

Research Note

On the Possible Function of the Proximal Lens Unit of *Notonecta glauca*

GÁBOR HORVÁTH*

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The water bug *Notonecta glauca* has doublet lenses corrected for spherical aberration. The proximal lens unit constitutes a refractive index transition between the distal lens unit and the crystalline cone. It inevitably reduces the reflectivity of the eye. Such correction for spherical aberration, however, could also be simply achieved by means of an aplanatic singlet lens. Therefore it seems possible to suppose that the proximal lens unit might produce both decreased reflection and increased transmission. To test this idea, the reflectivity of the doublet in *Notonecta* is calculated and compared with the reflectivity of two corresponding aplanatic singlets of different refractive indices for contact with air and water. Because of the lower lens unit, the absolute reflection suppression ΔR in the dioptric apparatus is about 2% in water and the relative reflectivity reduction $\Delta R/R$ amounts to 65%. In air this effect is negligible. The question of the evolutionary importance of this phenomenon is briefly discussed.

Notonecta glauca Dioptric apparatus Proximal lens unit Reflection suppression Transmission enhancement

1. INTRODUCTION

Bedau (1911) observed that the corneal lens of the water bug *Notonecta glauca* is composed of two layers. Schwind (1980) found that both lens units are optically homogeneous and that the refractive indices of the distal and proximal units are $n_d = 1.54$ and $n_p = 1.46$, respectively. The two units are separated by a thin transitional correction layer [Fig. 1(A)] which reduces the spherical aberration (Schwind, 1980; Horváth, 1989a). Schwind (1980) demonstrated that the dioptric apparatus of *Notonecta* has only a very small spherical aberration in air as well as in water. Horváth (1989a) calculated the optimal form of the lens of *Notonecta* and the optimal shape and position of the correction layer, and found that the dioptric apparatus of backswimmer is optically well optimized. Similar aplanatic doublet lenses were found also in the schizochroal compound eye of phacopid trilobites (Clarkson & Levi-Setti, 1975; Horváth, 1989b), and in the ocellar eye of the sawfly larva *Perga* (Meyer-Rochow, 1974).

Correction for spherical aberration results in an exact focal point which increases the light-collecting efficiency and sensitivity of the eye. Correction for spherical aberration can be achieved simply by means of an aplanatic singlet lens as designed first by Huygens (1690). The trilobite *Phacops rana milleri*, for example, saw sharply by its post-ecdysially developing schizochroal compound eye consisting of Huygensian

singlet lenses composed of calcite (Horváth & Clarkson, 1993). What is then the optical function of the proximal unit in the doublet lens of *Notonecta*?

In this note an attempt is made to answer this question. The lower unit in the doublet of *Notonecta* introduces a transition of refractive index between the upper lens unit and the crystalline cone, therefore it inevitably suppresses the amount of light reflected from the internal refracting surfaces of the dioptric apparatus. It is suggested that this reduction in reflectivity may be a possible optical function of the proximal lens unit in the backswimmer. To test this idea, the reflectivity of the doublet of *Notonecta* is calculated and compared with the reflectivity of two corresponding aplanatic singlets of different refractive indices. The relatively small effect of the proximal lens unit in suppressing internal reflection in *Notonecta* is quantitatively determined and the question of its evolutionary importance is briefly discussed.

2. METHODS

The dioptric apparatus in the foveal region of the eye of *Notonecta* was modelled by the optical system in Fig. 1(A). The doublet lens—consisting of two homogeneous units ($n_d = 1.54$, $n_p = 1.46$)—connects below with an optically homogeneous crystalline cone with index of refraction $n_c = 1.35$ and the focal point F lies at the proximal tip of the cone (Schwind, 1980). The shape of the correction layer was calculated by means of the geometric optical method presented previously (Horváth, 1989a). The upper and lower boundary surfaces of the correction layer coincide with the correction

*Universität Tübingen, Lehrstuhl für Biokybernetik, Auf der Morgenstelle 28, D-72076 Tübingen 1, Germany.

