

ACCOMMODATION IN THE CUTTLEFISH (*SEPIA OFFICINALIS*)

FRANK SCHAEFFEL¹, CHRISTOPHER J. MURPHY² AND HOWARD C. HOWLAND^{3,*}

¹Department of Experimental Ophthalmology, University Eye Hospital, Röntgenweg 11, D72076 Tübingen, Germany,

²Department of Surgical Sciences, School of Veterinary Medicine, University of Wisconsin, 2015 Linden Drive West, Madison, WI 53706, USA and ³Department of Neurobiology and Behavior, Cornell University, Ithaca, NY 14853, USA

*Author for correspondence (e-mail: hch2@cornell.edu)

Accepted 25 August; published on WWW 28 October 1999

Summary

We have studied natural accommodation in the eye of six specimens of cuttlefish (*Sepia officinalis*) as they were fed with fish and shrimp. Using infrared photoretinography, we observed (1) that the resting refractive state of the cuttlefish was emmetropic or slightly hyperopic, (2) that accommodation took place only a fraction of a second before a strike and (3) that accommodation focused selectively only in the frontal visual field while no change in refraction could be measured in the lateral field of view. Accommodation was bilateral and amounted to approximately 5 diopters (the reciprocal of the focal length

expressed in meters). Simultaneously, the eyes converged. It appears that, as in most teleost fishes, accommodation in the cuttlefish involves a movement of the crystalline lens perpendicular to the axis of the eye. In histological sections, we observed the position and arrangement of the ciliary muscles, confirming earlier anatomical descriptions, and developed a model of how accommodation could be achieved.

Key words: cuttlefish, *Sepia officinalis*, accommodation, physiological optics, photoretinography, histology, vision.

Introduction

Cephalopods have attracted considerable interest because they represent the most highly developed invertebrates and because they show numerous adaptations that have evolved convergently with vertebrates (Packard, 1972). In particular, their eyes are strikingly similar to those of vertebrates despite the fact that the developmental origin of their tissues is quite different.

Behaviorally, cuttlefish show a remarkably high visual acuity (approximately 8 cycles degree⁻¹; Muntz and Gwyther, 1989), which is better than that of the cat (Hughes, 1977). The axes of the cuttlefish eyes diverge by almost 160° and point upwards by 20° above the horizontal plane (Heidermanns, 1928). The eyes are highly mobile, however, because of 13 extraocular muscles (Packard, 1972; Budelmann and Young, 1993), and show both nystagmus and convergence (for a summary, see Packard, 1972). In contrast to those of teleost fishes (Sivak, 1991), cuttlefish eyes show a prominent light-induced pupillary constriction. Hess (1909) claimed that the pupillary responses are completely independent from the state of accommodation.

Evidence for active ocular accommodation in an invertebrate has been only indirect until now. Hess (1909) found that the refractive state of the cuttlefish eye could be changed both by electrical stimulation and by applying nicotine sulfate. By paralyzing the accommodation muscles using curare and atropine, Hess (1909) also showed that the

resting refractive state of the cuttlefish eye is near-emmetropic and not myopic as previously claimed (Beer, 1897). Later Alexandrowicz (1928) observed that there is both negative and positive accommodation during electrical stimulation; Sivak (1982) described movements of the lens both anteriorly and posteriorly in the short-finned squid *Illex illecebrosus* during anesthesia. Recent direct measurements of lens movement during accommodation are lacking, however, but the results of Hess (1909) using a pharmacological approach seem most convincing. With accommodation at rest, the refractive state was similar all over the visual field. Heidermanns (1928) admired the high imaging quality of the cuttlefish lens even for the far periphery of the visual field. Yet the mechanism that moves the spherical lens in the eye during accommodation remained unclear. Hess (1909) measured prominent changes in intraocular pressure in an *in vitro* preparation following both nicotine stimulation and electrical stimulation, and assumed that these pressure changes were fundamental for the movement of the lens towards the anterior aspect of the eye during accommodation. It is difficult to explain a lateral movement of the lens from pressure changes, however, and, from the arrangement of the ciliary muscles, it is not clear how the increase in intraocular pressure could be achieved.

The natural accommodation response in an invertebrate has not been documented previously. We report that cuttlefish do indeed accommodate during predatory behavior but that

accommodation selectively focuses only the anterior visual field. We also confirmed the anatomy of the ciliary muscles (e.g. Tompsett, 1939, Figs 66, 67) from histological sections, and we provide an explanation of how the accommodation mechanism can work to produce the kind of accommodation we observed.

Materials and methods

Animals

We observed three adult specimens of *Sepia officinalis* (approximate length L from the tip of the mantle to the eye 0.3 m) and three juvenile specimens ($L=0.2$ m) on two occasions at the Monterey Bay Aquarium. Individual large specimens were isolated in a 20 gallon (approximately 90 l) aquarium and fed small fish or shrimp attached to a rod. We recorded several predatory strikes as described below from both the frontal and lateral aspects.

