ELASTICITY OF TISSUES INVOLVED IN ACCOMMODATION

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Abstract—Uniaxial loading of human lens, zonules, ciliary muscle, and choroid shows a nonlinear relationship between stress and deformation of the specimen, and hysteresis on unloading. Spring constants, at 10% elongation, have been calculated for all specimens and for several combinations. Except for zonules they are significantly correlated with age. They will provide a basis for a model of accommodation. The mean force required for 10% elongation of the lens, at mean age 43, is about 22 × greater than for the zonules; and the mean elongation of the zonules is nearly 7 × that of the lens at a load of 0.01 N (∼ 1 g). Ranges of forces and pressures in the accommodated and nonaccommodated eye are estimated.

Accommodation   Elasticity   Lens   Lens capsule   Zonules   Choroid   Ciliary muscle

INTRODUCTION

Four structures are involved in accommodation: the lens, zonules, ciliary muscle and choroid. For an ultimate mechanical model it is necessary to know the force-displacement relations for each of these tissues, as well as the force exerted by the ciliary muscle.

The geometric arrangements of these four structures is indeed a complicated one, particularly for an experimental determination of their individual mechanical properties. The zonules are extremely thin, too thin to be clamped. The spherical shape of the lens, in a frontal plane, obviates simple experiments of a "standard" nature. Choroid and ciliary muscle are delicate and hard to cut into strips of uniform width.

More than a century after Helmholtz's (1856) famous study of lens changes during accommodation, it is still not clear why the changes in shape or movement of the posterior capsule are presumably minor compared to the much thicker anterior capsule. The role of the lens substance in accommodation is also unclear. O'Neill and Doyle (1968) in their theoretical studies (based on data from a diagrammatic sketch by Helmholtz, 1856) considered the lens to be a liquid-filled membrane, with the liquid serving only to provide an interior pressure resisting the capsule. Koretz and Handelman (1982) on the other hand assumed in their model that the entire lens was a solid elastic structure, with no distinction between the capsule and its contents. Since both studies consider only the anterior portion of the lens, and contain no reliable experimental data about even the order of magnitude of the material constants, a quantitative evaluation of their models is impossible.

In an effort to provide some measure of the physical properties of the lens, Fisher (1971) determined Young's modulus (E) of elasticity of human lens by spinning the lenses around the anterior–posterior polar axis. These measurements however required mechanical models to allow for material property evaluation. In the spinning experiment, for example, the model consisted of a series of rotating concentric rings, each generating circumferential stresses to resist the centrifugal forces generated by the spinning. Such a model is not capable of differentiating between the properties of the capsule and those of the lens substance; it is a two-dimensional thin disk model of a very three-dimensional body. In spite of these criticisms, these experiments are certainly the most sophisticated which have been performed for determining the material properties. That the numbers can be

criticized shows the difficulty of the problems facing experimenters.*

To provide further data on the elasticity of lens and zonules we deduced estimates from uniaxial stress–strain measurements on isolated specimen by loading the specimen in one direction (see Figs 1 and 2). We also include estimates for the elasticity of choroid and ciliary muscle.

The reason for loading lens and zonules uniaxially is firstly that their anatomical relations remain intact with an initial radial orientation of zonules when the lens is suspended at zero load. This does mean that on loading, there will be a slight loss of radial orientation but with a strong degree of compensation as pointed out later. Secondly, we are able to measure elasticity of lens and zonules simultaneously under the same load, which is important and not possible under any other conditions we know of. We cannot claim that the numbers obtained for the material constants will provide a specific value exact to x digits; but we do claim that our experiments provide order of magnitude estimates of material properties for structures of the eye involved in accommodation.

METHODS

Human eyes were enucleated and used for experiments within 24 hr after death. The test specimen is clamped at both ends for strips of choroid and ciliary muscle; and at 12 and 6 o'clock for CLC, CC and ZLZ specimens (Fig. 1). The lens alone is glued to a holder (see direct lens loadings). Some eyes were used for multiple tissue measurements, e.g. for "lens alone" and for choroid or ciliary muscle.