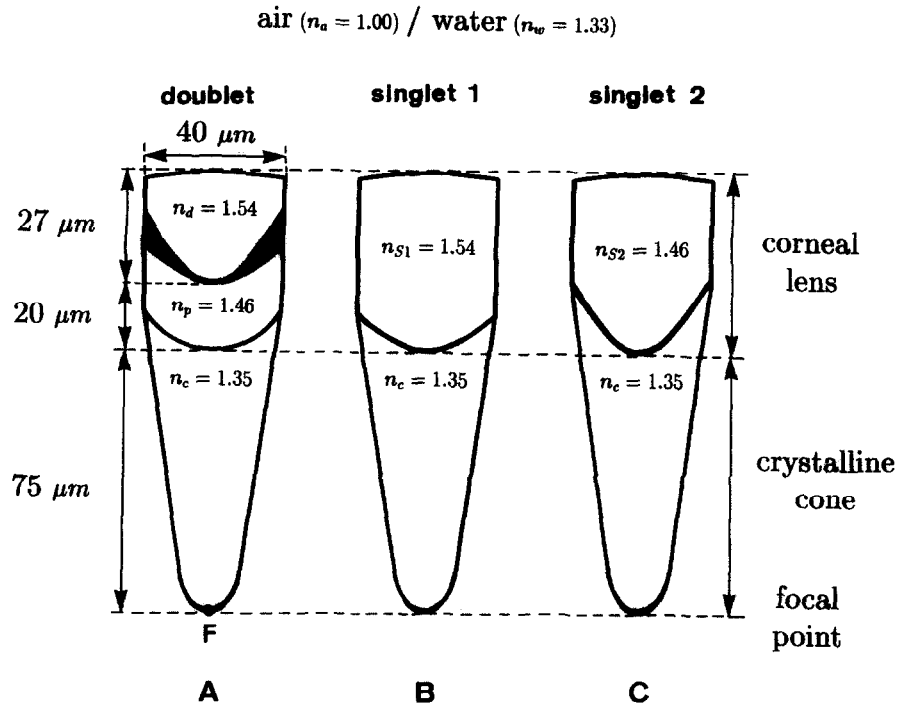


FIGURE 1. Schematic representation of the vertical section of the three dioptric apparatuses investigated, consisting of optically homogeneous elements. The geometrical parameters and the refractive indices are indicated. The focal point F lies at the proximal tip of the crystalline cone. The external medium is air or water. (A) The aplanatic doublet lens of the water bug *N. glauca* has a thin correction layer (black) between the distal and proximal lens units. (B, C) Aplanatic singlet lenses, whose distal surface coincides with that of the doublet and their proximal surface has a Huygensian correction profile.

interfaces calculated for contact with water and air, respectively. For the sake of simplicity, the thin correction layer was considered optically homogeneous with the intermediate refractive index $n_t = (n_d + n_p)/2 = 1.5$.

The dioptric apparatus of *Notonecta* was compared with the corresponding dioptric apparatuses in Fig. 1(B, C), consisting of an aplanatic homogeneous singlet lens and a crystalline cone. In both singlets the correction for spherical aberration is ensured by the proximal Huygensian lens profile, the shape of which was calculated by the same method as in Horváth and Clarkson (1993). The distal surface of the singlets coincides with that of the real doublet of *Notonecta*. The refractive indices of singlet 1 [Fig. 1(B)] and singlet 2 [Fig. 1(C)] are equal to that of the distal ($n_{s1} = n_d = 1.54$) respectively proximal ($n_{s2} = n_p = 1.46$) unit of the doublet. The thickness, diameter and focal length of the singlets are the same as those of the doublet.

With the help of the expression of the amplitude reflection coefficient ρ for optical interfaces, the reflectivity R of the different refracting surfaces in the dioptric apparatus of *Notonecta* is given in the Appendix. The reflectivity of the correction layer in the doublet was calculated in two steps. First the correction interface for contact with water and the corresponding reflectivity R_{upper} were determined; these give the upper surface of the correction layer and its reflectivity. In the second step the correction interface for contact with air and the corresponding reflectivity R_{lower} were determined, giving the lower surface of the correction layer and its reflectivity. The resultant reflectivity of the doublet will be the sum of the reflectivities of the different refracting

surfaces. The reflectivity of the two aplanatic singlets studied [Fig. 1(B, C)] can be calculated similarly.

3. RESULTS

Figure 2(A) shows the calculated correction layer in the doublet of *Notonecta* while Fig. 2(B, C) demonstrates the computed proximal Huygensian correction profiles of the aplanatic singlets 1 and 2 for contact with water. Figure 2 also represents the ray tracing through the dioptric apparatuses when they are immersed into water. *N. glauca* is an amphibious water bug and, therefore, its eye has to function in air as well as in water (Schwind, 1980). The three dioptric apparatuses were therefore studied in air ($n_a = 1.00$) and water ($n_w = 1.33$). The calculated values of the reflectivity R , reflectivity difference $\Delta R \equiv R_{\text{singlet}} - R_{\text{doublet}}$ and relative reflectivity difference $\Delta R/R_{\text{singlet}}$ are shown in Table 1 for contact with air and water.