Measurement of refractive state

Refractive state was recorded continuously using an infrared photoretoscope attached to an infrared-sensitive video camera. The infrared photoretoscope (Schaeffel et al., 1987) created a crescent-shaped reflex in the pupils of the animals which originated from the fundus. Myopic refraction could be identified by a reflex in the lower portion of the pupil (see Fig. 2) and hyperopic refraction by a reflex in the upper portion (see Figs 1, 4). The amount of defocus could be calculated from the relative height of the reflex, as previously shown by Howland (1985). We used a version of a photoretoscope with infrared light-emitting diodes (LEDs) placed at five different eccentricities. LEDs placed at different eccentricities create light crescents of different height in the pupil (Howland, 1985; see also Fig. 1). The LEDs were flashed in sequence, cycling through all five eccentricities at 3.3 Hz. In this situation, the height of the crescents changes with time, which is seen as an apparent movement of the fundus reflex (Schaeffel et al., 1987). The sign of refractive error could be more easily evaluated this way, and both precision and range of measurement were improved. Because the photoretoscope was in air and the animal in water in a glass aquarium, the apparent position of the photoretoscope in relation to the animal was approximately 1.337 times as far from the aquarium wall as its true distance. With the photoretoscope usually 1 m from the aquarium, the animal appeared to be approximately 0.25 diopters (D, the reciprocal of the focal length expressed in meters) more myopic than it actually was, and we have corrected the values in this paper for this artifact, expressing defocus relative to the virtual position of our refractor. We follow the convention with underwater animals of stating the defocus in diopters as measured under water (Hueter and Gruber, 1980). Several hours of observation were necessary to attain video recordings of predatory sequences in which the refractive state could be followed throughout the strike. Depending on the relative position of the prey item, animals were refracted from both the front and the side.

Histology

Eyes were obtained from three adult and two juvenile specimens immediately after death and were immersion-fixed in Bouin's solution ($N=2$), Trump's fixative ($N=4$) or 10 % neutral buffered formalin ($N=4$). The eyes were then examined grossly, opened in a parasagittal plane, and the central portion of each globe was processed routinely and embedded in paraffin. Sections were cut at 8 μ m thickness and stained with hematoxylin and eosin, periodic Schiff stain or Mason's trichome stain.

Results

Resting refractive states

While the animals moved around in the tanks, presenting various axes of their eyes to the photorefractor, their refractions ranged from near-emmetropia to slight hyperopia (+2 to +3 D). We did not see changes in refractive state due to spontaneous accommodation. Like Hess (1909), we did not see changes in refractive state of the eyes in the peripheral visual field.

Accommodation during prey capture

The only occasion when accommodation was seen was during fixation of prey. During seven prey attacks by four animals, the most striking observation was that the refractive state remained hyperopic or near-emmetropic during the strike if the refractions were obtained from the side (Fig. 1). In contrast, when refractions were obtained from the frontal field (Fig. 2), a myopic refraction was observed for a fraction of a second just before the animal attacked a shrimp offered on a stick. Simultaneously, the eyes showed some degree of convergence. The amplitude of natural accommodation amounted to approximately 5 D.

The strike duration could be crudely measured from the video sequences and was approximately 200 ms (six frames) in duration from the first detectable elongation of the capturing tentacles to the contact with the prey item (Fig. 1).

Histological observations

At first glance, the cuttlefish eye resembles a vertebrate eye (Fig. 3A, right panel). As is common in aquatic vertebrates, the acellular lens is almost spherical. In contrast to the vertebrate lens, it is divided into two halves by a septum that results from its dual origin from two separate ectodermal layers (Sivak, 1991). With the iris removed (Fig. 3A, left panel, after Hess, 1909), it can be seen that the ciliary body consists of two rings, a ciliary ring and a muscle ring attached to the sclera. The muscle ring has its largest extent in the horizontal plane (Hess, 1909). The division of the ciliary body (Fig. 3B) into two parts is also obvious in a transverse section of the anterior aspect of the eye. In cuttlefish, the iridial cartilage is very prominent and extends from the ciliary body to approximately half the width of the iris.

The iridial cartilage (CIr, Fig. 3B) is independent of a second, even more prominent, equatorial cartilage (eC, Fig. 3B), located in the equatorial region of the globe and

