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The Mechanism of Lenticular Accommodation in Chicks

ADRIAN GLASSER,*† CHRISTOPHER J. MURPHY,‡ DAVID TROILO,§¶ HOWARD C. HOWLAND§

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In the chick eye, accommodation for near objects is brought about by changes in the focal length of the lens and by changes in the corneal radius of curvature. Several different mechanisms of lenticular accommodation have been proposed for the avian eye. These include a role for the ciliary muscle, a role for the iris muscle, and a role for changes in intraocular pressure. We have studied accommodation in the chick eye using electrical stimulation of the Edinger–Westphal nucleus, electric-field stimulation of enucleated eyes, *in vitro* measurement of changes in back vertex distance of the lens, and histology. We present evidence showing that, in the chick eye, lenticular accommodation is induced primarily by a contraction of the muscle fibers at the peripheral edge of the iris. During accommodation, the peripheral muscle fibers of the iris contract to apply a force through the ciliary processes to the anterior equatorial surface of the lens. This increases the focal power of the lens. When accommodation is relaxed, the lens is returned to its unaccommodated state by the elasticity of the pectinate ligament and the ciliary body. Contractions of the posterior ciliary muscle and changes in intraocular pressure, forces that have previously been proposed to play major roles in lenticular accommodation, are shown to be of secondary importance only.

Chick Iris Lens Edinger–Westphal nucleus Iridectomy Ciliary muscle

INTRODUCTION

In chicks, up to 25 D of accommodation can be induced by electrically stimulating the Edinger–Westphal (EW) nucleus. Roughly 40% of this accommodation is due to changes in corneal curvature and 60% is due to changes in lens curvature (Troilo & Wallman, 1987; Glasser, Troilo & Howland, 1994). We have previously described the mechanism of corneal accommodation in chicks (Glasser *et al.*, 1994), and here we present new evidence for an iris-mediated mechanism of lenticular accommodation.

There are numerous and varied descriptions of lenticular accommodation in bird eyes. Among them are suggestions that changes in lens curvature are brought about by contractions of the ciliary muscle, by contractions of the iris muscle, or by contractions of both muscle groups together. Cramer (1853) observed that, in pigeon eyes, lens movements ceased after the iris had been removed. He therefore concluded that it was the iris that was chiefly responsible for increasing the lens power during accommodation. Pumphery (1961) reported that during accommodation the ciliary body is forced against the lens by a contraction of the posterior ciliary muscle. Similarly, Meyer (1977) stated that a contraction of the posterior ciliary muscle thrusts the ciliary body inward against the anterior surface of the lens, thus forcing the lens against the iris to produce an anterior lenticonus. This is essentially a repetition of Walls' (1967) earlier description of lenticular accommodation in birds. Walls (1967) stated that lenticular accommodation might be accomplished "[by] squeezing the lens at its equator positively and vigorously by means of the ciliary body, and with the sphincter of the iris sometimes called into play to help deform the anterior surface of the lens".

Aquatic birds have been shown to have a reduced ciliary musculature (Sivak & Vrablic, 1982), perhaps reflecting the irrelevance of corneal accommodation when the eye is under water. Some aquatic birds, however, have an enlarged iris muscle to support the strong lenticular changes that aquatic birds require in order to become emmetropic underwater (Hess, 1912; Duke-Elder, 1958; Goodge, 1960; Walls, 1967; Sivak & Vrablic, 1982). Two species of diving birds, each of which had up to 50 D of accommodation, were shown to have massive anterior lenticonus during accommodation (Levy &

*Section of Physiology, Cornell University, Ithaca, NY 14853, U.S.A.
†To whom all correspondence should be addressed at present address: School of Optometry, University of Waterloo, Waterloo, Ontario, Canada N2L 3G1.
‡Department of Surgical Sciences, School of Veterinary Medicine, University of Wisconsin—Madison, Madison, WI 53706, U.S.A.
§Section of Neurobiology and Behavior, Cornell University, Ithaca, NY 14853, U.S.A.
¶Present address: Department of Biosciences, New England College of Optometry, 424 Beacon Street, Boston, MA 02115, U.S.A.

Sivak, 1980). This study, and one other on diving birds (Sivak, Hildebrand & Lebert, 1985), suggested that the lens was being forced through the rigid disk of the contracted iris, and that the iris, therefore, played only a passive role in accommodation. Goodge (1960) noted that the eye of the dipper has an extremely well developed iris sphincter muscle, and he concluded that this was the only structural modification in the eye that could account for the dipper's increased accommodative range over other passerine birds. Sivak and Vrablic (1979) have, similarly, suggested that the extensive iris sphincter muscle of the penguin eye is well adapted to induce extensive lenticular changes during accommodation. Hess (1912) showed that the iris sphincter muscle caused lenticular accommodation in the cormorant eye by squeezing the lens, and he believed that this mechanism would apply across all bird species.

Similarly, numerous studies of accommodation in terrestrial birds have resulted in contradictory descriptions of how lenticular changes are brought about. Slonaker (1918) was not able to find any structure in the eye of the English sparrow that could deform the relatively firm lens. He concluded that lenticular accommodation must be brought about by changes in the axial diameter of the eye or in the position of the lens. Beer (1893) argued against an accommodative role for the iris muscle from his studies of the hawk eye. He noted that the movements of Purkinje images on the anterior surface of the lens could still be seen even after the entire iris had been removed. Müller (1857) believed that the muscle fibers at the peripheral iris were the primary muscle group involved in lenticular accommodation, and that the central iris muscle was responsible for pupillary constriction.

Several different mechanisms of lenticular accommodation have been proposed for the chick eye. Most recently, lenticular accommodation has been attributed to a contraction of the ciliary muscles forcing the ciliary processes against the anterior surface of the lens (West, Sivak & Doughty, 1991), and to an indirect pressure-mediated mechanism whereby a contraction of the ciliary muscles would stretch the choroidal coat and increase the vitreous pressure behind the lens (Suburo & Marcentoni, 1983).

Our own work on lenticular accommodation in the chick eye has produced findings which are largely in agreement with those of Müller (1857) from his studies on a variety of bird species. We attribute changes in the curvature of the chick lens primarily to a contraction of the peripheral circular and oblique iris muscle fibers located at the root of the iris, where the iris and the ciliary body join (Fig. 1). These muscle fibers lie on the ciliary processes on the anterior equatorial surface of the lens. When the muscle fibers contract, they push on the ciliary processes, to actively squeeze the peripheral edge of the lens and increase its curvature. Secondary roles are

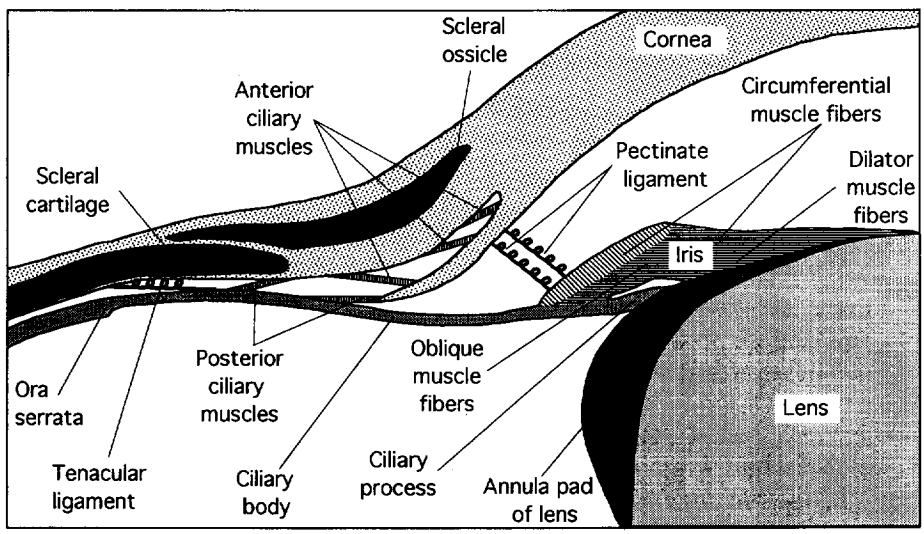

FIGURE 1. A diagrammatic representation of the nasal segment of the ciliary region of a chick eye showing the anatomical structures that contribute to lenticular accommodation. The structural rigidity of the chick eye is maintained by the ossicles and the cartilage in the sclera of the globe. The scleral cartilage extends throughout the posterior sclera of the globe to form the cartilaginous cup. The ciliary muscles are located at the inner angle of the scleral ossicles. This diagram shows only representative ciliary muscle fibers which have been drawn to show their orientation within the nasal ciliary region of the eye. The iris lies against the anterior surface of the lens and is firmly attached to the lens at the ciliary processes. The iris musculature consists primarily of circumferential muscle fibers throughout the iris, with the greatest density of muscle fibers approximately midway between the iris root and the pupillary margin. Although the entire cross-sectional length of the iris contains circumferential muscle fibers, it is primarily the peripheral portion of the iris (emphasized region) that is responsible for lenticular accommodation. This does not represent a separate muscle group. The radially oriented dilator fibers of the iris are arranged in a monolayer in the posterior iris adjacent to the pigment epithelium. The ciliary body is primarily composed of loosely arranged connective tissue and blood vessels, and it extends between the root of the iris and the sclera. The ciliary body is attached to the sclera by the posterior ciliary muscles and the tenacular ligament. The elements of the pectinate ligament extend between the inner lamella of the cornea at the corneal spur and the root of the iris. The elasticity of the pectinate ligament and the tenacular ligament is shown through their depiction as springs.

attributed to the actions of the posterior ciliary muscle and the vitreous pressure behind the lens. Brief reports of these results have appeared elsewhere (Glasser, Troilo & Howland, 1993; Glasser & Howland, 1993).

