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Butterfly Optics Exceed the Theoretical Limits of Conventional Apposition Eyes

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Abstract. Optical experiments on butterfly compound eyes show that they have angular sensitivities narrower than expected from conventional apposition eyes. This superior performance is explained by a theoretical model where the cone stalk is considered as a modecoupling device. In this model the Airy diffraction pattern of the corneal facet excites a combination of the two waveguide modes LP_{01} and LP_{02}. When the two modes propagate through the cone stalk the power of LP_{02} is transferred to LP_{01} alone which is supported by the rhabdom. This mechanism produces a higher on-axis sensitivity and a narrower angular sensitivity than conventional apposition optics. Several predictions of the model were confirmed experimentally.

1 Introduction

The accepted model of optics in apposition compound eyes is simple, consisting of a waveguide photoreceptor in the focal plane of a lens (Snyder 1975, 1977; Pask and Barrell 1980a, b; Van Hateren 1984). A major exception from this model was recently found in butterfly apposition eyes by Nilsson et al. (1984, 1987). With several optical techniques they demonstrated that the butterfly optical system behaves as an afocal telescope. The principal difference from conventional apposition optics is the addition of a small but powerful lens in the cone stalk. This second lens recollimates the light from a point source so that it reaches the rhabdom as a parallel bundle. This is indeed a new concept in apposition eye optics, but the existence of such an optical system still lacks a functional explanation. In a theoretical study by Dr. Colin Pask (pers. comm.) the afocal system is shown to perform no better than a conventional apposition system with focal optics, at least if the cone-stalk lens is considered as an ideal lens. It is intriguing, therefore, that butterflies have evolved such a substantial elaboration of their ommatidial optics with seemingly no improvement.

The main intention of this article is to provide a theoretical interpretation of butterfly optics that allows a functional explanation. As will be shown in this paper, the system is indeed superior to conventional apposition systems in two respects. First, it yields a higher on-axis sensitivity, second, it brings the angular sensitivity closer to the diffraction limit of the facet lens. We first provide experimental data on the performance of butterfly optics, and compare it with the conventional apposition system of the fly (see Van Hateren 1984). Although the afocal model of butterfly optics seems inevitable from the observations reported by Nilsson et al. (1987), we have here adopted quite a different interpretation. From the micrometer dimensions of the cone-stalk lens it is clear that it must act as a waveguide to some degree. If the entire cone stalk is considered part of the waveguide, the ommatidial optics can be modelled as a focal system with a funnel-shaped inhomogeneous distal end of the waveguide. In this paper we will show that predictions from such a model agree very well with experimental data, and also that the model provides important clues to the evolution of the butterfly optical system.

2 Methods

2.1 Animals and Preparation

Quantitative measurements were performed on the Sulfur butterfly, *Gonepteryx rhamni*. Results were obtained from seven ommatidia in two butterflies. The results were similar for all ommatidia. Additional qualitative observations were made on the following butterflies: *Clossiana euphrosyne*, *Aphantopus hyperantus*, and *Lycaena phlaeas*. The anatomy was inves-

tigated in all the above species and also in *Argynnis paphia*. For all optical experiments unanaesthetized animals were fixed with wax, and mounted on an $x-y-z$ stage. Care was taken not to impair ventilation.

2.2 Optical Methods and Rationale

The optical instrument used for the experiment of Fig. 1 is an extension of the one described previously (Van Hateren 1984). The main extension was a small halfmirror mounted in front of the objective, used for applying orthodromic light. This light travels through the ommatidia first in the orthodromic direction, is reflected by the tapeta, and propagated back in the antidromic direction. The light radiating out of the eye is then collected by the objective of the instrument, spatially filtered to select radiation coming from a single ommatidium, and finally imaged in the far field (see Franceschini 1975; Van Hateren 1984; Nilsson et al. 1987). The image is recorded photographically and then analyzed with a microdensitometer, which yields the intensity distribution of the far field radiation pattern of the eye.