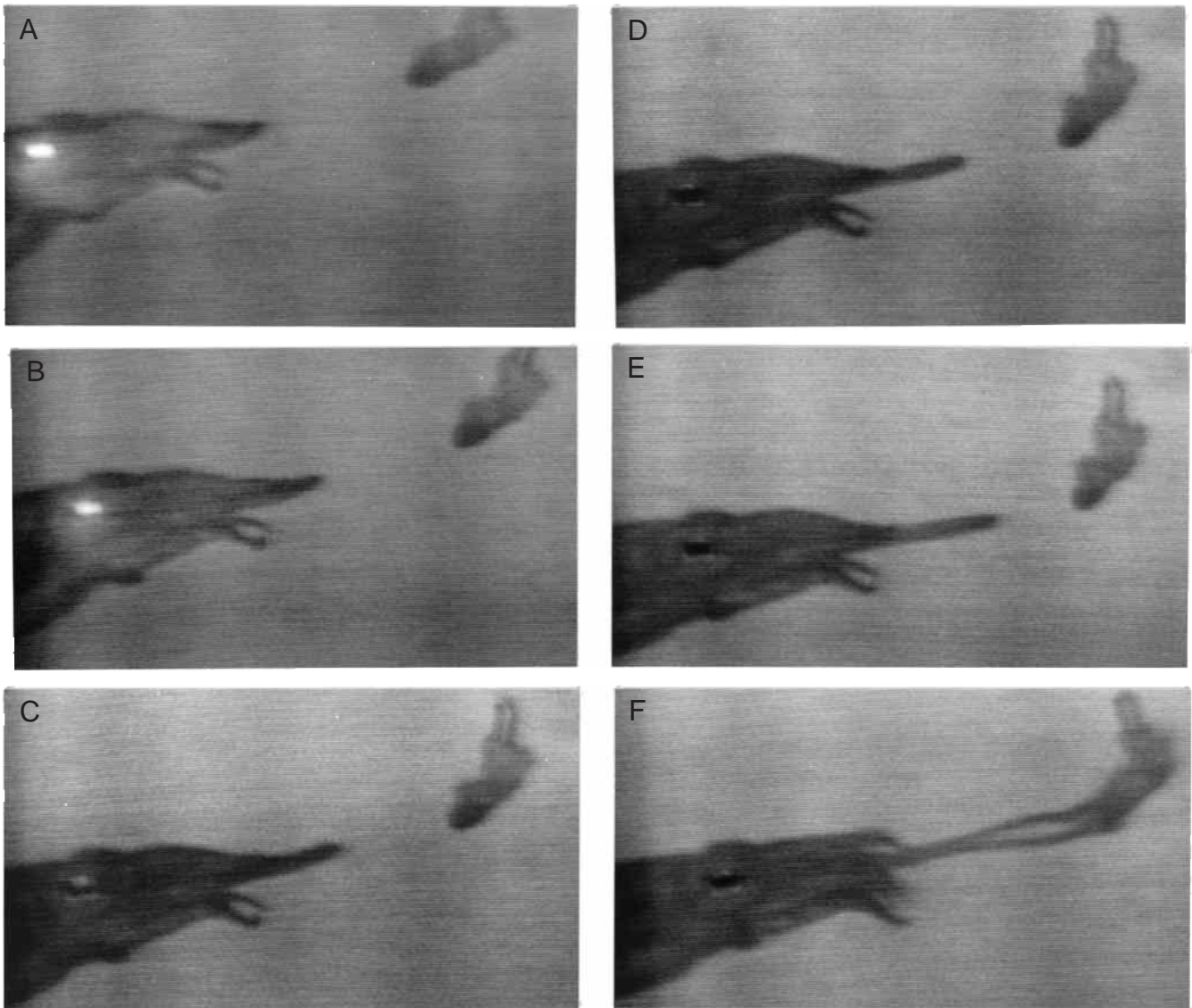


Fig. 1. (A–F) A juvenile cuttlefish catching a shrimp by propelling its tentacles. In the first frame, the pupil appears brightly illuminated because the least eccentric light-emitting diode (LED) of the retinoscope creates a bright reflex. Because of over-saturation, the orientation of the reflex crescent in the pupil cannot be recognized in this frame. However, for more eccentric LEDs (e.g. B,C), it is clear that the reflex appears in the upper part of the pupil, indicating hyperopia. For even higher eccentricities, the crescent becomes invisible because the amount of hyperopia is too small to create a reflex crescent (Howland, 1985). In a later frame (not shown, 100 ms after frame F), the LEDs had cycled through once, and the LEDs with the lowest eccentricity flashed again. It could be seen that the eye remained hyperopic as viewed laterally. The time taken between frames was 33 ms.

extends posteriorly to lie external to the retina. The anterior extent of the equatorial cartilage is located slightly anterior to the ora serrata. The ciliary muscle fibers are well developed and originate, at least in part, from the anterior border of the equatorial cartilage. They extend into the ciliary body in a radial direction. Also present are a number of fibres that are oriented obliquely and circumferentially. These latter appear to be located external to the radially oriented fibers. Contraction of these fibers would transmit a force to the lens, which is attached directly to the ciliary body by a continuation of the lenticular septum. Anterior to the lens there is a second chamber that is limited by a layer that is analogous to the vertebrate

cornea (Co, Fig. 3B). In the lower part of this chamber, numerous processes extend from the cornea, but they do not seem to impair vision because, within the optical zone, the 'cornea' is smooth and transparent (Hensen, 1865). The posterior chamber is tightly closed and has no connection to the environment (Hess, 1909; Packard, 1972). The everted retina (Fig. 3C) includes a prominent layer of rhabdomes, ranging in length from 20 μm in the periphery to 50–80 μm in the central part of the retina. Their average diameter is 4 μm in the center and 10 μm in the periphery, and they show a pronounced orientation towards the pupil (Heidermanns, 1928) with up to 45° of tilt towards the pupillary axis in the far