MATERIALS AND METHODS

Subjects

Cornell K-Strain White Leghorn chicks at 4 weeks of age were used to study the accommodative mechanism. Chicks were obtained at hatching and housed in groups under a 12/12 hr light/dark cycle with *ad libitum* feed and water.

EW stimulation

Electrical stimulation of the EW nucleus (EW stimulation) was used to study lenticular accommodation in eight 4-week old chicks (Troilo & Wallman, 1987; Glasser *et al.*, 1994). To measure the extent of EW-stimulated accommodation, chicks were refracted using infrared photorefraction with lens neutralization as described previously (Glasser *et al.*, 1994). In addition to the measurements explained below, chick eyes were observed during EW-stimulated accommodation using an ophthalmic slit-lamp (Bausch & Lomb) as described previously (Glasser *et al.*, 1994).

Ultrasound

A-scan ultrasound (Echorule, 3-M) was used to measure changes in the axial dimensions of the eye during EW-stimulated accommodation. Anesthetized chicks were immobilized in a stereotaxic apparatus and their eye-lids were held open with lid retractors. A drop of topical anesthetic (0.5% Proparacaine HCl, Bausch & Lomb) was applied to the cornea, followed by a small amount of ultrasound transmission gel (Aquasonic, Parker). The ultrasound transducer was positioned in front of the eye using a micromanipulator, while the ultrasound output was monitored to ensure optimal positioning of the transducer. The axial dimensions of the eye were measured while the eye was relaxed and unaccommodated. The measurements were then repeated during EW stimulation for a range of stimulus currents that had previously been determined to induce accommodation without eye movements. Anterior chamber depth, lens thickness, vitreous chamber depth, and axial length were measured as a function of stimulus current.

Partial iridectomies

Partial iridectomies were performed on the right eyes of 10 1-day old chicks. This surgical procedure resulted in the removal of the central iris muscle fibers while leaving a relatively uniform band of the most peripheral iris musculature intact. Chicks were anesthetized with isoflurane inhalant anesthesia (Anaquest, Arrane, 99.9%) administered via a vaporizer (Isotec 3, Cyprane, England) through which oxygen was passed at 1.5 l/min. Lidocaine anesthetic (1%) was injected s.c. around the orbit, and a drop of topical anesthetic (Proparacaine HCl ophthalmic solution USP 0.5%, Bausch & Lomb) was applied to the cornea. The eyelids were held open with lid retractors and a 1–2 mm incision was made vertically in the temporal margin of the cornea. Fine forceps were inserted through the incision into the anterior chamber to grasp the nasal margin of the iris. The iris was cleanly extracted in a single movement as the forceps were withdrawn. This procedure caused minimal bleeding and little or no trauma to the cornea or lens. Any remaining debris was expelled from the anterior chamber by pressing gently on the cornea. A single suture was tied in the corneal incision using 10-0 surgical silk (0.2 metric Ethicon black microfilament nylon). A drop of topical antibiotic (Dexasporin, Pharmafair) was applied to the cornea. Chicks began using the partially iridectomized eye within an hour after surgery.

Chicks were observed twice daily during post-surgical recovery and over the following 4 weeks for any signs of discomfort or infection. No chicks were removed from the study due to indications of discomfort or infection. However, post-surgical slit-lamp inspection revealed that, in four birds, either the pupil was occluded by pigment epithelial tissue or the lens capsule had been perforated. These four chicks were dropped from the study and euthanized.

At 4 weeks of age, the remaining six partially iridectomized chicks were used for EW stimulation as described previously. As with the normal chick eyes, the eyes of the six partially iridectomized chicks were measured during accommodation using infrared photorefraction and infrared keratometry, and the eyes were examined using an ophthalmic slit-lamp.

In vitro electric-field stimulation

To study the accommodative mechanism of the eye, an *in vitro* technique of electric-field stimulation was used. Chicks ($n = 10$) were euthanized (urethane: 1 ml/100 g of 40% in buffered saline), and their eyes were enucleated and placed in oxygenated Tyrode's solution (Pilar & Tuttle, 1982). The eyes were cleaned of extraorbital tissue and glued (Krazy Glue, Borden, Columbus, Ohio), at the sclera of the limbal region of the eye, into a bevelled hole in a plexiglas plate so that the cornea protruded through the hole. The cornea and the posterior segment of the eye were then removed to leave the lens naturally suspended within the scleral ring. The eye preparation could thereafter be handled using the plexiglas plate.

The plexiglas plate with the attached eye preparation was inserted into a slot in a 3 cm long (4 cm wide × 4 cm high) transparent plexiglas observation chamber which was filled with oxygenated Tyrode's solution. Wire stimulating electrodes were introduced into the Tyrode's solution on either side of the plate to allow the intraocular muscles to be stimulated using a Grass stimulator (50 Hz, 15 msec duration, 10–150 V). This procedure has been shown to induce neurogenic contractions of the intraocular muscles (Yoshitomi, Ito &

Inomata, 1988). The eyes remained viable for up to 2 hr under these conditions.

These eyes were studied with an ophthalmic slit-lamp to observe lenticular and iridial changes during electrical-field stimulation. When the eye was viewed from the front, the iris, pectinate ligament, and the anterior surface of the lens could be seen, and when viewed from the back, the ciliary body and the posterior lens surface were visible (Fig. 2). This setup enabled the anterior and the posterior surfaces of the lens to be observed directly and independently to ensure that the movements observed were real physical changes, and not simply apparent movements as seen through the changing optics of the lens.

A-scan ultrasound was used to monitor changes in lens thickness and lens position during electric-field stimulation and during a sequential dissection. The ultrasound transducer was placed against the front surface of the plexiglas observation chamber. The lens thickness and lens position were measured within the chamber while the eye was unstimulated. Electric-field stimulation caused changes in lens thickness and lens position, and these changes were recorded using the ultrasound. In addition, the eye preparation could be further dissected by removing the plexiglas plate from the observation chamber and placing it in a dissecting dish. Varying degrees of dissection were undertaken to reveal the ciliary muscles, or to remove the iris or the lens. The eye preparation was then returned to the slot in the observation chamber for further ultrasound measurements.

Dissection

We did a sequential dissection on six eyes to determine how the pectinate ligament and ciliary body contribute towards maintaining lens position and the lens thickness. The enucleated, but still intact globes were glued to the plexiglas plate as described previously. The plate was inserted into the slot in the observation chamber and the chamber was then filled with Tyrode's solution. The ultrasound transducer was positioned against the front surface of the observation chamber and clamped in position. The lens thickness and the lens position were then measured in the intact eye as the eye was held in the chamber.

The eye was removed from the chamber by simply removing the plexiglas plate to which it was glued, and the sequential dissection was performed as follows: (1) the cornea was removed; (2) the posterior sclera and vitreous were removed; (3) the tenacular ligament was cut; and (4) the pectinate ligament was cut. Each step of the dissection was completed easily and rapidly with no physical contact or disruption of the lens. The anterior segment of the eye remained firmly glued to the plexiglas plate throughout the procedure. After each stage in the dissection, the plexiglas plate was returned to the slot in the observation

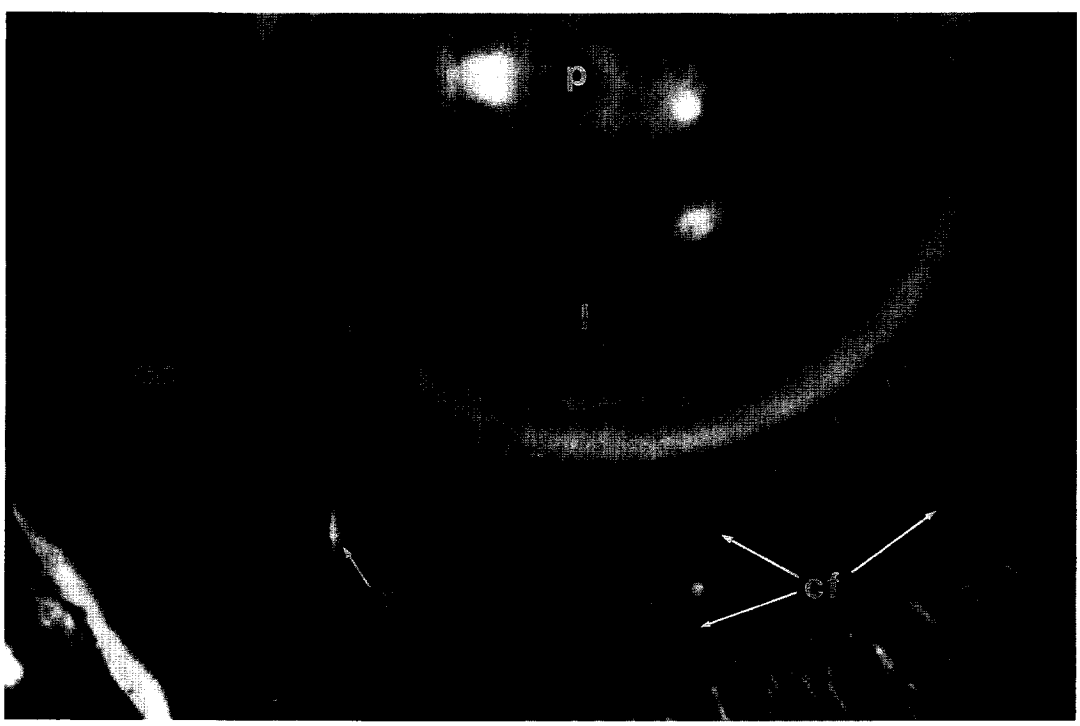

FIGURE 2. Photograph of the lens (l) and ciliary body (cb) of the anterior segment of a dissected chick eye, as viewed from the vitreous chamber. The pupillary aperture (p) and the iris can be seen through the lens. The posterior surface of the ciliary body is folded to form the ciliary folds (cf) which radiate towards the lens. The ciliary folds are attached to the anterior peripheral margin of the lens by the ciliary processes (black arrows). These can be seen around the peripheral edge of the lens and through the lens as magnified by the optics of the lens. The radially oriented ciliary folds of the ciliary body extend outward to join the retina at the *ora serata*. The vestigial embryonic fissure (ef) is visible as a white scar on the inferior nasal ciliary body. The outer edge of the ciliary body at the region of the *ora serata*, from where the posterior segment of the eye has been removed, can be seen as a white tissue at the lower left.

chamber, and the ultrasound measurements repeated. This allowed a comparison of lens position and thickness relative to the intact eye at each stage of the dissection.