Loading of the specimen is done in a tension machine described elsewhere (Graebel & van Alphen, 1977). Essentially, the top clamp of the test specimen is attached to a transducer and the bottom clamp to an arm, descending or ascending at a speed of 0.9 mm/min, driven by a screw connected to a timing motor. The output is recorded on a Grass 7C polygraph. The change of length of the specimen is directly proportional to the time scale. The clamps were redesigned from the original description into simple pinching devices for easier manipulation,

with beaks 10 mm wide and 6 mm high. The Grass force displacement transducer (FT03) carrying the top clamp was made vertically adjustable by a rack and pinion to simplify attaching the specimen to the lower clamp.

The mounted specimen is submerged in a saline bath with flat walls to prevent optical distortion. Photographs of the specimen were taken at the beginning and end of loading and unloading as well as at intermediate intervals. The magnification is found from the size of the beaks or other attachment devices. To isolate various components that might affect lens or zonule strain, three types of test specimen were employed: CLC, CC and ZLZ, see Fig. 1.

CLC specimens

The ciliary body with pars plana, lens and zonules is *en bloc* excised from the eye. The top clamp is placed at the pars plana at 12 o'clock and connected to the transducer. The specimen is then lowered by means of the rack and pinion into the bottom clamp which is fixed to the apparatus. Length–tension curves were recorded during both loading and unloading (Fig. 2).

CC specimens (loading the ciliary body without lens)

After an initial loading–unloading experiment was run on a CLC specimen, the lens was removed by cutting the zonules with the specimen still between clamps. A similar loading–unloading experiment was then run on the CC specimen to find the effect of the lens plus zonules on the CLC system.

In additional experiments the lens was excised from the *loaded* CLC specimen. The machine was stopped and the lens removed under tensile forces varying between 2.5 and 6.7 g to estimate the value of the ZLZ spring.
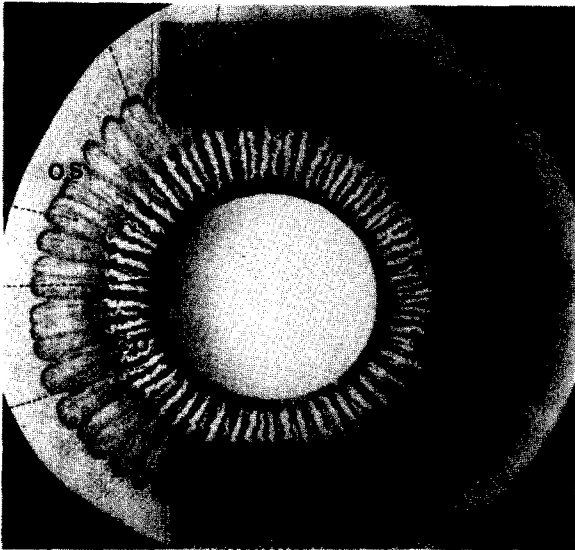
ZLZ specimens

The ciliary body was cut with scissors at the 3 and 9 o'clock positions when the specimen was unloaded, to avoid damaging lens capsule or zonula fibers. The results allow direct estimates for the spring constant (and the Young's modulus) of lens and zonula fibers.

Direct lens loadings

The equator of the lens was glued with methacrylate to a copper ring segment from 10 to 2 o'clock. The ring has a profile with a radius
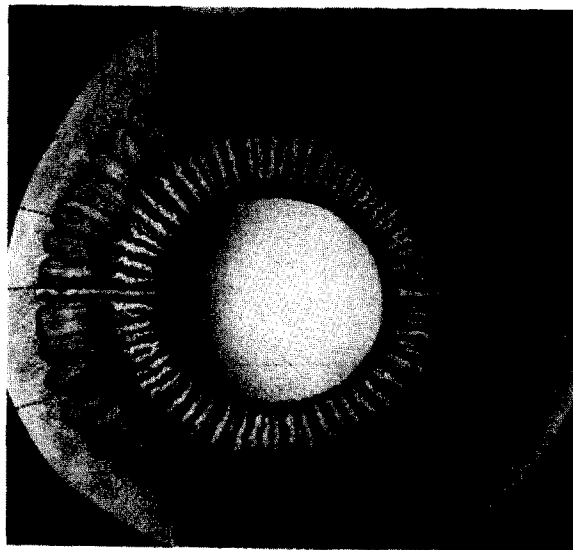
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*Fisher (1977) also measured the tensile force on the zonules, applied indirectly through the ciliary body. By subsequent spinning of the lens, he related dioptric power to lens profile and lens profile to zonular force.

