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# Study of taurine and tauret content in the compound eye of locust with light and dark adaptation

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**Summary.** Taurine as well as tauret (retinyliden taurine) levels were measured in locust *Locusta migratoria* compound eyes. HPLC measurements revealed relatively low taurine levels ($1.9 \pm 0.16$ mM) in dark-adapted eyes. Glutamate, aspartate and glycine levels were $2.0 \pm 0.2$, $2.7 \pm 0.4$ and $3.0 \pm 0.37$ mM, respectively, while GABA was present only in trace amounts. After about 4 h of light adaptation at 1500–2000 lx, amino acid levels in the compound eye were as follows: taurine, $1.8 \pm 0.17$ mM; glutamate, no change at $2.1 \pm 0.2$ mM; aspartate sharply increased to $4.7 \pm 0.7$ mM; glycine slightly decreased to $2.8 \pm 0.3$ mM; and GABA trace levels. In the compound eye of locust *Locusta migratoria*, the existence of endogenous tauret in micro-molar range was established. In the dark, levels were several times higher compared with compound eye after light adaptation 1500 lx for 3 h, as estimated by TLC in combination with spectral measurements. Existence of tauret in compound eye is of special interest because in the compound eye, rhodopsin regeneration is based on photoregeneration.

**Keywords:** Taurine – Tauret – Compound eye – Aspartate – Glutamate glycine

## Introduction

After the 1970s, the range of biological phenomena associated with taurine has progressively expanded to include pregnancy, birth, development, brain, heart, liver, and kidney function, osmoregulation, antioxidant and membrane stability (see Huxtable and Sebring, 1986; Huxtable, 1990; Van Gelder, 1990). With time, it became evident and currently there is no doubt that taurine plays an essential role in vision in vertebrates (Pasantes-Morales et al., 1989; Lima et al., 1990, 2004; Petrosian and Haroutounian, 1990, 2000; Lombardini, 1991; Militante and Lombardini, 2002). First of all, a high level of taurine, up to 40 mM concentration, is characteristic for the retina of all vertebrates tested, even for those species which have low taurine content in other tissues and organs (Orr et al., 1976; Voaden et al., 1977; Lima et al., 1990, 2004; Petrosian et al., 2006). The highest level of taurine in the retina (50–80%) has been observed in the photoreceptors (Orr et al., 1976; Voaden et al., 1977; Lake and Vardone-Smith, 1989; Lima et al., 1990). The importance of taurine for vision of vertebrates was emphasized after 1975 when it was recognized that a taurine-free diet causes blindness in cats (see Hays et al., 1975; Schmidt et al., 1977). For visual systems based on wave-guide optic principles such as that specific to insect compound eyes (see Gribakin and Govardovski, 1975), rhodopsin regeneration is based on photoisomerization (Smith and Goldsmith, 1991), and for these systems, there are only rare reports about taurine content. Taurine like immunoreactivity was noted in compound eye of *Drosophila* and *Locusta* (Bicker, 1992; Pirvola and Panula, 1992) and *Honeybee* (Schaffer et al., 1988; Eichmuller and Schaffer, 1995). However, there are almost no direct measurements of tissue levels of taurine or its derivatives in the compound eye.

The other point of interest is tauret (retinyliden taurine), an endogenous taurine conjugate and newly discovered in vertebrate retinae and RPE cells (Petrosian and Haroutounian, 1990, 2000; Petrosian et al., 1996, 2000a, b, 2006). It was suggested that taurine associates with specific retinoid binding proteins and plays an essential role in 11-cis and all-trans retinoid transport between RPE and retina, and that this mechanism involves tauret. Thus, tauret may be involved in rhodopsin regeneration and prevention of light induced damage of photoreceptor cells (Petrosian and Haroutounian, 1990, 2000; Petrosian et al., 1996). Until now, there is no data concerning the existence of tauret in the compound eye where, unlike vertebrate retinal rods, rhodopsin regeneration

is based exclusively on photoregeneration. In the current study, along with efforts to measure taurine in compound eye under dark and light adaptation, we also tried to estimate whether there exists endogenous tauret in the compound eye of locust *Locusta migratoria*.

