

Adaptation mechanisms in the dorsal ocelli of *Periplaneta americana*

(Orthopteroidea: Blattaria, Blattidae)

Von H. WUNDERER, P. SEIFERT & G. WEBER

Abstract

Light- and dark-adapted ocelli of the cockroach *Periplaneta americana* were investigated using an ultrastructural and histochemical approach. The degradative route of photoreceptive membrane observed during light adaptation is comparable to that in insect compound eyes. A peculiar photoreceptor organelle is histochemically shown to be lysosome-related. During dark adaptation, the rhabdoms are reorganized; endoplasmic cisternae assemble as palisades around the rhabdoms.

Introduction

Many insects have three dorsal ocelli at the vertex of the head; only two ocelli in a slightly different position are present in some groups like moths and cockroaches (rev. GOODMAN 1981). The ocelli may be involved in very variable functions, e. g. polarotaxis in desert ants (FENT & WEHNER 1985), horizon detection in locusts (rev. ROWELL 1988), flight equilibrium control in dragonflies (STANGE 1981), triggering of the circadian activity in arctiid moths (WUNDERER & DE KRAMER 1989). The cockroach ocelli show a well organized retina (COOTER 1975, WEBER & RENNER 1976) and complex nervous connections (COOTER 1975, TOH & HARA 1984, TOH & SAGARA 1984). With regard to their function, several contradictory investigations exist (see discussion by RIVAULT 1983) but it remains unclear as yet. Moreover, these ocelli show prominent adaptation mechanisms which will be reported here.

Materials and methods

1. **Animals.** Male adults or last instars of *Periplaneta americana* L. were used from a culture at the Zoological Institute of Munich. Their light/dark cycle was 12:12 h. Light adaptation by indirect daylight plus fluorescent lighting (in total about 800 lux) occurred during the normal day, dark adaptation during the normal night period.

2. **Transmission electron microscopy** followed conventional techniques. After 2 h adaptation, parts of the head bearing the ocelli were fixated for 4 h at 4°C with 5% glutaraldehyde in Sørensen's phosphate buffer with 4% sucrose, pH 7.4 (cf. GLAUERT 1975). After several buffer rinses and postfixation with 2% osmium tetroxide in the same buffer (2 h at 4°C), the specimens were dehydrated in graded ethanol and embedded in Durcupan ACM (Fluka/Buchs, Switzerland) via propylene oxide. Serial 0.5–1.0 µm semithin sections through an ocellus alternated with 60–90 µm ultrathin sections. Light microscopical control was done with the semithin sections stained with a mixture of methylene blue and Azur II. Ultrathin sections were stained with uranyl acetate and lead citrate, and examined with a Zeiss EM 9A or EM 10 at 60 kV.

3. **Histochemistry.** Contents of acid phosphatase were demonstrated using the method of KREUTZBERG & HAGER (1966). The above fixation but with 1M cacodylate buffer was applied. The incubation medium (15 min at 37°C) consisted of 0.05M acetate buffer pH 5.0 with 0.19% sodium-glycerophosphate, 0.13% lead nitrate, and 0.006% sucrose, followed by several washes in 0.1 M acetate buffer and dehydration. Controls were treated with i) incubation medium without sodium-glycerophosphate; ii) complete medium with 0.01 M NaF added as inhibitor. Unstained ultrathin sections were examined in the electron microscope.

Results and Discussion

1. Photoreceptors after light adaptation.

The structural features of the light-adapted ocellus have been described in general by COOTER (1975) and WEBER & RENNER (1976). The rhabdom configurations (Figs. 1, 4) are built by a fusion of 2–6 rhabdomeres from neighbouring photoreceptor cells. A distinct borderline between the single rhabdomeres is typically visible in sectioned profiles of light-adapted rhabdoms (Figs. 1, 2). Thus, the rhabdomeres comprise microvilli of equal length (approx. 1 μm). At the rhabdomeric borders (where the microvilli originate), coated pits and membrane whorls are adhering. The subrhabdomeric region of the light-adapted photoreceptor cells exhibits sacculi of the smooth endoplasmic reticulum in a random distribution (Fig. 2). Additional organelles can be observed in this region: numerous Golgi stacks, different types of dense bodies, lipid droplets (Fig. 3), and multitubular bodies (Figs. 2, 3). The multitubular bodies have been described by WEBER & RENNER (1976) as peculiar organelles of the photoreceptor cells within the *Periplaneta* ocellus. They are only present during light adaptation.

