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Title The gross and microscopic structure of the hamster eye with special reference to accommodation

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Gross and histologic studies were made of the hamster eye and of its adnexa. The structure was found to resemble in general the eye of most mammals. An extensive cornea and strategic placement of pigment give it a striking brilliance. The greater portion of the orbit is filled with a bulky, bilobed Harderian gland. Lacrimal and Meibomian glands are as commonly described.

Dioptric features are those of an accommodating eye. Ciliary processes are well developed but a diminutive ciliary muscle was noted. The muscle cells are slightly atypical and few in number and lack an obvious functional arrangement. The lens is of moderate size and centrally located. A circular pupil is capable of changing its diameter. Retinal composition is that of a seeing eye but is probably adapted scotopically. No cones were recognized and neither macula lutea nor fovea centralis is present.

Insertion of the extrinsic ocular muscles of Mesocricetus auratus is not via the classic tendon. No smooth muscle or structure of the cardiac type is present in the region of the insertions. Other modifications that could serve as involuntary contractile elements associated with these muscles were sought but nothing was found. Recti and oblique muscles were not differentiated structurally from the retractor bulbi muscle.

Various mechanisms of accommodation are discussed with particular emphasis on the scheme of Dr. William Bates. Innervation studies are reviewed as they apply to involuntary activity of the extrinsic musculature.

It was concluded that although rodents in general are said to not accommodate, all necessary structures are present in the hamster. It must be assumed, however, that if accommodation is dependant upon precise and definite activity of the ciliary musculature this faculty is limited.

THE GROSS AND MICROSCOPIC STRUCTURE OF THE HAMSTER EYE WITH SPECIAL REFERENCE TO ACCOMMODATION

by

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THE GROSS AND MICROSCOPIC STRUCTURE OF THE HAMSTER EYE WITH SPECIAL REFERENCE TO ACCOMMODATION

INTRODUCTION

The question of accommodation by the vertebrate eye is not settled. The ability to adjust for near and far vision has been ascribed to certain structures and modifications thereof, and presence or absence of the same has been the criterion by which individual groups of animals have been judged to possess or lack this sense-ability. Departing from the classic explanations, Dr. William Bates in 1918 assigned accommodative function to the extrinsic eye muscles and postulated the presence of involuntary contractile elements to be found associated with the striated musculature by means of which bulbar distortion could be produced (6, p.5). According to his hypothesis then, focusin for near and far vision would resemble in a dynamic manner the pathologic conditions known as myopia and hypermetropia which are known to be the result of an elongation or shortening of the eyeball beyond the normal range (2, p.37).

It is said (23, p.686) that rodents in general are not able to accommodate. Mesocricetus was investigated for three reasons: 1) to establish the gross and microscopic morphologyof the ocular apparatus in preparation for accommodation studies, 2) to determine whether the classic features designated as being necessary for accommodation are present and, 3) to note whether any structural modifications of the extrinsic musculature exist and, if so, whether by their nature they could so affect vision.

MATERIALS AND METHODS

Mature hamsters, many past breeding prime, were observed in various ways. Eight heads were preserved in formalin for binocular dissection. Three skulls were prepared. A variety of staining techniques were attempted. <u>In vitam</u> methylene blue according to Hines (7, p.9), Guyer (14, p.255) and modifications of both for nerve endings produced no satisfactory results. In every instance the animals were killed rapidly with ether. Injection of the warm dye solution was made through the conus, carotid artery or especially through the left ventricle. The postcaval vein and the aorta were ligated and the jugulars slit for drainage. Guyer's method was modified to 30 minutes in 1:100 methylene blue following rapid excision of the orbital contents, two hours in saline in an open Petri followed by fixation for 24 hours in picrate solution. The prparations exhibited a confusing pattern of nuclear contents stained blue but no certain nerve terminations. The Hines technique for the rabbit was repeated and varied; methylene blue concentrations to 1:100 and 1:1000, time reduction up to 75% for each step, and employing an isotonic carrier rather than a hypertonic solution of the dye. Injection time and quantity of solution were also varied depending upon reaction of the individual subject.

The gold chloride method of Cole (5, p.240) for motor end plates was the most successful of the nerve preparations. His schedule for the rat was used without modifcation. The entire ocular contents was treated and following the alcohol-glycerine step the muscles were dissected off using a binocular dissecting microscope, and were either mounted entire in glycerine, dehydrated and made into permanent whole mounts, or imbedded in paraffin and sectioen at 5, 12, or 28 microns.

Twenty-four eyes were fixed in Bouin's, Zenker's, or formalin and sectioned. Mallory and hematoxylin-eosin stains were used generally. Some attempts were made to stain nerve endings using a direct albumen method ($AgNO_3$) but the preparations were unreliable. Muscle-tendon transition should have been demonstrated in borax carmine-picric acid preparations. Eleven complete series sectioned in various planes and at different thicknesses were examined.

Live studies were made on the hamsters of the Department of Zoology of Oregon State College and on several pet animals from different sources. No distnction was made between male and female animals.

