Effect of Formoguanamine on Structure and Function of the Compound Eye of the Butterfly, Papilio xuthus

Authors: Miyako-Shimazaki, Yumiko, Shimazaki, Youji, and Eguchi, Eisuke

Source: Zoological Science, 14(1) : 29-35

Published By: Zoological Society of Japan

URL: https://doi.org/10.2108/zsj.14.29

ZOOLOGICAL SCIENCE **14**: 29–35 (1997)

Effect of Formoguanamine on Structure and Function of the Compound Eye of the Butterfly, *Papilio xuthus*

Yumiko Miyako-Shimazaki[1], Youji Shimazaki[2]
and Eisuke Eguchi[1]*

[1]*Department of Environmental Science, Yokohama City University, 22-2 Seto, Kanazawa-ku, Yokohama 236, Japan*
[2]*Department of Chemistry, Ehime University, Matsuyama 790, Japan*

ABSTRACT—Formoguanamine hydrochloride (FG) is known as a potent chemical to induce blindness in chick eyes by disrupting the pigment epithelium and visual cells in the retina. In this study, we examined the effect of FG on the structure and function of the compound eyes of the butterfly, *Papilio xuthus* (Lepidoptera, Insecta). We administrated 2 mg FG per 1 g body weight of the pupa at about the first one third of the whole pupal period, because accomplishment of morphogenesis of the compound eye occurs in the last half of the pupal period. As a result, unusual membranous structures such as trophospongium-like structures and myeloid bodies were observed in the cytoplasm of the retinular cells besides the normal rhabdom. This result suggests that FG treatment influences on some steps in the formation of rhabdom membranes. However, the amount of chromophore, 3-hydroxyretinal and the responses to white light recorded by the ERG method from FG-treated specimens were not different from the control animals.

INTRODUCTION

Formoguanamine (Fig. 1) is one of the amino-s-triazine compounds. Among them 4 chemicals: ammeline, formoguanamine (FG), 2-amino-s-triazine, and 2-amino-4-hydroxy-s-triazine are known to induce blindness, and FG is the most potent (Matsubara *et al.*, 1975). FG is also known as a classical diuretic triazine which suppresses sodium reabsorption in the renal tubules (Goodman and Gilman, 1975). Obara *et al.* (1985) reported that subcutaneous injection of FG induced blindness in newly hatched chicks within 28-32 hr. According to their paper, FG administration induced degeneration of the pigment epithelial cells and visual cells followed by retinal detachment. In addition, the specific activity of retinal ornithine aminotransferase, which is exclusively localized in the mitochondria of the retinal pigment epithelium, was remarkably decreased, and the retinal vitamin B6 content depressed rapidly.

In this study, we examined the effect of FG on the structure and function of the compound eye of the butterfly *Papilio xuthus*. In many lepidopteran compound eyes, the formation of the rhabdom occurs in the last half of the pupal period (*Manduca*: White *et al.*, 1983; *Bombyx mori*: Eguchi *et al.*, 1962). It is most likely that in *Papilio xuthus*, the formation of the rhabdom occurs in the same period, and for this reason we injected FG during the first one third of the pupal stage.

* Corresponding author: Tel. +81-45-787-2213;
FAX. +81-45-787-2213.

The present study is the first report of the formation of the trophospongium-like structure (TPL) and myeloid body (MB) in the retinular cells caused by a specific chemical reagent.

MATERIALS AND METHODS

Experimental animals

We used both sexes of Japanese yellow swallowtail butterfly, *Papilio xuthus*. The butterflies were taken from a laboratory stock culture derived from eggs laid by wild females captured in Yokohama, Japan. Larvae were reared on citrus leaves under the light regime of 16 hr light : 8 hr dark at 20 ± 1°C, which was maintained throughout the pupal period. The larvae reared under this condition become non-diapausing pupae. Pupal duration (between pupal ecdysis and adult emergence) was typically 18 ± 1 days at 20 ± 1°C.

Administration of formoguanamine hydrochloride

Formoguanamine hydrochloride (FG) was kindly donated by Dr. T. Oishi of Nara Women's University. 2 mg of FG solubilized with 50 µl of saline solution was injected per 1 g body weight of the pupa. FG injections were performed on 5 to 7 day old pupae (following pupal ecdysis) at the intersegmental soft cuticle of the abdomen. As a control (CNTL), saline solution was injected under the same conditions. The effect of FG on the compound eyes of adult butterflies was examined within 3 days after emergence.

In addition to the preliminary experiment, 3 experiments were done. Among 17 FG injected pupae, 10 pupae survived and successfully emerged to adult butterflies.

