that in color vision the trait to be optimized is the power to resolve individual spectral energy distributions or physical surface reflectances. They present no argument that the adaptiveness of color vision depends upon this ability; indeed, they provide no argument that this ability would be biologically adaptive. Instead, they simply assume that spectrophotometric resolution is the appropriate measure of performance. By contrast, I have emphasized the adaptive feature of color vision suggested by Jacobs

(1981), namely, increased discriminability of object surfaces. The appropriate measure of the adaptiveness of trichromacy over dichromacy on this conception hinges on new or enhanced discriminability of surfaces in an animal's environment.

The extant studies of the relation between environment and evolution in color vision do not support the Barlow approach. The evolution of distinct cone pigments, a prerequisite for color vision, probably was not initially driven by a demand for spectral differentiation. Pigments with a range of sensitivity maxima would increase the range of optic sensitivity of the eye, thereby permitting increased discriminations among surface reflectances without necessarily permitting differential spectral sensitivity. (In order for multiple cone types to be exploited for color discrimination, the available neural machinery must be sensitive to differences in activity between or among cone types; a system that summed across cone types would enjoy enhanced optic range without color vision—see Goldsmith 1991, 301-304, Jacobs 1981, 178-179.) In an extensive study of the relation between environmental conditions and cone types, McFarland and Munz (1975) concluded that in certain tropical fishes, a system of two cone types evolved in order to enhance the contrast between objects and their background in spectrally restricted underwater photic environments. In such environments, dark objects can best be discriminated with a receptor whose sensitivity matches the peak spectral transmission of sea water (which, at a depth of 25 m, is nearly monochromatic). Light objects can best be discriminated with a pigment whose sensitivity is offset from the background light. On the basis of comparing several species with different feeding habits and inhabiting different photic environments, McFarland and Munz argued that "the evolutionary selection of multiple photopic systems, and of color vision itself, is probably related to to the maximization of contrast against monochromatic backgrounds" (1975, 1045). Although little work has been done measuring the environment in which primate trichromacy evolved, Jacobs reports that investigation of the environment of one South American primate supports the view that the principal color discriminations are "among subtle shades of green or between contrasting colors and green" (Snodderly 1979, as quoted in Jacobs 1981, 175). Here, ecological considerations suggest that the finest discriminations are needed within the greens, and otherwise between the greens and the entire red/yellow end of the spectrum.

The physical instruments approach of Barlow and his followers is not without its place. Optimization arguments can help to guide the formulation of functional and evolutionary hypotheses; maximization of sensitivity to various physical properties of stimulation is one form of optimization. Rigorous specification of the physical capacities of sensory systems can thus arm the investigator with candidate hypotheses about function. It would be a mistake, however, simply to assume that there has been evolutionary pressure to optimize sensitivity for the stimulus dimensions of greatest interest to physicists or to video engineers. Judgments of function must be tested by taking the animal/environment relation into account. Only by learning how sensory systems actually are used can we determine what they are for.

5. Conclusion

Assume that the function of early vision in primates is to provide representations of adaptively-significant features of the distal environment. The task of the system should then be described by denominating the adaptive significance of the distal properties. On this conception, the visual system is not a physical instrument for recording the values of the proximal stimulus as described in physical optics. Rather, it is a perceptual system with the function of representing surfaces as an aid to detecting food and other significant objects. Extended to the case of color vision, this approach suggests that metameric matching need not entail a loss of information. If color vision has the function of discriminating particular environmentally-given classes of object surfaces, the mere possibility of metamerism may be irrelevant to an assessment of its performance. Further, environmentally extant metamers need not entail a discriminatory deficiency if their discrimination would not yield a biologically significant partition of environmental surfaces. The representational content of color perception might best be conceived in terms of partitions of object surfaces into discrimination classes that are conjoined with adaptively-significant objects, and not in terms of a physical specification of spectral energy distributions.

Notes

[1] An earlier version of this paper was presented at the Cornell Cognitive Science Symposium and to the Departments of Psychology and Philosophy of Dalhousie University, both in June, 1991. I thank each audience for their stimulating discussion. Larry Shapiro has given me helpful comments and criticisms on a more recent draft.

[2] For the purposes of this section, as in the rest of the paper, "color" is used to mean what color scientists call "hue", or "chromatic color" (Boynton 1990, Hurvich 1981).

[3] Metamerism can be defined for samples of light received at the eye, or for surfaces illuminated by a given light source; my discussion takes surface metamers as its primary example.

[4] This conception of color as a property of objects is similar to Beck's definition of color as "the property of light by which two objects of the same size, shape, and texture can be distinguished" (1972, 181; his definition extends to achromatic color). It is opposed to the philosophical analyses of Hilbert (1987, 99), who equates colors in objects with individual physical surface reflectances, and of Hardin (1988, 111-112), who contends that, failing a reduction of color to a physical property such as surface reflectance, it should be categorized as an illusion.

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