

Correspondence

Spectral filtering enables trichromatic vision in colorful jumping spiders

Daniel B. Zurek^{1,*}, Thomas W. Cronin²,
Lisa A. Taylor^{1,3,4}, Kevin Byrne¹,
Mara L.G. Sullivan⁵,
and Nathan I. Morehouse^{1,*}

Jumping spiders (family Salticidae) are masters of miniature vision, achieving higher spatial resolution in relation to body size than any other animal [1]. While most members of this family do not use color in intraspecific communication, several genera serve as emerging examples of rapid evolutionary radiation in sexual display coloration [2]. These include the Australasian *Maratus* ‘peacock’ spiders, and the American genus *Habronattus*. Males of these genera are often brilliantly colored on body surfaces they showcase to females during elaborate courtship dances (Figure 1A). However, molecular and electrophysiological data suggest that color vision in the acute ‘principal’ eyes of most jumping spiders is based on only two types of photosensitive pigment, one sensitive to ultraviolet (UV) light, the other to green light [3–5]. We report here that *Habronattus* jumping spiders may achieve substantially better color vision via a mechanism previously unknown in spiders: the shifting of sensitivity of a subset of their photoreceptors from green to red via a long-pass filter positioned in their retina. Trichromatic vision resulting from this filter system should markedly enrich these animals’ perception of color, including reds, oranges and yellows often found in their courtship displays.

Like all salticids, *Habronattus* has a modular visual system formed by four specialized eye pairs. The large principal eyes serve spatial vision and also support color vision. Their small retinas have a characteristic boomerang shape (Figure 1B,C), and are composed of four photoreceptor tiers (Figure 1D–F) [6]. In salticids with known principal retina sensitivities, the two proximal tiers (1 and 2) consist

of a dense, regular mosaic of green-sensitive photoreceptors, while the two distal tiers (3 and 4) are UV-sensitive with a less organized mosaic structure [4,5].

We investigated the sensitivity of the photoreceptors in the principal eye retinas of *Habronattus pyrrihrix*, a species in which males display green, cream, orange, and red ornaments to females during complex courtship sequences (see Supplemental Movie S1). Previous research has established that long-wavelength colors

play a role in foraging and courtship [7,8]. However, the dichromatic vision of closely related species would provide limited color perception for short wavelength colors, and no ability to discriminate long wavelength colors. Such poor spectral discrimination seems mismatched to the diverse color palette of *H. pyrrihrix* and its congeners.

Using spectrophotometric techniques, we determined transmittance of optical structures