For scotopic vision as much light as possible has to be collected. Many nocturnal *Lepidoptera* possess a corneal nipple array to suppress reflection of light from their corneal surface and to enhance the transmissivity of their dioptric apparatus (Bernhard, Gemne & Sällström, 1970). Scanning electron microscopic studies showed that the corneal surface of the *Notonecta* eye is smooth and lacks corneal nipples (Horváth, unpublished data).

Because of the amphibious life of *Notonecta* its external lens surface is very flat (Schwind, 1980) and has a low refractive power. Consequently, the internal refracting surfaces, the correction layer or the proximal lens surface, require significant curvature (Fig. 2) in both the

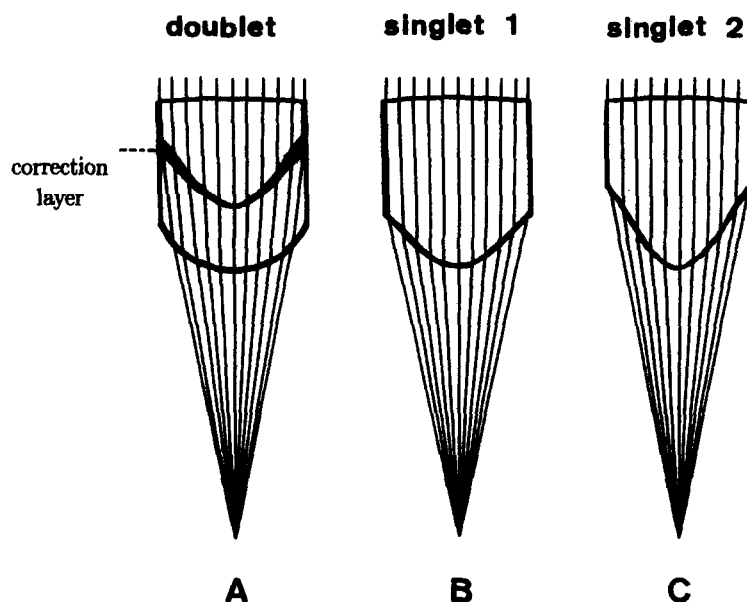


FIGURE 2. The calculated correction layer in the backswimmer's doublet (A) and the proximal Huygensian profiles in the singlets (B, C) with ray tracing for contact with water. For the sake of simplicity, the contours of the crystalline cones are omitted.

singlet and doublet lenses to ensure the necessary refractive power of the dioptric apparatus. The smaller the refractive index of the singlet, the steeper must be its proximal Huygensian correction profile for the same power [Fig. 2(B, C)]. From equation (1) of the Appendix one can see that the amount of light reflected from a refracting surface increases with the incident angle ϕ and with the refractive index difference Δn between the two adjacent optical media. In water, where backswimmers spend most of their life, the amount of light reflected from the flat distal lens surface is negligible: from Fresnel's formula $R_{\perp} = (n_1 - n_2)^2 / (n_1 + n_2)^2$ for normal incidence (Guenther, 1990) with n_1 (water) = 1.33 and n_2 (cornea) = 1.54 one can obtain a reflectivity value of about 0.5%—unnecessary to reduce it further by corneal nipples. The resultant reflectivity of the lens is thus principally determined by the internal refracting surfaces of the dioptric apparatus.

As shown in Table 1, the reflectivity of singlets 1 and 2 in water amounts to 1.94 and 2.60%, respectively. In spite of the smaller refractive index of singlet 2 its reflectivity is larger in water than that of singlet 1 because of the steeper rise of the proximal Huygensian correction profile [Fig. 2(B, C)]. This demonstrates the dominant role of the steep slope of the proximal lens surface in determining lens reflectivity in water. In air

this dominance disappears, and singlet 1 has larger reflectivity (5.43%) than singlet 2 (5.00%).

It is clear from Table 1 that the doublet has smaller reflectivity than the singlets in air as well as in water. This effect is the inevitable consequence of the reflectivity suppression by the correction layer and the proximal lens unit: both constitute a refractive index intermediate between the optical media they separate. In air, this reflectivity reduction is negligible: 0.10–0.53% in absolute value and 2.0–9.8% relatively (Table 1). However, in water, the absolute reflectivity suppression amounts to 1.04–1.70%, which means some 54–65% relative reduction and a very small reflectivity of 0.90% (Table 1). Because the index of refraction of the correction layer is not homogeneous as it was assumed for simplicity, the calculated reflectivity reduction in the doublet of *Notonecta* is underestimated (Table 1).