We demonstrated the direct action of the iris on the lens using a dissected lens with the ciliary processes and iris still attached. The lens and iris were removed from an eye by making a circumferential cut through the ciliary body and the pectinate ligament around the peripheral edge of the lens. This tissue was maintained in Tyrode's solution and electrically stimulated via two electrodes placed in the dissecting dish. During electric-field stimulation the iris contracted and the thickness of the lens increased.

Lens back vertex distance measurements

With the ability to induce lenticular changes using electric-field stimulation, we were able to measure optical changes in lens power *in vitro*. For this we developed a computer-assisted method to measure lens back vertex distance using a scanning laser technique (Fig. 3) similar to that described previously (Sivak *et al.*, 1985; Sivak, Gershon, Dovrat & Weerheim, 1986a; Sivak, Hildebrand, Lebert, Myshak & Ryall, 1986b). Lens back vertex distance was measured in excised eyes from which the cornea and the posterior segment (retina, scleral, vitreous etc.) had been removed. The intraocular muscles were unaffected by the dissection and the lens remained naturally suspended within the scleral ring formed by the scleral ossicles at the limbus of the eye. The eye preparation was stimulated either electrically or pharmacologically using a Tyrode's/nicotine solution (0.011%), and measurements were made before and during stimulation.

To determine if the iris muscle contributes to the change in lens power during stimulation, laser scanning measurements were made in relaxed and electrically stimulated eyes before and after a total iridectomy. The back vertex distance was first measured while the iris remained intact. The plexiglas plate to which the eye was glued was then removed from the laser scanning apparatus and placed in a dissecting dish. The whole iris was then removed by cutting it circumferentially at the root of the iris with fine iridectomy scissors. This could be accomplished without disturbing any other intraocular tissues. The plexiglas plate was then returned to the glass chamber, and the lens back vertex distance was again measured before and during electric-field stimulation.

Histology

Histology of the anterior segment was performed on 10 4-week old chick eyes to verify the arrangement of the lenticular accommodative apparatus. Chicks were euthanized with CO_2, and the eyes were enucleated and

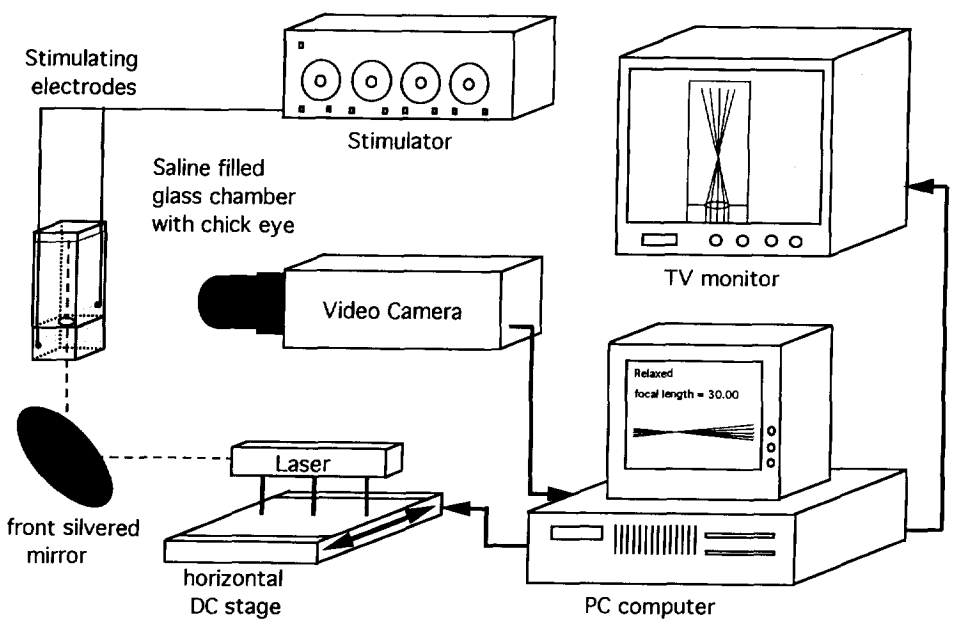

FIGURE 3. A diagrammatic representation of the scanning laser technique that was used to measure changes in back vertex distance of chick lenses. The anterior segment of the eye is positioned in the glass chamber and an electrical stimulus is applied using wire electrodes placed in solution. The laser beam, reflected off a front silvered mirror below the chamber, passes through the lens. The laser is mounted on a motor-driven stage. The stage is controlled by the PC so that when the stage is moved the laser beam will scan across the pupillary aperture. A video camera, connected to an image processor board in a PC, views the side of the glass chamber, and the output from this video camera is displayed on the TV monitor. As the laser is scanned across the pupil, the laser beam is located by the image processor and the position and slope of each of the refracted laser beams is then calculated by the computer. Following each scan across the lens, all the laser beams passing through the lens are reconstructed by the computer, the convergence point of all the laser beams is determined, and the lens back vertex distance is calculated. This information is stored to disk together with any user supplied information to identify the particular scan (i.e. "relaxed" or "stimulated"). This procedure is conducted while the tissue is relaxed (unstimulated), as shown on the PC monitor, and again when stimulated. The difference between the values obtained for the relaxed lens and the accommodated lens provides a measure of the change in back vertex distance of the lens.

dissected in oxygenated Tyrode's solution. The cornea, the posterior sclera, and the vitreous gel were removed, and the remaining anterior segment preparations were fixed in chilled 4% glutaraldehyde fixative for 48 hr. The scleral ossicles were decalcified by soaking them in 10% EDTA for 2–4 days. The anterior segment preparations were dehydrated, embedded in plastic, serially sectioned at 10 μm, and stained on a hotplate with basic fuchsin/methylene blue.

To examine the iridial musculature in more detail, seven chick eyes were fixed in 10% formalin and decalcified as before. Two eyes were opened in the mid-horizontal plane, and two eyes the mid-sagittal plane. Central portions of the globes were processed routinely for paraffin embedding, sectioned at 8 μm, and stained with Hematoxylin and Eosin (H&E) and Masson's trichrome stains. Three eyes, from which the cornea and posterior segment had been removed, were processed for paraffin embedding. These were serially sectioned in the frontal plane until the posterior margin of the iris had been passed.

Additional sections (8–10 μm) were obtained from 25 eyes which had been fixed in either 10% formalin or Bouin's fixative and embedded in paraffin. These specimens were from chickens of various breeds and ages. Sections from each globe were stained with H&E and Masson's trichrome stains.

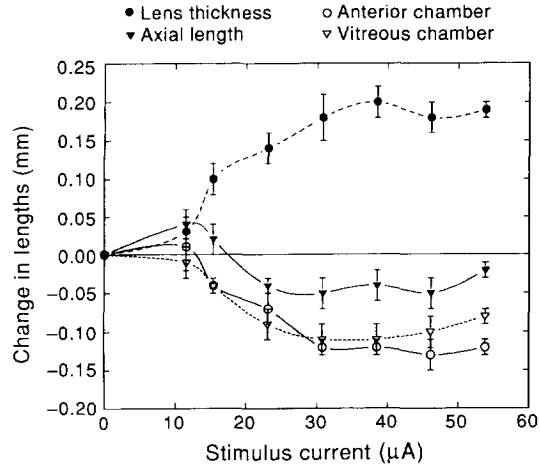

FIGURE 4. Changes in axial dimensions of the eyes from eight chicks in which the EW nucleus was stimulated to induce accommodation. The anterior chamber depth, the lens thickness, the vitreous chamber depth, and the axial length of the eyes were measured using A-scan ultrasound. Measurements were made when the eye was relaxed and again during stimulation of the EW nucleus. The lens thickens and bulges into the anterior and vitreous chambers equally during EW-stimulated accommodation, thus producing a decrease in the anterior and vitreous chamber depths. A slight decrease in axial length is observed at stimulus currents above 20 μA. The data points are connected by smoothed lines to aid readability, not by curves of best fit.

RESULTS

EW-stimulated accommodation

In all chicks used for EW stimulation, the tip of the stimulating electrode was verified to be within the EW nucleus using histological methods. The exact position within the EW nucleus varied slightly, which resulted in some variability of accommodative amplitude among chicks.

