The Dorsal Compound Eye of Simuliid Flies:

An Eye Specialized for the Detection of Small, Rapidly Moving Objects

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Compound Eye, Light-Quantum Noise

The highly specialized dorsal compound eye of male Simuliids is especially adapted to detect during flight the females which are very small animals (1×3 mm). At dawn, the eye functions close to the physical limit imposed by the quantum fluctuations of light. In bright illuminations, light-qauntum noise is not a limiting factor as can be shown by behavioural experiments.

Simuliid flies have subdivided compound eyes. The dorsal eye differs in several characteristic features when compared with the ventral one. Three major differences have been previously described[1].

1) The corneal facets are considerably larger in the dorsal eye (diameter 25 to 40 µm) than in the ventral eye (diameter 10 to 15 µm).

2) In the dorsal eye, the retinular cells and their rhabdomeres are extremly elongated (length approximately 300 µm), whereby they penetrate the basement membrane and extend into the ventral region of the head. The retinular cells and rhabdomeres of the ventral eye, in contrast appear similar to those in other Dipterans (length 50 µm).

3) The screening pigment in the dorsal eye is trans-lucent for light of longer wavelengths and is of a light brown colour, whereas the ventral eye has a dense dark red-brown screening pigment.

The eye of the female has features similar to those described above for the ♂ ventral eye. This indicates that the eye of the males that is functionally specialized is the dorsal one. During the last few summers when animals were available we analysed the optical properties of the eyes, interpreted the data in terms of a possible function and performed field experiments in order to validate the given interpretation. The results of our considerations are the following:

1) The combination of large-facet lenses and elongated rhabdomers in the ♂ dorsal eye, allows for a high angular resolution, combined with a high absolute sensitivity (rate of absorbed quanta of light per second).

Both parameters are important, since according to our behaviour analysis it is the function of the dorsal eye to detect the females against the blue sky as they cross above the swarm of males. The females are then persued by the males and caught for mating. To detect a rapidly moving female (size approximately 1×3 mm) over a distance of some 50 cm (angular subtense approx. 0.2°) is a difficult task for a small insect eye, since quantum fluctuations of light might become a limiting factor for detectability.

In order to determine if this is really the case, we performed dummy-experiments in which a small leadball of a size similar to a female was moved above swarming males. We observed whether the dummy induced a chasing response in the males. The result is that at noon-time males stop chasing the dummy if it is more than approximately 50 cm away, even against a bright sky. Under these conditions light-quantum noise is small compared with the signal induced within one photoreceptor. That, is, males were also able to detect females at larger distances from a signal-to-photon noise point of view, but they actually do not follow them, probably because they are not fast enough to have a chance to catch the females. The neural mechanism that allows males to discriminate between females more than 50 cm away from those that are closer is not based on binocular distance perception. The relevant parameters for the distinction are angular velocity and modulation of the signal induced within the receptors.

At dawn, light-quantum fluctuations become closer to the size of the signal, and consequently the dummies are no longer followed even if they are moved at as short a distance as 10 cm above the swarm. We would like to mention here that the threshold for contrast in the optomotor turning response in *Musca* is also photon-noise limited at lower light intensity levels[2].

The rhabdomeres of the dorsal eyes are 5 to 6 times longer than those of the ventral one. This increases the number of absorbed quanta by approximately a factor of 4. With regard to the function of how brightness decreases with time this increased absorption rate may be interpreted *e. g.* as a prolongation by 1 to 2 hours of the time at dawn in which the males are able to detect females. This, in turn, increases the probability af mating and explains the high selection pressure for the elongated rhabdomeres.

The third specialisation mentioned above, the translucent screening pigments of the dorsal eye, also fits the concept developed here. Microspectrophotometric measurements show that the screening

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pigment absorbs between 370 and 520 nm. This suggests that the rhodopsin within the retinular cells absorbs in the short-waveength part of the spectrum. This again is an adequate adaptation since in the short-wavelength spectral range the angular resolution of the ommatidia is better due to the diffraction of light. It is possible to show, using reasonable assumptions, that a second absorption peak of the visual pigment in the longer-wavelength part of the spectrum even though it would cause an increase in the number of absorbed photons and therefore reduce the relative noise of the signal, would not improve the signal-to-noise ratio for small objects. This is mainly due to the fact that angular resolution of the receptors decays with increasing wavelength. If the visual pigment absorbs in the short-spectral range, it would be an advantage to use a screening pigment that is translucent outside of this range and allows for a high-absorption rate of metarhodopsin for exactly the reason discussed by several authors[3], that is, to keep the concentration of rhodopsin high.

Actually, Dietrich[1] already suggested that the dorsal eye of Simuliid flies as well as that of other subdivided compound eyes is specially adapted for the detection of small objects like females. We have tried to understand the way they are adapted for this special task in biophysical terms.

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