As shown in Van Hateren (1984) this far field radiation pattern is – at least in lens-waveguide systems – identical to the angular sensitivity. Although we will argue in this article that the butterfly has a system more complex than just a lens-waveguide system, the far field radiation pattern is identical to the angular sensitivity also in this system. The reason for this is that the Helmholtz reciprocity theorem used in the argument in Van Hateren (1984) is also valid for the optical system we propose here for the butterfly. The reciprocity theorem, however, is only applicable to one mode at a time because, if e.g. two modes are present, the one that is most efficiently absorbed by the photopigment will contribute least to the light that is returned from the eye and is used for the optical measurements (Van Hateren 1984; Nilsson et al. 1987). To avoid this problem we have, for the optical experiments, selected butterfly species that only support the first mode (LP_{01}) in their rhabdoms (see Land et al. 1987).

Further details on the optical setup, the photography, and the calibration are given in Van Hateren (1984). The photographs of radiation patterns (Figs. 4 and 6) were made on another optical setup which is based on the same general principle as the one mentioned above. More details on this setup and the various ways of imaging the output of butterfly eyes are given in Nilsson et al. (1987).

2.3 Anatomy

For electron microscopy, shallow eye cups were cut from fresh eyes. The cups were fixed in a solution consisting of 2% formaldehyde, 2.5% glutaraldehyde, 4% sucrose and 10 m*M* EGTA in 0.2 *M* sodium cacodylate buffer (pH 7.3). Postfixation was carried out in 1% OsO_4 solution. The material was dehydrated in an alcohol series and embedded in Araldite. Ultrathin sections were cut and stained with lead citrate and uranyle acetate.

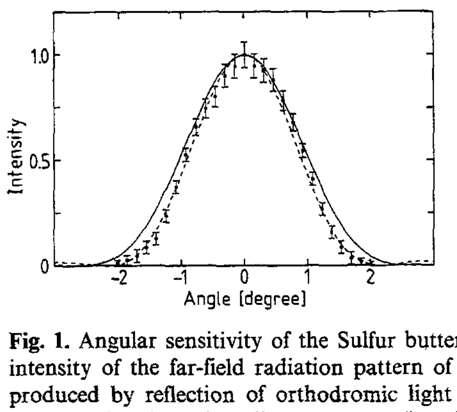

Fig. 1. Angular sensitivity of the Sulfur butterfly. *Data points:* intensity of the far-field radiation pattern of an ommatidium produced by reflection of orthodromic light at the tapetum; wavelength 650 nm, lens diameter 21 µm (inscribed circle 20 µm, circumscribed circle 22 µm). Broken line: Airy diffraction pattern for a 21 µm lens. Continuous line: angular sensitivity for a lens-fiber system with the same lens diameter and an *F*-number that yields an optimum on-axis efficiency ($F = 2.2$, rhabdom diameter 2 µm)

3 Results

3.1 Measurements of the Angular Acceptance Function

Figure 1 shows the acceptance function measured (see Methods) in the Sulfur butterfly (data points), and two theoretical angular sensitivities. The dimensions of the ommatidial lens were also determined. For the theoretical calculations we assumed a circular lens with a diameter equal to the mean of the inscribed and circumscribed circles of the hexagonal lens. This diameter yielded the Airy diffraction limit of the lens (broken line). The second theoretical curve (continuous line) is the one that corresponds to a conventional apposition eye: a facet lens with a waveguide in its focal plane (as is found e.g. in the fly's eye, see Van Hateren 1984; Smakman et al. 1984). The F-number of the lens was optimized here for maximum on-axis efficiency (about 80%).

We see in Fig. 1 that the measured points are closer to the Airy diffraction limit than to the curve corresponding to a pure lens-waveguide system. This was the case in all ommatidia where this measurement was done. The optics of butterfly ommatidia appear to produce angular sensitivities narrower than expected