One technique deserves special mention. In an attempt to determine whether or not the hamster is able to change the shape of his eyeball under relatively normal conditions, i.e. without direct faradic or chemical stimulation of the adjacent nervous or contractile tissue, photographs were taken following deep etherization of the test animal. A series of ten snaps at 1-2 minute intervals were taken, the first while the animal was completely relaxed by the ether and subsequent shots during recovery. Restoration of muscle tonus was ascribed to the third minute because the bulbus was retracted following release of pressure in the temporal region, whereas previously the eyeball had remained extruded. Also, constriction of the palpebrae behind the protruding bulbus was perceptible in subsequent manipulations. Measurements of the cornea (all of which was exposed), limbus diameter and depth from the anterior margin of the cornea to the limbus were made from the prints. No distortion of the bulbus could be noted.

This method is accompanied by certain obvious fallacies. A stationery set-up is not possible with a conscious animal so that positioning and focusin pose real problems. Although almost the entire cornea is exposed when the palpebrae are parted normally the sclera shows rarely and then only at the angle of the eyelids. To secure ppints of reference and to insure including the entire cornea the eye is readily popped out of its socket by gentle pressure posterior and ventral to it. This protruded position is abnormal and account must be taken of not only the pull of the extrinsic eye muscles proper but also of the pressure of a stretched retractor bulbi pulling from its extensive, multiple insertions just posterior to the equator of the bulbus. Considering only the mechanical aspects of the situation it is apparent that such pull could distort the bulbus into an egg-shape rather than a spheroid figure, a phenomenon which should be ascertainable from corneal measurements.

No drugs other than the anesthesia were used in this study (see later for miotic effects). It was supposed that any normal change of shape of which the eye were capable could be detected in the transition from the relaxed to the aroused condition.

OBSERVATIONS

The prominence of the hamster eye is not a function of its large relative size but is rather due to an interplay of factors, the most notable of which is the placement of pigmentation. Heavy distribution of pigment on the smooth free borders of the palpebrae with gradual recession toward both lateral and medial canthi give an illusion of roundness to the exposed portion of the cornea, when in reality the palpebral fissure is only biconvex in outline. Occasionally patches of blue-white sclera are visible in the temporal canthus when the animal is disturbed and so moves his eye. In general, however, only cornea can be seen.

Within the medial canthus a splotchily pigmented, triangular caruncula lacrimalis is situated, within the conjunctival sac. Measuring 1.5mm along each side, one base is shaped to the nictitating membrane and is applied to it between its midline and lateral edge. Hairs occurring in no apparent pattern or relationship to the pigment spots direct their free ends toward the medial canthus.

Cilia along the "external" border of pigment at the edge of the palpebrae are not striking and actually are shorter than body hairs in general and are uniformly black. On the superior eyelid the cilia occur in regular arrangement with a dorsal sweep; those on the inferior lids are shorter and less orderly.

A prominent nictitating membrane lies within the nasal canthus, its center bearing a small pigmented protuberance on its anterior surface. Actually located medially in that the caruncle placed at the junction of the two palpebrae is located between the protuberance and lateral border of the third eyelid it is seen to be heavily pigmented on its distal border with the pigment diminishing progressively toward the proximal portion. The structure measures ca. 2 mm across its rectangular form and is supported by quite an extensive cartilage rod. Folds of conjunctiva which cover it taper off on either side of the rectangle and thus surround about a third of the eyeball, forming the plica semilunaris.

The skin of the hamster head is easily removed for observation of the relationship of the eye to the other cephalic structures. Upon removing likewise a tough fascia which extends from the superior lids to insert dorsally on the fascia of the head muscles a finer, more delicate connective tissue membrane is seen. This is deflected ventrally so that it formas a capsule around the lacrimal gland and the vein lying above it, serving as a carrier for the lacrimal ducts (seven or more) leading from the gland to their openings in the upper lid. A strong attachment to the orbital process of the frontal bone at a deeper level conveys a branch of the blood vessel to a foramen leading into the brainbox.

Fitting snugly in an angle formed by the supraorbital ridge and the bulky temporalis muscle the lacrimal gland possesses contours adapted entirel to its surroundings. Rounded on the dorsal surface and viewed from that angle it measures 9 mm along its antero-posterior axis and seldom achieves a thickness beyond 0.6-1 mm. As it approaches the bulbus it conforms to it, sending a process laterally and one medially and directed into the orbit proper a distance of 3 mm, exhibiting here a width of 7 mm. Essentially a convex-concave form persists. The series of ducts emanate from the antero-medial portion.

Puncta lacrimalia occur on each eyelid, one easily located on the external margin of the upper eyelid, the other lying internal to the edge of the inferior palpebra on the opposite side of the lacrimal lake at the level of the caruncle. Pigment is present around the punctum but it diminishes in intensity within the duct. The duct aperture itself measures ca 0.4 x 0.3 mm. After traveling anteriorly 2 mm the ducts of a single eye converge abruptly and enter the base of a large triangular shaped papilla which is hollow and has a single opening directed into the nasolacrimal duct. At this level a slight enlargement of the duct forms the lacrimal sac. This duct is flattened laterally. The walls are tough and are not collapsed in preserved specimens. A pocket in the maxillary bone with a posteriorly directed opening accommodates the duct. Dorso-ventral measurements show a diminution of 2 to 1 mm absolute size in its anterior progress. Curving medially 3-4 mm anterior to the medial canthus the duct enters the ventral meatus of the turbinate system and opens finally in its extreme anterior portion.