For this group of chicks, we have previously shown that EW-stimulated accommodation produced a mean accommodative amplitude of 25 D that saturated at a stimulus current of about 55 μA. We have also shown that lenticular changes account for roughly 60% of this accommodation, the remainder being due to corneal accommodation (Glasser *et al.*, 1994).

Figure 4 shows the ultrasound measurements of changes in lens thickness, anterior chamber depth, vitreous chamber depth, and axial length in the eyes of chicks used for EW stimulation. The values represent changes relative to the unaccommodated eye and they are plotted as a function of stimulus current. Lens thickness increases by up to 0.2 mm (at 39 μA, mean = 0.195, $t = 10.37$, $P < 0.001$) with resulting decreases in both anterior (at 39 μA, mean = -0.115, $t = -12.9$, $P < 0.001$) and vitreous (at 39 μA, mean = -0.11, $t = -6.91$, $P < 0.001$) chamber depths by about 0.1 mm each. This reflects no net forward or backward movement of the lens within the eye. There is also a decrease in axial length of the eye which attains statistical significance at current amplitudes of 23 and 30 μA (23 μA, $t = -2.62$, $P < 0.05$; 30 μA, $t = -2.40$, $P < 0.05$).

As reported previously, slit-lamp observations of the eye show that EW stimulation produces a contraction of the muscle fibers at the peripheral iris which increases the tension on the pectinate ligament. When the stimulus is terminated, the iris returns to its relaxed position and the tension on the pectinate ligament is relieved (Glasser *et al.*, 1994). We now report that while the peripheral muscle fibers of the iris were always observed to contract, pupillary constriction did *not* always occur during EW stimulation. Lens thickening and increases in both the anterior and posterior lens curvatures were observed under slit-lamp illumination, showing that the lens bulges into both the anterior and vitreous chambers. This uniform bulging of both lens surfaces accounts for the ultrasound measurements showing a decrease in both chamber depths during accommodation.

Partial iridectomies

Partial iridectomies were performed on 1-day old chicks, allowing them a sufficient period of recovery before examining the accommodating eye at 4 weeks of age. Varying degrees of iris removal were accomplished due to the difficulty of the surgical procedure in the small eyes of day-old chicks. Most commonly, some iris muscle remained functional in some quadrants of the eye, while little or none remained in other parts. In the most successful cases ($n = 2$), a uniform partial iridectomy resulted in a more or less uniform band of muscle fibers at the peripheral edge of the iris which remained functional. One such example is shown in Fig. 5. Under slit-lamp illumination, functional lenticular

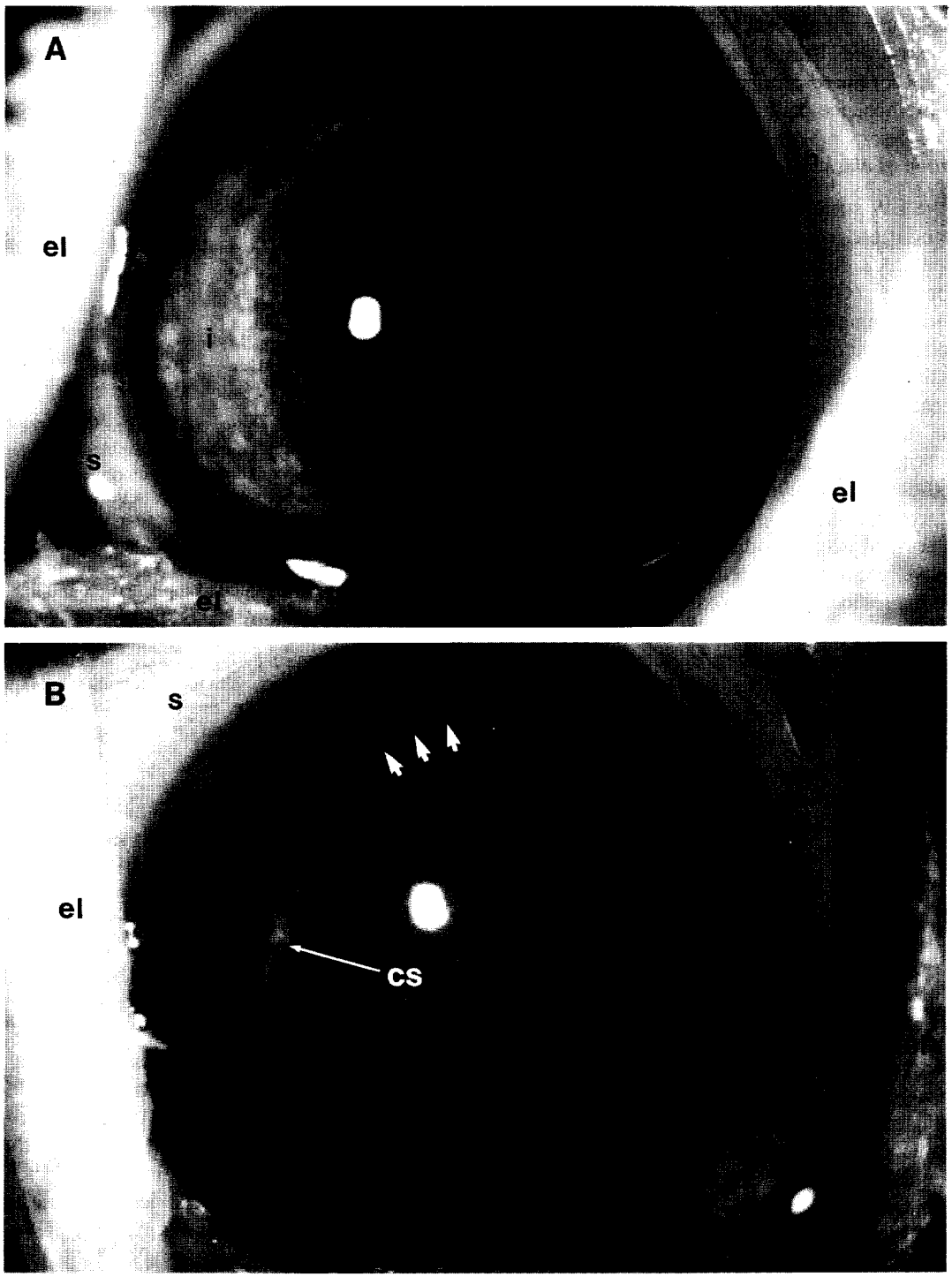

FIGURE 5. Photographs of a normal (A) and a partially iridectomized right eye (B) from two different 4-week old chicks. The bright spot seen within the pupil of each eye is the corneal reflection (first Purkinje image) from the optic fiber illumination. The eye-lid (el) is held open with a lid retractor. At the left of the photographs the sclera (s) can be seen, and on the right the nictitating membrane (n) is visible at the nasal corneo-scleral margin of the eye. (A) The iris (i) and blackened pupil can be seen through the cornea. The dark ring around the peripheral iris (seen here as a blackened ring at the outer edge of the iris) represents the region of the more deeply pigmented fibers of the iris sphincter muscle. The extensive vascularization of the iris can be seen as a network of fine dark lines throughout the intact iris. (B) The right eye of a 4-week old chick which had received a partial iridectomy at 1 day of age. The corneal scarring (cs) can be seen on the temporal (left) corneal margin. This is all that remains of the corneal incision through which the iris was removed at 1 day of age. Note that this scar is on the far temporal margin of the cornea and so would not interfere with normal vision. In this example, the muscle fibers of the most peripheral iris remained intact following the partial iridectomy. This is essentially the same group of muscle fibers as the more deeply pigmented ones seen in (A). The ciliary processes are firmly attached to the anterior surface of the lens and hold the iris against the lens. These finger-like projections can be seen through the remaining muscle fibers of the peripheral iris at the lower-left edge of the pupil. The tips of the ciliary processes can be seen protruding from under the remaining iris muscle at the upper-left edge of the pupil (small arrows).

accommodation could be clearly observed in these two chicks. Both chicks freely accommodated under light hand-held restraint. The eyes appeared normal in all respects, except for the scarring in the peripheral temporal cornea and the absence of the more central iris.

EW stimulation of chicks with partially iridectomized eyes

As with the EW-stimulated normal chicks, the extent of accommodation was measured in the partially iridectomized chick eyes using infrared photorefraction and keratometry (Glasser *et al.*, 1994). Lenticular accommodation remained functional to varying degrees in the partially iridectomized chicks, and corneal scarring resulted in disruptions of the normal corneal curvature. Because of the variability of the partial iridectomies, no attempt was made to compile these measurements for comparison with the results from the normal chick eyes. However, these chick eyes had a mean maximal accommodative amplitude of 17 D, of which 52% was due to corneal accommodation. In each chick, the total refractive change exceeded the corneal change, indicating the presence of both corneal and lenticular accommodation.

In these partially iridectomized eyes from which the central iris sphincter muscle fibers had been removed, the tips of the ciliary processes could be viewed under slit-lamp illumination. In addition, the ciliary processes on the anterior surface of the lens were visible beneath the optically translucent muscle fibers at the peripheral iris (Fig. 5). A contraction of the peripheral muscle fibers of the iris was seen to directly force the ciliary processes against the lens. The pectinate ligament, which remained intact in the partially iridectomized eyes, was stretched during a contraction of the peripheral muscle fibers of the iris, just as in the normal eyes.

In vitro electric-field stimulation

Electric-field stimulation of enucleated, dissected eyes induced strong contractions of the intraocular muscles. Pupillary constriction, lenticular changes, and ciliary body movements were observed. The most pronounced and consistent effect was a strong contraction of the iris, particularly the peripheral muscle fibers at the root of the iris. It is a portion of these muscle fibers that remained intact in the partially iridectomized eyes (Fig. 5).