CLC
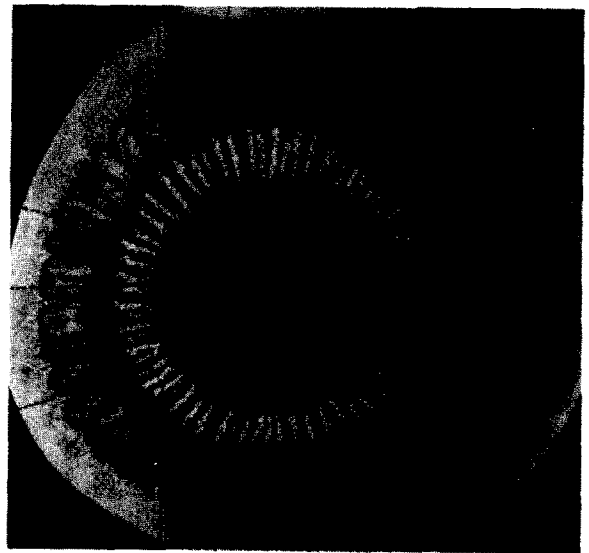
CC

ZLZ

Fig. 1. Three specimens viewed from the vitreous side. CLC: clamps are placed at 12 and 6 o'clock just behind the ciliary processes (cp). The clamp at 12 o'clock is hooked up to a force displacement transducer (T) and the clamp at 6 o'clock to a lever, descending or ascending at a rate of 0.9 mm/min. The ora serrata (os) is clearly visible. In CC specimens the lens has been removed at zero force after an initial run of the original CLC specimen. In ZLZ specimens the ciliary body is cut at 3 and 9 o'clock with or without an initial run of the CLC specimen.
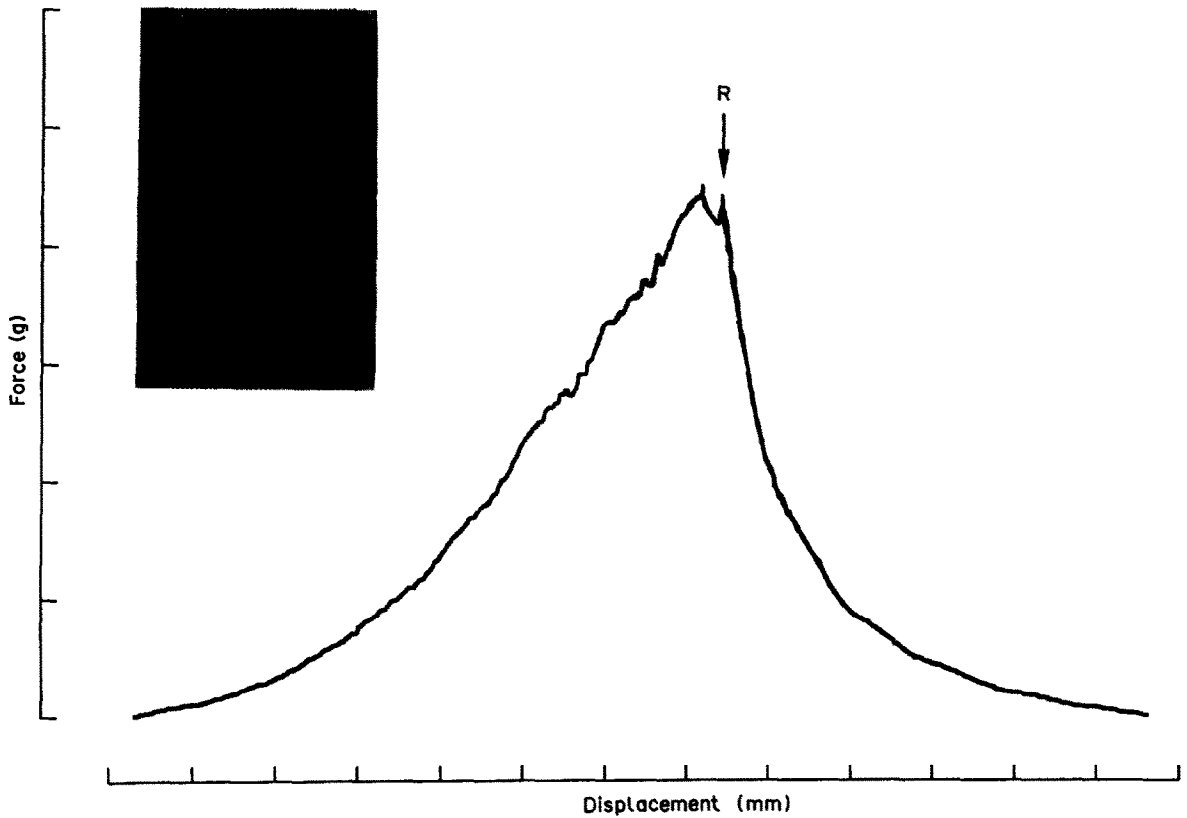
Fig. 2. Length–tension recording of a CLC specimen showing hysteresis after reversal of force at R. Abscissa: displacement, units of 1 mm; ordinate: force, units of 1 g (0.01 N); inset—C, ciliary muscle; Z, zonules (in between cil. proc.); L, lens; S, spring constant. In terms of elasticity, a CLC specimen is essentially a system of springs: three springs in series (ZLZ) and two in parallel (C, C). By cutting the two CC springs we find the spring constants of the ZLZ system; by taking out the lens we find S'_{CC}.