Before a discussion of the ocular sockets contents can be entertained the boundaries of this socket must be circumscribed as they occur _in situ_.

Just under the skin dorsal boundaries are well defined. Framing the eyeball and its attached structures on the posterior sector is the lacrimal gland, laterally the zygomatic arch, anteriorly the 60 degree angle formed by the zygomatic arch, and medially the frontal bone. Walls of the socket consist of the masseter muscle extending ventrally from the zygomatic arch, the temporalis filling the posterior and postero-lateral margins (both inserting on medial portions of the mandible) and cranium medially. The anterior angle is open essentially in that here the naso-lacrimal duct passes from the region of the nasal canthus to its opening in the maxilla, bypassing the lacrimal bone which is loosely attached to the dorso-anterior region of the orbit. A flattened muscle originating on the dorso-lateral margin of the maxilla and also inserting on the mandible, effects a 90 degree turn as it passes over the zygomatic arch and directs its fibers more laterally than posteriorly, morphologically associating with the arch as a chain to a pulley. Ventrally the orbital contents become closely apposed to the buccal walls, associated facial muscles and the mandible.

However, very little association of the eye proper and its immediate adnexa occurs with the above "basket". Palpebral fasciae serve to suspend the bulbus in this cavity. The tunica conjunctiva palpebrarum forms the inner lining of the lid which, from the fornix conjunctivae is deflected over the corneal surface as the tunica conjunctiva bulbi. In the medial canthus a fold of the conjunctiva serves as the outer layer of the plica semilunaris. A lesser fold is noted in histological section between the plica and the tunica conjunctiva bulbi which is not supported by cartilage. The Harderian gland opens adjacent to this fold. Within the socket the ocular structures are also isolated from immediate association with their environment. Originating from the limbus conjunctiva the periorbita completely encapsulates the posterior hemisphere of the bulbus and the eye's muscles and nerves. This sac is of variable thickness. It appears elastic because, while exhibiting no tension _in situ_, it rolls when its attachments are severed. All ocular accessories are accompanied to their entrance into the orbit by this sheath. The infraorbital nerve trunk as such is not included but is rather covered dorsally by the periorbita penetrated by branches of the nerve to the eye.

Entry of the optic nerve into the orbit is through a large circular foramen in the orbital process of the presphenoid. Postero-lateral to the foramen is the larger opening of a tunnel formed by frontal, palatine, basisphenoid and presphenoid processes through which the infraorbital nerve travels from the brainbox.

An excessively bulky, bilobed Harderian gland occupies the greater portion of the orbit. It is closely applied to the bulbus in the region of the limbus and extends the length of the eye socket. Enclosing the inferior, external and internal recti almost completely, the lateral, major lobe of the gland is 4 mm across its anterior margin and 5 mm long, tapering into a triangular shape. The lesser lobe occupies the medial portion of the socket, is also triangular (2 mm/side), and overlies the anterior portion of the superior rectus. A single duct carries the secretion peripherally into the conjunctival sac. The mouth of the duct is adjacent to the nictitating membrane. Secreting epithelium is simple columnar constituted in a compound tubular pattern. A high secretory state was observed in every gland as judged from the abundance of granules and vacuoles. The secretion appears to be merocrine.

Types of mechanical accessories are as generally described for mammals. A retractor bulbi muscle of relatively extensive mass is prominent. Originating on the orbital process of the presphenoid just posterior to the optic foramen the retractor approaches the bulbus partially spiraled in a counter-clockwise direction (as viewed from the posterior aspect) around the optic nerve, and inserts at four points alternating with the recti insertions but in a more posterior latitude. Just postero-dorsal to the optic foramen is the origin of the superior rectus. This muscle is about 20% longer than the remaining three recti which originate as a single trunk antero-ventral to the optic foramen. A broad, flat inferior oblique travels laterally in an equatorial direction just posterior to the limbus from its origin lateral to the nasolacrimal duct on the zygomatic process of the maxilla. This muscle, as well as the superior oblique, is found external to the Harderian gland and just under the periorbital sac. The superior oblique originates on the orbital process of the frontal bone approximately in the center of the median wall of the orbit. It proceeds directly dorsally to the limbus where it makes an abrupt right angle turn toward the bulbus over the anterior margin of the lesser lobe of the Harderian gland. Contacting the scleral coat the muscle is directed equatorially for a short distance before inserting posterior to and at right angles with the superior rectus. No trochlea, either fibrous or cartilaginous is apparent.

Measurements were made of excised eyes which had been preserved in Bouin's and formalin. External length of the eye is 5 mm and the greatest diameter 5.2 mm. The cornea occupies almost the entire anterior hemisphere, being about 2.2 mm in depth. Its diameter is 4.7 mm. The hamster eye is acorn shaped like that of the chinchilla.