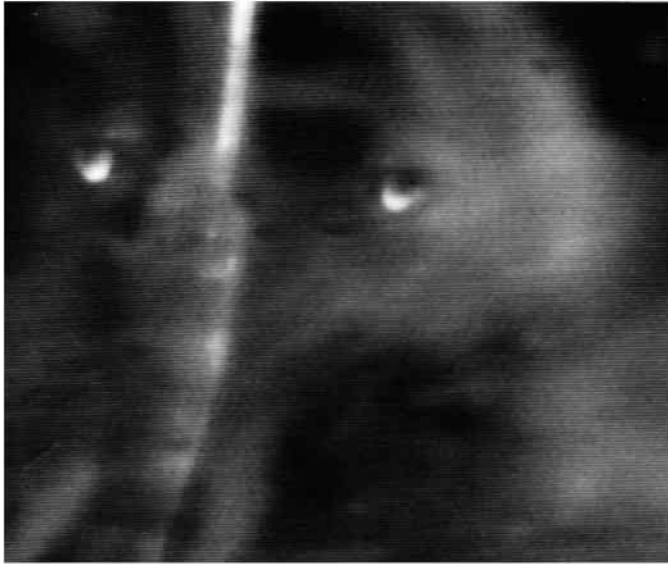


Fig. 2. Myopic refraction in a cuttlefish fixating a shrimp offered on a stick, shortly before it struck. The reflex crescent appears in the lower part of the pupil; from its height, it can be calculated that accommodation amounted to approximately 5 D. Note the binocular accommodation.

periphery. Below the rhabdome layer there is the basement membrane, the nuclear layer of the photoreceptors, a fiber layer, a layer containing mainly nuclei of nerves, another fiber layer and, finally, a layer containing the fibres running to the optic tract.

Discussion

Possible mechanisms of accommodation and comparison with accommodation mechanisms of teleost fishes

We have observed that accommodation in the cuttlefish changed the refractive state differently in two axes of the eye. Such behavior can be explained only by a lateral movement of the lens, perpendicular to the pupillary axis of the eye. A lateral movement of the lens is also common among teleost fishes (Sivak and Howland, 1973; Fernald, 1990). Hess (1909) has described how, in the cuttlefish, the lens is suspended *via* the 'ciliary ring' (Fig. 3A,B) by a 'muscle ring' (Fig. 3A,B) consisting of radially oriented fibres (Fig. 3B). We have observed that these fibres are attached to the equatorial cartilage, and their constriction can, therefore, be controlled very precisely despite the fact that, in general, the eye is quite soft. By constricting these fibers in radial segments, and relaxing them on the opposite side of the lens, the lens could be moved in any direction perpendicular to the pupillary axis. Strikingly, the muscle ring is also wider in the horizontal axis (Fig. 3A, left panel), which would allow for more accommodation in the frontal field than in the upper or lower field. Our simple model differs from that of Hess (1909) in that no pressure changes in the eye are necessary to explain the movement of the lens, and the crucial point is that the movement of the lens is not parallel to the axis of the eye but

perpendicular to it. Hess (1909) did observe drug-induced accommodation in the axial direction of 14 D. Axial accommodation is more difficult to explain with our simple model because constriction of the ciliary muscles moves the lens backwards and this results in accommodation for distant objects. To explain his observation of drug-induced accommodation, additional forces such as pressure changes must be considered, but their relevance for natural accommodation is unclear.

Optical features of the cuttlefish eye and comparison with the teleost eye

Sivak (1991) showed that, just as in fishes, the lens is the only image-forming structure in the cephalopod eye. Accordingly, high optical quality in the lens is desirable. A high optical quality can be deduced from the appearance of the photoretinoscopic reflexes (Fig. 4), which are smooth and have a distinct horizontal border. In fact, they look much clearer than in a cat eye, in which many optical disturbances show up in the lens (H. C. Howland, unpublished observation). The optical features of the cephalopod lens resemble those of the teleost fish lens because they also have an index gradient designed to minimize spherical aberration (Heidermanns, 1928). Heidermanns (1928) has examined the off-axis image quality of the isolated cuttlefish lens and found no appreciable decline in image quality. Large amounts of chromatic aberration were also observed, but they are not important because cuttlefish are probably monochromats (Heidermanns, 1928; Packard, 1972; Messenger, 1981).

Clues to the sign of defocus

The W-shaped pupil of the cuttlefish has a number of optical consequences (Murphy and Howland, 1991). Points of light in the environment (such as those reflected from the scales of a fish) will be imaged as an M if the fish is located beyond the focal plane of the eye and as a W if the fish is located in front of the eye's focal plane, thus potentially supplying a clue to the sign of defocus for the accommodation mechanism.

Under conditions of extreme miosis (pupillary constriction), two apertures are formed at the medial and lateral aspects of the pupil. This creates a situation similar to that of Scheiner's disk where only those objects in the plane of focus form a single image on the retina. Again, this can potentially function as a monocular in- or out-of-focus detector.