We have made slit-lamp observations of the dissected eye during electric-field stimulation. We see that, when the iris sphincter muscle contracts, the anterior and posterior lens curvatures increase, and the pectinate ligament and the ciliary body stretch. When the stimulus is terminated, the peripheral iris returns towards its rest position, and the lens curvatures flatten as the elasticity of the pectinate ligament and ciliary body is taken up.

By viewing the posterior surface of the lens during electric-field stimulation, one can see that it undergoes a marked increase in curvature and an obvious decrease in diameter (no measurements were made). The ciliary body is stretched radially towards the lens as the iris contracts. The ciliary processes which are attached to the anterior surface of the lens, are forced against the lens. This can be observed through the clear optics of the lens. The posterior ciliary body is attached to the sclera of the globe by the tenacular ligament (Fig. 1). During electric-field stimulation, it can be seen that the ciliary body is pulled forward to stretch the tenacular ligament. When the stimulus is terminated, the ciliary body is pulled back to its rest position as the elasticity of the tenacular ligament is taken up.

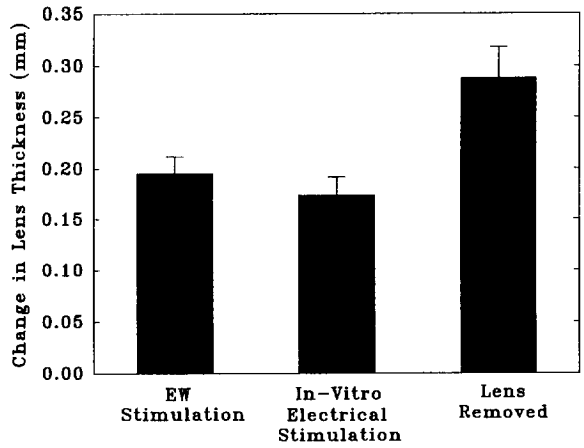

FIGURE 6. This graph shows the extent to which the lens thickness increases in three cases: (1) during EW-stimulated accommodation; (2) during electric-field stimulation of the anterior segment of the eye; and (3) after the lens has been removed from the eye. The changes in lens thickness were measured using A-scan ultrasound. EW-stimulated accommodation ($n = 8$) and electric-field stimulation ($n = 8$) caused the lens thickness to increase by the same amount. This serves to demonstrate that the lenticular changes that occur during electric-field stimulation are equivalent to those resulting from EW-stimulated accommodation. Once the lens is removed from the eye, it gets significantly thicker than during either EW-stimulated accommodation or electric-field stimulation. This indicates that the lens is normally held in a relatively flattened state, and when it is completely free of other influences, it will round up under its own elasticity.

Ultrasound measurements show that the lens thickness increases by the same amount during electric-field stimulation *in vitro* as during EW-stimulated accommodation (Fig. 6). The two cases are slightly different, however, because as shown in Fig. 7, there is a net backward movement of the lens during electric-field stimulation *in vitro* which is absent during EW-stimulated accommodation.

Dissections

We were able to determine the role that the various elements of the eye play in accommodation by measuring changes in lens thickness and lens position during a sequential dissection. At each stage of the dissection, ultrasound was used to measure these changes in six eyes as they were held in a slot in a plexiglas chamber. The dissection followed the same sequence as described earlier: (1) the cornea was removed; (2) the posterior segment was removed; (3) the tenacular ligament was cut; and (4) the pectinate ligament was cut. The results show that the tenacular ligament holds the lens flattened because, after it is cut, the lens thickness increases by

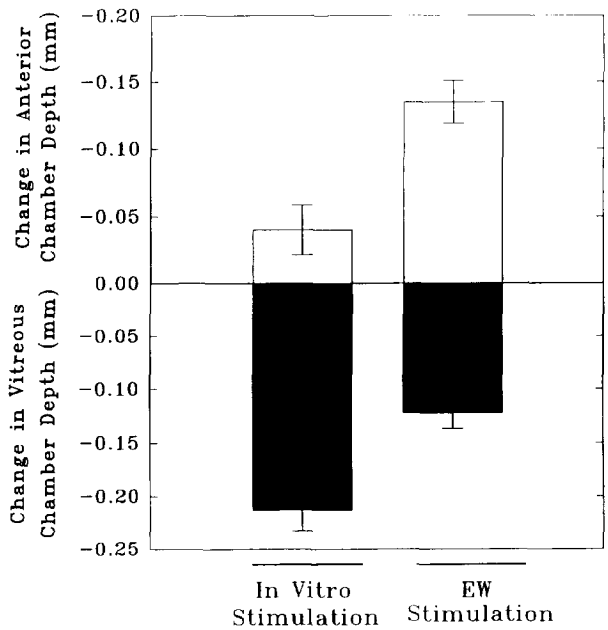

FIGURE 7. The changes in lens thickness and lens position that occur during EW-stimulated accommodation and electric-field stimulation of the anterior segment of the eye. The changes in lens thickness and position were recorded using A-scan ultrasound. The data show changes relative to the unstimulated, relaxed lens. They are presented as negative values because during stimulation, both the anterior chamber depth and the vitreous chamber depth *decrease* as the lens bulges into them. In the anterior segment of the eye, from which the cornea and the back of the globe have been removed, "anterior chamber" represents the distance from the front surface of the plexiglas observation chamber to the anterior surface of the lens and "vitreous chamber" represents the distance from the posterior surface of the lens to the back of the observation chamber. It is clear that the two stimulation conditions produce different effects. However, for each stimulation condition the increase in lens thickness (obtained by adding both changes) is the same (0.25 mm). During electric-field stimulation, the posterior surface of the lens bulges more than the anterior surface of the lens producing a net backward movement of the lens. During EW-stimulation, however, the two surfaces of the lens bulge by approximately the same amount.

0.4 mm (Fig. 8). The pectinate ligament holds the lens forward in the eye because, after it is cut, the lens moves backward. This demonstrates that the resting tension of the tenacular ligament and pectinate ligament is responsible for holding the lens in the unaccommodated position.

Electric-field stimulation of an isolated iris–lens preparation was used to demonstrate that the iris alone can induce lenticular changes. A lens was dissected from an eye with the iris still attached by the ciliary processes. The posterior surface of the lens was placed on the bottom of a dissecting dish filled with Tyrode's solution. Electric-field stimulation caused iris muscle contractions which were similar to those seen during electric-field stimulation of the anterior segment preparation and those seen in the intact eye during EW-stimulated accommodation. With each contraction of the iris, the lens thickness increased noticeably. This resulted in the iris and anterior surface of the lens being pushed upward in the dissecting dish. When the stimulus was terminated, the iris relaxed and the lens returned to its unstimulated thickness. No measurements of lens thickening were made.

Scanning laser measurements of changes in back vertex distance

Scanning laser measurements were used to show that *in vitro* electric-field stimulation did cause optical changes in lens power, and that these changes no longer occurred after the iris had been removed.

While unstimulated and in the relaxed state, the mean back vertex distance of chick lenses ($n = 11$) was 33.58 mm. This represents a resting back vertex power of 39.70 D (Fig. 9). Electric-field stimulation caused a 9.5 D mean increase in lens power when the irises were intact ($P < 0.05$, $t = -7.453$, paired t-test). After the irises had been removed, the mean resting back vertex distance increased slightly to 35.82 mm. Now, with the irises removed, there was only a 1.8 D change in back vertex power when eyes were electrically stimulated. Thus, removal of the iris resulted in an 85% loss in change of power of the lens.

Pharmacological stimulation was also used to induce changes in lens power. On a group of eyes ($n = 8$) in which the irises remained intact, a 0.011% Tyrode's/nicotine solution was found to cause a mean change in back vertex power of 18 D. This was considerably more than the 10 D change that resulted from electric-field stimulation.

Histology

Figures 10 and 11 are representative histological sections through the anterior segment of the chick eye, showing the arrangement of the accommodative apparatus (see also Fig. 1). The iris lies against the anterior surface of the lens and, at its periphery, the iris is continuous with the ciliary body. The ciliary body is firmly attached to the anterior surface of the lens by the ciliary processes. The fibers of the pectinate ligament extend between the inner lamella of the cornea at the corneo-scleral spur and the anterior surface of the peripheral iris.

The chicken iris has an extensive group of circumferential muscle fibers which are located more or less throughout the cross-sectional extent of the iris (Fig. 10). The circumferential muscle fibers thin out in proportion to the total iris thickness, and they are predominantly associated with the anterior iris stroma.

A distinct group of oblique muscle fibers is present in the peripheral one-half to one-third of the iris (not shown). Generally, these fibers are short and sparse and are most obvious in the region of the iris root. They are found immediately subjacent to the circumferential fibers, and remain within a single plane of the iris passing parallel to the iris surface.

The iris dilator is a thin strap-like muscle that consists of 1–4 muscle fibers spanning the entire length of the iris (Fig. 10). The fibers adjacent to the pupil margin are typically obscured from view by melanin associated with the pigment epithelium of the iris. The most peripheral dilator fibers lie posterior to the oblique muscle fibers.