Histology

For light and electron microscopy, the compound eyes were removed from the head and prefixed with 2% glutaraldehyde plus 2%

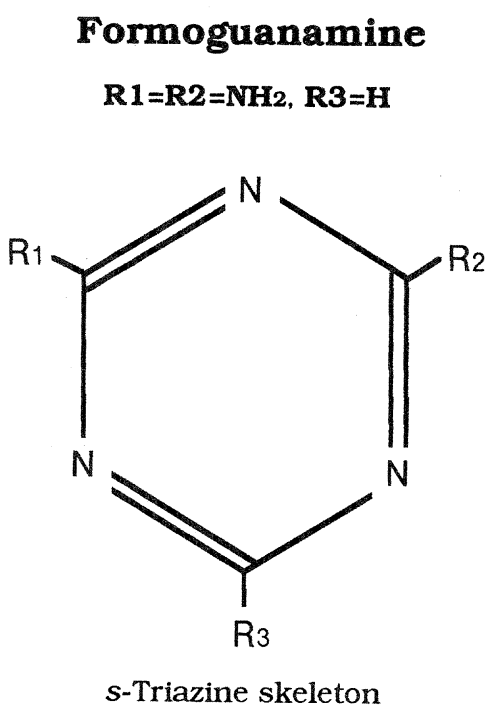

Fig.1. Structural formula of formoguanamine (2,4-diamino-s-triazine). In the present study formoguanamine hydrochloride which was the neutralized formoguanamine with HCl was used.

paraformaldehyde in 0.1 M sodium cacodylate buffer at pH 7.2 (CB) for 12 hr at 4°C. The tissues were then washed in CB, postfixed in 2% OsO_4 in CB for 2-3 hr at room temperature, dehydrated in a graded acetone series and embedded in Epon 812. Semithin sections were cut with a glass knife and stained with 0.2% toluidine blue. Ultrathin sections were cut with a diamond knife, double-stained with uranyl acetate and lead citrate, and examined under a JEM 1200EX electron microscope.

Electrophysiology

The electrophysiological methods used in the present experiments are basically the same as described previously (Bandai *et al.*, 1992; Nakagawa and Eguchi, 1994).

Wings and legs of a butterfly were removed. The animal was then fixed, dorsal side up, to a plastic stage with bee's wax and put at the center of a reflecting ball. The inner surface of the ball was painted with silvery material. A white-light stimulus was provided by a 500 W Xenon arc lamp and led into the Faraday Cage by fiber optics. The tip of the optic fiber was introduced into the reflecting ball through a narrow slit. A small hole was made at corneal surface and a 3 M KCl filled glass-micro electrode was inserted in the center of the eye just below the corneal layer; an indifferent electrode was placed at the dorsal side of the neck. ERG's were measured at different light intensities over a range of 3 log units.

Chromophore analysis

The procedure for extracting 3-hydroxyretinoids and quantitative analyses of 11-*cis* and all-*trans* 3-hydroxyretinals were as described previously (Shimazaki and Eguchi, 1993). The extracted 3-hydroxyretinoids were analyzed by HPLC-system (Waters Corporation) equipped with a YMC SIL column (6 × 150 mm). The peak locations of 3-hydroxyretinoids in the chromatogram were checked by using standards.

RESULTS

General remarks

In a preliminary experiment, different concentrations of FG were injected into pupal bodies of the early pupal stage (5 to 7 days after pupation) to determine the lethal amount of FG to the butterfly. It was confirmed that a FG amount of over 2 mg/1 g body weight caused pupal death. Therefore, in all of the further experiments an amount of 2 mg FG/1 g body weight was injected. The compound eyes of adults within 3 days after emergence were used for all our experiments (EM, ERG, HPLC).

FG-treated butterflies showed no noticeable abnormalities regarding their external appearance; antennae, legs and wings etc. were apparently normal. As to the compound eyes, their shape, size and blackish eye color, etc. also seemed identical to those of control butterflies.

The compound eye of *Papilio xuthus* is of the apposition type. An ommatidial retinula is composed of totally 9 retinular cells; 4 distal, 4 proximal and 1 basal retinular cell can be distinguished according to their contributions to the rhabdom (Bandai *et al.*, 1992).

EM observations revealed that the FG treatments caused unusual membranous structures such as trophospongium-like structure (TPL) and myeloid body (MB) in the cytoplasm of retinular cells (Fig. 2A, B). Beside these structures, many electron dense granules of ca. 50 nm in diameter were observed in the extracellular space between each retinular cell of an ommatidium containing TPL and/or MB (Fig. 2A-C, arrowheads). These granules were not observed in normal compound eyes.