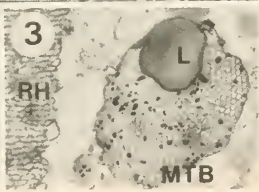
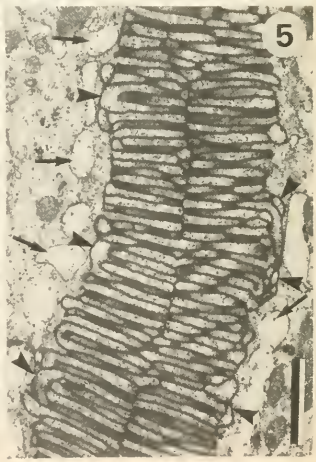
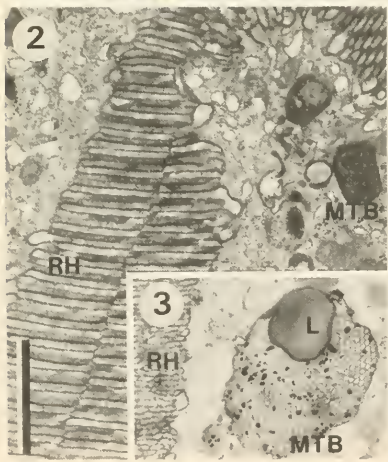
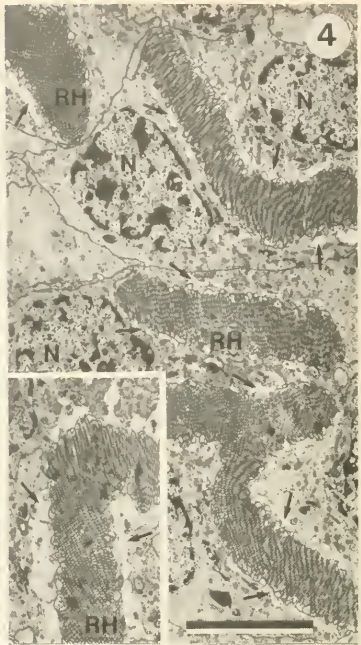
These organelles can be further characterized by a histochemical test for acid phosphatases. Incubation of the ocellar retina with sodium glycerophosphate (see Methods) reveals positive, fine-granular lead precipitates only within multitubular (Fig. 3) and dense bodies. Precipitates are never found in lipid droplets nearby (Fig. 3), or in any other compartment; they are completely absent in controls. Hence, multitubular and dense bodies in the ocellar photoreceptors can be classified as lysosome-related bodies (cf. HAFNER et al. 1980; rev. BLEST 1988).

2. Photoreceptors after dark adaptation.

Several profound changes of the photoreceptor cell structure occur during dark adaptation. In contrast to the light-adapted rhabdoms, the clear middle borderline between adjacent rhabdomeres disappears (Fig. 4). Parts of the rhabdomeres interdigitate (Fig. 5); now, it is no longer possible to definitely ascribe them to the respective photoreceptor cells. A number of microvilli with lengths of up to 2.5 μm reach over the whole width of such rhabdom profiles (Fig. 5). Several microvillar rows show a U-shaped appearance as they become cross-connected at the rhabdom border by membrane layers (Fig. 5). This feature reminds of "membrane loops" in the development of this ocellus (TOH & YOKOHARI 1988), in dark-adapted ocelli of wasps (PABST & KRAL 1989) and of arctiid moths (GRÜNEWALD & WUNDERER 1990).

After dark adaptation, voluminous perirhabdomeral palisades are obvious along the entire rhabdom length (Fig. 4). Similar palisades have also been described in dark-adapted ocelli of *Schistocerca gregaria* (GOODMAN 1970, 1981). Simultaneously, smaller vesicles and sacculi of the smooth endoplasmic reticulum have disappeared from the receptor cell cytoplasm in this state. It may be concluded, therefore, that the palisades have been formed by an aggregation and fusion of vesicular profiles near the rhabdom border. Other organelles described above for the light-adapted state are less frequent or completely absent, in particular the multitubular bodies.

It follows that obvious structural differences of the ocelli in *Periplaneta americana* are correlated with light and dark adaptation. At the same time, these differences give an indication of the pathways for membrane turnover. The light-adapted photoreceptor cells are characterized by containing certain types of degradative organelles. The observed pinocytotic events and vesicles can be assumed to mediate the incorporation of microvillar membranes into the receptor cell, events which are well known in other invertebrate photoreceptors (revs. WHITE et al. 1980, BLEST 1988). In these cases, multivesicular bodies are formed following pinocytosis (l. c.) which are seldom in the ocellar photoreceptors of *P. americana*. Here, the frequent multitubular bodies may serve this function; this is suggested by their enzyme content. The tubuli within these bodies are structurally comparable with the rhabdomeric microvilli (Fig. 3). Therefore, these bodies could be directly formed by a phagocytotic uptake of rhabdomeric pieces, an alternative to the mostly described formation by assemblies of pinocytotic vesicles



(compare BLEST 1980). The further way of degrading incorporated membranes usually leads to dense bodies, and finally to lipid droplets (rev. BLEST 1988). Both these organelles are present in the light-adapted ocellar photoreceptors of *P. americana*.