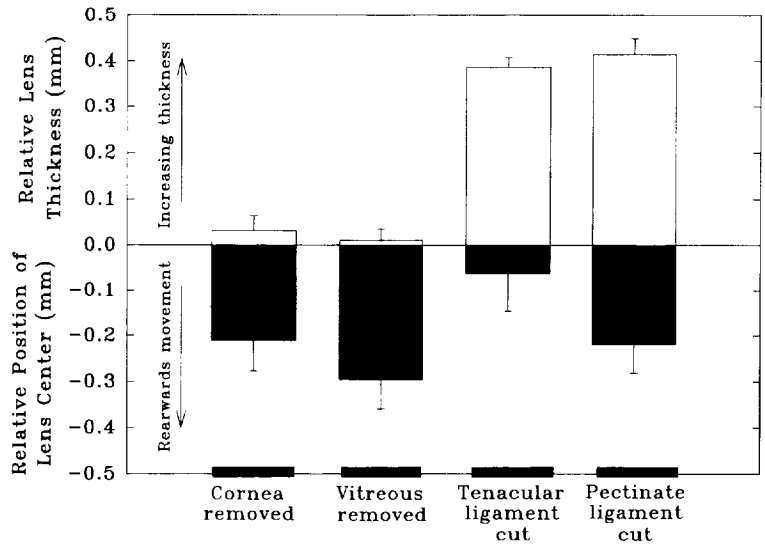

FIGURE 8. Changes in lens thickness (open bars) and changes in lens position (solid bars) during the sequential dissection. At each step in the dissection the lens thickness and lens position were measured using A-scan ultrasound. All values represent changes relative to the intact eye prior to dissection (n = 6 eyes, SEM). (1) After the cornea is removed, there is no increase in lens thickness, but the lens moves backward in the eye. (2) After the vitreous is removed, there is still no change in lens thickness, but the lens moves further backward. (3) When the tenacular ligament is cut, there is an increase in lens thickness, and the lens moves forward towards its original position. (4) When the pectinate ligament is cut there is no further increase in lens thickness, but the lens moves backward again. This sequential dissection shows that the lens is held forward by a combination of the intraocular pressure, the vitreous, and the pectinate ligament, and the lens is held flattened by the tenacular ligament and the ciliary body.

DISCUSSION

The mechanism of lenticular accommodation

During accommodation the peripheral muscle fibers of the iris contract to apply a force against the ciliary processes on the anterior equatorial surface of the lens. The ciliary processes push on the annular pad at the anterior equatorial margin of the lens. This results in an increase in lens thickness and an increase in the curvature of the anterior and posterior surfaces of the lens. The

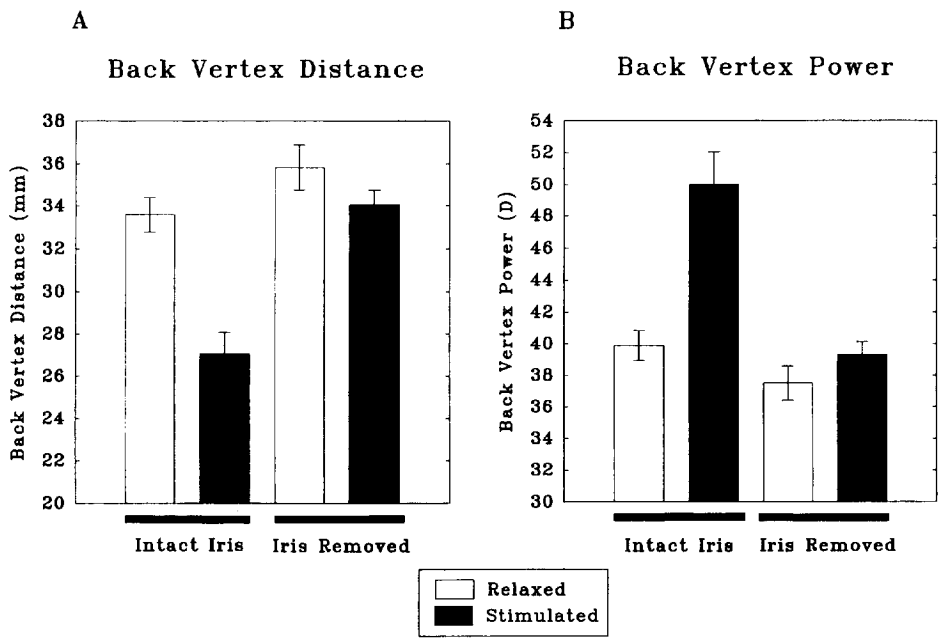

FIGURE 9. The results of scanning laser measurements of chick lenses showing (A) changes in back vertex distance and (B) the same measurements expressed as changes in back vertex power. The back vertex distance was measured while the lens remained suspended in the anterior segment of the eye (n = 11). Electric-field stimulation was used to induce changes in lens power. During stimulation, the mean back vertex distance decreased from 33.6 to 27.0 mm (39.9 to 50.0 D). The iris was then removed from the anterior segment of the eye and the back vertex distance was again measured. The removal of the iris caused a slight increase in the mean back vertex distance (33.6 to 35.8 mm), although this change was not significant. Once the iris had been removed, electric-field stimulation produced only a small (1.8 mm) decrease in back vertex distance (35.9 to 34.1 mm). This represents only about 20% of the change in lens power that occurred when the iris was intact. This provides evidence that the iris is primarily responsible for changing the focal power of the lens.

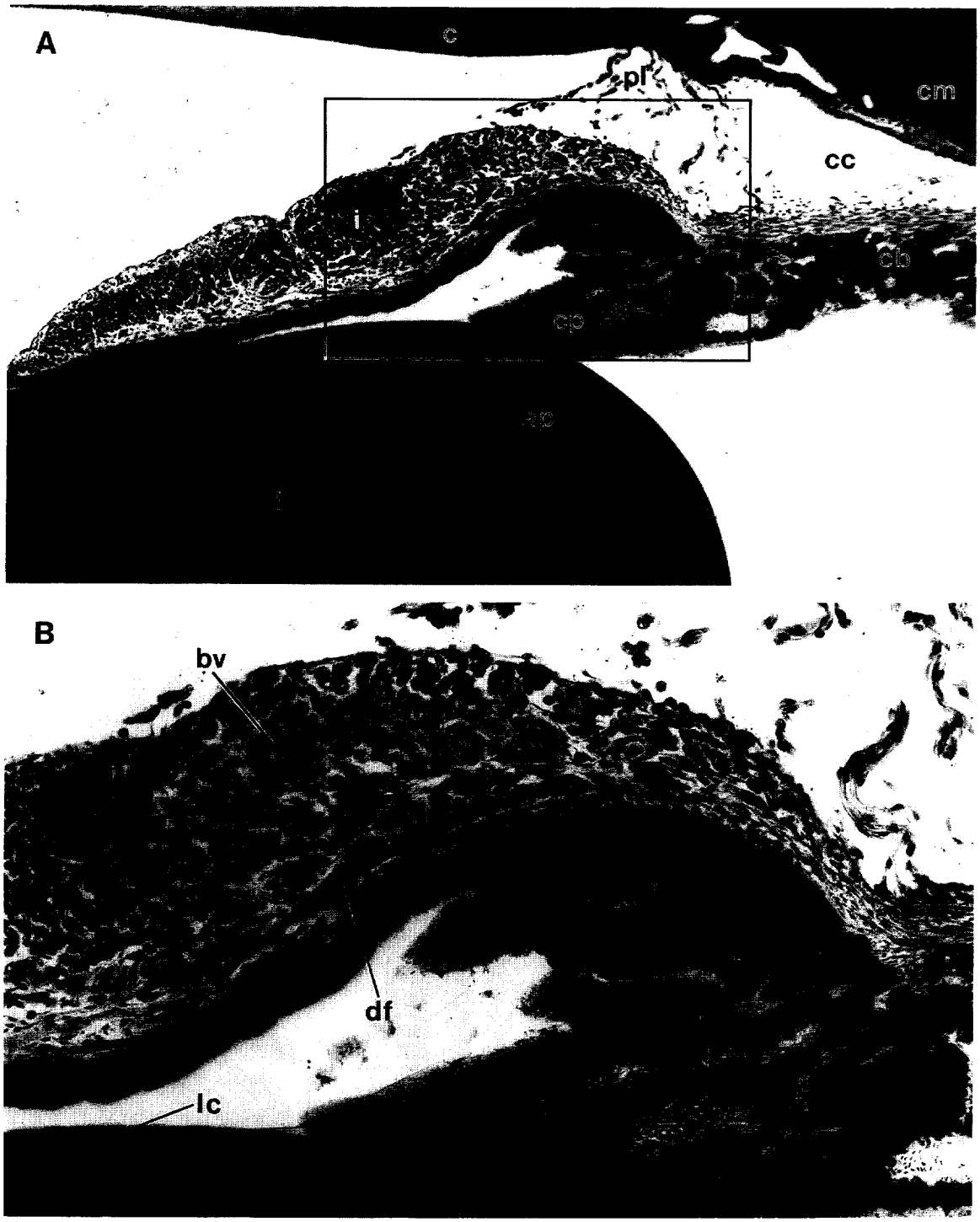

FIGURE 10. A horizontal histological section of the iris, ciliary processes, and lens of the chick eye at low (A) and high (B) magnification. The iris (i) lies against the anterior surface of the lens (l) and is attached to the lens through the ciliary process (cp). The pectinate ligament (pl) spans the ciliary cleft (cc). It extends between the cornea (c), at the corneal spur, and the root of the iris where the iris is joined to the ciliary body (cb). A small part of the anterior ciliary muscle (cm) is just visible in (A). (B) The fibers of the peripheral iris sphincter muscle can be seen in cross section. Their positioning over the ciliary process allows the force of contraction to be transferred directly to the lens through the ciliary process. Numerous small dark-staining nuclei, and larger diffuse staining fat droplets are scattered among the muscle fibers. Note that the ciliary body forms a firm contact on the lens through the lens capsule (lc). The striated dilator fibers (df) can be seen in longitudinal section and a blood vessel (bv) can be seen in cross section. Plastic embedded, 10 μm thick, basic fuchsin/methylene blue-stained tissue.

pectinate ligament and the ciliary body are stretched towards the axis of the eye as the iris muscle fibers contract.