Morphological observations

(1) Myeloid bodies

The myeloid bodies described here (Fig. 2B) were similar in appearance to those reported previously by White and Bennett (1989) and Eguchi *et al.* (1991). MBs were only observed in the distal region of the proximal retinular cells. A single MB is composed of piles of 10-30 flattened membranous sacs of ca. 20 nm in width (Fig. 2B, inset) which can be regarded as specialized modifications of smooth-surfaced endoplasmic reticulum (sER). A membrane of MB of 7-8 nm in thickness is folded at its margin (Fig. 2 B, inset, arrowheads) which shows a structure of hair-pin loops rather like a disc membrane of the outer segment of the vertebrate retina.

The lumen enveloped by the MB membrane is electron lucent without any noticeable structures. Some of the MB membranes were continuous with the rough-surfaced endoplasmic reticulum (rER), exhibiting numerous ribosome particles at the peripheral region of the MB. The planes of MB membranes were arranged in parallel with the optical ommatidial axis, which is perpendicular to those of the rhabdom microvilli.

(2) Trophospongium-like structure (TPL)

Most of TPLs were located in the distal region of the

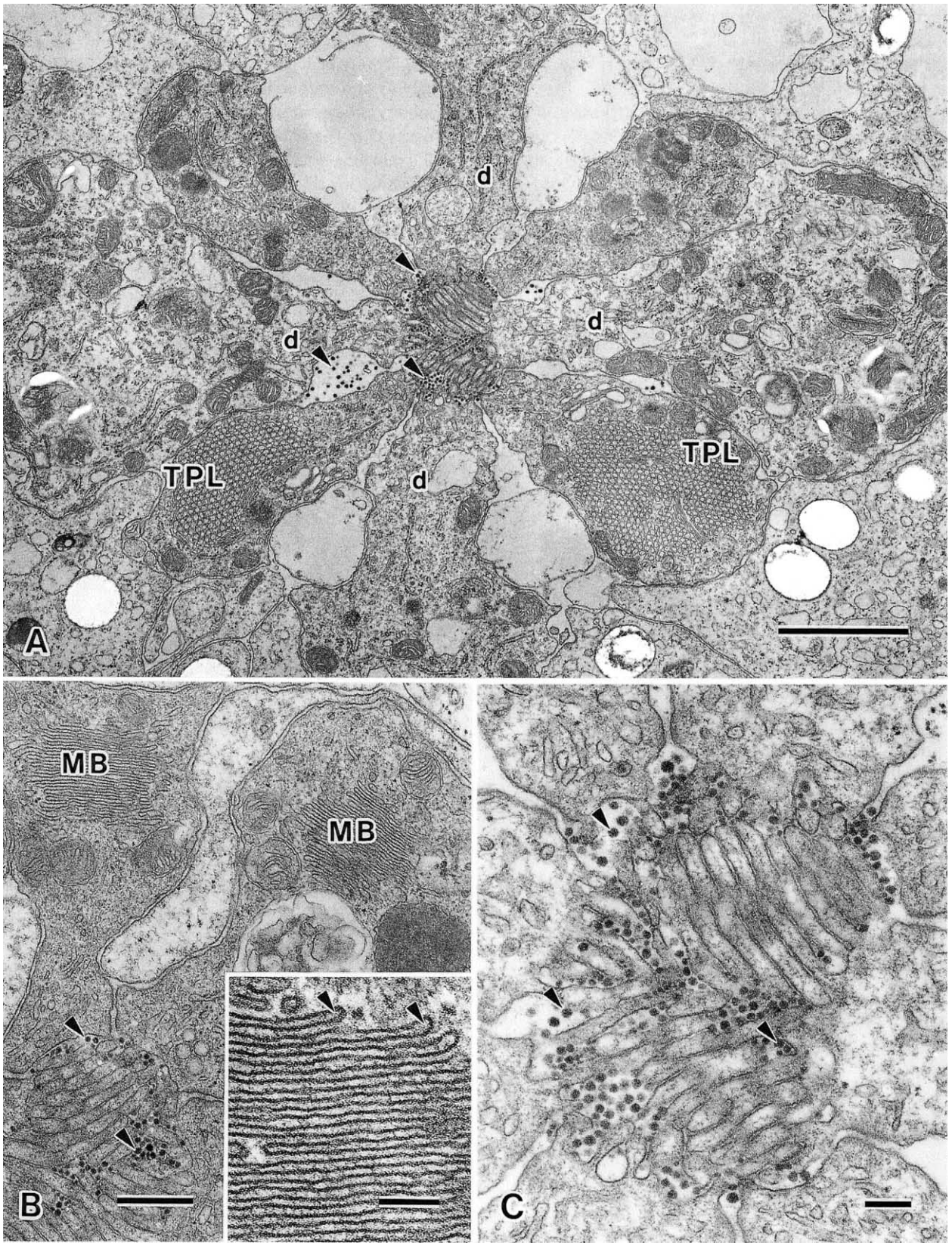

Fig. 2. Cross section of an ommatidium at the very distal layer, just beneath the crystalline cone of FG-treated specimen. (**A**) Trophospongium-like structures (TPLs) are observed in the cytoplasm of the proximal retinular cells (TPL). Distal retinular cells are labelled as "d". (**B**) Myeloid bodies (MBs) are also observed in the cytoplasm of retinular cells (MB). The inset shows a marginal