The Spectral Sensitivity of the Ocelli of *Calliphora* (Diptera)

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Insect Ocelli, Spectral Sensitivity, Colour Vision

The spectral sensitivity of the ocelli of *Calliphora* was determined by means of the electroretinogram (ERG). Sensitivity is high in the spectral range from 340 to 450 nm; with still increasing wavelengths it rapidly decreases. Analysis of the shape of the ERG resulting from stimuli of different wavelengths, as well as experiments with selective chromatic adaptation, indicate that there is mainly one spectral mechanism contributing to the response.

The spectral sensitivity of flies as determined by means of behavioural responses has been investigated with different methods. One would like to interpret these results in terms of the sensory input from the compound eyes since considerable knowledge of spectral sensitivities of ommatidial photoreceptors has been accumulated [1]. However, in behavioural experiments using, for example, optomotor response or phototactic orientation [1, 2], ocellar input, because of the wide visual fields of the ocelli, might also have contributed to the responses.

In order to obtain information on the spectral properties of such a possible contribution, we determined sensitivities of the ocelli of a fly species by means of the electroretinogram (ERG).

Methods

Calliphora, ♀, wild type, aged 4 to 8 days, from laboratory strains were used for the experiments. The convex surface of the ocellus investigated was carefully cut away using a razor blade. This allows a more homogeneous illumination of the ocellar retina by means of a light guide, and it also lowers the resistance of the cornea to a value (approx. 5 – 20 kohm) that enables the ERG to be recorded easily by just touching the remaining cornea with a capillary electrode. The electrodes (tip diameter approx. 10 μm, R approx. 10 – 20 kohm) were filled with Ringers solution [3]. The indifferent electrode was placed in the tissue below the ocellus. In order to get rid of ERG-contributions from the compound eyes, these eyes were carefully removed by means of a razor blade in a way similar to that described by Metschl [4]. The open surface of the head was covered with vaseline to prevent drying out of the tissue. Recordings from such preparations are stable for several (up to 6) hours.

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Light stimuli were delivered by means of a UV-transmittant light guide (diameter 4 mm), the end of which was placed at a distance of 5 to 7 mm and perpendicular to the ocellar cornea surface.

Light sources were two Xenon arcs (Osram XBO, 150 Watt), the beams of which were combined by means of a half-silvered mirror and, using quartz optics, imaged onto the input end of the light guide. Heat protecting-, neutral density and interference-filters (Schott, types Depal and UV-pil) as well as electromechanical shutters provided the monochromatic stimuli. The second light source allows the ocelli to be adapted with monochromatic light.

The preparation was first dark adapted for at least 30 min. The stimuli of a duration of 1 to 2 sec were given at intervals of 10 sec. The intensity at each wavelength was increased until the signals were somewhat larger than a criterion response of 0.15 – 1.5 mV. Then the next wavelength was chosen and again the intensity increased until the response reached the criterion. Under these conditions a stimulus interval of 10 sec was sufficient to prevent detectable adaptation effects.

Results

The ERG usually starts with a small (cornea-positive) on-effect, followed by a negative maintained potential and a negative off-effect. The shape varies with the intensity as shown in Fig. 1. Occasionally the transients of the responses have been more oscillatory.

Stimuli of different colours always produced equivalent shapes of the ERG as long as the relative

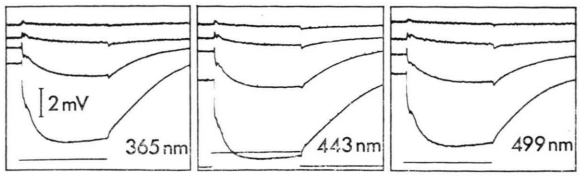

Fig. 1. Electroretinograms of a median ocellus (*Calliphora* ♀, wildtype), induced by light stimuli of different intensities and colours. Top: cornea positive. Four stimuli, differing in intensity by a factor of ten, were given at each of the three wavelengts. The relative intensities at the different colours have been adjusted to produce ERG-amplitudes of similar size. Duration of stimulus 2 seconds.

intensities were adjusted to give the same ERG amplitude; there is no colour-specific effect detectable within the shape of the ERG (Fig. 1).

With increasing intensities the maximal amplitude ΔU (measured between on- and off-effect) increases monotonically. The curves for different wavelengths of light are shifted parallel to each other over a relative quantum rate scale (Fig. 2 c). The relative number Q of quanta of different wavelengths, sufficient to elicit a criterion response in the range of a $0.15-1.5$ mV, can be found from such curves. The relative sensitivity $S=1/Q$ of several ocelli is drawn in Fig. 2 a, b. Sensitivity is usually maximal in the UV, but is still considerable at wavelengths up to 450 nm. Sometimes a second maximum occurs in this wavelength range, followed by a rapid decrease in sensitivity at still longer wavelengths. No significant difference between median or lateral ocelli was found (Fig. 2).

The fact that no colour-specific change of the shape of the ERG can be demonstrated suggests that there is probably only one kind of spectral mechanism contributing to the response. This view is also supported by experiments with selective chromatic adaptation; adaptation with UV-light or light of longer wavelengths suppresses the sensitivity at all wavelengths to a similar degree (Fig. 3). Due to limits in the light intensities available, it cannot be excluded, however, that with stronger selective adaptation colour specific effects of a kind as described for dragonfly ocelli [5] might occur.