A fibrous capsule of Tenon envelopes the eye without including the Harderian gland or other adnexa. The extrinsic musculature travels through it and through a region of loosely organized connective tissue in which are frequently found fat deposits. Here is provided a socket in which the eye might be freely rotated.

The sclera is composed of dense connective tissue whose collagenous fibers are arranged in an orderly pattern conforming to the bulbar contours. The extrinsic muscle fibers follow this same direction for a short distance before terminating on the periphery of the scleral layer.

The cornea is constituted as for mammals in general. The epithelium is stratified squamous 4 to 6 layers deep. Beneath this layer is a structureless lamella which stains deeply with eosin (Bowman's membrane). A substantia propria about 40 microns deep is composed of a regular connective tissue which shows an inter-lacing of fibers. These appear grossly to form a continuous network rather than a collection of unassociated fibers. A membrane of Descemet is present which takes no stain in the above preparations but rather is amber colored and appears homogeneous. Internal to this is a single layer of epithelial cells difficult to make out in most sections.

The uvea is heavily pigmented. Pigment is also found in lesser amounts in the lamina fusca of the sclera and is continued into the ciliary body, ciliary processes and iris. An occasional ligh-staining cell could be seen which resembled those found in the ciliary body. No tapetum is present in the hamster.

The ciliary apparatus, exclusive of the muscle, is well developed. Extensive groupings of processes resemble strongly the human condition. More than 160 finger-like processes were counted. These are covered by simple cuboidal epithelium containing pigment in its proximal area. Dense pigment fills the stroma which is permeated with blood vessels extending to the far end of each process. In the ciliary body proper was sought indication of a smooth muscle system. Cells which stained differently from the surrounding connective tissue cells occurred among the pigment cells of the ciliary body. In H&E preparations these cells took a light blue color. Their nuclei are relatively large and elongate (Fig.2). The cellular outlines are not distinct and fibers of collagenous appearance are interspersed among the cells. No apparent order exists in their distribution unless it be an inclination towards a radial dispersion. Their position at least predisposes one to interpret them as being related to ciliary muscle. And, indeed, they seem to represent atypical involuntary smooth muscle cells, perhaps primitive, perhaps degenerate.

The iris of Mesocricetus is black with a heavy complement of pigment. Occasionally cells resembling those of an epithelium and which stained a pale blue with H&E stains could be seen but their borders could not be defined precisely. Most notable is the presence of a prodigious quantity of blood vessels. At least a third of the volume of the organ is made up of blood sinuses.

In a group of seven week old animals killed rapidly with ether and whose eyes were then fixed in Bouin's, the diameter of the pupillary aperture averaged 2.6 mm with a range of 2.2-2.9 mm. A study of live animals showed that whether dilated or constricted the pupil is circular. Variation in size was induced through topical administration of certain drugs. Two 100 watt lamps at a distance of 12 inches were used to observe the pupillary changes and in this strong illumination the opening was seen to be 0.8-1.0 mm in diameter. Two drops of 0.1% atropine were applied to the right eye. Within five minutes the pupil had opened to somewhat less than 2 mm, the left (control) eye remaining as before. After fifteen minutes both apertures measured 2.5 mm and reached a maximum dilation of 3 mm by 30 minutes after application of the atropine. A slight decrease in diameter was observed shortly after applying a 0.1% solution of pilocarpine to the right eye of another animal. Apliaction of pilocarpine powder to the cornea likewise induced a pupillary constriction. Atropine reversed this situation when placed on this experimental eye. An attempt to stimulate a contraction of the superior oblique muscle by the intraorbital injection of a drop of 0.1% adrenalin in another animal led to the observation that the opposite pupil constricted markedly while the eye receiving the drug showed no change in that respect.

The wave length of light producing maximum efficiency or response in the human eye is 0.5550 microns (24, p.642). It is said (23, p.256) that the optimal diameter of a (pin-hole) aperture is equal to twice the square root of the product of the screen distance and the wave length of light. If the hamster eye were to respond similarly to the human eye the optimal aperture of his eye should be 0.7968 mm. This figure is based on screen distance being that distance from the pupil to the fundic portion of the retina.

As far as could be determined at the magnification available the visual layer of the retian contains only rods. These contain cylindroids of pigment in their basal portions. Neither macula lutea nor fovea centralis is present. In the fundic region of the retina up to 12 layers are seen in the outer nuclear layer but in general only seven to eight rows of nuclei are found. Two to three rows constitute the inner nuclear layer, while the ganglion cells form a single incomplete row which is frequently interrupted by blood vessels. (Fig. 6)

These blood vessels are branches of arteries and veins which have entered with the optic nerve. Pigment is found surrounding their trunks as deep as the ganglion layer. All retinal layers are represented at the visual margins, i.e. on either side of the blind spot and approaching the pars ciliaris retinae but there is a diminution in extent of the plexiform layers especially, and a gradual loss in depth of the nuclear layers.