part of MB at higher magnification. MB consists of stacks of flattened cisternae (arrowheads) of ca. 20 nm in width with a space constant of ca. 10 nm. (**C**) Rhabdom region in (**A**). A number of granules (arrowheads) are seen in the intercellular space among retinular cells. Scales: 2 μm (**A**), 500 nm (**B**), 100 nm (**B**, inset), 200 nm (**C**).

proximal retinular cells. The general appearance of the TPL observed here was rather similar to the structures revealed in the retinular cells of the compound eye of Papilio irradiated by strong UV light (Eguchi and Meyer-Rochow, 1983). The cross section to the array of longitudinally arranged tubules of TPL showed a typical honeycomb-like structure (Figs. 2A, 3A).

The diameter of TPL tubules was approximately 50-70 nm (Fig. 3A) which is smaller than that of a rhabdomeric microvillus (ca. 90 nm, Fig. 2C). Some filamentous elements were observed within the lumen of TPL tubules when sectioned transversely (small arrows in Fig. 3A).

Various features of the TPLs sectioned in different directions at the distal layer of the ommatidia are shown in Fig. 3. The typical features of the TPL are shown in cross (Fig. 3A) and in longitudinal sections (Fig. 3D). From the evidence presented in Fig. 3, it is concluded that the TPL consists of stacked tubules of ca. 70 nm in diameter, each 1 to 2 μm in length and arranged in parallel with a space of ca. 15 nm between them. In longitudinal sections along the long axis of the TPL tubules, one end of a tubule is closed (Fig. 3C, arrows); the opposite end, however, is open to the cytoplasm of the retinular cell (Fig. 3D, arrows).