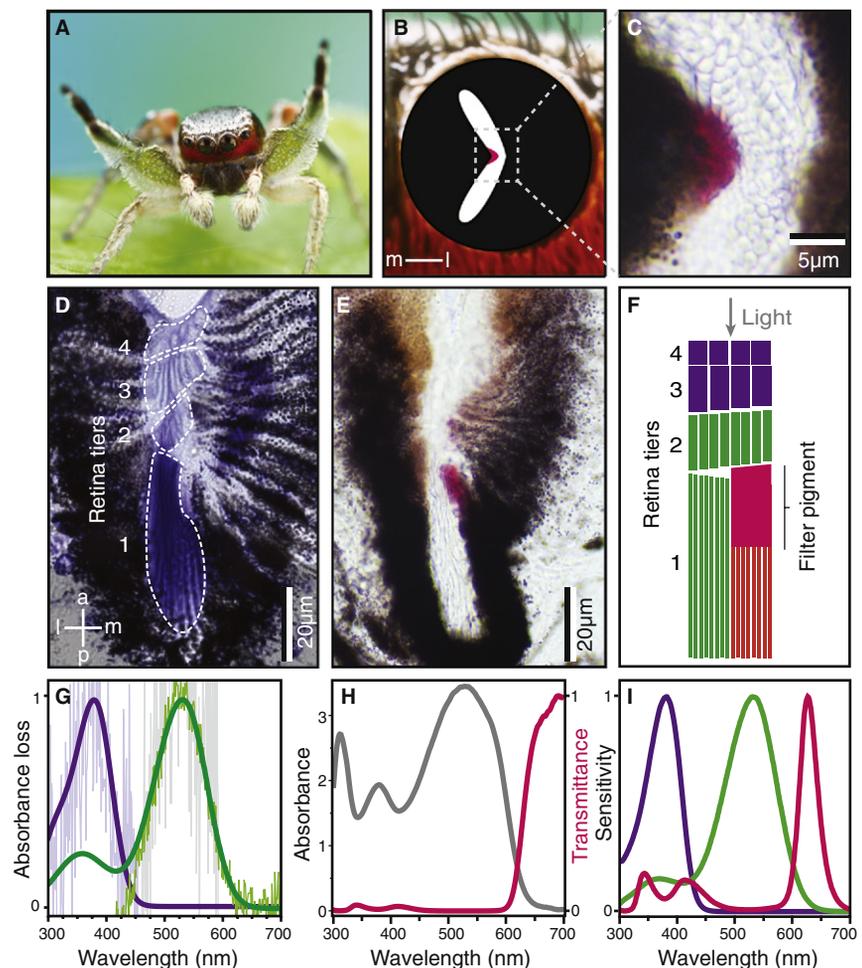


Figure 1. Spectral filtering of *Habronattus pyrrihrix* photoreceptors.

(A) Courtship display of male *H. pyrrihrix* (photo: Colin Hutton). (B) Boomerang-shaped retinas superimposed on principal eye lenses, small red area indicates filter position. (C) Red filter pigment visible in unstained coronal cryosection (14 μm thick) of the principal retina. (D) Tiered retina structure in thin horizontal section of principal retina: a, anterior; p, posterior; l, lateral; m, medial. (E) Red filter pigment visible in unstained horizontal cryosection (14 μm thick) of the principal retina. (F) Diagram of tiered arrangement of green and UV-sensitive photoreceptors in longitudinal view of principal retina center of *H. pyrrihrix*. Red area indicates long-pass filter pigment, shifting sensitivity of tier 1 photoreceptors from green to red. (G) Normalized visual pigment absorbance difference spectra in proximal (green, $n = 11$) and distal (violet, $n = 2$) retinal tiers with best-fit templates. (H) Absorbance (grey) and transmittance (red) of filter at maximal observed thickness ($n = 6$). (I) Predicted sensitivity of three photoreceptor classes, UV (377 nm), green (530 nm), red (626 nm), after light filtering by optics and filter pigment. All axes in G–I are linear.

in the light path (Supplemental Results), and measured absorbance spectra of visual pigments in unfixed, cryosectioned retinas. Consistent with previous work, we found two photopigments (Figure 1G), one green-sensitive (tiers 1 and 2, $\lambda_{\max} = 530$ nm) and one UV-sensitive (tiers 3 and 4, $\lambda_{\max} = 377$ nm). UV-sensitive photoreceptors exhibited a second peak at ~ 530 nm, similar to the double-peaked UV-green photoreceptors described previously in other species [3]. In addition, we found an unexpected, ruby-red photostable pigment positioned in the light path of a population of foveal tier 1 rhabdoms (Figures 1C–F and Supplemental Figure S1B,C). The pigment is found in both sexes, and functions as a spectral long-pass filter (Figure 1H) that allows only red light to reach the underlying green-sensitive photoreceptors. This would produce a large shift of their λ_{\max} from 530 nm to 626 nm, making this spatially acute part of tier 1 specifically sensitive to red light. As a result, these now ‘red’ photoreceptors provide a third color channel (Figure 1I). Another unique feature of this filter system is its restriction to a small region of the retinal center, which results in a trichromatic area surrounded by an otherwise dichromatic retinal field.

In most eyes where they occur, spectral filters function to sharpen the sensitivity peaks of their associated photoreceptors, but members of some taxa, such as butterflies and stomatopods, multiply spectral sensitivity using filtering [9]. This strategy comes with a decrease in sensitivity of filtered photoreceptors. Consistent with this, a recent study of *H. pyrithrix* shows that behavioral responses to color stimuli weaken under dim light [8]. However, the bright habitats typical of *Habronattus* species should allow filter-based trichromacy to functionally increase the discriminable color gamut, thereby aiding color-based prey selection and female assessment of colorful male courtship displays. We simulated perceived contrasts of four male color ornaments using a dichromatic (UV, green) and a trichromatic (UV, green, red) model of the *H. pyrithrix* visual system. Compared to a dichromatic system, adding a third, red-sensitive receptor increases discriminability of long

wavelength colors (for example, it more than doubles the perceptual distance between green 1st legs and orange 3rd legs; see Supplemental Figure S2). However, because of the spatial extent of the filter, only a small area in the center of the visual field of each eye is trichromatic. This suggests that complex male displays may present specific challenges for female color vision, and that the gaze movements observed in salticids [10] may play a role in extracting spectral information from the visual scene.

