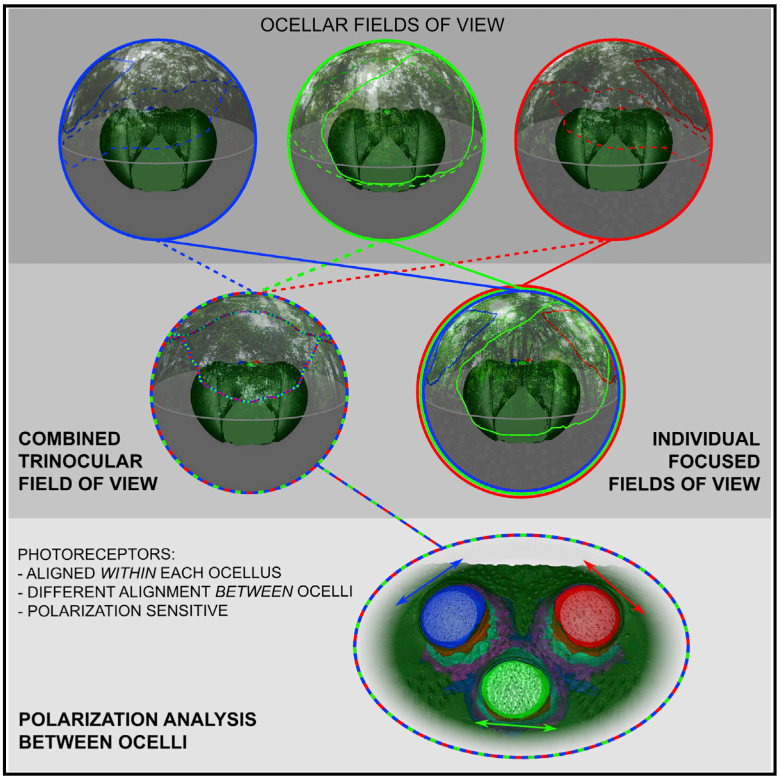
Report

Current Biology

The Dual Function of Orchid Bee Ocelli as Revealed by X-Ray Microtomography

Graphical Abstract



Highlights

- Optical ray-tracing was performed on 3D models of ocelli from microtomography data
- Orchid bee ocelli have retinal regions to detect focused light
- The retinae also have polarization-sensitive regions with trinocular overlap
- The organization of rhabdoms would enable polarization analysis between the eyes

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In Brief

Using X-ray microtomography and ray tracing, Taylor and Ribi et al. show that the ocelli of the orchid bee would provide information for both flight stabilization and polarization analysis—regions of each eye receive focused light, and other regions form a trinocular visual field from differentially aligned polarization-sensitive rhabdoms.

Taylor et al., 2016, Current Biology *26*, 1319–1324
May 23, 2016
http://dx.doi.org/10.1016/j.cub.2016.03.038

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The Dual Function of Orchid Bee Ocelli as Revealed by X-Ray Microtomography

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http://dx.doi.org/10.1016/j.cub.2016.03.038

SUMMARY

Visually guided flight control in the rainforest is arguably one of the most complex insect behaviors: illumination varies dramatically depending on location [1], and the densely cluttered environment blocks out most of the sky [2]. What visual information do insects sample for flight control in this habitat? To begin answering this question, we determined the visual fields of the ocelli—thought to play a role in attitude stabilization of some flying insects [3–5]—of an orchid bee, *Euglossa imperialis*. High-resolution 3D models of the ocellar system from X-ray microtomography were used for optical ray tracing simulations. Surprisingly, these showed that each ocellus possesses two distinct visual fields—a focused *monocular* visual field suitable for detecting features elevated above the horizon and therefore assisting with flight stabilization [3–5] and, unlike other ocelli investigated to date [4, 6, 7], a large *trinocular* fronto-dorsal visual field shared by all ocelli. Histological analyses show that photoreceptors have similar orientations within each ocellus and are likely to be sensitive to polarized light, as in some other hymenopterans [7, 8]. We also found that the average receptor orientation is offset *between* the ocelli, each having different axes of polarization sensitivity relative to the head. Unlike the eyes of any other insect described to date, this ocellar system meets the requirements of a true polarization analyzer [9, 10]. The ocelli of *E. imperialis* could provide sensitive compass information for navigation in the rainforest and, additionally, provide cues for visual discrimination or flight control.

RESULTS AND DISCUSSION

The prominent dorsal ocelli of *E. imperialis* each possess a biconvex lens, a distinct iris, and a cupped retina (Figure 1). In contrast to several other bee species, whose dorsally facing ocellar retinae appear to receive only unfocused light [11, 12], a substantial vitreous body separates each retina from its lens, indicating that they may receive a focused view of the world. Although our optical analysis showed that light parallel to the optical axis of each lens was focused behind the rear of the retina (Figure 2A), our 3D models indicated that cupped areas in the proximal rim of both the lateral and median retinae were positioned at the correct distance from the lens to receive focused light (Figure 2B). In its normal orientation during flight (measured from films of flying orchid bees), our ray-tracing algorithm predicted that the median ocellar retina receives focused light from a frontal region that extends from just below the horizon up to an elevation of approximately 70°, whereas the lateral ocelli receive focused light from smaller rearward looking regions elevated from the horizon to approximately 50° (Figures 3A and 3B). A hypothesis for the function of ocelli in diurnal flying insects is that they act as horizon detectors for attitude stabilization [3, 4]. This idea has been supported by anatomical data from dragonflies showing that the lens of their median ocellus focuses horizontal features in the environment onto the retina [13, 14]. The presence of focused visual fields looking horizontally in different azimuthal directions (Figure 3D) in the ocelli of *E. imperialis* suggests that they too play a role in attitude stabilization. Furthermore, the complete visual fields of orchid bee ocelli have a similar extent to the dorsally positioned but poorly focused ocelli of the blowfly *Calliphora* [15], which have been confirmed to measure low-latency visual cues for flight stabilization [5, 16].

The entire retina of each ocellus does not receive well-focused light (Figure 2A), and, likewise, the regions in the world from which this focused light originates also represent a minor portion of the large field of view of each ocellus (Figure 3). The ocelli of *E. imperialis* therefore appear to have functions in addition to providing information for attitude stabilization. Intriguingly, a substantial region of the world is viewed by all three ocelli, forming a large dorsal region of trinocular overlap centered around the optical axes of the lenses (Figure 3C). Given that the majority of the common visual field does not fall on focused areas of the retinae (Figure 2A), what could be the benefit of having three underfocused views of a patch of canopy and sky? To understand the possible function of the trinocular overlap, we