4. DISCUSSION AND CONCLUSION

According to Giller and McNeill (1981), backswimmers prefer dim, turbid and standing waters with a dense growth of aquatic plants and phytoplankton. The peripheral photoreceptors R1–R6 of backswimmers act as a scotopic system and are associated with adaptation to a dimly lit environment (Schwind, Schlecht & Langer, 1984). The light-collecting efficiency of the eye is of particular importance under these conditions and is mainly ensured by means of correction for spherical aberration of the lens. The only other possible way to increase the light-collecting efficiency is to minimize the amount of light reflected from the refracting surfaces of the dioptric apparatus, because the effect of light scattering within the substance of the lens and the crystalline cone is negligible (Miller, 1979).

Reflections of light occur wherever there are sharp transitions in refractive index. In the case of a common

TABLE 1. The calculated values (in %) of the reflectivity R , reflectivity difference $\Delta R \equiv R_{\text{singlet}} - R_{\text{doublet}}$ and relative reflectivity difference $\Delta R/R_{\text{singlet}}$ for the three aplanatic dioptric apparatuses in Figs 1 and 2 in air and water

	R (%)		ΔR (%)		$\Delta R/R_{\text{singlet}}$ (%)	
	Air	Water	Air	Water	Air	Water
Doublet	4.90	0.90	—	—	—	—
Singlet 1	5.43	1.94	0.53	1.04	9.8	53.6
Singlet 2	5.00	2.60	0.10	1.70	2.0	65.4

arthropod cornea with a refractive index of 1.5 the upper limit for the reflectivity is about 4% at normal incidence in air (Miller, 1979) so the effects are small. But in the eye of many Lepidoptera corneal nipples were evolved (Bernhard *et al.*, 1970) to reduce the reflectivity by about 2–4% depending on the wavelength of light. Internal reflections within the dioptric apparatus may also be minimized by gradients of refractive index: fish or amphipods possess such lenses (Land, 1981). The lack of a nipple array in backswimmers may be explained by the fact that they spend their life mainly in water so that the reflectivity of their flat corneal surfaces amounts to about 0.5%, considerably lower than the reflectivity value of about 4% of a smooth corneal lens surface in air.

Notonecta is one of the few animals that have doublets, whose spherical aberration is eliminated by means of a special interface between the optically homogeneous lens units and not by a special gradient index of refraction. Taking this fact as a starting-point, I tried to determine the possible optical role of the proximal unit in the doublet. One of the optical functions that I could establish for this lower lens unit is the moderate, 2%, suppression of internal reflection. The collection of this extra light from a turbid, dimly lit environment might explain why is it advantageous for *Notonecta* to use aplanatic doublets instead of the simpler Huygensian singlets. On the other hand, the presence of two single intermediate regions, the correction layer and the lower lens unit, in the dioptric apparatus is not very good for transmission enhancement—a lens with a gradient index of refraction, like in fish or amphipods, would be better still. However, the simple solution employed by *Notonecta* reduces the reflectivity of the dioptric apparatus by about 54–65% in comparison with the singlets (Table 1). One could argue that this transmission enhancement is too small and not a sufficient cause for evolving the proximal unit in the lens. If so, the biological function and optical role of the backswimmer's proximal lens unit remain unrevealed. But such an argument would undercut explanations of the development of corneal nipples in many Lepidoptera and Trichoptera, whose nipples also have only 2–4% reflectivity suppression and transmissivity enhancement (Bernhard *et al.*, 1970; Miller, 1979).

A possible alternative explanation to the reflection hypothesis is that because of the correction layer the doublet has better off-axis correction than the singlets in air as well as in water (Horváth, 1989a), which may matter a bit as *Notonecta* has an open rhabdom structure (Schwind, 1980), and would need a somewhat extended image. It is also conceivable that the lower lens unit has some other biological (e.g. biomechanical) function rather than any optical role. The lower unit might simply support the upper one. This seems unlikely, because the distal unit with index of refraction of 1.54 is composed of a hard chitinous material, but the refractive index of 1.46 of the proximal unit implies a fairly soft substance—not ideal for an internal support. On the basis of the above I may conclude the following.