The formation of perirhabdomeral palisades during dark adaptation is typical for photoreceptors in the ocelli of *P. americana*, in its compound eyes (BUTLER 1973), and in those of several other insects (rev. GOLDSMITH & BERNARD 1974). It is discussed as an optical consequence of such palisades near the rhabdom that the refractive index between rhabdomeric microvilli and receptor cytoplasm becomes modified (see the above review). This results in a total reflection of light at the rhabdom border, hence a better guiding of light within the dark-adapted rhabdoms. Beside this function, the ample system of cisternae formed by such palisades could serve as an effective and local calcium sink which would modify the sensitivity of the receptor cells (rev. WALZ & BAUMANN 1989).

In conclusion, our examination has shown that the ocellus of the cockroach *Periplaneta americana* undergoes adaptational changes in the light and dark which involve a considerable turnover of photoreceptive membranes.

Zusammenfassung

Hell- und dunkeladaptierte Ocellen der Schabe *Periplaneta americana* wurden ultrastrukturell und histochemisch untersucht. Bei Helladaptation kann ein Abbau fotorezeptiver Membranen über mehrere Abbaustufen festgestellt werden, wie er von Komplexaugen bekannt ist. Ein spezielles Degradations-Organell wird histochemisch nachgewiesen. Bei Dunkeladaptation kommt es zu einer Rhabdom-Umbildung und zur Entstehung von rhabdomnahen Palisaden.

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Ocellar retina of *Periplaneta americana*, **left**: in light adaptation, **right**: in dark adaptation.

Fig. 1: Rhabdom configurations (RH) are formed by several neighbouring photoreceptor cells with nuclei (N). Middle borderline between contributing rhabdomeres indicated by arrows. Scale: 5 μm . **Fig. 2:** Multitubular body (MTB) neighbouring (electron-lucent) sacculi of endoplasmic reticulum and several electron-dense profiles. Rhabdom (RH) with distinct middle borderline. Scale: 1 μm . **Fig. 3:** Electron-dense, dot-like precipitates indicating activity of acid phosphatase within multitubular body (MTB) enclosing lipid droplet (L). Note similarity of MTB contents with microvilli of rhabdom (RH) nearby. ($\times 16.800$).

Figs. 4, 5: RH: dark-adapted rhabdoms, N: photoreceptor nuclei. Subrhabdomeric palisades indicated by small arrows. 5 shows aggregation of smaller perirhabdomeral cisternae (arrows), **Inset in 4** shows large palisades. Note absence of middle borderlines within rhabdoms (RH) (only partially in 5). Arrowheads in 5 indicate U-shaped microvilli and membrane loops. Scale bars: 5 μm in 4, 1 μm 5.

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Anschrift der Autoren:

Hansjörg WUNDERER, Zoolog. Institut/Biol. 1,

Universitätsstraße 31, D-8400 Regensburg, F.R.G.

Peter SEIFERT, Zoolog. Institut, Luisenstraße 14, D-8000 München 2, F.R.G.

Gerhard WEBER, Planegger Straße 24 A, D-8000 München, F.R.G.

Wie sehen Insekten polarisiertes Licht?

(Diptera, Syrphidae, Tabanidae)

Von Franziska PILSTL, Andreas LANGE, Peter SEIFERT und Ulrich SMOLA

Abstract

For three dipteran species highly specialized visual cells in the dorsal rim area of the compound eye are described. Within these ommatidia the eight retinula cells are morphologically different from those of normal ommatidia. The retinula cells R1–6 have reduced rhabdomeres and cell somata, the rhabdomeres of the central cells R7 and R8 are enlarged. These two cells form short rhabdomeral segments, which are aligned one after another so resembling the rhabdoms found in some Crustaceans. Judging from their morphology these highly specialized ommatidia are extremely sensitive for polarized skylight.

Im Gegensatz zu uns Menschen besitzen Insekten verschiedener Ordnungen die bemerkenswerte Fähigkeit, linear polarisiertes Licht wahrnehmen zu können.

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