A contraction of the anterior ciliary muscle causes a change in the curvature of the cornea for corneal accommodation (Glasser *et al.*, 1994). The posterior ciliary muscle pulls the posterior ciliary body forward against the tension of the tenacular ligament. This releases

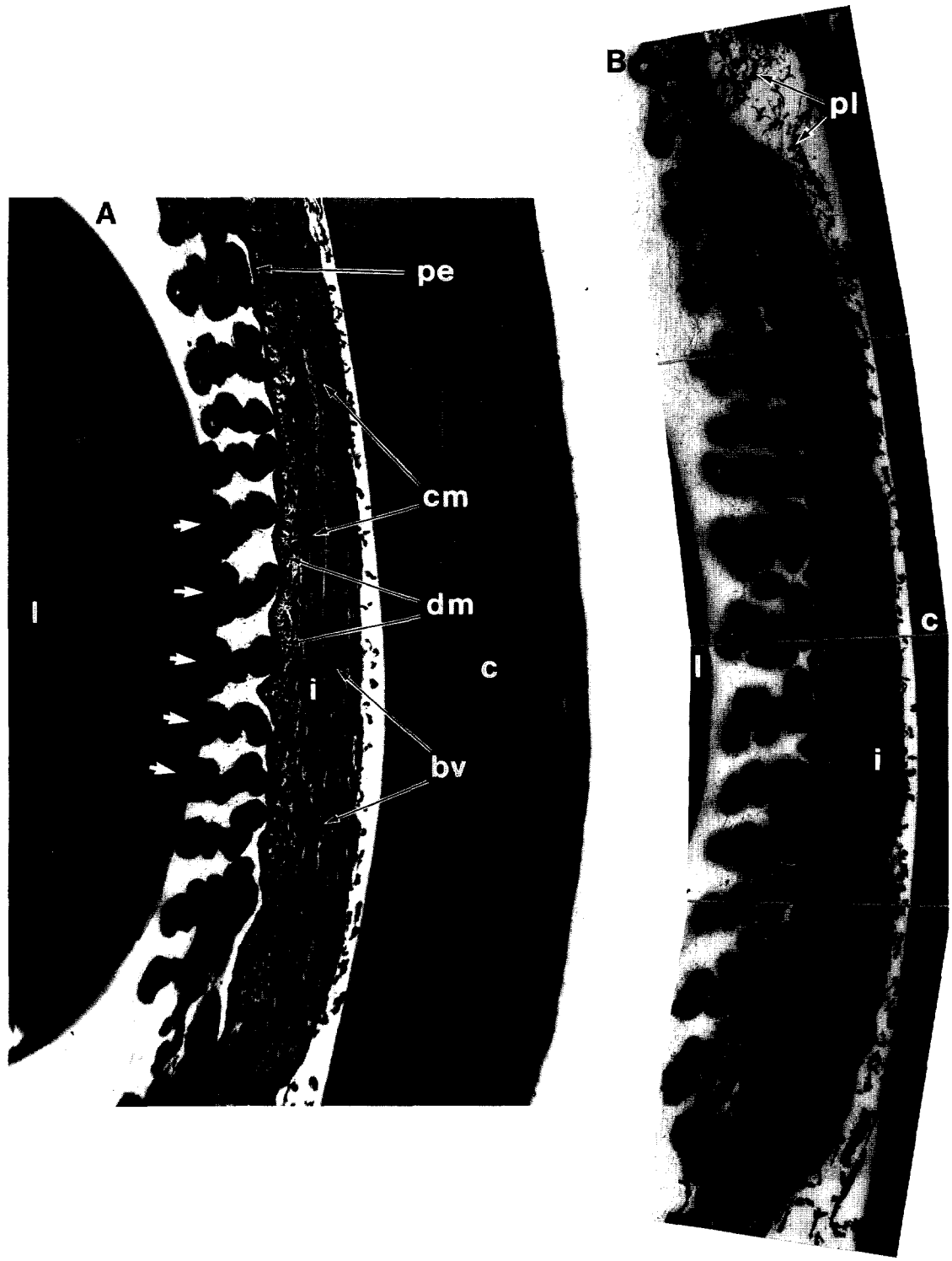

FIGURE 11. Two separate horizontal histological sections near the peripheral ciliary margin of the iris (i) at the inferior margin of the eye. (A) A representative section at the region where the ciliary processes (arrow heads) are still fused to the annular pad of the lens. (B) A subsequent serial section about 30 μm (three sections) inferior to the section in (A). This shows a higher magnification of the peripheral iris musculature and associated ciliary folds where the ciliary processes no longer contact the lens. The iris is densely packed with circumferential muscle fibers (cm), shown here in longitudinal section. In (B), note that although the ciliary processes no longer contact the lens, the iris is still thick and muscular in this region. This musculature at the far peripheral region of the iris can provide no pupillary constrictive function, but it serves to accommodate the lens. A contraction of these muscle fibers would act to push the ciliary processes on the annular pad of the lens. Adjacent to the deeply pigmented epithelial (pe) layer of the iris, the dilator muscle (dm) fibers can be seen in cross section. Scattered elements of the pectinate ligament (pl) can be seen in the anterior chamber of the eye between the cornea (c) and the iris, particularly at the upper region of (B). In (A) a series of blood vessels (bv) can be seen in longitudinal section within the iris. The darkly stained nuclei of the avian erythrocytes can be seen within the vessels. Plastic embedded, 10 μm thick, basic fuchsin/methylene blue-stained tissue.

some of the resting tension of the ciliary body, and allows the peripheral iris musculature to act directly on the lens, rather than having to pull against the resting tension of the ciliary body.

Dissections and histology show that the peripheral iris is attached to the ciliary processes at the root of the iris and that the ciliary processes are themselves attached to the annular pad of the lens. The site of attachment of the ciliary processes to the annular pad of the lens, and the position of the muscle fibers of the peripheral iris on the ciliary processes, suggest that the annular pad serves to spread the contractile force of the iris evenly around the equatorial margin of the lens. The elasticity of both the pectinate ligament and the tenacular ligament assist in returning the iris, ciliary body, and lens to their unaccommodated rest positions.

Our physiological evidence is supported by the anatomical arrangement of the peripheral muscle fibers of the iris. The arrangement of the iridial musculature suggests several distinct yet related mechanisms whereby iris-induced changes in lens curvature would take place. The following proposed mechanisms would necessarily act in concert to produce lenticular accommodation. (1) The peripheral circumferential muscle fibers of the iris squeeze the lens through the ciliary processes to bring about a change in lens curvature. (2) The circumferential fibers in the central iris impart an axial pull to the ciliary processes through a "purse string" effect. The bulk of the circumferential muscle fibers in the peripheral one-third of the iris, clearly not required for pupil constriction, would pull the iris root and associated ciliary body axially. (3) A contraction of the oblique fibers might draw the peripheral muscle fiber group together to create a more compact ring. This would help the peripheral muscle fibers to deliver a more concentrated force on the ciliary processes.

Contrary to previous reports (Slonaker, 1918; Gundlach, Chard & Skahen, 1945) we see no deformation of the ciliary region of the globe during accommodation. The structural rigidity that the scleral ossicles provide to the ciliary region of the bird eye ensures that the accommodative tension from the pectinate ligament, the ciliary muscles, and the tenacular ligament do not deform the globe.

Until now the conventional description of the mechanism of lenticular accommodation in terrestrial birds (including chicks) has been that the ciliary body is forced against the lens by a contraction of the ciliary muscles (Duke-Elder, 1958; Pumphery, 1961; Walls, 1967; West *et al.*, 1991). There are several serious objections to this proposed mechanism. First, in the chick eye, the ciliary cleft is often up to 5 times the width of the entire ciliary muscle. For the ciliary muscle to apply a force on the lens it would, therefore, be required to *expand* more than 5 times its *width* before even contacting the lens. This is an action which is incompatible with the orientation of the ciliary muscle fibers (Glasser *et al.*, 1994; Murphy, Glasser & Howland, 1995). Second, the ciliary body consists largely of pigmented epithelial cells and blood vessels lying beneath a fine layer of connective tissue fibers. If the ciliary body were to be forced against the lens to induce lenticular changes, it would have to be composed of more rigid and less compressible tissues. The tissues of the ciliary body seem more suited to withstand tensile forces, and the orientation of the ciliary muscle fibers seem more suited to release resting tension on the ciliary body. These observations cast serious doubt on the validity of previous descriptions of avian accommodation, but they are consistent with the mechanisms that we have proposed here.