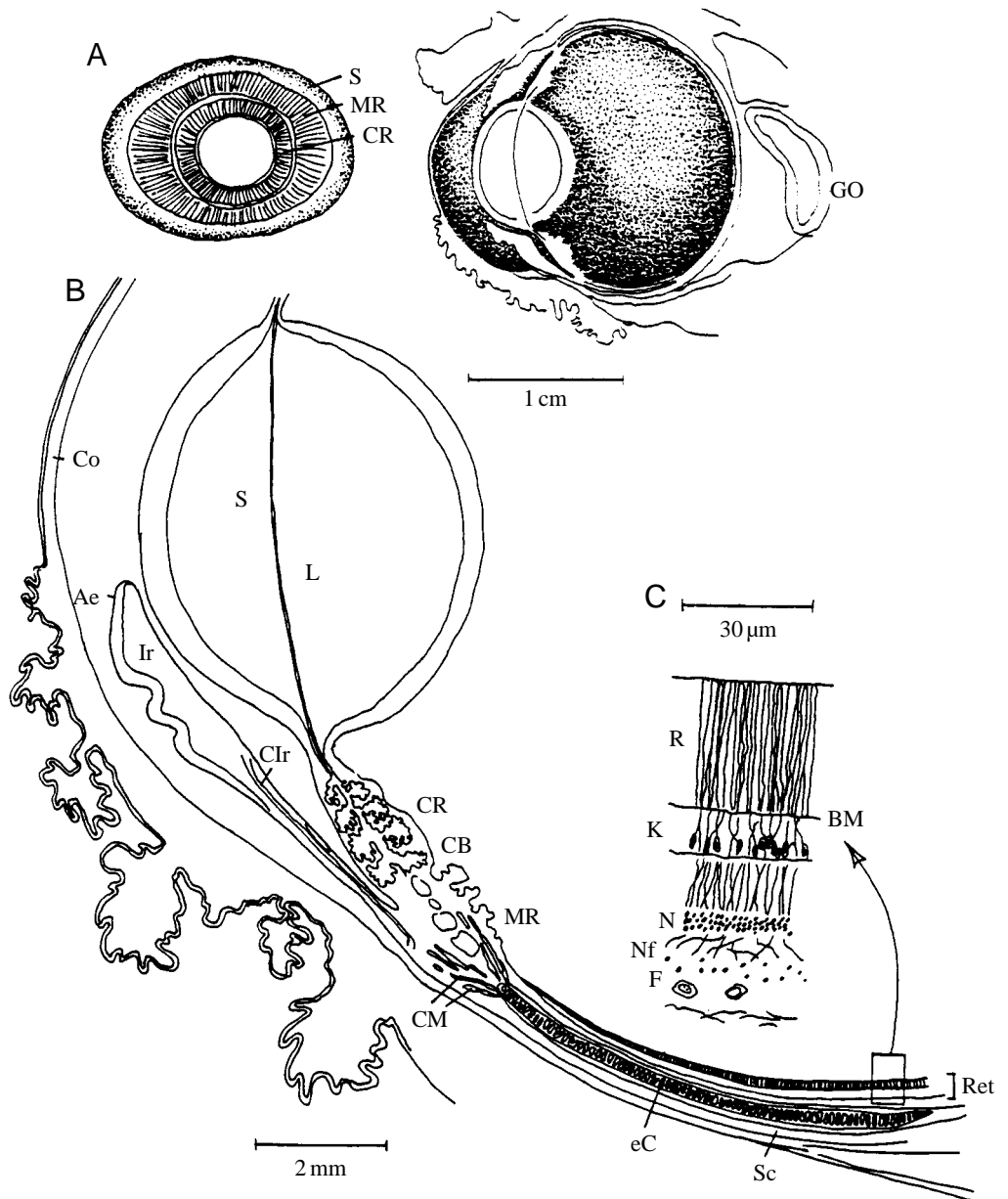
Mathiessen's ratio and the refractive index of the lens

The ratio of focal length to lens radius (Mathiessen's ratio) in excised cephalopod lenses (*Rossia* sp.) is similar to that of teleosts (2.55; Walls, 1942), ranging from 2.36 to 2.78 (Sivak, 1991). The values we calculated from data measured in two excised lenses of *Sepia officinalis* by Heidermanns (1928) were slightly lower (2.11 and 2.12).

Computation of the effective refractive index of the lens

Our sample of cuttlefish included one animal with bilateral

Fig. 3. Histology of the cuttlefish eye. (A) Right: the cuttlefish eye *in situ*, sectioned vertically. Note the almost spherical lens and the remarkable similarity to a vertebrate eye (GO, ganglion opticum). Left: anterior aspect of the eye of the cuttlefish (as seen from outside along the optical axis) after complete removal of the iris. Removal of the iris exposes the ciliary ring (CR, see also Fig. 3B), and the muscle ring (MR), which are attached to the sclera (S). Note that, in the horizontal plane, the muscle ring is broader than in the vertical plane (redrawn after Hess, 1909). (B) Magnified view of a transverse section of the anterior segment of the eye oriented as shown in A (right side). Most strikingly, the lens (L) of cephalopods is divided by a septum (S) that results from the fact that the lens develops from two layers of ectoderm. The lens is connected to the ciliary body (CB) which Hess (1909) has considered to be divided in two parts, the ciliary ring (CR) and the muscle ring (MR). The ciliary muscles (CM) are prominently developed. They are radially and obliquely oriented and are attached to a cartilaginous ring around the equatorial diameter of the eye (equatorial cartilage, eC). The ocular coat consists of numerous layers including the retina (Ret) and the sclera (Sc). In the iris (Ir), the iridial cartilage (CIr) is particularly well developed. Sphincter and dilator iridis were not obvious in our preparation, but are said to be located anterior to the iridial cartilage (Ae, argentea externa; drawing prepared from histological section). Co, cornea. (C) Transverse section through the retina. At first glance, the retina has some similarity to the vertebrate retina, although it is everted (rhabdomes, R, point towards the incoming light). The rhabdomes are quite long (up to 80 μm in the central part of the retina). Photoreceptor cells are attached to the basement membrane (BM). Subsequent layers are the nuclear layer of the photoreceptors (K), the nuclear layer of the nerves (N), the nerve fibre layer (Nf) and a layer of fibres projecting to the optic nerve (F). Below, two arteries are shown (drawing prepared from histological section).