Is filter-based trichromacy specific to *H. pyrithrix* limited to certain genera that particularly profit from increased color discrimination, or common to all jumping spiders? We found similar filters in four other *Habronattus* species selected from across the *Habronattus* phylogeny (*H. conjunctus*, *H. dossenus*, *H. virgulatus*, *H. hirsutus*; Figure S1A). Thus, filter-based trichromacy may be a general feature of this genus. However, such filters are absent in other salticid genera we sampled, such as *Salticus* and *Phidippus*, which do not use color ornaments during courtship. This suggests that a shift from dichromacy to trichromacy may have played an important role in the evolution of the distinctively colorful courtship displays of *Habronattus* jumping spiders. Future studies will examine if improved color discrimination ability, conveyed by intraretinal filtering, represents a key innovation that enabled the extensive radiation and success of the genus *Habronattus*.

In conclusion, our study offers a solution to the long-standing puzzle of how some salticids see color and opens the door for future studies on co-evolution of color vision and coloration. Future work should focus on the taxonomic extent of this filter-based trichromacy, as well as the adaptive benefits most likely to have favored its evolution. In particular, we suggest that trichromatic species may realize significant advantages when foraging in prey communities that include red and yellow aposematic prey.

SUPPLEMENTAL INFORMATION

Supplemental information contains experimental procedures and supplemental results, two figures, and one movie and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2015.03.033>.

ACKNOWLEDGEMENTS

We thank Damian Elias and Wayne Maddison for sharing field site coordinates, Donna Beer Stolz and the technical staff of the Center for Biological Imaging for assistance with histological methods, and Riley Timbs and Zarreen Amin for supplementary cryosectioning and microscopy. Funding for this work was provided by the University of Pittsburgh and the Air Force Office of Scientific Research (FA9550-12-1-0321).

REFERENCES

- Harland, D.P., Li, D., and Jackson, R.R. (2012). How jumping spiders see the world. In *How Animals See the World: Comparative Behavior, Biology, and Evolution of Vision*, O.F. Lazareva, T. Shimizu, and E.A. Wasserman, eds. (New York: Oxford University Press), pp. 133–164.
- Maddison, W.P., and Hedin, M. (2003). Phylogeny of *Habronattus* jumping spiders (Araneae: Salticidae), with consideration of genital and courtship evolution. *Syst. Entomol.* 28, 1–22.
- DeVoe, R.D. (1975). Ultraviolet and green receptors in principal eyes of jumping spiders. *J. Gen. Physiol.* 66, 193–207.
- Blest, A.D., Hardie, R.C., McIntyre, P., and Williams, D. (1981). The spectral sensitivities of identified receptors and the function of retinal tiering in the principal eyes of jumping spiders. *J. Comp. Physiol. A* 145, 227–239.
- Nagata, T., Koyanagi, M., Tsukamoto, H., Saeki, S., Isono, K., Shichida, Y., Tokunaga, F., Kinoshita, M., Arikawa, K., and Terakita, A. (2012). Depth perception from image defocus in a jumping spider. *Science* 335, 469–471.
- Land, M.F. (1969). Structure of the retinae of the principal eyes of jumping spiders (Salticidae: Dendryphantinae) in relation to visual optics. *J. Exp. Biol.* 51, 443–470.
- Taylor, L.A., Maier, E.B., Byrne, K.J., Amin, Z., and Morehouse, N. I. (2014). Colour use by tiny predators: jumping spiders show colour biases during foraging. *Anim. Behav.* 90, 149–157.
- Taylor, L.A., and McGraw, K.J. (2013). Male ornamental coloration improves courtship success in a jumping spider, but only in the sun. *Behav. Ecol.* 24, 955–967.
- Cronin, T.W., Marshall, J., Johnsen, S., and Warrant, E. (2014). Visual pigments and photoreceptors. In *Visual Ecology* (Princeton, New Jersey: Princeton University Press), pp. 37–65.
- Land, M.F. (1969). Movements of the retinae of jumping spiders (Salticidae: Dendryphantinae) in response to visual stimuli. *J. Exp. Biol.* 51, 471–493.

¹Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA 15260, USA.

²Department of Biological Sciences, University of Maryland Baltimore County, Baltimore, MD, USA. ³Entomology and Nematology Department, University of Florida, 1881 Natural Area Dr., Gainesville, FL 32611, USA. ⁴Florida Museum of Natural History, University of Florida, 3215 Hull Rd., Gainesville, FL 32611, USA. ⁵Center for Biologic Imaging, Department of Cell Biology, University of Pittsburgh School of Medicine, Pittsburgh, PA 15260, USA.

*E-mail: dbz1@pitt.edu (D.B.Z.), nim@pitt.edu (N.I.M.)