CORRESPONDENCE



Spiders possess tapeta lucida to enhance photodetection in their inverse secondary retinas but not in their everse primary retinas

Sir,

In volume 44, issue 10 of this journal, Vee et al. proposed that the tapetum lucidum-the reflective structure found in the retina of some nocturnal vertebrates-evolved as a compensatory co-adaptation for the inverted nature of the vertebrate retina.^[1] The tapetum enhances the sensitivity of visual perception through the reflection of photons that initially pass through the photoreceptor layer unabsorbed back toward the anterior direction. This gives these photons a second chance to collide with a photoreceptor, boosting photosensitivity under low illumination, and producing the phenomenon known as "eye shine" when viewed under high light conditions (e.g., the headlights of a car).

The photoreceptors of vertebrates are oriented in the posterior direction such that they appear backwards compared to the photoreceptors of cephalopods (octopuses, squids, and nautiloids). This backward-facing arrangement places structural constraints on the histology of the vertebrate retina and limits its photosensitivity as a result of light scattering and absorption by the cellular components that precede the photoreceptive segments in the path of incoming light. In contrast, with their photoreceptors oriented in the anterior direction, cephalopod retinas form a densely packed and unbroken sheet of photosensitive tissue.

While the tapetum has never been discovered in a cephalopod, Vee et al. show that the tapetum has evolved dozens of times among vertebrates with a striking degree of diversity in the histological arrangements and even their chemical composition, indicating homoplasy and repeated convergent evolution. Thus, the hypothesis holds that the tapetum has evolved many times throughout the vertebrate clade because of the limitations and suboptimal arrangement of the inverted retina, while the cephalopod retina, with the superior sensitivity of its everse design, has no need for a tapetum.

There is an additional piece of corroborating evidence for this hypothesis left undescribed by Vee et al. in relation to their thesis. As noted by the authors, some spiders also possess tapeta. Similar to vertebrates, spider visual systems are composed of simple "camera" eyes containing a single corneal lens that focuses light on an underlying retina.^[2] However, spider eyes come in two forms: a single pair of "principal" eyes, and up to three pairs of "secondary" eyes. [3] These eye types differ in their evolutionary histories, developmental trajectories, and retinal morphology.^[3] It is the latter that provides corroboration for the hypothesis put forward by Vee et al.

The principal eye retinas have everted photoreceptive segments facing outwards towards incoming light, and universally lack tapeta. [4] This everted morphology provides higher sensitivity, and the opportunity for densely packed retinal mosaics that offer remarkable acuity, most notably in the principal eyes of jumping spiders. [3] In contrast, the retinas of the secondary eyes are inverted, with photoreceptive segments often below or to the side of the photoreceptor cell bodies.^[4] This inverted retinal morphology presents a challenge for photosensitivity, one solved by many spider groups using a tapetum lucidum composed of highly reflective guanine crystals.^[5] Thus, spider tapeta represent another example of convergent evolution, sharing no evolutionary ancestry with that of vertebrates. Tellingly, tapeta have only evolved in the secondary retinas-the inverted ones-and not in the principal retinas. Thus, the principal and secondary retinas of spiders are akin to the retinas of cephalopods and vertebrates, respectively, with the former being anterior-facing and lacking tapeta and the latter being inverted and sometimes aided by tapeta.

Therefore, the tapeta of spiders offer additional evidence, if circumstantial, that the tapetum lucidum tends to evolve in animal eyes with inverted photoreceptors due to their suboptimal photosensitivity, but offers little or no benefit when photoreceptors are oriented in the more optimal everse orientation. This suggests that the selective pressures shaping tapetal evolution in vertebrates, identified by Vee et al., may be of more widespread importance to understanding the diversity of visual systems in the natural world.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

wileyonlinelibrary.com/journal/bies

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

> Nathan I. Morehouse¹ Nathan H. Lents²

¹Department of Biological Sciences, University of Cincinnati, Cincinnati,

²Department of Sciences, John Jay College, The City University of New York, New York, New York, USA

Correspondence

Department of Sciences, John Jay College, 524 W. 59th Street, New York, NY 10019, USA.

Email: nlents@jjay.cuny.edu

REFERENCES

1. Vee, S., Barclay, G., & Lents, N. H. (2022). The glow of the night: The tapetum lucidum as a co-adaptation for the inverted retina. *BioEssays*, 44(10), 2200003.

- Morehouse, N. (2020). Spider vision. Current Biology, 30(17), R975-R980
- Morehouse, N. I., Buschbeck, E. K., Zurek, D. B., Steck, M., & Porter, M. L. (2017). Molecular evolution of spider vision: new opportunities, familiar players. The Biological Bulletin, 233(1), 21– 38.
- 4. Homann, H. (1971). Die augen der Araneae. Zeitschrift für Morphologie der Tiere, 69(3), 201–272.
- 5. Land, M. F. (1985). The morphology and optics of spider eyes. In *Neurobiology of arachnids* (pp. 53–78). Springer.