## Materials and methods

*Light adaptation*

In this study, we used crickets *Locusta migratoria* which were collected not far from Yerevan, in the Eghward region, during September and October of 2004 and 2005. Some groups of the insects were dark adapted for 14–20 h at 20 °C for further determination of taurine, glycine, GABA, aspartic and glutamic acid levels as well as tauret levels. The other groups were light adapted at 1500–2000 lx during 3–5 h at 20 °C for the same purpose.

*Chemicals*

Methanol, HPLC grade, was obtained from Roth (Germany). O-phthalaldehyde and standards of aspartate (1 mg/ml), glutamate (5 mg/ml), glycine (1 mg/ml), taurine (1 mg/ml) GABA (1 mg/ml) and homoserine (1 mg/ml) were obtained from Biokhrom (Russia). All-trans tauret was synthesized in a one step reaction for use as a standard.

*HPLC and TLC analysis of endogenous neuroactive amino acids*

Compound eyes of crickets *Locusta migratoria* were prepared for dark or light adaptation under dim red or white 1500 lx light, respectively. Samples, each containing 6 compound eyes, were immediately weighed to avoid loss of mass. Then, the samples were homogenized by glass–glass homogenizer in 300 µl 0.1 N $HClO_4$ and left to stand at least for 2 h for free amino acid extraction. After that, samples were centrifuged at 15000 rpm for 15 min. After o-phthalaldehyde derivatization, 50 µl of the supernatants were used for amino acid content determination by high-pressure liquid chromatography (ED-108, Biokhrom, Russia). Homoserine was used as an internal standard for amino acid quantification. Column $C_{18}$ 150 × 4.6 (Phenomenex) was employed for amino acid separation. Taurine content was also estimated in parallel with TLC. TLC was performed on starch pre-coated silica gel plates (Armsorb). For this procedure, 3 µl 0.1 N $HClO_4$ extracts and standard synthetic taurine and other amino acids solutions were spotted on Armsorb sheets which were then developed for about 2 h in butanol:acetic acid:water combined in a 36:9:15 ratio. After development, spots on sheets were treated with a acetone:acetic acid mixture in a 36:4 ratio plus 100 mg ninhydrin, then were visualized by heating at about 120 °C for 5–6 min.

*Estimation of tauret content*

After collecting in conditions described above, compound eyes were rapidly frozen in dry ice. Then, 6 samples of dark and light adapted compound eyes, each sample containing 12 compound eyes, were freeze dried (freeze-dryer LGA 05, WML, Germany) at −20 °C under vacuum ($1 \times 10^{-3}$ Pa) for about 30 h. The freeze-dried samples were weighed and homogenized, and 100 µl dry methanol was added to the homogenates. After 2 h of extraction, samples were centrifuged (15 min at 15000 rpm) and methanol excess was evaporated until about 30 µl supernatant remained which was then further analyzed. TLC of the samples was performed in combination with spectral measurements. For this purpose, 30 µl of 100% methanol extracts of dried compound eye and 30 µl of standard synthetic tauret (1 mM in 100% methanol) were spotted on the Armsorb sheets. These were then developed for about 20 min with the mixture of chlorophorm:methanol:trifluoroacetic acid in a ratio 20:6:0.4. In some cases during development, trifluoroacetic acid was removed from the developing system. After development, Armsorb sheets were cut into separate strips. Then strips with spots corresponding to tauret standards ($R_f$ equal to about 0.65) were placed into 1.2 ml of 100% methanol solution for compound extraction. Then absorbance spectra of methanol extracts of such spots were recorded. In case of development without trifluoroacetic acid, absorbance was recorded twice, before and after protonation, by adding 10 µl 0.1 N HCl. In this way one can establish whether there exists Schiff base bearing molecule in samples such as tauret. Absorbance was recorded on spectrophotometer Specord (Carl Zeiss Jena) or Hitachi 150-20 (wavelength range 334 to 500 nm).