Eyes which had been fixed in Bouin's were enucleated and measurements made of the lenses. These were spheroids flattened antero-posteriorly to a diameter of 2.8 mm in this plane. Equatorial diameters ranged from 3.2-3.8 mm, averaging 3.5 mm. In specimens so prepared the lens is seen to occupy approximately 23% of the bulbar volume. A circular pattern of adhering pigment about 2.3 mm in diameter was noted anterior to the lens equator and appeared to be a portion of the iris. This was not present in the formalin fixed preparations. In all fixed specimens the lens was clear, amber-colored and showed longitudinal striae. It was firm and easily handled, while in fresh specimens it was soft and difficult to remove. All histological sections were made of aphakic eyes. In these sections no zona ciliaris was noted. The position of the lens is approximately central in the living eye being bounded anteriorly and posteriorly by non-living structures. The absence of direct contact with the cornea eliminates the possibility of corneal influence in any shift in lens position that might occur.

This study was first undertaken as a search for involuntary contractile elements which might be found at the insertion of the extrinsic eye muscles. Neither smooth muscle nor muscle of the cardiac type is present (Fig.4). The extrinsic eye muscles insert without a tendon (tendon here being defined in the classic sense, i.e. a structure containing closely packed, parallel collagenous bundles the cells of which are arranged in long parallel rows between these bundles (22, p.71).[1] Having passed through the capsule of Tenon they approach the bulbus directly. The muscle fibers may then course parallel with the scleral fibers for a short distance before ending in a rounded or conical margin. Their sheaths become continuous with the peripheral layers of the sclera. Cross-striations persist up to this very abrupt termination. These insertions are spread over a large portion of the sclera and are always in apposition to it rather than being dispersed in the space of Tenon. The retractor bulbi muscle follows the same general pattern with its multiple insertions.

No obvious division into thick and thin fibers could be made. In squash preparations mounted in glycerine fiber

[1] Barber (1, p.6) defines tendon as "The argyrophilic fibrillae which intervene between the muscle fiber and the collagenous elements of its insertion."

diameters ranged from 25 to 49 microns with a well distributed series between these margins. Recti and oblique muscles were not differentiated in this respect from the retractor. Many fibers could be traced for almost the entire length of the muscle. Anastomosis of fibers and a spiral configuration were not seen. No staining for argyrophilic or elastic fibers was attempted.

In vitam staining for nerve endings was not successful. Gold chloride preparations showed nicely the distribution of nerve fibers to and within the muscles. These nerves enter in a trunk whose volume is at least half that of the muscle at this point and are then dispersed to the individual muscle fibers. Finally, the nerve fibers terminate without any structural modification that might be called an end-plate. Judgment on this point must be reserved pending confirmation by another method. That the ocular muscles carry a heavy complement of innervation is certain. Whether the peculiar endings described for certain other vertebrates are present is not known, nor can we determine from these preparations whether the fibers are medullated or not. Muscle spindles are not present in the eye muscles of *Mesocricetus*.

DISCUSSION

Mechanical means of adjusting directly for vision at near and far points are not necessary for a range of vision in two instances. Depth of focus may be achieved on a tilt-retina as in the horse (23, p.254) so that objects at varying distances may be viewed simultaneously, or the object may be brought into sharp focus by raising or lowering the head. The other alternative is elongation of the visual cells so that rays focused in a series of planes are interpreted with equal clarity (23, p.254).

At least four major mechanisms for accommodation are postulated for vertebrates. The simplest is contraction of the pupil to a stenopaic aperture, a narrow slit. This condition holds in the chinchilla (9, p.138) who apparently possesses no other structure capable of visual adaptation. Diminution in aperture increases the depth of focus, which is then expressed in centimeters difference between the maximum nearness and distance which an object may be shifted and still be interpreted on the retina with no blur (8, p. 238).

An alteration in corneal diameter of two to three millimeters was reported for the pigeon by Gundlach, Chard and Skahew (13, p.30) which may account for accommodation up to 15 diopters! These contour changes were measured using a "very old style ophthalmometer" (13, p.29).

Contraction of the ciliary muscle (Crampton's and Brucke's) pulls against the cornea and sclera. Muller's muscle[2] acts as a tightening doughnut around the base of the cornea and through its pull on the scleral ossicle forces an increase in intraocular pressure to sharpen the curvature of the cornea. Corneal refraction is thus greatly increased. Young (as cited in Duke-Elder, 10, p.753) immersed the eye in water so that corneal refraction was eliminated and found that accommodation was not effected.

The majority of modern investigators place the greatest emphasis on the lens. In certain vertebrates below mammals the lens is known to shift in position (23, p.272; 13,p.41). For mammals in general since the time of Descartes (1637) changes in lens shape have been postulated (10, p.753). Observations summarized by Davson (8, p. 242) prove its plasticity. During accommodation, i.e. adjustment for near vision, it is seen to lose the fine wrinkles found at the equator in non-accommodated eyes and to be tremulous "as though its normal suspension had been relaxed". The explanation for this is that the contraction of the meridional ciliary muscle fibers drag the ciliary body forward while the circular fibers reduce the circle which they describe thus reducing tension on the zonule. As the tension on the lens equator is eliminated the lens

[2] This is not the same Muller's muscle of mammals (23,p.272)

rounds up and in consequence exerts greater converging power. Hypermetropic changes were produced in cats and dogs by Layton and coworkers (21, p.568) by injection of solutions of various tonicity into the vitreous. Amyl nitrate (a vasodilator) diminishes the effect and adrenalin or stimulation of the cervical sympathetic supply enhances the effect of the injection. They conclude (21, p.570) that the flattening of the lens is the direct result of increased tension of the zonule fibers which are put on the stretch by the shrinking toward the sclera of the ciliary body in consequence of the contraction of its blood vessels and diminution of its volume.