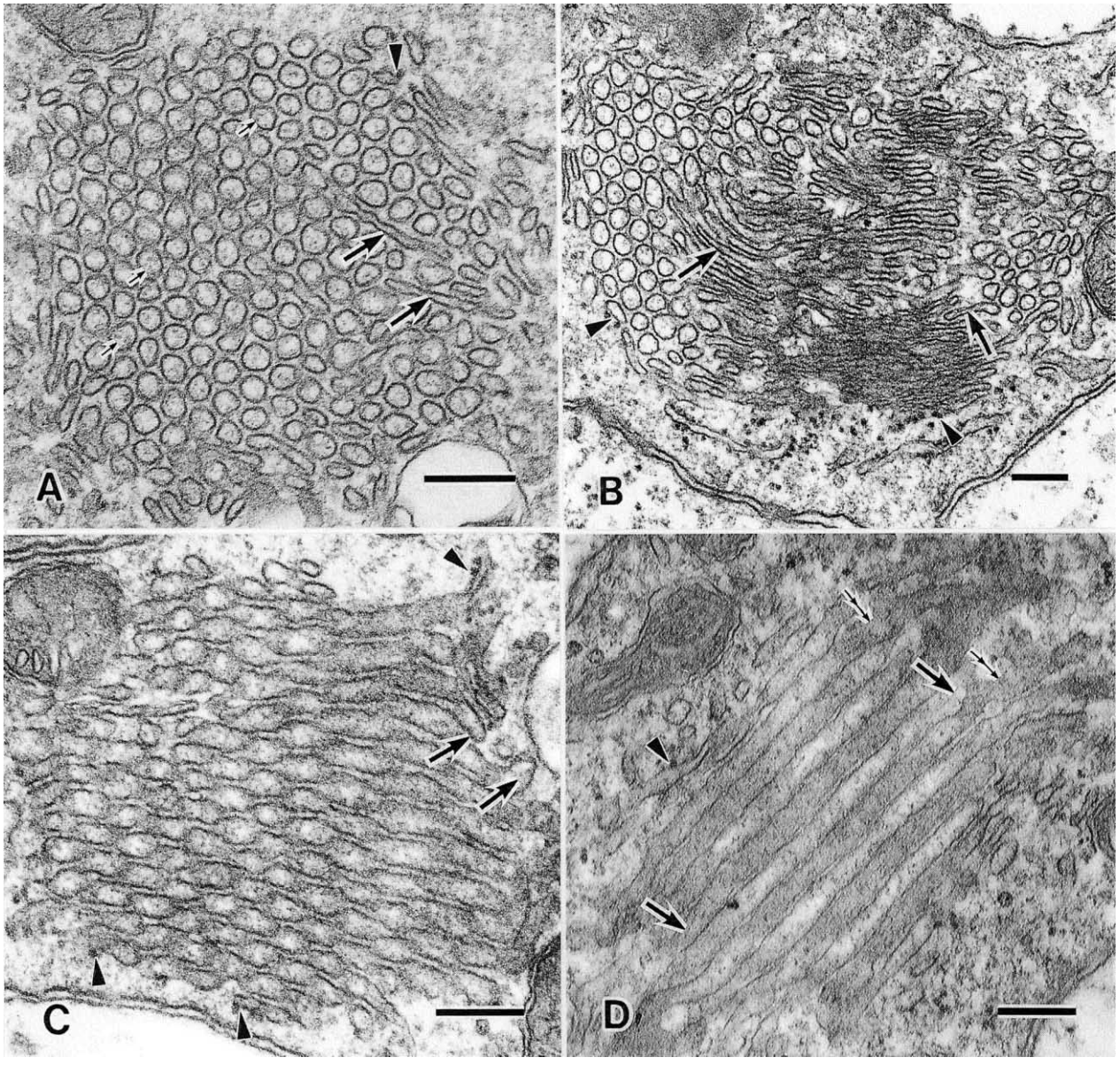

Fig. 3. Various features of TPL, cross- (**A**, **B**), oblique- (**C**) and longitudinal (**D**) sections along the longitudinal axis of tubules of TPLs. The diameter of the tubules of TPL is ca. 50 nm in (**A**), but in another section, it reaches a value of ca. 70 nm. Flat membrane sacs (arrows in **A**, **B**) occasionally exist in TPL. Some filamentous elements are observed in the cisternae of tubules (small arrows in **A**). The edges of the TPL tubules are closed (arrows in **C**) and open (arrows in **D**). Continuity between the tubules of TPL and rER (arrowheads in **A**-**D**) and sER (double arrows in **D**) is frequently observed. Scales in **A**-**D**: 200 nm.

As to the direction of TPL tubules in relation to the ommatidial axis, their tubules are mostly arranged in parallel to the longitudinal optical axis. Longitudinal and oblique profiles of TPL were observed less frequently than transverse sections.

In some TPL, a considerable amount of flattened membranous sacs of ca. 20 nm in width were intermingled with the TPL tubules (Fig. 3A, B, arrows). Continuity between the tubules of TPL and rER (arrowheads in Fig. 3A-D) is frequently observed particularly in the peripheral region of TPL, and also in some instances, TPL tubules were continuous with swollen sacks of sER (Fig. 3D, double small arrows).

Electrical responses

The relation between the amplitudes of the electrical responses and the different intensities of the white lights used as stimulus were investigated by the ERG method. Five individuals each from control and FG treated butterflies were used. The ERG response from normal *Papilio* compound eye is negative and monophasic with a fast transient phase followed by a sustained phase, it is a typical "slow type ERG" according to Autrum's classification (Autrum, 1958). There was no noticeable difference in the wave forms of ERG between the control and FG treated butterflies. ERGs were recorded for light intensities covering 3 log unit. Stimulus-response (V-log I) curves were fitted to the Naka and Rushton equation (Naka and Rushton, 1966a, b) as modified by Norman and Werblin (1974),

$$V / V\,max = In / (In + Kn),$$

where I is the stimulus intensity, V is the amplitude of the response, Vmax is the maximum response, K is the light intensity yielding a response of 50% Vmax and n is the exponential slope of the function.

Figure 4 shows the averaged response amplitudes to the different light intensities (V-log I curves) from control and FG treated butterflies. Highest stimulus intensity used in the practical experiment is 0 in log unit, but in this figure more intense light is indicated in abscissa, to represent the light intensity which is expected to yield a response of estimated Vmax. Basically, V-log I curves of the two groups showed similar sigmoidal curves (Fig. 4).

The measured response amplitudes and the estimated Vmax of FG-treated butterflies were all smaller than those of the control animals (Table 1). For example, the Vmax of FG-treated animals was approximately 7.15 mV, which was 1.37 mV smaller than that (8.52) of the control ones. From the results, the responsiveness of the compound eyes of FG-treated animals to the light stimuli seems smaller than those of the control animals. A statistical analysis by student t-test, however, revealed no significant difference between the two groups ($p>0.05$).