## Results

*TLC estimation of taurine in locust compound eye*

The first series of TLC using taurine standards revealed relatively high levels of taurine in locust compound eyes kept in the dark, roughly estimated to be in the range 10–20 mM. It is interesting to note that there is a noticeable decrease in taurine levels after 1500–3000 lx/3 h light adaptation (see Fig. 1) in each series of TLC determination. Another TLC study of cricket compound eyes was performed using different amino acid standards. Rather high levels of glutamate, aspartate and glycine, as compared with taurine, and relatively low GABA content was revealed with dark adaptation (Fig. 2). During this series of TLC determinations, it was difficult to get any quantitative estimation of taurine content. In the same series, a decrease in taurine content in the cricket compound eye and an increase in aspartate and glutamate (Fig. 2) were noted with light adaptation at 1500–2000 lx/3 h.

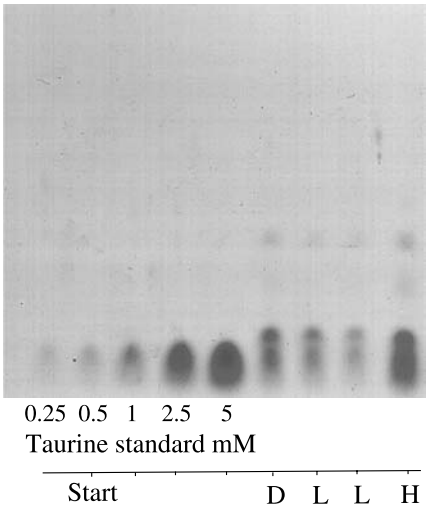


**Fig. 1.** TLC determination of taurine content in the locust compound eye. First 5 spots are taurine standards 0.25, 0.5, 1.0, 2.5, 5.0 mM. Samples of compound eye in dark (*D*) under light (*L*) and extract from head (*H*) from dark-adapted insect

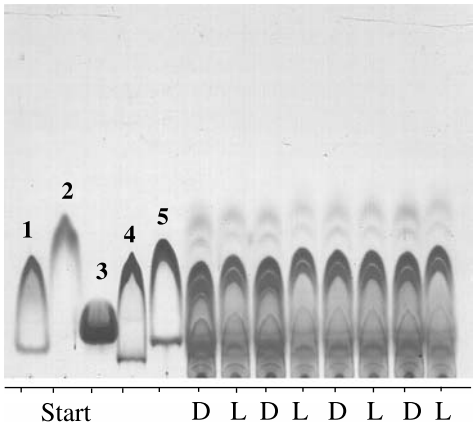


**Fig. 2.** TLC determination of glycine, GABA, taurine, aspartic acid and glutamic acid content in the locust compound eye at dark and light adaptation. First 5 spots are 1-glycine, 2-GABA, 3-taurine, 4-aspartic acid and 5-glutamic acid standarts each at 1.0 mM concentration. Spots ## 6–13 are samples of compond eye in dark (*D*) and in light (*L*) correspondingly. During each spotting of standards as well as from extracts of compound eye 3 µl samples were spotted

### *HPLC measurements of taurine and free amino acids in cricket compound eye*

The average wet weight of one compound eye was about 4.6 mg. A typical HPLC profile is represented in Fig. 3. In dark-adapted cricket compound eyes, taurine level is remarkably low ($1.9 \pm 0.16$ mM) when compared to TLC estimation. Glutamate, aspartate and glycine levels were $2.0 \pm 0.2$ mM, $2.7 \pm 0.4$ mM and $3.0 \pm 0.37$, respectively; while there were only trace amounts of GABA. After about 4 hour-light adaptation at 1500–2000 lx, amino acids levels in the compound eye were as follows; taurine $1.8 \pm 0.17$; glutamate, no change at $2.1 \pm 0.2$; aspartate sharply was increased to $4.7 \pm 0.7$ mM; glycine decreased to $2.8 \pm 0.3$; and GABA only trace amounts. It is interesting to note that aspartate increase was more dramatic upon light adaptation.

