the concept of the universality of the single-peaked, tuned receptor.

After allowing for the above errors, I interpret Hillman's response as a claim that my hierarchical ordering of the tuned receptor as one part of traditional color theory was inappropriate and misleading. Indeed, Hillman says that: "The essence of the Palmer-Young paradigm . . . has *nothing to do* [italics mine] with the shape or narrowness of these curves." This assertion is only intelligible to me (although not necessarily correct) if the word "paradigm" in the preceding quotation is read as Hillman's "classical color vision paradigm" and not as the tuned-receptor paradigm actually described by me. The real issue would have been more clearly defined had Hillman simply made this claim more directly and then proceeded to document it. Unfortunately, Hillman's claim is not supported by any documentation from the extensive literature on color vision but is instead buttressed solely by Hillman's comment "that [he knows] of no claim to the contrary in the literature."

This claim and its consensual validation are quite extraordinary: My review incorporated explicit quotations from Palmer and Thomas Young which, ab initio, described the tuning of the receptor spectral sensitivity function as well as a quotation from MacNichol which is representative of current thinking on this problem. These quotations were intended to be representative rather than exhaustive; however, it would not be difficult for me to present the readers of *Science* with many more "claims to the contrary." But the quotations in the original article were already incompatible with the phrase: "nothing to do." Hillman's difficulty in accurately reading what I said seems to extend to what Palmer and Young said as well; Hillman does not distinguish between "shape" and "narrowness" (in the bandwidth sense). As I said in my review, a tuned receptor ". . . is maximally sensitive to a given wavelength and progressively less sensitive to other wavelengths" (*1*, p. 269). The narrowness (in the bandwidth sense) is not a part of this definition, nor was it a part of Palmer's and Young's descriptions.

It has been necessary to deal with these issues at length because they do seem to represent views that now have some currency. In my view, it would be much better if we examine the new data, recognize that they do differ from our expectations, and concentrate on exploring the substantive implications of this unexpected outcome.

Hillman does make several substantive points: First, he says that: "The intensities required for substantial pigment bleaching are well known and accessible to most visual researchers." Had Hillman tried to document this point by returning to the primary literature cited in my article, he would have had difficulty extracting the absolute intensities actually used in such experiments. Until the recent introduction of silicon photodetectors, absolute calibrations of monochromatic lights were so difficult that investigators in this area frequently presented only relative data. For this reason, my own comments on this point were presented cautiously and tentatively. Second, Hillman's belief that rapid pigment regeneration provides a more likely explanation for these bleaching failures also requires documentation from the primary literature. There are several ways of carrying out such bleaching experiments and Hillman's explanation could only be valid for sequential rather than intercurrent bleaching experiments. Third, Hillman's speculation about two interconvertible states of one pigment carries with it the necessary corollary that transitions from either state to the other state are, in most species, capable of producing *identical* membrane excitations; this corollary derives from the evidence presented in the review that there is no specific effect of color on the receptor response in most preparations. As noted in my review, the preparations studied by Hillman are unusual. These substantive points raised by Hillman may ultimately be shown to be correct, but we need to be provided with considerable additional evidence before we can evaluate their validity.

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Mitochondrial Morphology

Hoffmann and Avers (*1*) reported results of their studies of mitochondrial morphology in bakers' yeast, *Saccharomyces cerevisiae*, which indicate that cells of a diploid strain, iso-N, contain but one large, branched mitochondrion per cell regardless of the functional state of the organelles. They urged caution in drawing conclusions about mitochondrial number, size, and shape when random-section analysis is used, and they suggested that the situation observed by them may be quite general. Thus, not just yeast but many eukaryotic cells may contain a unit mitochondrion instead of the larger numbers, as often cited.

Our data on quantitative estimations of mitochondrial numbers in yeast are somewhat at variance with those of Hoffmann and Avers (*1*) and can be used to reassess the unit mitochondrion hypothesis.