The "k" value, the light intensity which produces half of the amplitude of the Vmax of FG treated animals was -0.68 in log I unit which is 0.42 log unit brighter than that (-1.10) of the control animals (Table 1). Granted that "k" values represent

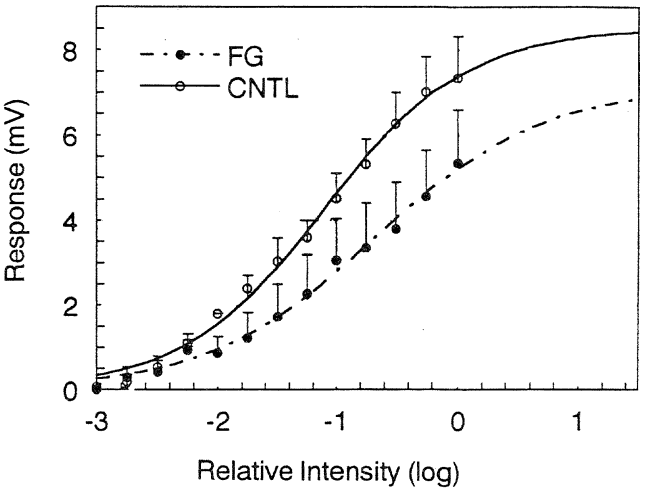

Fig. 4. V-log I curves of ERGs from FG-treated (filled circles) and control (open circles) compound eyes. The theoretical lines are derived from Naka and Rushton's equation.

the sensitivities of the eyes, FG treated eyes ought to be about 2.6 times (converted to light intensity) less sensitive than the control animals. However, according to the statistical analysis, once again no significant difference between the two sets of data was demonstrable.

The "n" value represents the slope in the linear part of the V-log I curve and higher "n" means steeper in gradient and a narrower dynamic range (linear part) of V-log I curve. The "n" of FG-treated butterflies was 0.62 which is a little bit smaller than that (0.73) of the control animals (Table 1). But here again, there was no significant difference between the two groups.

Chromophore contents

As reported by Vogt (1984) and Shimazaki and Eguchi (1993, 1995), the chromophore of the visual pigment is 3-hydroxyretinal. In the present experiments, the amounts of 3-hydroxyretinal were quantitatively measured from FG-treated and control eyes. The amounts of 3-hydroxyretinal per compound eye of FG treated and control butterflies were 30.5 pmol and 35.8 pmol respectively, and statistically there was no significant difference between them.

Table 1. The averaged amounts of chromophore, 3-hydroxyretinal of FG treated and control animals, and the values of "Vmax", "k", "n" of averaged V-log I functions of two groups

	3-hydroxyretinal pmol/eye	ERG		
		V_{max} (mV)	k	n
FG	30.5	7.15	−0.68	0.62
CNTL	35.8	8.52	−1.10	0.73

DISCUSSION

TPL and MB as unusual membranous structures

The structure known as MB is characterized by massed parallel and flattened membranous sacks. MBs are normally observed in the pigment epithelial cells of vertebrate retinas especially of amphibians (Porter and Yamada, 1960; Whittle, 1976). In invertebrates they occur abundantly in the inner segments of visual cells of cephalopod eyes (Yamamoto *et al.*, 1965). But in insect compound eyes, MBs are not normally observed in retinular cells and considered as unusual and abnormal structures. In insect eyes, the formation of MBs can be induced by abnormal treatments such as carotenoid deprivation (*Manduca sexta*: White and Bennett, 1989, 1992), by exposure to unusually bright light during the pupal stage of *Bombyx mori* (Eguchi *et al.*, 1991), and adulthood of beetles (*Anoplognathus pallidicollis*: Meyer-Rochow and Horridge, 1975).

The trophospongium was originally described as a membranous structure in the cytoplasm of nerve cells. The typical example of trophospongium was reported in large nerve cells of the cerebral ganglion of a planktonic crustacean *Leptodora kindtii* (Scharrer, 1964). In this case, trophospongium is composed of an infolding of the cell membrane of a neuron. Later on, Eguchi and Meyer-Rochow (1983) reported the trophospongium-like structure (TPL) in the retinular cells of *Papilio* compound eyes irradiated by UV light. The structure observed in the present study resembles well the TPL except for the diameter of their constituent tubules. Therefore we called it as TPL in the present study.