### *TLC and spectral estimation of tauret in locust compound eye*

The average weight of one dried compound eye was about 2.0 mg. Each sample for tauret measurement contained 10–12 compound eyes. TLC of standard tauret was done after about 20 minute elution without any other additional treatment. This revealed tauret as a well-defined dark orange colored spot with $R_f = 0.65$ (Fig. 4). On the line where the methanol extract of dark adapted compound eye was spotted on the same plate, the appearance of dark orange colored tauret-like spot was noted after development with $R_f$ around 0.65 (Fig. 4). A less intensely colored tauret-like spot was noted on the same plate in the case of light adapted compound eye extract (Fig. 4). Spectral measurements of the spots corresponding to standard tauret and dark- and light-adapted compound eye samples obtained from the spotting line (situated in circle, see Fig. 4) revealed an absorbance maximum at 440 nm for standard tauret (curve 1 on Fig. 5) and around 440 nm for dark- (curve 2 on Fig. 5) and light-adapted (curve 3 on Fig. 5) compound eye samples. It is necessary to note that tauret is noticeably higher in dark-adapted compound eye

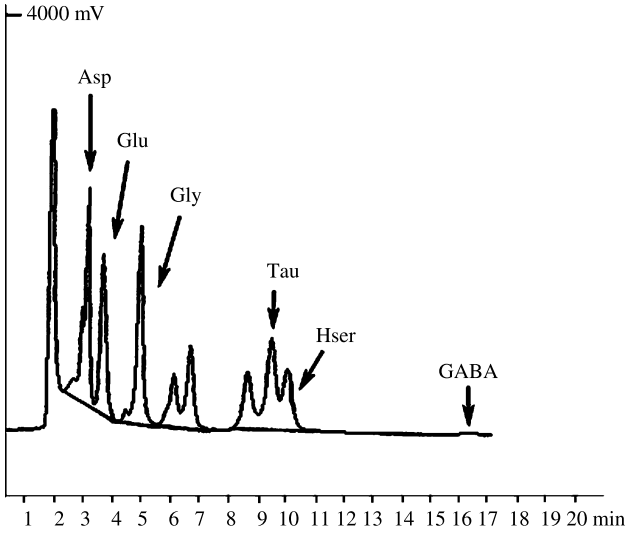


**Fig. 3.** Typical HPLC profile of taurine, glutamate, aspartate, glycine, GABA and internal standard homoserine content in locust compound eye in dark (flow rate 1 ml/min)

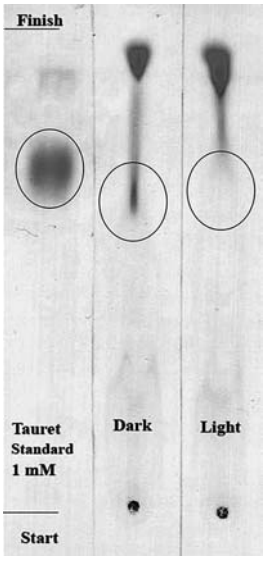


**Fig. 4.** TLC estimation of tauret content in the dark and light adapted locust compound eye. Tauret in standard and in compound eye is encircled

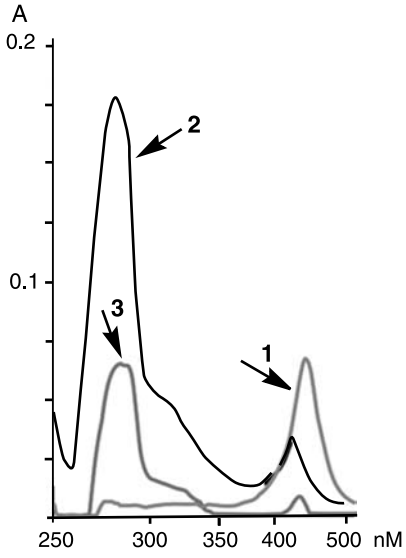


**Fig. 5.** Absorbance spectra of TLC spot corresponding to tauret in extract of dark (*2*) and light (*3*) adapted locust compound eye. Absorbance spectra of standard tauret spot is marked by *1*. TLC development system with trfluoroacretic acid. The region of absorbance maximum of tauret is around 440 nm

compared with light-adapted eyes (compare absorbance maximum on curve 2 and curve 3 around 440 nm in Fig. 5). In the next study, TLC was carried out in the system where trifluoro acetic acid was specially omitted. After development, spots corresponding to the tauret position for standard and dark- and light-adapted compound eyes were removed and the 100% methanol extract absorbance spectra recorded. Initial absorbance spectra in a spot corresponding to tauret position in sample of dark-adapted compound eye is represented on Fig. 6 (bottom curve). The absorbance maximum around 350 nm is hardly visible. After protonation by the addition of 10 µl of 0.1 N HCl, the appearance of absorbance spectrum was observed with a clearly visible maximum around 440 nm (Fig. 6, upper curve). This well-defined shift in absorbance maximum in combination with TLC records clearly indicates on the presence of Schiff base bearing tauret molecule in dark-adapted compound eye. The obtained data strongly support the presence of endogenous tauret in cricked compound eye.