cataracts that appeared to be on the rear surface of the lens, i.e. at a distance of twice the radius of the lens from the anterior surface (Fig. 4). Because the cornea has no power under water, the cataract was seen as the virtual image created from the anterior surface of the lens. By using the iris as a marker for the position of the anterior surface of the lens and measuring the relative movement of the anterior surface and the virtual image of the cataract, we could compute the distance of the virtual image from the anterior surface of the lens b and, hence,

the effective refractive index of the lens, according to the equation:

$$n_2 = 2n_1(1 - r/b), \quad (1)$$

where r is the radius of the lens, n_1 is the refractive index of sea water and n_2 is the refractive index of the lens (see Appendix). The calculation yielded a mean value of 1.624 ± 0.086 (mean \pm S.E.M., $N=4$) for the refractive index of the homogeneous lens model. This may be compared with

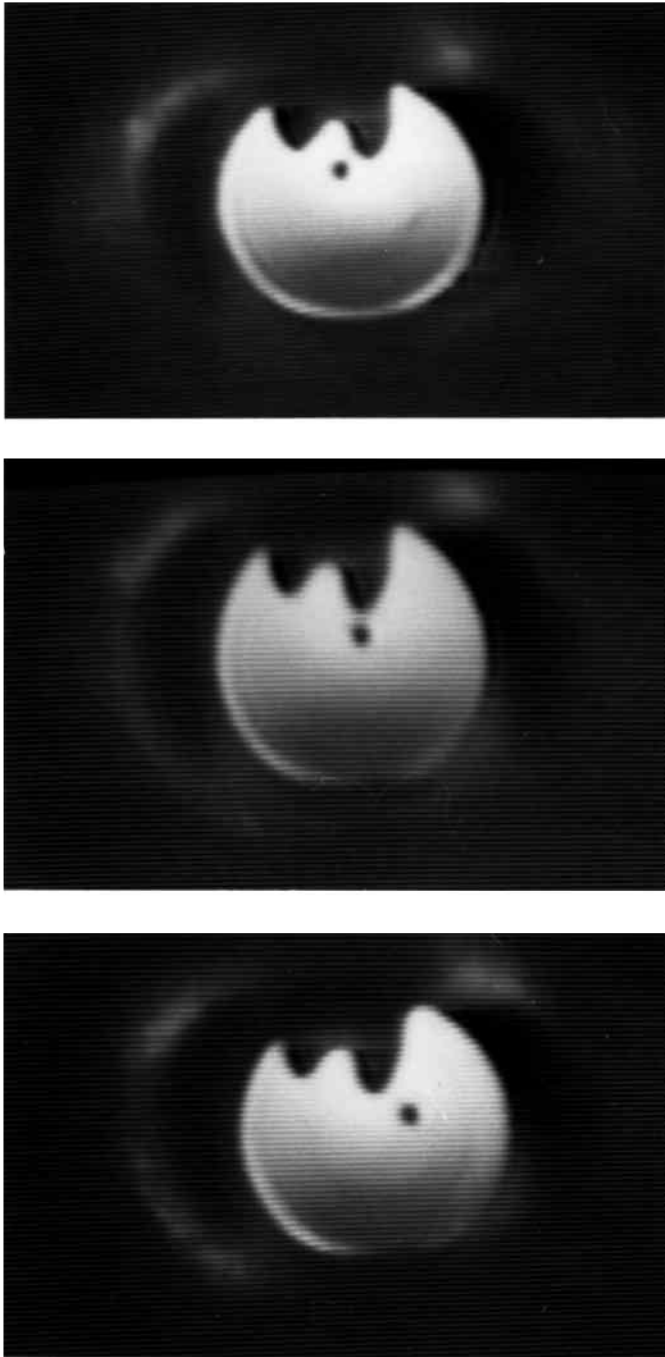


Fig. 4. Optical quality of the cuttle fish eye and the use of a lens cataract to determine its refractive index. The upper portion of the pupil is brightly illuminated from the photoretinoscopic reflex. The position of the reflex indicated hyperopia, and its height permits one to calculate its amount. Note that the reflex appears crisp and clear, indicating the good optical quality of the eye. The black dot visible in all frames is the virtual image of a cataract at the rear side of the lens. From its movement relative to the movement of the lens, we could calculate the refractive index of the lens (for details, see text and Appendix).

Sivak's (1982) measurements of the equivalent power of the spherical, gradient index lens of another cephalopod, the short

finned-squid *Illex illecebrosus*. Sivak found that the equivalent refractive power of that lens was 1.72, while the refractive index of its gradient ranged from 1.441 in the periphery to 1.485 in the core of the lens.