The fourth structural adaptation for visual accommodation is contained within the extrinsic musculature and may exert force to distort the entire bulbus. This was suggested in 1697 by Sturm, Listing (1851) subscribed to it (10, p. 753), and in 1918 Dr. William Bates reformulated the idea. A current histology text (22, p. 602) states that not only is intraocular pressure a factor influencing bulbar shape but the "additional deformation is produced by the pressure of the several extrinsic eye muscels." In this regard recent work by Bennati and Isola (3, pp.147-158) seems applicable. From an abstract of their work it is noted that they injected intravenously acetyl choline and adrenaline and found that the former produced contraction of one external rectus and inhibition of the same muscle of the other side. The inferior rectus also was stimulated and its antagonist inhibited. The adrenaline caused the superior oblique muscle to contract.

Thomas Young attempted to prove in 1801 that no elongation of the eyeball could occur by the following experiment: he placed a ring at the inner angle of the orbit pressing against the globe and a second at the outer angle exerting pressure on the sclera over the macular region. The pressure of the latter stimulates the retina and produces a bright spot in the field of vision. But on strong accommodation neither of the rings was displaced nor did the pressure image alter (10, p. 753).

Citing from Bates' work Hauser (15, p.8) notes that "Dr. Bates...discovered and proved that it is not the crystalline lens but the six external muscles that act upon the eyeball and give the eye its ability to adjust and accommodate." This statement is substantiated by the fact that aphakic human eyes may accommodate. And Corbett (6, p.5) further elaborates: "Dr. Bates further established that we have no control over these changes in shape of the eyeball to accommodate for vision at the near or far point, since they are brought about by the involuntary muscles...because each involuntary muscle is actually an extension of one of the long muscles attached to the outside of the eyeball."

Strain to see at a distance produces myopia, according to Bates (2, p.38). This occurs only in animals with two active oblique muscles because "animals in which one of these muscles is absent or rudimentary are unable to elongate the eyeball under any circumstance." Similarly, an eye, straining to see at the near point becomes flatter in one or all meridions (2, p.37). Experimentally he found that accommodation could not be paralyzed unless the atropine reached the oblique muscles, "the real muscles of accommodation" (2, p.17). Without inhibiting the recti muscles in the same manner, electrical stimulation of the eyeball produced hypermetropia.

The mammalian extrinsic ocular muscles are decidedly different from mammalian skeletal muscle. Irvine (19, p.851) noted that many of the peculiar characteristics of these muscles are typical of skeletal muscles of reptiles and amphibians. The muscle fibers are relatively small in diameter. Two types of fibers within a muscle may be differentiated: those rich in sarcoplasm, dark, and containing many nuclei; and fibers relatively poor in sarcoplasm. A division into thick and thin fibers in a single muscle is reported generally (27, p.218, 17, p.11, et al). Barber (1, p.9), working with the lateral rectus of common forms representing all six classes of vertebrates, found little or no elastic tissue with Verhoef's stain. Three fiber patterns were noted by Thulin (19, p.849) in his work with man and monkeys. First, that in some muscles there were bundles of fibrillae running irregularly. In other instances a regular arrangement of fibers rich in sarcoplasm but with relatively few bundles were seen and these had likewise special nerve endings. Thulin saw, especially at the origin end of some of his muscle preparations, that some of the fibrillae were long and circled the muscle hypolemmally. An interlacing of fibers as in the heart and a characteristic small diameter are also reported. A variation in structure along the length of the extraocular muscles of the rabbit was noted by Hines (17, pp.12,13). She found the largest fibers together with the smallest myofibrils and fine cross-striations in the origin third. Large fibers showing coarse striation were characteristic of the insertion two-thirds, while in the final third of the muscle were found smaller fibers that were not continuous with the larger, and which stained darkly with methylene blue.

Neither observations of the hamster eye muscles nor a survey of the literature offers data to add credence to the postulates of Bates. While a great many specific peculiarities observed in the eye muscles of certain mammals do not seem to be of general application yet there is a notable lack of any allusion to involuntary muscle which might be a part of or associated with the extrinsic eye musculature. Although Dr. Bates does not present a tabulation of his data in his book, Better Eyesight Without Glasses, his text implies that his information was largely secured through the single objective method of retinoscopy

(2, p.9). Histologic evidence is not reported.