EW-stimulated accommodation

During EW stimulation the peripheral muscle fibers of the iris always contracted during accommodation, but the pupil did not always contract. In our case, this may have been due to the positioning of the stimulating electrode within the EW nucleus. Müller (1857), however, described seeing accommodative contractions of the peripheral muscle of the iris without accompanying pupillary constriction in the eye of a freely accommodating falcon. During EW-stimulated accommodation, an electrode positioned in the more lateral EW nucleus might cause strong pupillary constriction without inducing accommodative changes. The occasional absence of pupillary constriction during EW-stimulated accommodation, together with Müller's (1857) observations, argues for a separation of the parasympathetic innervation to the accommodative and pupillary subdivisions of the iris muscle. If the iris is controlling lenticular accommodation, pupillary constriction must necessarily be able to occur without inducing accommodative changes. This would require separate parasympathetic control over the more central pupillary constrictor muscle fibers and the more peripheral accommodative muscle fibers of the iris. Although accommodative and pupillary subdivisions occur within the EW nucleus (Reiner, Karten, Gamlin & Erichsen, 1983), the most comprehensive descriptions of the innervation of the chick iris muscle to date indicate no such functional subdivisions (Zenker & Krammer, 1967; Oehme, 1969). Evidence does exist, however, for a differential distribution of muscle fiber types within the chick iris that may correspond with the functional subdivisions of the iris (Scapolo, Peirone, Filogamo & Veggetti, 1988). Although there is no previous evidence for the role of the chick iris in lenticular accommodation, it is possible that the differential distribution of muscle fiber types may correspond with the two separate functions of the iris.

In vitro electric-field stimulation

In the dissected eyes there is a net backward movement of the lens during electric-field stimulation which is not seen during EW-stimulated accommodation. This may be because the intraocular pressure and the vitreous are not present in the dissected eyes. During EW-stimulated accommodation in chicks, there is an increase in intraocular pressure on the order of 1–3 mm Hg (Glasser *et al.*, 1994) which may act to apply a force against the posterior lens surface and so translate greater changes in

curvature to the anterior surface of the lens. In the dissected eye, without the force of the vitreous against the posterior surface of the lens, the lens is free to move backwards in the eye during electric-field stimulation. This probably results in smaller changes in curvature of the anterior lens surface than would occur during accommodation in the intact eye.

Other observations from electric-field stimulation of dissected eyes have verified our description of the mechanism of lenticular accommodation. When the lens and its attached iris are removed from the eye, placed in Tyrode's solution and electrically stimulated, the iris muscle fibers contract to cause an increase in the thickness of the isolated lens. This clearly demonstrates that the iris musculature alone is sufficient to increase the curvature of the lens. When the pectinate ligament and the ciliary body are cut to remove the lens and iris, the lens tends to ball up slightly. This is because the pectinate ligament and the ciliary body exert a radial tension on the iris to hold the lens in the unaccommodated state. In the intact eye the forces of lenticular accommodation must act against these two elastic elements to bring about a change in lens curvature. We believe that the posterior ciliary muscles play a major role in overcoming the intrinsic elastic forces of the ciliary body during lenticular accommodation.

The role of the vitreous in lenticular accommodation

Hess (1912) observed that lenticular accommodation occurs even once the globe has been opened, and he therefore concluded that changes in intraocular pressure were not a motivating force for lenticular accommodation. Walls (1967), however, suggested that Hess's experiments proved only that there can be no increase in pressure on the vitreous during accommodation. We have previously shown that there *is* an increase in pressure in the chick eye during accommodation and that normal intraocular pressure is required for corneal accommodation to occur (Glasser *et al.*, 1994). The results presented here show that, when the posterior segment of the eye is removed, the lens will move backward in the eye during electric-field stimulation, but this does *not* occur during EW-stimulated accommodation (Fig. 7). These observations argue in favor of a passive mechanical role of the vitreous gel and posterior segment of the eye in accommodation in chicks.

The observation that the ciliary body is pulled forward during accommodation may provide an explanation for the source of the increase in intraocular pressure during accommodation. The posterior ciliary muscle inserts on the *pars plana* of the ciliary body at the anterior insertion of the tenacular ligament (Murphy *et al.*, 1995). When the ciliary muscles contract, the ciliary body is pulled forward against the elasticity of the tenacular ligament. A contraction of the peripheral muscle fibers of the iris would also act in concert on the ciliary body, pulling it radially. This could pull the choroid, the retina, and the vitreous forward against the posterior surface of the lens, increasing the intraocular pressure and potentially causing the decrease in the axial length (cornea to retina) of the eye. Alternatively, it is possible that EW stimulation could cause a thickening of the choroid through increased blood flow (Fitzgerald, Vana & Reiner, 1990). Either interpretation remains consistent with experimental findings reported here and elsewhere (Glasser *et al.*, 1994).

Lens back vertex distance measurements

We have shown that electric-field stimulation of enucleated eyes results in a 10 D change in back vertex power. This is *not* likely to represent the true extent of lenticular accommodation in the chick eye, for two reasons. First, there is a backward movement of the lens during electric-field stimulation that is not seen during *in vivo* EW-stimulated accommodation (Fig. 7), indicating that the two cases are not identical and so other differences may exist. Second, we have measured much stronger changes in back vertex power, up to 18 D, using nicotine stimulation (0.011%). This clearly indicates that the lens is capable of much stronger changes in back vertex power than those measured during electric-field stimulation. These drug induced changes, however, are presumably also accompanied by backward movements of the lens that do not occur in the intact eye.

In spite of this, our measurements of changes in back vertex power provide evidence for the role that the iris muscle plays in lenticular accommodation. The fact that there is such a small change in lens power once the iris has been removed argues strongly in favor of a direct iris-mediated mechanism of lenticular accommodation. The small changes in back vertex power that occur after the iris has been removed might be attributed to two causes. First, the posterior ciliary muscle is attached to the *pars plana* of the ciliary body and so the ciliary muscle pulls the ciliary body towards the lens during accommodation. This would relieve the outward tension on the ciliary body and permit the lens to ball up slightly under its own elasticity. Second, it is possible that the iris was incompletely removed, leaving some fibers intact to act directly on the lens. Beer (1893) observed Purkinje images on the lenses of hawk eyes during electrical stimulation. He noted that movements of the Purkinje images persisted even after the iris had been removed and concluded from this that the iris could not be involved in lenticular accommodation. Our own findings show that small changes in lens power do still occur in the chick eye even after the iris has been removed. These changes are presumably due to the action of the posterior ciliary muscle on the lens. It is likely that the lens movements that Beer (1893) observed were those movements caused by to the action of the still intact ciliary muscles.

We have seen that electric-field stimulation causes increases in the curvature of the lens even after the pectinate ligament has been cut. From his observations of hawk eyes, Beer (1893) stated that lenticular changes could no longer be induced after the pectinate ligament had been cut. He concluded that the pectinate ligament maintained the lens in its flattened, unaccommodated state and that a contraction of the ciliary muscles released this tension and allowed the lens to ball up. This is similar

to the mechanism described for the mammalian eye, where the zonula fibers and Müller's muscle work synergistically during accommodation. Given the morphological differences between chick and raptor eyes, it is possible that, in the hawk eye, the pectinate ligament is responsible for holding the lens flattened in its unaccommodated state. In the chick eye, however, the pectinate ligament is stretched during accommodation and our measurements show that it serves to hold the lens forward in the eye. Our sequential dissections also show that the lens is maintained in its flattened state primarily by the tension of the ciliary body. In the chick eye, a contraction of the posterior ciliary muscle does release some of the resting tension that the ciliary body imposes on the lens. This is in accord with Beer's (1893) observation on the hawk eye, but is only of secondary importance to the accommodative role played by the iris muscle.

The apparent contradiction between Beer's (1893) findings and our own most likely represents species differences in the accommodative mechanism. Although we have done a comprehensive study of the accommodative mechanism of the chick eye, the extent to which this mechanism can be applied to other bird species is unclear because of the extreme diversity of bird eyes. Hess believed that the accommodative mechanism was the same among different bird species, and that only the extent of accommodation differed. However, it is now well known that aquatic birds have a substantially greater range of accommodation than terrestrial birds, and that they must rely on lenticular accommodation more than terrestrial birds (Sivak, 1980; Sivak *et al.*, 1985; Goodge, 1960). Terrestrial birds have been shown to have corneal accommodation (Beer, 1893; Schaeffel & Howland, 1987; Troilo & Wallman, 1987; Glasser *et al.*, 1994) which would serve no function in aquatic birds (Sivak, 1980). The iris musculature is extraordinarily diverse between different bird species (Goodge, 1960; Oehme, 1969; Sivak & Vrablic, 1982). The owl iris, for example, has none of the peripheral circumferential muscle fibers (Oehme, 1969; Oliphant, Johnson, Murphy & Howland, 1983) that provide the major force of lenticular accommodation in chicks. The apparent absence of lenticular accommodation in the English sparrow (Slonaker, 1918), the widely varying morphology of various bird eyes (Lord, 1956; Rochon-Duvigneaud, 1943), the diversity of habitats, and visual requirements of birds all suggest that the accommodative mechanism in bird eyes may vary more widely than Hess (1912) and others had previously considered.

SUMMARY

We have presented the first demonstration of an active role of the chick iris in lenticular accommodation. In sharp contrast to previous reports (Suburo & Marcantoni, 1983; West *et al.*, 1991), our evidence supports the observation, first made by Müller (1857) in the hawk eye, that the peripheral muscle fibers of the iris are primarily responsible for lenticular accommodation. We have shown that a contraction of these fibers imparts an axially directed force to the ciliary processes that lie against the anterior equatorial surface of the lens. The ciliary processes, which lie on the annular pad of the lens, are actively squeezed by the peripheral muscle fibers of the iris to increase the curvature of the anterior and posterior surfaces of the lens. The role of the ciliary muscle, formerly thought to be the primary muscle involved in changing the curvature of the lens, has been shown to play only a minor secondary role.

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