References and Notes

1. K. Takahashi, K. Hayashi, T. Kinoshita, *Plant Physiol.* **159**, 632–641 (2012).
2. T. Kinoshita, K. Shimazaki, *EMBO J.* **18**, 5548 (1999).
3. G. Pearce, D. S. Moura, J. Stratmann, C. A. Ryan Jr., *Proc. Natl. Acad. Sci. U.S.A.* **98**, 12843–12847 (2001).
4. M. Haruta, C. P. Constabel, *Plant Physiol.* **131**, 814–823 (2003).
5. M. Haruta, G. Monshausen, S. Gilroy, M. R. Sussman, *Biochemistry* **47**, 6311–6321 (2008).
6. J. L. Matos, C. S. Fiori, M. C. Silva-Filho, D. S. Moura, *FEBS Lett.* **582**, 3343–3347 (2008).
7. J. Wu *et al.*, *Plant J.* **52**, 877–890 (2007).
8. J. V. Olsen *et al.*, *Cell* **127**, 635–648 (2006).
9. G. Pearce, Y. Yamaguchi, G. Munske, C. A. Ryan, *Peptides* **31**, 1973–1977 (2010).
10. K. G. Kline-Jonakin, G. A. Barrett-Wilt, M. R. Sussman, *Curr. Opin. Plant Biol.* **14**, 507–511 (2011).
11. J. J. Sanchez-Serrano, Arabidopsis *Protocols* (Springer, New York, 2013).
12. P. J. Bertics *et al.*, *J. Biol. Chem.* **263**, 3610–3617 (1988).
13. J.-M. Escobar-Restrepo *et al.*, *Science* **317**, 656–660 (2007).
14. H. Lindner, L. M. Müller, A. Boisson-Dernier, U. Grossniklaus, *Curr. Opin. Plant Biol.* **15**, 659–669 (2012).
15. K. Chae *et al.*, *Plant J.* **71**, 684–697 (2012).
16. D. J. Cosgrove, Z. C. Li, *Plant Physiol.* **103**, 1321–1328 (1993).
17. T. Nomura *et al.*, *J. Biol. Chem.* **280**, 17873–17879 (2005).
18. J. Hu *et al.*, *Plant Cell* **20**, 320–336 (2008).
19. D. Lee, D. H. Polisensky, J. Braam, *New Phytol.* **165**, 429–444 (2005).
20. G. Felix, J. D. Duran, S. Volko, T. Boller, *Plant J.* **18**, 265–276 (1999).
21. T. S. Nühse, A. R. Bottrill, A. M. E. Jones, S. C. Peck, *Plant J.* **51**, 931–940 (2007).
22. E. L. Rudashevskaya, J. Ye, O. N. Jensen, A. T. Fuglsang, M. G. Palmgren, *J. Biol. Chem.* **287**, 4904–4913 (2012).
23. M. Haruta *et al.*, *J. Biol. Chem.* **285**, 17918–17929 (2010).
24. A. Goossens, N. de la Fuente, J. Forment, R. Serrano, F. Portillo, *Mol. Cell. Biol.* **20**, 7654–7661 (2000).
25. G. Wu, E. P. Spalding, *Proc. Natl. Acad. Sci. U.S.A.* **104**, 18813–18818 (2007).

Acknowledgments: We thank H. Burch for technical assistance; M. Ivancic for advice on mass spectrometry data analyses; R. Wrobel, B. Fox (National Institute of General Medical Sciences Protein Structure Initiative, U54 GM074901), and S. Litscher for assistance with *E. coli* expression experiments; G. Barrett-Wilt for mass spectrometric instrumentation; M. A. Beg, M. Hoffman, and O. Ginther for assistance with the iodination experiments; F. Li for advice on *Nicotiana* expression; S.-H. Su and the Plant Imaging Center for assistance with microscopy; and W. Aylward for advice on Etruscan mythology. Supported by NSF grant MCB-0929395 and U.S. Department of Energy Office of Basic Energy Sciences grant DEFG02-88ER13938 (M.R.S.), NSF grant DGE-1256259 (K.S.), and the National Human Genome Research Institute–University of Wisconsin Genomic Sciences Training Program (NIH grant 5T32HG002760, B.B.M.). Phosphoproteome data are deposited in PRIDE (Proteomics Identification Database) with accession numbers 31655 to 31656 and ProteomeXchange accession number PXD000515. Microarray data are deposited in ArrayExpress (E-MEXP-3994).