Behavioral and anatomical visual acuity

Muntz and Gwyther (1988, 1989) have examined the visual acuity of the octopus behaviorally and found surprisingly high values of close to 10 cycles degree⁻¹. Heidermanns (1928) has measured the average diameter of the rhabdoms and gives a value of 4 µm. Apparently, this diameter is independent of age and eye size, which indicates that visual acuity increases with age. Nevertheless, from the formulae given by Reymond (1985), the anatomical resolving power (ARP) of an adult cuttlefish can be calculated:

$$\text{ARP} = \text{PND} / (\sqrt{3} \times d \times 57.3), \quad (2)$$

where ARP is the anatomical resolving power (in cycles degree⁻¹), PND is the posterior nodal distance (in mm), and d is the average rhabdome-to-rhabdome spacing (in mm). The calculation gives a value of 19.1 cycles degree⁻¹ using data from Heidermanns (1928) for the adult cuttlefish (p. 626ff; PND 7.6 mm, average rhabdom/rhabdom spacing 4 µm). However, it has been pointed out by Heidermanns (1928) that the average rhabdome diameter varies from 4 µm close to the optical axis of the eye to 10 µm in the periphery. The calculated acuity must, therefore, be considered as the optimal value with considerable decline for off-axis vision.

Depth of field of the cuttlefish

Depth of focus depends critically on the size of the pupil. Since the cuttlefish has a W-shaped pupil, the depth of focus cannot be calculated using a simple formula such as the one provided by Green et al. (1980). For a maximal rhabdome length of 80 µm and a posterior nodal distance of 7.2 mm, a maximal depth of field of 1.52 D results from the assumption that the image plane can be moved along the length of the rhabdoms with no decline in resolution. Estimates based on the optics of the eye are not possible because of the complex shape of the pupil, but inspection of Fig. 4 indicates that the optics may be good enough to allow for such a small depth of field. In contrast to Heidermanns (1928), who considered accommodation as not important for monocular distance estimation, we cannot exclude the possibility that accommodation provides a hint (Harkness, 1977) as to how far away a prey item is located. The amount of accommodation observed matched the required value within the depth of field.

Appendix: computation of the refractive index of a lens from the image of a posterior cataract

Infrared photoretinography illuminated the lens of the cuttlefish and, in these experiments, allowed us to visualize the image of a posterior cataract, which we assumed was on the posterior face of the spherical lens, as well as the iris, which is draped over the front surface of the lens. Because the cornea

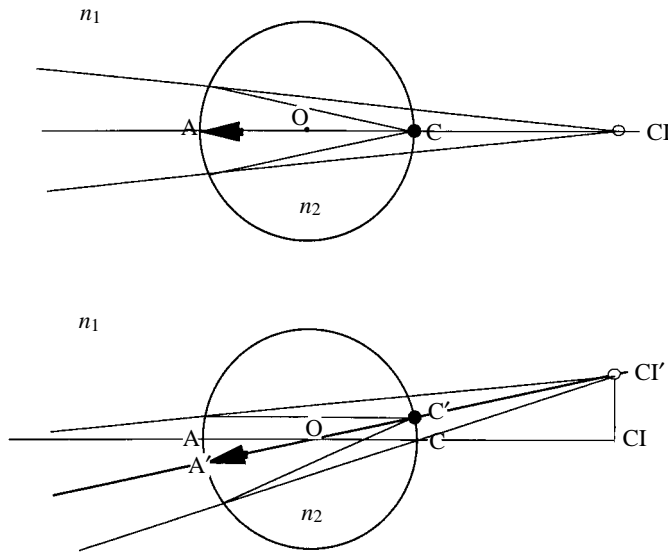


Fig. 5. (A) The image of a small cataract, C at the posterior pole of the lens appears at point CI. (B) When the lens is rotated so that a point on the front of the lens moves from A to A' the image of the cataract moves from CI to CI'. The refractive index of the lens can be calculated from the ratio of these movements (see text). O, the center of the lens; n_1 , the refractive index of sea water; n_2 , the refractive index of the lens.

has virtually no refractive power, we could treat the optics of this situation as that of a single surface with sea water in front (refractive index $n_1=1.337$) and the effective refractive index of the lens (homogeneous model) n_2 behind the anterior surface of the lens (Fig. 5).

Letting the radius of the lens be unity, the distance of the cataract from the front surface of the lens, AC, is 2, i.e. the diameter of the lens. Letting the distance of the image of the cataract from the front of the lens be ACI or, more conveniently, $ACI=b$, we can write the equation for the two distances:

$$n_1/b + n_2/2 = (n_2 - n_1). \quad (\text{A1})$$

Solving this equation for n_2 , we find:

$$n_2 = 2n_1 + 2n_1/b. \quad (\text{A2})$$

The sign of b will be negative because it is a virtual image. Hereafter, we treat all distances as positive, and equation A2 becomes:

$$n_2 = 2n_1 - 2n_1/b. \quad (\text{A3})$$

From Fig. 5, it may be seen that, if the lens is viewed from two positions, a spot on the front of the lens, e.g. a portion of the iris, will be seen to move through the distance AA', while the image of the cataract will move through the distance CICI'. It is also clear from the diagram that, if we consider that the system has been rotated about the center of the lens, O, the ratio of these distances for small movements will be approximately:

$$CICI'/AA' = (b - 1)/1 = b - 1. \quad (\text{A4})$$

Letting g equal $CICI'/AA'$, i.e. the measured ratio of the

movement of the cataract image to that of the movement of the iris, and substituting into equation A2, we have:

$$n_2 = 2n_1 - 2n_1/(g + 1). \quad (\text{A5})$$

Taking the refractive index of sea water, n_1 , as 1.337, we have:

$$n_2 = 2.674 - 2.674/(g + 1). \quad (\text{A6})$$

Making measurements on photographs such as that of Fig. 4 to find four values of g , we calculated the mean value of the effective refractive index of the cuttlefish lens to be 1.624 ± 0.086 (mean \pm S.E.M., $N=4$).