An autonomic control of these muscles would be an alternative. Two particularly exhaustive coverages of the innervation of the extraocular muscles are worthy of attention. In 1927 Hines concluded from a survey of work done to that time that sympathetic innervation for some skeletal muscles at least may exist but "without anything assigned for it to do" (16, p.175). Five types of nerve terminations together with subdivisions of some were worked out and classified by Hines for the extrinsic eye muscles of the rabbit. Removal of the superior and inferior cervical ganglia together with their fibers produced no change in these nerve endings, and cutting of the oculomotor nerve just at its exit from the brain caused degeneration of all endings but hose on the blood vessels (a combination of the two operations producing degeneration of all nerves to the muscles) (17, p.38). She is inclined to doubt the sympathetic innervation of muscle fibers on the basis of her own observations. It is interesting that she further postulates a primitiveness for the extrinsic eye muscles. She says: "In the mammal this abundance of innervation seems to be characteristic of aberrant muscles - muscles which may have remained primitive - muscles which do not move bony structures" (17, p.35).

The question of double innervation of the extrinsic eye muscles was dealt with authoritatively by Woollard in

1927 (26, p.498). He employed normal mammals, mammals suffering from deficiency diseases, cats with the abdominal sympathetic chain out on one side and cats with the ventral roots of the lumbosacral plexus divided on one side. His conclusions are as follows: "In the ocular muscles two distinct fibers were observed, one the ordinary medullated nerve fiber with the typical motor terminal plate, the other a non-medullated fiber ending in a grape-like termination. Each kind of fiber was distributed to a separate muscle fiber. The muscle fibers were easily distinguished as thick and thin, the thin being associated with the non-medullated fibers. These non-medullated fibers are in the light of the experimental results of Sherrington and Boeke believed to be sympathetic fibers. Comparison with Dogiels description and figures suggest that they have nothing to do with the sensory fibers in the eye muscles." From his own experimental work Woollard (27, p.222) rather attributes to these non-medullated fibers a sensory function although different in arrangement from other sensory innervation elsewhere in the body.

Corbin and Oliver (7, p.184) traced the fibers supplying the insertion-third grape-like terminations to the brain stem of III and there found them intermingled with the motor fibers of the oculomotor nerve. The gold impregnation method of Hunter and Latham (18, p.36), using hens and goats, led them to conclude that the muscle fibers were divided into separate bundles served respectively by branches from the somatic and sympathetic nervous systems, the former subserving contractile and the latter plastic tonus.

Woollard (27, p.218) wishes to discount the primitiveness of the eye muscles and consider them rather highly specialized in order to have a philosophical basis for supposing a valuable proprioceptive function for some of the peculiar end organs. Yet Irvine and Ludvigh (20, p.1049) found proprioceptive sense lacking in the exrinsic eye muscles upon applying the usual criteria, namely: 1) histologic and anatomic evidence, 2) vibration sense, 3) myotatic reflexes, and 4) position sense.

Two techniques, in vitam methylene blue and gold chloride are used quite consistantly in nerve-muscle studies, and were especially notéd in work reviewed for this paper. Discrepancies in the literature and the inconclusiveness of the situation to date may therefore be attributed to the great amount of variation among mammalian ocular structures which makes for unreliable generalizations and interpretive fallacies.

SUMMARY AND CONCLUSIONS

1. The structure of the eye of Mesocricetus auratus resembles generally that of most mammals.
2. Dioptric features are those of accommodating animals.
3. Cells of possibly contractile nature were noted in the ciliary body but division into discrete acting groups was not possible.
4. Zonule fibers were not seen.
5. Retinal composition is that of a seeing eye. Cones are probably absent. Neither macula lutea nor fovea centralis is present.
6. The pupil is circular and capable of changing its diameter.
7. Insertion of the extrinsic eye muscles is not via the classic tendon. Involuntary muscle cells of smooth or cardiac type are not found in the region of extraocular muscle insertion.
8. No association with the cornea or any retractor muscle is possible for the lens.

Although rodents in general are said to not accommodate the necessary apparatus is seen to be present in the hamster. If accommodation is dependant upon a well-developed ciliary musculature it will need to be assumed that this faculty is limited. Whether or not autonomic innervation is supplied to the extrinsic eye muscle fibers remains to be determined.

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Explanation of Figures

Fig.1. Ciliary apparatus. (100X, 5u sec., H&E stain)

Fig.2. Ciliary muscle. (430X, 5u sec., H&E stain)

Fig.3. Cross section of approaching insertion of extrinsic ocular muscle. (430X, 7u sec., H&E stain)

Fig.4. Longitudinal section of extraocular muscle insertion. (430X, 7u sec., H&E stain)

Fig.5. Extraocular muscle insertion, whole mount. (50X, squash prep., gold chloride-formic acid stain)

Fig.6. Retina. (100X, 5u sec., H&E stain)

