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on NE responses of Purkinje cells have been established (1, 2, 5, 7, 10). Although individual pharmacological results cannot provide definitive evidence, all results obtained are consistent with our proposal.

21. E. G. Anderson, H. L. Haas, L. Hosli, *Brain Res.* **49**, 471 (1973); of 68 cells tested, 79 percent were depressed by cyclic AMP.
22. B. S. Bunney and G. K. Aghajanian, personal communication; of 27 cells tested in caudate nucleus, nucleus accumbens, and olfactory tubercle, 89 percent were depressed by cyclic AMP.

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The Tuned-Receptor Paradigm

Wasserman (1) presents an excellent systematic review of the spectral sensitivities of invertebrate photoreceptors, but he has built out of them a straw man in his attempt to show that "the tuned-receptor paradigm is not universally valid." His demonstration arises from his own distortion of the classical color vision paradigm. This paradigm, as he states clearly enough, is that "color discrimination must involve a comparison of the relative responses in a set of receptors. An array of paradigmatic receptors tuned to different portions of the spectrum will . . . produce different relative receptor responses to lights of different wavelengths." Since "this is also true of a contraparametric system," it is not clear in what sense a narrowly tuned receptor is paradigmatic while a broadly tuned one is contraparametric. The essence of the Palmer-Young [1, references 2 and 3] paradigm is surely the necessity for the intercomparison of the responses of receptors with different tuning curves, and has nothing to do with the shape or narrowness of these curves. I know of no claim to the contrary appearing in the literature. The existence of a limited continuum of receptor types, arbitrarily classified into α and β groups, is no evidence for qualitatively different color vision mechanisms. The paradigm-contraparametric formulation therefore appears to me a false dichotomy.

In this context, I fail to understand the author's statement that the tuning notion is "distinct from" the concepts that Palmer's and Young's "particles" correspond to light sensitive pigments and that "information about color is not extracted from the response of one receptor but by comparing the relative responses of receptors which differ in their sensitivities to different spectral stimuli." The tuning notion, as I understand it, clearly embraces these concepts.

Finally, I am surprised at the suggestion that most authors who failed to find selective bleaching of one of the two peaks of the β -receptors did so for lack of adaptation intensity. The intensities required for substantial pigment bleaching are well known and accessible to most visual researchers. Rapid regeneration of the pigment or pigments (2) appears a more likely explanation. I also note, in addition to the explanations offered, that the two spectral peaks may represent two interconvertible states of a single pigment rather than two independent pigments (3).

There is no doubt that scientific investigators sometimes "adhere to a paradigm even when there is evidence that is incompatible with the paradigm," but Wasserman presents no such evidence.

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Evidence incompatible with an established concept is frequently ignored or rejected at first. Later, if this new evidence becomes compelling, it is often said, unfortunately, that the evidence really conforms with that which was always known. My purpose in writing my review of invertebrate receptors (1) was to draw attention to new evidence that I thought had become compelling; I had hoped that a review of this new evidence would stimulate a serious consideration of its implications for receptor function. Hillman's response (2) to my review is that I misrepresented the prior belief

structure and that a proper portrayal of these prior beliefs would be consistent with the evidence presented in my review. Hillman's criticism was consensually validated by three distinguished referees and has to be taken as a statement of widely held views. Obviously, if we are to make future substantive progress in this area, we must analyze Hillman's position carefully. Unfortunately, Hillman has not made the clearest possible case for his position; his response exhibits a number of errors, including the logical error of equivocation. A careful analysis is therefore doubly required.

From the title to the end of my review, I explicitly distinguished between the subordinate concept of the tuned-receptor paradigm, which referred solely to the shape of the receptor spectral sensitivity function, and the superordinate concept of color vision in general, which subsumes auxiliary subordinate concepts (such as the concept that color vision involves a comparison between receptors). In my review, the term "paradigm" never referred to anything other than the shape of the receptor function.

The assertion that I created a "straw man" in my review of invertebrate photoreceptors derives from the confusion created by Hillman's equivocation between the tuned-receptor paradigm described by me and the "classical color vision paradigm" described by him. The equivocation is to be found in Hillman's third sentence which represents me as "clearly stating" something that I never did say. The further statement that ". . . it is not clear in what sense a narrowly tuned receptor is paradigmatic . . ." rests on this earlier equivocation: Clarity depends on keeping the terms of the discussion consistent.

Hillman's subsequent complaint that he ". . . fail[s] to understand . . ." me is a quite understandable result of this equivocation-dependent lack of clarity, which has made it difficult for him accurately to read my review. For example, he asserts that I argued for ". . . qualitatively [italics mine] different color vision mechanisms." I actually said the opposite, namely, that β ". . . receptors undoubtedly would involve a color vision system that is quantitatively [italics added] different . . ." (1, p. 269). I never said nor did I ever imply that the data under review disconfirmed any concept of color theory other than

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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References and Notes

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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