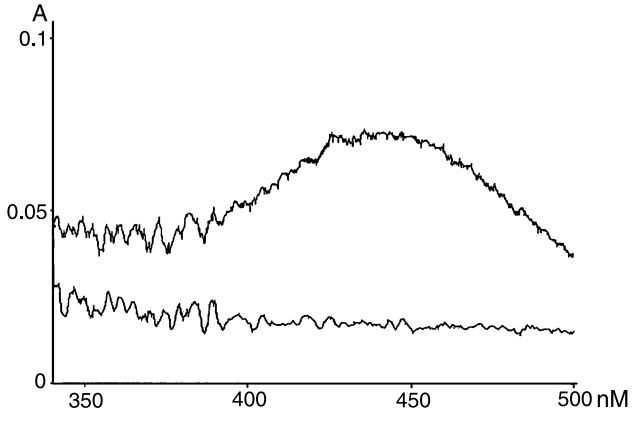


**Fig. 6.** Absorbance spectra of tauret in extract of TLC spot from dark-adapted compound eye. Lower curve: before protonation; upper curve: after protonation

## Discussion

With initial estimates of taurine content by TLC (Fig. 1), we demonstrated relatively high concentrations in the range of 10–20 mM in the compound eyes of crickets (*Locusta migratoria*). However, the following TLC test (Fig. 2) clearly shows that with the system we have used, it is difficult to have adequate separation of taurine from other free amino acids. So, we conclude that with the first TLC, we overestimated taurine content in the compound eye. For more precise measurements, HPLC analysis was used. Regardless, both types of TLC analyses have confirmed immunohistochemical data on taurine like reactivity in compound eye (Bicker, 1992; Pirvola and Panula, 1992; Schaffer et al., 1988; Eichmuller and Schaffer, 1995). Moreover, a decrease in compound eye taurine content was demonstrated upon illumination.

HPLC measurements revealed that taurine content in dark-adapted compound eye was 1.9 mM. However, if we will take into account that water content was about 60%, then one can assume that taurine content in the compound eye will be a little higher. Even with such correction, taurine content in cricket compound eye is still rather low when compared with the large amounts of taurine measured in the retina of all vertebrates so far tested (Orr et al., 1976; Voaden et al., 1977; Lima et al., 1990, 2004; Petrosian et al., 2006). It is important to note that with HPLC measurements, a slight, but steady decrease in taurine content of about 5% was observed upon illumination.

Another difference from vertebrate retina, as one can see in Table 1, is that taurine in crickets compound eye is not dominant among the free amino acids. Rather, aspartate and glycine are dominant. Aspartate could be a possible neurotransmitter in compound eye photoreceptor cells because of the very dramatic increase of aspartate content upon illumination (almost 75%).

As has been noted before, the importance of taurine is well documented, for the viability of vertebrates retinal cells (Hays et al., 1975; Orr et al., 1976; Schmidt et al.,

**Table 1.** Amino acid content of the locust compound eye in mM at light and dark adaptation

| Compound eye | Aspartate | Glutamate | Glycine | Taurine | GABA |
|---|---|---|---|---|---|
| Dark | $2.7 \pm 0.4$ | $2.0 \pm 0.2$ | $3.0 \pm 0.37$ | $1.9 \pm 0.16$ | Traces |
| Light | $4.7 \pm 0.7$ | $2.1 \pm 0.2$ | $2.8 \pm 0.3$ | $1.8 \pm 0.17$ | Traces |
| Change | +74% | +5% | −7% | −5% | – |