Dedicated to the memory of Walter Heiligenberg who died on 8 September 1994. This study was supported by EY-02994 to H.C.H., by a grant from the DFG (SFB307-TP A7) to F.S. and by a grant from the Veterinary Optometric Society to C.J.M. We thank members of Monterey Aquarium for their help with this project.

References

- Alexandrowicz, J.-S.** (1927). Contribution a l'etude des muscles, des nerfs et du mechnisme de l'accommodation de l'oeil des cephalopodes. *Arch. Zool. Exp. Gen.* **66**, 71–134.
- Alexandrowicz, J.-S.** (1928). Sur la fonction des mussels intrinseques de la oiell des cephalopods. *C.R. Soc. Biol. Paris* **99**, 1161–1164.
- Beer, T.** (1897). Die Akkommdation des Cephalopodenauges. *Pflügers Arch.* **67**, 541–586.
- Budelmann, B. U. and Young, J. Z.** (1993). The oculomotor system of decapod cephalopods: eye muscles, eye muscle nerves and the oculomotor neurons in the central nervous system. *Phil Trans. R. Soc. Lond. B* **340**, 93–125.
- Fernald, R. D.** (1990). The optical system of fishes. In *The Visual System of Fish* (ed. R. H. Douglas and M. B. A. Djamgoz), pp. 45–61. London: Chapman & Hall.
- Green, D. G., Powers, M. K. and Banks, M. S.** (1980). Depth of focus, eye size and visual acuity. *Vision Res.* **20**, 827–835.
- Harkness, L.** (1977). Chameleons use accommodation to judge distance. *Nature* **267**, 346–349.
- Heidermanns, C.** (1928). Messende Untersuchungen über das Formensehen der Cephalopoden und ihre optische Orientierung im Raume. *Zool. Jhb.* **45**, 609–650.
- Hensen, V.** (1865). Über das Auge einiger Cephalopoden. *Z. Wiss. Zool.* **15**, 155–242.
- Hess, C.** (1909). Die Akkommodation der Cephalopoden. *Arch. Augenheilkunde* **64**, 125–152.
- Howland, H. C.** (1985). Optics of photoretinoscopy: results from ray tracing. *Am. J. Optim. Physiol. Opt.* **62**, 621–627.
- Hueter, R. E. and Gruber, S. H.** (1980). Retinoscopy of aquatic eyes. *Vision Res.* **20**, 197–200.
- Hughes, A.** (1977). The topography of vision in mammals of contrasting life style: comparative optics and retinal organization. In *Handbook of Sensory Physiology*, vol. VII/5 (ed. F. Crescitelli), pp.615–687. Berlin: Springer Verlag.
- Levy, B. and Sivak, J. G.** (1980). Mechanisms of accommodation in the bird eye. *J. Comp. Physiol.* **137**, 267–272.
- Messenger, J. B.** (1981). Comparative physiology of vision in molluscs. In *Comparative Physiology and Evolution of Vision in*

- Invertebrates, Handbook of Sensory Physiology*, chapter 2, vol. VII/6C (ed. H. Autrum, L. S. Goodman, J. B. Messenger and R. Wehner), pp. 93–200. Berlin: Springer-Verlag.
- Muntz, W. R. and Gwyther, J.** (1988). Visual acuity in *Octopus pallidus* and *Octopus australis*. *J. Exp. Biol.* **134**, 119–129.
- Muntz, W. R. A. and Gwyther, J.** (1989). The visual acuity of octopuses for gratings of different orientations. *J. Exp. Biol.* **142**, 461–464.
- Murphy, C. J. and Howland, H. C.** (1991). The functional significance of crescent-shaped pupils and multiple pupillary apertures. *J. Exp. Zool. (Suppl.)* **5**, 22–28.
- Packard, A.** (1972). Cephalopods and fish: the limits of convergence. *Biol. Rev.* **47**, 265–273.
- Reymond, L.** (1985). Spatial acuity of the eagle *Aquila audax*: a behavioral, optical and anatomical investigation. *Vision Res.* **25**, 1477–1491.
- Schaeffel, F., Farkas, L. and Howland, H. C.** (1987). Infrared photoretinoscope. *Appl. Optics* **26**, 1505–1509.
- Sivak, J. G.** (1982). Optical properties of a cephalopod eye (the short finned squid, *Illex illecebrosus*). *J. Comp. Physiol. A* **147**, 323–327.
- Sivak, J. G.** (1991). Shape and focal properties of the cephalopod ocular lens. *Can. J. Zool.* **69**, 2501–2506.
- Sivak, J. G. and Howland, H. C.** (1973). Accommodation in the Northern Rock Bass (*Ambloplites rupestris rupestris*) in response to natural stimuli. *Vision Res.* **13**, 2059–2064.
- Tompsett, D. H.** (1939). *Sepia*. *L.M.B.C. Memoirs on Typical British Marine Plants and Animals* **32**, 1–184.
- Walls, G.** (1942). *The Vertebrate Eye and its Adaptive Radiation*. New York: Hafner.