A lumen of each sack of MB is entirely enveloped with membrane same as an endoplasmic reticulum. While in TPL, a terminal end of a tubule was closed on one side (Fig. 3C, arrows), but the end of the opposite side was open (Fig. 3D, arrows) - at least in some of the tubules. Therefore, inside of a tubule is continuous with cytoplasm, and indeed some of the lumens contain cytoplasmic filaments (Fig. 3A, small arrows). These filaments might act as core filament to support the cylindrical structure of the TPL tubules. The open structure of TPL tubule is quite unique, because, in general, all the membranous cell organelles in the cytoplasm such as endoplasmic reticulum, mitochondria, lysosomal elements etc. are known to be closed systems.

From a morphological point of view, there are similarities and differences between TPL and the rhabdom. On the similarities of TPL to rhabdom microvilli, TPL tubules contain some filamentous structures in their lumens, and one terminal end of a tubule is open to the cytoplasm. On the other hand, the difference between TPL and rhabdom is that the diameter (50-70 nm) of a tubule of TPL in the present study is smaller than that of the rhabdom microvillus (90 nm, Fig. 2C). It seems noteworthy that the diameter of the TPL tubules in the present study is also smaller than that (100 nm) of TPL which was observed in the same butterfly by irradiation with strong UV light (Eguchi and Meyer-Rochow, 1983). The three dimensional structure of TPL in the present study which consists of straight tubules is clearly different from the paracrystalline body described by White and Bennett (1989) which is a network of sinuous tubules representing one of many variations of the tubular and reticular sER. Most of TPLs are arranged in parallel to the optical longitudinal axis of an ommatidium. If the membranes of the TPLs contain visual pigment although which was not confirmed in the present study, this directional arrangement of the TPLs is least effective to absorb incident light passing through an ommatidial optic axis.

Now, another question arises; namely what is the underlying mechanism for the formation of TPL and MB in retinular cells. TPLs and MBs were seen mainly in the distal region of the proximal retinular cells where no rhabdom microvilli protrude from them; the bulk of the rhabdoms of the compound eyes of even those treated with FG were almost completely normal. These facts might suggest that MBs and TPLs are the results of excess production of membranes caused by FG.

The now generally accepted model of turnover of rhabdomeric photoreceptive membrane was proposed by Schwemer (1986). Based on his model, the formation of microvilli membrane involves the following sequence of processes in the retinular cells. At first, photoreceptive membranes containing visual pigments are originally synthesized at rough surfaced endoplasmic reticulum (rER) with numerous ribosomes; rER becomes smooth ER (sER) by the removal of the ribosomes from the rER; small membranous vesicles derived from sER are transported to Golgi bodies where some modifications of the membranes and condensation of the visual pigments occur; small vesicles budding off the Golgi bodies are transported to basal region of the rhabdom and finally incorporate into the rhabdom microvilli.

Itaya (1976) proposed an alternative route of formation of rhabdom membrane, where vesicles derived from endoplasmic reticulum are directly transported to rhabdom without passing through the Golgi apparatus. In the present study, continuity between the tubules of TPLs and rER (arrowheads in Fig. 3A-D) was frequently observed particularly in the peripheral region of TPLs, and also in some instances, TPL tubules were continuous with swollen sacks of sER (Fig. 3D, double small arrows). From these facts it is more likely that the TPLs may be formed directly from the rough and smooth endoplasmic reticulum.

By taking the present results into consideration, MB may be formed by blocking of the release of the small vesicles from sER with FG, followed by the accumulation of sER which are normally synthesized even under the FG treatment. On the other hand, TPL may result from rhabdom formation at the wrong locations, i.e. elsewhere in the cytoplasm other than in the ommatidial center.

Photoresponse and Chromophore content

In the present study, no noticeable differences in the amounts of 3-hydroxyretinal and the photoresponses were

detected between FG and control butterflies. This fact does not necessarily mean that the morphologically abnormal retinular cells caused by FG-treatment have the same functions as those of the control animals. Because the described morphological changes following FG treatment were observed only in about 10% of the total number of ommatidia. Therefore, the function of the majority of the remaining ommatidial retinulae which were unaffected by FG may conceal the expected retarded photoresponse and lower amount of chromophore of the retinular cells affected by FG.

ACKNOWLEDGMENTS

We thank Dr. T. Oishi (Dept. Biol. Nara women's university) for his kind gift of formoguanamine hydrochloride and for critical reading of the manuscript, and Prof. V. Benno Meyer-Rochow (Department of Zoology, Oulu University, Finland) for his kind review of the manuscript. This research was supported in part by Grants-in-Aid for Scientific Research from the Ministry of Education, Science, Sports and Culture of Japan.