Key to figure code

I - iris

CP - ciliary process

CM - ciliary muscle

S - sclera

R - retina

EM - extraocular muscle

N - nucleus of ciliary muscle cell

G - ganglion cell layer

IN - inner nuclear layer

ON - outer nuclear layer

RDS - rods

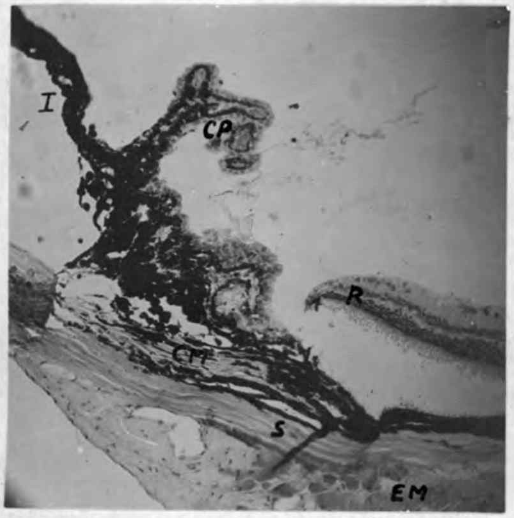

FIG. 1

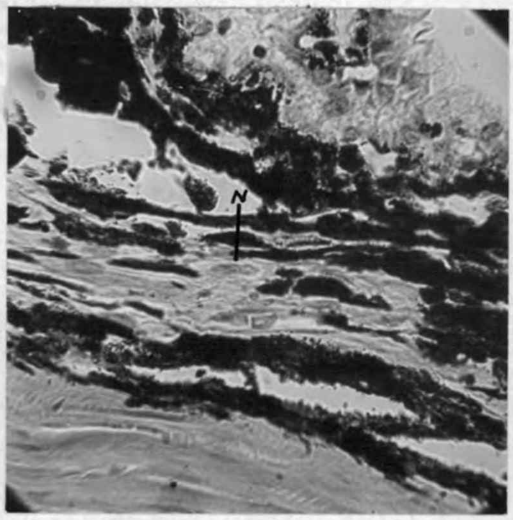

FIG. 2

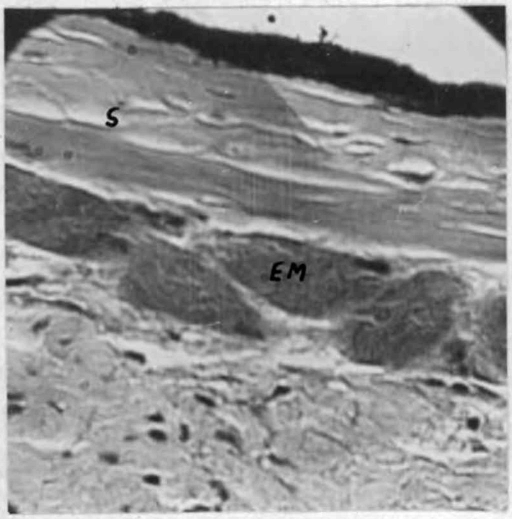

FIG. 3

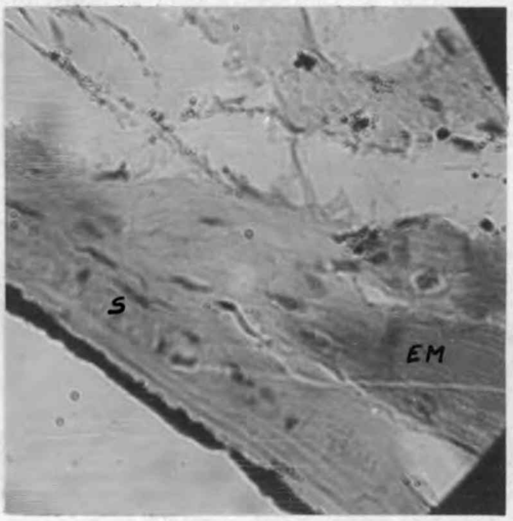

FIG. 4

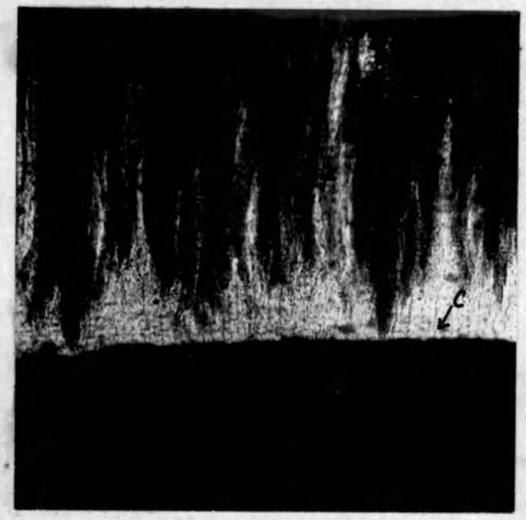

FIG. 5

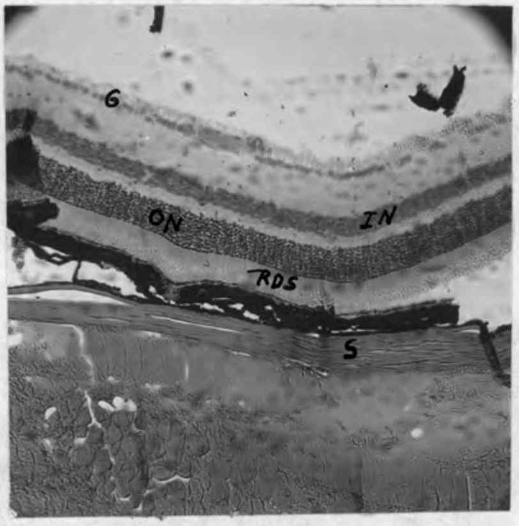

FIG. 6