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Review

Evolution of color and vision of butterflies

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Abstract

Butterfly eyes consist of three types of ommatidia, which are more or less randomly arranged in a spatially regular lattice. The corneal nipple array and the tapetum, optical structures that many but not all butterflies share with moths, suggest that moths are ancestral to butterflies, in agreement with molecular phylogeny. A basic set of ultraviolet-, blue- and green-sensitive receptors, encountered among nymphalid butterflies, forms the basis for trichromatic vision. Screening pigments surrounding the light-receiving rhabdoms can modify the spectral sensitivity of the photoreceptors so that the sensitivity peak is in the violet, yellow, red, or even deep-red, specifically in swallowtails (Papilionidae) and whites (Pieridae), thus enhancing color discriminability. The photoreceptor sensitivity spectra are presumably tuned to the wing colors of conspecific butterflies.

Keywords: Visual pigments; Corneal nipples; Tapetum; Wing color; Spectral sensitivity

1. Introduction

Butterflies include the most colorful living objects and never fail to charm the spectator, especially because of their association with flowers. It thus has been a long-standing assumption that butterflies possess color vision, but that this is indeed the case has only recently been demonstrated unequivocally (Kelber and Pfaff, 1999; Kinoshita et al., 1999). Unfortunately, the neural systems mediating color vision have remained virtually unexplored, but our knowledge about the photoreceptor systems and their possible evolution is steadily accumulating (Briscoe and Chittka, 2001). The differences in the eyes of butterflies studied so far suggest that the capacity to discriminate colors varies among species, which is understandable, as different behaviors and habitats impose different visual tasks (Arikawa, 2003).

The diversity in butterfly species is extremely rich, and studies of the anatomy, physiology and development of butterfly eyes and optical ganglia (Yagi and Koyama, 1963; Strausfeld and Blest, 1970; Arikawa, 1999; Briscoe and Chittka, 2001; Warrant et al., 2003) as well as of the architecture and development of the wings and their scale cells indicate the great potential of butterflies for understanding central questions of evolution and development (Nijhout, 1991; Brakefield et al., 1996).

Butterflies belong to the insect order Lepidoptera, but most of the lepidopteran families are moths. There is considerable evidence that the moths are ancestral to the butterflies. The evolutionary tree of moths branches off into the rhopalocerans, i.e., the Hedylidae, Hesperiidae (the skippers), and Papilionoidea; the latter superfamily consists of the butterfly families Papilionidae, Pieridae, Nymphalidae, Lycaenidae, and Riodinidae (Wahlberg et al., 2005).

Most butterflies are adorned with bright wing colors, which are presumably tuned to the properties of the visual systems of observers, be they potential partners or predators. Notably, intraspecies recognition is often achieved via the displayed wing

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colors, and this will be especially the case in butterfly species with sexual dichroism, that is, where the sexes have markedly different colors (Obara and Majerus, 2000; Kemp et al., 2005).

In this paper we will first describe the anatomy of butterfly eyes and the properties of the photoreceptors and their visual pigments. Subsequently, we will present a comparative survey of the eyes of butterflies and related insect species, with a perspective on the spectral properties of butterfly wings.

2. The butterfly eye and retina

2.1. Anatomy of butterfly eyes

The compound eyes of butterflies consist of numerous anatomically identical units, the ommatidia, which are more or less arranged in a hemisphere. Each ommatidium is recognizable from the outside by a facet lens. Together with the associated crystalline cone the facet lens forms the imaging optics that projects incident light onto the photoreceptors (Fig. 1).

A butterfly ommatidium contains nine photoreceptors. Their light-sensitive organelles, the rhabdomeres, jointly constitute the fused rhabdom, a long cylinder that acts as an optical waveguide. Depending on the quality of the imaging optics as well as the size of the rhabdom, each ommatidium samples a different spatial area, with widths typically of the order of 1°. The visual fields remain restricted owing to pigment cells that surround each ommatidium as a protective light screen (Land, 1981; Nilsson, 1989).

A specialty of most butterfly eyes is the presence of a tapetum located proximally to the rhabdoms. Incident light propagates along the rhabdom, and when it is not absorbed it is reflected by the tapetum. The light travels then in the reverse direction and, if not absorbed, eventually leaves the eye again, where it is visible as eye shine (also called eye glow).

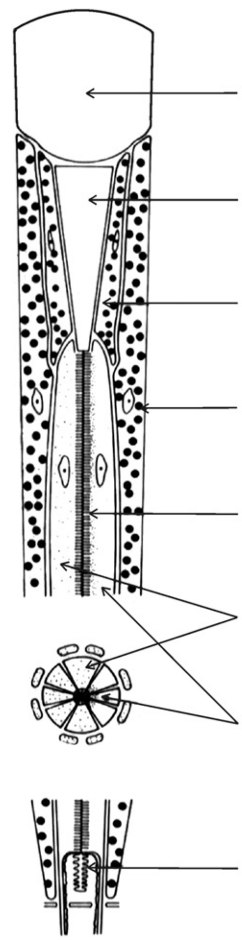

Fig. 1. Anatomy of an ommatidium of a diurnal butterfly. The facet lens focuses incident light into the rhabdom. This is the cylindrical structure that consists of the rhabdomeres of the photoreceptors, which are fused together. The rhabdomere is the organelle that contains a photoreceptor's visual pigment. The fused rhabdom acts as an optical waveguide, which functions to enhance the chance of light absorption by the visual pigments, and thus to enhance light sensitivity. Proximally of the rhabdom a basal tracheole exists, which acts as a reflector for light that has not yet been absorbed. Part of the reflected light is not absorbed at the way back, and this light leaves the eye again, so that it is visible as eye shine.

2.2. Spectral receptor classes and eye regionalization

Vision starts with the absorption of light by the visual pigments, which are localized in the rhabdomere, a special, strongly folded part of the photoreceptor cell membrane. The visual pigments, rhodopsins, are opsin proteins combined with a chromophore. In humans and bees this is retinal and in lepidopterans it is 3-hydroxyretinal, derivatives of vitamins A1 and A3, respectively (Vogt, 1989; Seki and Vogt, 1998). Photon absorption by the rhodopsin causes isomerization of the chromophore and subsequently a photochemical process that ends in a photostable metarhodopsin. The metarhodopsin (M) can be photoreconverted to the rhodopsin (R) state (Fig. 2).

The general organization of butterfly color vision is similar to that of honeybees and bumblebees. The bee color vision system is based on three photoreceptor classes, with maximal sensitivity in the ultraviolet (UV), blue (B) and green (G) wavelength ranges (Menzel and Backhaus, 1989; Spaethe and Briscoe, 2005). Extensive electrophysiological recordings in a large number of hymenopteran species have demonstrated the universal presence of the three basic receptor classes (Peitsch et al., 1992). Intracellular electrophysiology of photoreceptors of nymphalid butterflies has demonstrated a similar basic set of UV, blue and green receptors (Kinoshita et al., 1997).

The distribution of receptor types appears not to be homogeneous, however. For instance, in the eyes of the honeybee drone, which are divided into a dorsal and ventral eye half, the set of UV-, B- and G-receptors is only present in the ventral eye, whilst the dorsal half only has UV- and B-receptors (Peitsch et al., 1992), in line with optical observations (Menzel et al., 1991). Similar regionalizations, often sex-related, have been encountered in many insect species (Stavenga, 1992). Specialized dorsal areas can be readily observed in butterfly eyes by utilizing the eye shine, for instance in the small white *Pieris rapae* and the satyrine *Bicyclus anynana* (Miller, 1979; Stavenga, 2002a,b).