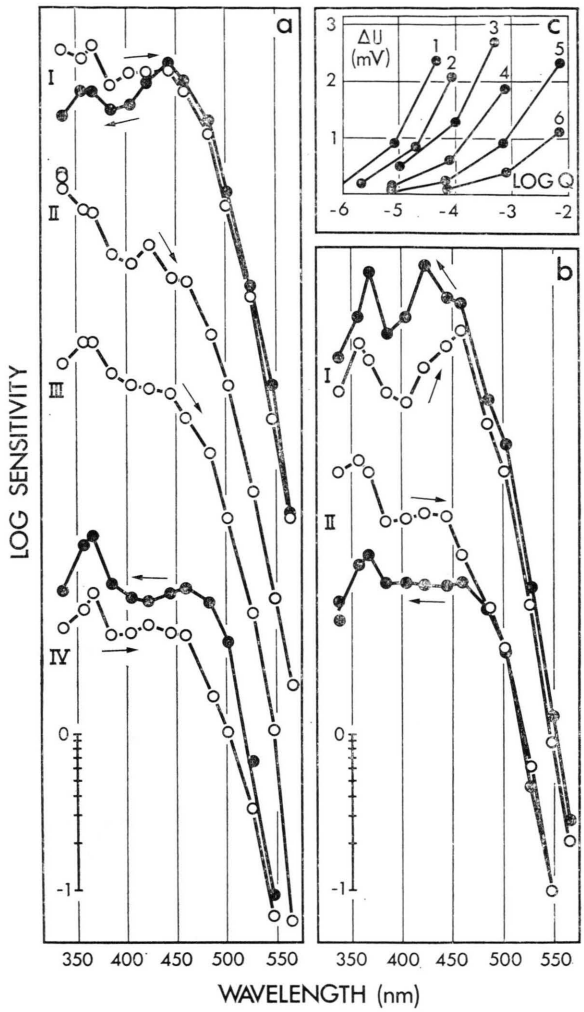

Fig. 2 a. Spectral sensitivities of four median ocelli (I–IV). For presentation, the sensitivity spectra of the different ocelli have been shifted vertically relative to each other. 2 b. Spectral sensitivities of two lateral ocelli (I, II). Points in all cases were measured proceeding from the short-wavelength end of the spectrum to the long-wavelength end (○), or in the opposite direction (●) (see arrows). 2 c. Amplitude of the ERG as a function of relative quantum intensity of the stimulus for several different wavelengths of light. 1: 355 nm, 2: 382 nm, 3: 457 nm, 4: 499 nm, 5: 524 nm, 6: 545 nm.

Discussion

The spectral sensitivity of the ocelli of *Calliphora* as determined by means of the ERG is different from the spectral sensitivity of other known insect ocelli. The cockroach ocellus contains – as does the ocellus of the fly – only one kind of spectral mechanism. The sensitivity in the cockroach ocellus, however, is maximal at longer wavelengths (500 nm) with only a small shoulder in the UV [6]. In the bee there are two sensitivity maxima present, one in the UV (335 – 340 nm) the other in the green (490 nm). This spectral sensitivity curve, however, is composed of contributions from two kinds of spectral mechanism with two different kinds of spectral

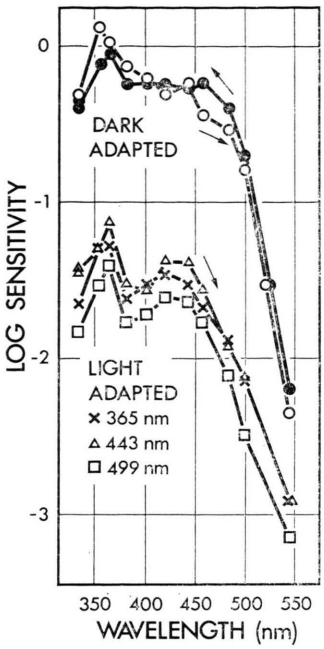

Fig. 3. Spectral sensitivity of a lateral ocellus as measured dark adapted (○), or measured adapted continously to light at wavelengths 365 nm (×), 443 nm (△), 499 nm (□) and then measured dark adapted again (●).

sensitivities [6]. The spectral sensitivity of intracellularly recorded photoreceptors of dragonfly ocelli show maxima in the UV ($\approx$ 360 nm) and the green ($\approx$ 500 nm). Selective adaptation shows that two spectral mechanisms can be recorded from each cell [5]. In one species (*Anax*) also a third peak in the blue ($\approx$ 440 nm) together with the one in the UV and the green spectral range occurred.

A comparison of spectral sensitivities shows that the receptors of the ocelli are different from the receptors so far found in the dipteran compound eye [1]. Hence, the ocelli combined with these receptors, could provide the input of a system capable of "colour-vision". Since the ocelli affect at least phototactic responses [7], their influence probably introduces colour-specific effects into this kind of behaviour. Therefore it seems worthwhile to check also in other kinds of optically induced behavioural responses if and how the ocelli contribute to the response. If the ocelli give a main contribution to colour-specific effects, it is clear that such effects cannot be a proof for "colour vision" in the sense that a colour can be ascribed to a detailed object; for the task the optical resolution of the ocelli is obviously too poor [7].

Recently an unsuccessful attempt was made to induce a prolonged afterpotential (PDA) in the ocelli of *Drosophila* by means of blue light [9]. This light is optimal for PDA-induction in receptors 1 – 6 of *Drosophila* [8]. However, if the ocelli of *Drosophila* are different in spectral sensitivity from the receptors 1 – 6 as in *Calliphora*, blue light might not have been the optimal wavelength for a PDA-induction in these receptors.

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