(i) Because the proximal lens unit in the *Notonecta* eye is too thick, about 20 μm axially, in comparison with the wavelength of light in the visible range of the spectrum, coherent reflection of light in the corneal lens is out of the question. A maximum transmission enhancement of 2% is achieved in the *Notonecta* eye by suppression of internal incoherent reflection with a similar result to that achieved by the Lepidopteran eyes which reduce external reflectivity by coherent interference due to corneal nipples. *Notonecta* is not a nocturnal insect, but lives in the dim light of turbid bodies of water and small enhancement of internal transmission may aid scotopic vision.

(ii) The small suppression of internal reflection in the *Notonecta* eye is an inevitable consequence of the presence of regions (correction layer and proximal lens unit) of intermediate refractive indices. The transfer of contrast is enhanced and confusing optical signals resulting from internal reflections are somewhat reduced by this small suppression of internal reflection. This will hold for any doublet. The lower lens unit in the schizochroal-eyed trilobites or in the ocelli of the sawfly larva *Perga* also has a similar transparency enhancement.

(iii) The dioptric apparatus of *Notonecta* is adapted to its dimly lit aquatic environment in two different ways. (1) The exact focusing of light on the distal tip of the rhabdom is ensured by a corneal lens corrected for spherical aberration because of the bell-shaped correction layer. (2) The correction layer and the proximal lens unit suppress reflection from the internal refracting surfaces of the dioptric apparatus and thus achieve secondary transmission enhancement.

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APPENDIX

Reflectivity of the Aplanatic Doublet Lens of Notonecta

The amplitude reflection coefficient ρ of an interface between two adjacent optical media of refractive indices n_i and n_j (Guenther, 1990) is

$$\rho[\varphi, n_i, n_j] = \sqrt{\frac{A^2(2 - A^2 - B^2)}{2B^2(1 - A^2)}}$$

with

$$A = \frac{\sin \varphi}{n_j} \left(\sqrt{n_j^2 - n_i^2 \sin^2 \varphi} - n_i \cos \varphi \right),$$

$$B = \frac{\sin \varphi}{n_j} \left(\sqrt{n_j^2 - n_i^2 \sin^2 \varphi} + n_i \cos \varphi \right) \quad (1)$$

for incident angle φ if the unpolarized light propagates from medium i towards medium j . Let the refractive indices of the environment, the distal and the proximal lens units and the crystalline cone be n_e, n_d, n_p and n_c , respectively. The aplanatic doublet of *Notonecta* has four refracting surfaces: the distal lens surface, the upper and lower surfaces of the correction layer and the proximal lens surface. If the refractive index of the correction layer, considered optically homogeneous for simplicity, is n_i , then the first-order incoherent reflectivities of these refracting surfaces are respectively

$$R_{\text{distal}} = \frac{2}{r^2} \int_0^r x \rho[\varphi_d(x), n_e, n_d]^2 dx, \quad (2)$$

$$R_{\text{upper}} = \frac{2}{r^2} \int_0^r x \{1 - \rho[\varphi_d(x), n_e, n_d]^2\} \rho[\varphi_u(x), n_d, n_i]^2 dx, \quad (3)$$

$$R_{\text{lower}} = \frac{2}{r^2} \int_0^r x \{1 - \rho[\varphi_d(x), n_e, n_d]^2\} \times \{1 - \rho[\varphi_u(x), n_d, n_i]^2\} \rho[\varphi_l(x), n_i, n_p]^2 dx, \quad (4)$$

$$R_{\text{proximal}} = \frac{2}{r^2} \int_0^r x \{1 - \rho[\varphi_d(x), n_e, n_d]^2\} \times \{1 - \rho[\varphi_u(x), n_d, n_i]^2\} \times \{1 - \rho[\varphi_l(x), n_i, n_p]^2\} \rho[\varphi_p(x), n_p, n_c]^2 dx \quad (5)$$

where r is the lens radius. The incident angles $\varphi_d(x), \varphi_p(x)$ and $\varphi_u(x), \varphi_l(x)$ of rays of light at the distal and proximal lens surfaces and at the upper and lower surfaces of the correction layer, respectively, can be determined as given in Horváth (1989a). The resultant reflectivity of the doublet of *Notonecta* is then

$$R = R_{\text{distal}} + R_{\text{upper}} + R_{\text{lower}} + R_{\text{proximal}} \quad (6)$$

Similarly can be determined the resultant reflectivity of an aplanatic singlet lens that has only two refracting surfaces: the distal lens surface and the proximal Huygensian correction surface (Horváth & Clarkson, 1993).