We have examined, by serial section analysis, cells of four (two diploid and two haploid) strains of *S. cerevisiae*, all of which are, to our knowledge, unrelated to iso-N. We find that mitochondrial shape and number per cell are highly strain dependent; furthermore, in contrast to Hoffmann and Avers' statement we find that the parameters shape, number, and mitochondrial mass are modified by altering cellular physiology and ploidy. Cells of all strains contained few (one to seven) large mitochondria *only* while they were growing exponentially on glucose (glucose-repressed); cells in the exponential phase that were grown in lactate (or glycerol) (derepressed) contained a much larger number of small mitochondria (25 in the case of one diploid strain and more than 100 in another). Under these conditions each of the isochromosomal haploids used in the construction of the first diploid contained only half the number of otherwise identical mitochondria per cell. The percentage of cellular mass constituted by the mitochondria was constant in all three strains. We conclude that, although cell mass increases with ploidy, the relative mitochondrial mass (as a percentage of total mass) and the mitochondrial number are determined only by qualitative differences in the cellular (mitochondrial) physiology, which in our strains may vary by as much as 4-fold and 30-fold, respectively.

Therefore, the data of Hoffmann and

Avers probably demonstrate only that iso-N represents one extreme of mitochondrial morphological polymorphism in *S. cerevisiae*; our data show that the hypothesis of a generalized unit mitochondrion as a morphological entity cannot be held generally valid even when applied to this organism (*2*). It is, of course, possible that mitochondria in a cell may constitute a functional unit even when they are not morphologically unified. If discrete mitochondria are capable of rapid and random fusion and fission [as has been observed in some organisms (*3*)], then all or a group of organelles in a cell may still constitute a single functional or genetic unit.

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While strain differences in yeast may explain some disparities in results reported by us (*1*) and those found by Grimes, Mahler, and Perlman, it is difficult to compare the data without more information concerning their methods of preparation and analysis. It would be important to know if three-dimensional reconstructions were made from intact ribbons of serially sectioned cells, and how many such series were analyzed for each strain in repressed and derepressed growth. We analyzed nine cells from complete series of thin sections earlier (*1*) and have since analyzed five more iso-N cells from aerobic cultures. All 14 cells contained branching, tubular mitochondrial forms, and only one of these showed two mitochondrial masses; all others contained a single giant mitochondrial network.

We found no differences in mitochondrial number or morphology for cells growing exponentially or in stationary phase (*1*); Grimes *et al.* mention only exponentially growing cells. We found no differences in mitochondria from repressed cultures compared with ethanol-derepressed cells (*1*). Grimes *et al.* neglected to mention the morphology of the mitochondria in their materials. This is a crucial comparison, especially in considering morphometric methods and artifacts of preparation. It would be important to know whether cells were prefixed in glutaraldehyde, and if glusulase was used to digest the cell wall before fixation. According to our observations and those of others (*2*), mitochondrial membrane continuity is modified by prior treatment with glusulase usually resulting in more than one mitochondrial mass in the cell.

Morphometric analysis (*3*) showed one branched, tubular mitochondrion in early stationary-phase yeast cells photographed with the high-voltage electron microscope. Their three-dimensional reconstructions were made from six to ten serial thick sections of whole cells, with computer-assisted analysis. Brandt *et al.* (*4*) reported branching, tubular mitochondrial structure in normal adult rat liver cells. In addition to these recent studies, earlier published reports had shown tubular mitochondrial morphology in algae (*5*), fungi (*6*), and insects (*7*). Far from being a peculiarity of one strain of yeast as suggested by Grimes *et al.* it would appear that tubular complexes rather than simple rod-shaped mitochondria are characteristic of many eukaryotic cells and species. Each study has demonstrated the presence of one or a few mitochondria rather than the hundreds or thousands that had been assumed from random-section analysis or when three-dimensional reconstructions were not attempted.

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