REFERENCES

Autrum H (1958) Electrophysiological analysis of the visual systems in insects. Exp Cell Res (Suppl) 5: 426–439

Bandai K, Arikawa K, Eguchi E (1992) Localization of spectral receptors in the ommatidium of butterfly compound eye determined by polarization sensitivity. J Comp Physiol A 171: 289–297

Eguchi E, Naka KI, Kuwabara M (1962) The development of the rhabdom and the appearance of the electrical response in the insect eye. J Gen Physiol 46: 143–157

Eguchi E, Meyer-Rochow VB (1983) Trophospongium-like structures in an insect eye: response of retinula cells of *Papilio xuthus* (Lepidoptera) to irradiation with ultraviolet light. Cell Tissue Res 231: 519–526

Eguchi E, Maeda S, Shimizu I (1991) The formation of myeloid bodies in retinular cells of the pupal compound eyes of silkworm moths (*Bombyx mori*) exposed to a constant bright light. Cell Tissue Res 265: 381–384

Goodman LS, Gilman A (1975) The Pharmacological Basis of Therapeutics. Macmillan, New York

Itaya SK (1976) Rhabdom changes in the shrimp, *Palaemonetes*. Cell Tissue Res 166: 265–273

Matsubara H, Obara Y, Kuba N (1975) On revelation of blindness in baby chicks caused by administration of guanamines, guanides and their related compounds. (Studies on the biological activity of heterocyclic compounds. Part II) J Agric Chem Soc Japan (Nogeikagaku kaishi) 49: 505–511

Meyer-Rochow VB, Horridge GA (1975) The eye of *Anoplagnathus* (Coleoptera; Scarabaeidae). Proc Roy Soc London B 188: 1–30

Naka K, Rushton WAH (1966a) S-potentials from color units in the retina of fish (Cyprinidae). J Physiol 185: 536–555

Naka K, Rushton WAH (1966b) S-potentials from luminosity units in the retina of fish (Cyprinidae). J Physiol 185: 587–599

Nakagawa T, Eguchi E (1994) Differences in flicker fusion frequencies of the five spectral photoreceptor types in the swallowtail butterfly's compound eye. Zool Sci 11: 759–762

Norman RA, Werblin FS (1974) Control of retinal sensitivity 1. Light and dark adaptation of vertebrate rods and cones. J Gen Physiol 63: 37–61

Obara Y, Matsuzawa T, Kuba N, Fujita K (1985) Retinal damage in hatched chicks induced by formoguanamine. Decrease in ornithine aminotransferase activity and vitamin B6 content. Exp Eye Res 41: 519–526

Porter KR, Yamada E (1960) Studies on the endoplasmic reticulum V. Its form and differentiation in pigment epithelial cells of the frog retina. J Biophysic Biochem Cytol 8: 181–205

Scharrer E (1964) A specialized trophospongium in large neurons of *leptodora* (crustacea). Z Zellforsch 61: 803–812

Schwemer J (1985) Turnover of photoreceptor membrane and visual pigment in invertebrates. In "The Molecular Mechanism of Photoreception" Ed by H Stieve, Springer, Berlin Heidelberg New York Tokyo, pp 303–326

Shimazaki Y, Eguchi E (1993) Synthesis of 3-hydroxyretinal in the cytosol of the butterfly compound eye. Vision Res 33: 155–163

Shimazaki Y, Eguchi E (1995) Light-dependent metabolic pathway of 3-hydroxyretinoids in the eye of a butterfly, *Papilio xuthus*. J Comp Physiol A 176: 661–671

Vogt K (1984) The chromophore of the visual pigment in some insect orders. Z Naturforsch 39c: 196–197

White RH, Brown PK, Hurley AK, Bennett RR (1983) Rhodopsins, retinula cell ultrastructure, and receptor potentials in the developing pupal eye of the moth *Manduca sexta*. J Comp Physiol A 150: 153–163

White RH, Bennett RR (1989) Ultrastructure of carotenoid deprivation in photoreceptors of Manduca sexta: myeloid bodies and intracellular microvilli. Cell Tissue Res 257: 519–528

White RH, Bennett RR (1992) Assembly of rhabdomeric membrane from smooth endoplasmic reticulum can be activated by light in chromophore-deprived photoreceptors of *Manduca sexta*. Cell Tissue Res 270: 65–72

Whittle AC (1976) Reticular specializations in photoreceptors: a review. Zool Scripta 5: 191–206

Yamamoto T, Takasaki K, Sugawara Y, Tonosaki A (1965) Fine structure of the octopus retina. J Cell Biol 25: 345–359

(Received August 26, 1996 / Accepted December 4, 1996)