Supplementary Materials

www.sciencemag.org/content/343/6169/408/suppl/DC1
Materials and Methods
Figs. S1 to S14
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9 August 2013; accepted 17 December 2013
10.1126/science.1244454

A Different Form of Color Vision in Mantis Shrimp

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One of the most complex eyes in the animal kingdom can be found in species of stomatopod crustaceans (mantis shrimp), some of which have 12 different photoreceptor types, each sampling a narrow set of wavelengths ranging from deep ultraviolet to far red (300 to 720 nanometers) (*1*–*3*). Functionally, this chromatic complexity has presented a mystery (*3*–*5*). Why use 12 color channels when three or four are sufficient for fine color discrimination? Behavioral wavelength discrimination tests (Δλ functions) in stomatopods revealed a surprisingly poor performance, ruling out color vision that makes use of the conventional color-opponent coding system (*6*–*8*). Instead, our experiments suggest that stomatopods use a previously unknown color vision system based on temporal signaling combined with scanning eye movements, enabling a type of color recognition rather than discrimination.

Stomatopods are benthic marine crustaceans that are generally found in tropical and temperate waters. Their compound eyes possess the largest number of photoreceptor types known in any animal [between 16 and 21 different receptors in some species (*1*, *3*, *9*)], allowing them to discriminate color (*5*) as well as both linear and circular polarized light (*3*, *10*). Such retinal complexity is unrivaled in the animal kingdom, although papilionid butterflies may have up to eight spectral sensitivities (*11*). Theoretical approaches have predicted that between four and seven photoreceptor types are all that is needed to accurately encode the colors of the visible spectrum (*12*–*14*). The four-channel (tetrachromatic) solution that birds and reptiles use to sample a spectral range from 300 to 700 nm is optimally arranged to encode the known colors within this range. Where the spectrum examined loses the ultraviolet (UV) or red end, three photoreceptors suffice, and trichromacy is the solution that many animals exhibit (*12*).

Our question was therefore, why do the stomatopods use 12 different photoreceptors to encode color? Before the experiments described here, Marshall *et al.* (*5*) demonstrated that stomatopods are capable of simple color discriminations based on color-card tests, similar to those devised by Carl von Frisch for bees and now used widely for a number of animals (*15*). We hypothesized two alternative mechanisms for color information processing in stomatopods: (i) a multiple dichromatic color-opponent system (as described below), or (ii) the binning of colors into 12 separate channels, without any between-channel comparisons (*4*, *16*).

Like butterflies, stomatopods have a variety of colorful body patterns, even using fluorescence to enhance color display (*17*). Furthermore, many of these species inhabit shallow coral reefs, one of the most colorful environments on Earth. The stomatopod's colors are thought to be involved in particularly complex communication systems, both between and within species (*18*), but little of this complexity requires a 12-dimensional color space to distinguish the colors available. Osorio *et al.* (*19*) speculated that stomatopods use their color sense to make reliable and quick judgements of color signals from conspecifics under changing light conditions, their steep-sided spectral sensitivities allowing particularly good color constancy. This would require comparison of the spectrally adjacent sharply tuned spectral sensitivities, and there is some anatomical evidence supporting this idea (*6*).

Stomatopod eyes are made up of a dorsal and ventral hemisphere, divided by a region of distinct

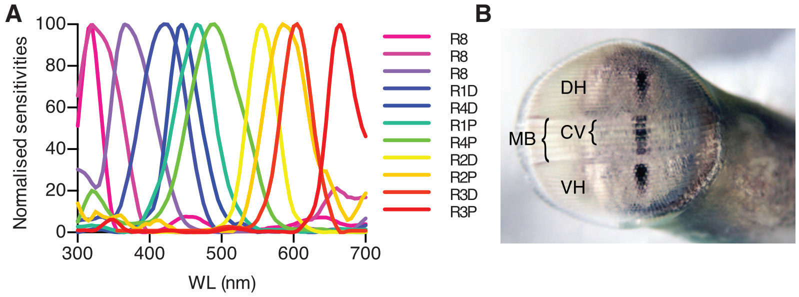

Fig. 1. (A) Spectral sensitivities of *H. trispinosa*. Spectral sensitivity curves obtained from intracellular electrophysiological recordings. The figure shows smoothed data (four neighbors on each side, second-order polynomial), normalized to 100% (see table S1). (**B**) Eye of *H. trispinosa.* Showing the dorsal hemisphere (DH) and ventral hemisphere (VH), divided by the midband (MB) containing the color receptors in the four top rows (CV).

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