(n = 5) Confidence interval 90%

1977; Voaden et al., 1977; Lake and Vardone-Smith, 1989; Pasantes-Morales et al., 1989; Lima et al., 1990, 2004; Lombardini, 1991; Petrosian and Haroutounian, 2000; Militante and Lombardini, 2002), in its involvement in osmoregulation (Pasantes-Morales et al., 1989), for calcium ion balance (Pasantes-Morales et al., 1989; Lombardini, 1991; Militante and Lombardini, 2002), in retinal protein phosphorylation (Lombardini, 1991; Militante and Lombardini, 2002), and for retinoid transport (Petrosian and Haroutounian, 1990, 2000; Petrosian et al., 1996, 2000a, b). Taurine exerts also a trophic action on the vertebrate retinal cells (Lima et al., 1990, 2004). With respect to localization of these effects, the problem with the vertebrate retina is that it is multimodal, consisting of different types of neuronal cells. In case of the compound eye, the situation is much simpler because the distal part of the compound eye that we prepared for analysis can be considered as a relatively pure cellular fraction containing mostly photoreceptor cells plus a few pigment cells.

Such understanding with respect to the existence of tauret in the compound eye as established in the current study may be helpful for clarifying tauret localization in the vertebrate retina. On the existence of tauret in compound eye, are indicating at least 3 points. First, upon TLC of the compound eye sample, a spot with $R_f$ around 0.7 was found which corresponds to standard tauret in the system (see Fig. 4 and Petrosian et al., 1996, 2000b). Second, the comparison of the absorbance spectrum of these samples has shown almost the same absorbance maximum (see Fig. 5). Third, in TLC analysis where trifluoroacetic acid was specially omitted, the maximum of absorbance spectrum of compound eye sample after protonation was shifted about 80 nm (Fig. 6), which strongly indicates on Schiff base bearing molecules in sample. Tauret was found in micro molar concentration in dark adapted compound eye and showed remarkable decrease upon illumination, as is seen in vertebrates retinae (Petrosian et al., 1996, 2000b, 2006). From these data, one can expect that tauret in vertebrate retina is concentrated in the photoreceptor cells. The fact that tauret exists in compound eye photoreceptor cells, where rhodopsin regeneration is based on photoisomerization (Smith and Goldsmith, 1991), is a hint that along with rods, one can assume the existence of tauret in the cone cells, where rhodopsin regeneration is a bit different from rhodopsin regeneration in rods (Imai et al., 1997). Summarizing, one can conclude that tauret is probably found in 3 types of photoreceptor cells; $1^{st}$ – in rods, where bleaching takes place after light absorbance and then a slow regeneration of rhodopsin follows; $2^{nd}$ – in cones, where bleaching takes place after light absorbance but afterwards regeneration is fast; $3^{rd}$ – in rhabdoms of ommatidia of compound eye where recovery rather is based on very fast photoregeneration via photoisomerization.

For rods and cones, the assumption was made that taurine is involved in transport of retinoids via tauret (Petrosian and Harouiounian, 1990, 2000; Petrosian et al., 1996, 2000a, b, 2006). In case of 11-cis retinal, it was suggested that along with specific retinoid binding proteins, taurine may play an essential role in 11-cis retinal transport between RPE and retina and thus it may be involved in rhodopsin regeneration (Petrosian and Harouiounian, 1990, 2000; Petrosian et al., 1996, 2000a, b, 2006). In case of all-trans retinal, it was suggested that taurine may be involved in removal of all-trans retinal from photoreceptor cells. Taurine may thus help to prevent photoreceptors from light induced damage (Petrosian and Harouiounian, 1990, 2000; Petrosian et al., 1996, 2000a, b, 2006) because all-trans retinal itself can enhance light induced damage (see Kalamkarov and Ostrovsky, 2002). However, at first glance, such understanding of the role of tauret is not useful in case of compound eye where rhodopsin regeneration is based on photoisomerization (Smith and Goldsmith, 1991) which does not need all-trans retinal removal. Tauret existence in the compound eye thus seems paradoxical. On the other hand, there exists another, slow component of rhodopsin regeneration which may involve tauret, specifically, its *de novo* synthesis. This applies as well in the case of vertebrates photoreceptors, which continually need renewal of rhodopsin stores because of shedding. In any case, tauret is probably essential for primary vision in the vertebrate retina and in the compound eye as well. However, its precise function for each case needs further clarification.

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