Vision, pigments and structural colouration of butterflies
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Summary of the PhD thesis

“Vision, Pigments and Structural Colouration of Butterflies”

The theme of this thesis is the interplay of seeing and being seen.
Butterflies are wonderful study objects for this question.

In Chapter 1, a general introduction is given to the topics of physiology of insect vision, physiological optics of butterfly eyes, and the optics of butterfly wing colouration.

In Chapter 2, we studied the primary processes of phototransduction (light sensing) in the visual sense (photoreceptor) cells of the fruitfly Drosophila melanogaster. We studied the interplay between the visual pigment, rhodopsin and its controlling protein, arrestin, under stimulation with light of different intensities and wavelengths. The role of arrestin is to inactivate the active form of visual pigment, metarhodopsin. If all available arrestin is used up, the photoreceptors remain spuriously activated even in the absence of light. We compared the electrical responses to light in the white-eyed wild-type fruitfly and in a hypomorphic mutant containing low levels of arrestin2 at a range of stimulus wavelengths and intensities. The reduced level of arrestin2 in the mutant modestly increased the light sensitivity, decreased the photoreceptor dynamic range and made the termination of the electrical response to light slow; the transition between full repolarization and spurious afterpotential occurred at a lower metarhodopsin fraction than in the wild type. We hypothesise that fruitflies, in comparison to bigger flies, economise on safety mechanisms: the only price paid under natural circumstances seems to be a reduced speed of light sensing.

The next two chapters are dealing with the physiological optics of butterflies. Their compound eye consists of ommatidia. Their central parts, the rhabdoms, are fused and form a wave guide. The ommatidia of pierid butterflies have three tiers: the distal tier has four photoreceptors. Two of them express UV or violet/blue rhodopsins. The other seven photoreceptors express a green rhodopsin.

In Chapter 3, we studied the eye regionalisation and the ultrastructure of the eye of the pierid butterfly, the Eastern Pale Clouded Yellow, Colias erate (family Pieridae). Its eye has distinct dorsal and ventral parts. In the ventral eye part, there are three types of ommatidia, which all use a red screening pigment to modify the spectral sensitivities of the photoreceptors. The UV cells always contribute less microvilli to the rhabdom than the violet/blue cells. All three ommatidial types have a constriction of the waveguide between the two tiers, which adds to the efficiency of the screening of the red pigment. The eye shine, resulting from tapetal reflections, peaks in the red (at 660 nm) or in the far red (730 nm), indicating that the sensitivity of proximal photoreceptors is shifted from green to red. The red ommatidia fluoresced under violet excitation, implying the presence of a violet-absorbing pigment that acts as a short-wavelength filter. The ommatidia in the dorsal part of the eye are devoid of screening pigments. The dorsal part of the eye has a brighter red eyeshine and is presumably only sensitive in the UV-green spectral range.

In Chapter 4, we studied the photoreceptors in the eye of Colias. We stimulated the eye with pulses of monochromatic light and used intracellular electrodes to measure the spectral and polarisation sensitivities of individual photoreceptors. We have identified one UV, four violet-blue, two green and two red photoreceptor classes, presumably based on rhodopsins peaking in the UV, violet, blue and green (360, 420, 460 and 560 nm, respectively). The four violet-blue photoreceptor classes are presumably based on a mixture of the two violet/blue rhodopsins, screened by a violet-absorbing distal pigment. The green classes have reduced sensitivity in the ultraviolet range. The two red
classes have primary peaks at about 650 and 665 nm. This peak shift, achieved by tuning the effective thickness of the red perirhabdomal screening pigment, is so far the largest among insects.

The next three chapters are dealing with the colouration of butterflies. Their wings are covered with two layers of scales, which form pixelated patterns. We have studied the optics of colouration of the iridescent males from a few pierid butterflies from the Coliadinae subfamily (Colias erate, Gonepteryx rhamni, G. cleopatra, G. aspasia) and the Colotis group (Hebomoia glaucippe, Colotis regina).

In Chapter 5, we have dealt with the morphology of single scales and reflectance spectra from the wings of iridescent pierid males. We used scanning electron microscopy (SEM) to describe the ultrastructure of their scales. The pigmentary colouration is based on pterin pigments which are located in small beads in the scales. The ridges on the upper surface of the scales are elaborated into multilayers, which result in iridescent structural colouration. The integrated reflection efficiency is correlated with the number of multilayers. We have measured the dependence of the peak reflectance wavelength on the illumination angle and found that it is in agreement with classical multilayer theory. The iridescence in pierid butterflies is in most cases in the ultraviolet wavelength range, but some species have a blue-peaking iridescence. We hypothesise that the spectral properties of the pigmentary and structural colouration are tuned to the spectral sensitivities of the butterflies’ photoreceptors.

In Chapter 6, we have described an instrument, tailored for studies of spatial and spectral patterns of colouration. The instrument, an imaging scatterometer (ISM) is built around an ellipsoidal mirror and essentially compresses a full hemisphere of reflections into a smaller angle which is then imaged with a commercial CCD camera. The instrument’s performance is illustrated by measurements of the scattering profiles of the blue-iridescent dorsal wing scales of the nymphalid Morpho aega and the matte-green ventral wing scales of the lycaenid Callophrys rubi.

In Chapter 7, we have studied spatial reflection patterns of the wings of iridescent pierid males. Imaging scatterometry demonstrated that the pigmentary colouration is diffuse whereas the structural colouration is more or less directional. The scattering pattern of structural colouration is elongated into a line. The directionality of structural correlation depends strongly on the scale curvature. In the case of the males of the Cleopatra brimstone Gonepteryx cleopatra, the fore- and hindwings have scales with different pigments and different scale curvatures. We hypothesise that the curvature modifies the spatial visibility of iridescence and may play a role in intraspecific signalling.

In Chapter 8, in an essay, we compared different senses, with an emphasis on imaging senses. The thesis is concluded by a short discussion in Chapter 9.