of 12 mm to fit the anterior and a radius of 6 mm to fit the posterior lens surface. Glueing was done in a horizontal plane on a glass plate by drying the equator of the lens with filter paper and touching the lens to the methacrylate in the groove of the holder. After 1 min the bond is firm enough to attach the holder in a vertical position to the transducer. The specimen was then lowered by rack and pinion onto a second methacrylate-containing holder at 6 o'clock. After another minute, loading machine and lens were submerged in saline and loading-unloading experiments were conducted. In other experiments the lens poles were glued to plastic discs (dia. = 7 mm) to stress the lens along an anterior–posterior polar axis. Both methods allow for direct estimates of the spring constant of the lens.

Choroidal strips were cut in a meridional or equatorial plane. Meridional choroidal strips were cut running over the posterior pole, and equatorial strips excised behind and parallel to the equator. Strips were cut using a double knife, with parallel blades set 5 mm apart, to make a nonpenetrating incision of the sclera. Penetration into the vitreous was done by scissors. Clamps were placed at both ends of the sclera-choroid strip, which was then attached to the loading machine. In the unloaded position the sclera was cut midway between clamps. The procedure ensured a flat preparation of uniform width, as well as a reliable measurement of its unstretched length.

Ciliary muscle strips were cut in a meridional or equatorial plane. Longitudinal ciliary muscle strips were also cut with the double knife, the incision extending into the cornea. A suture was inserted at the limbus and attached to the transducer, and a clamp was placed just behind the ciliary processes. For equatorial strips the muscle was disinserted from the scleral spur, and cut parallel to the limbus just behind the ciliary processes. Clamps were placed at both ends.

Reliability of measurements. All measurements were made on enlarged photographs (2.7–3.6×) to the nearest 0.5 mm. Magnification was determined by measuring either beak width or length. One series of measurements was accidentally duplicated, thus providing a double mask trial for accuracy. No difference was found in 98 of the 146 measurements. Differences of ±0.5 mm were about equally divided and were present 15× on 56 beaks (28 upper and 28 lower); 9× on 32 beak distances;

and 22× on 58 lens measurements (29 lengths and 29 widths). There was a difference of 1 mm on one lens measurement and a difference of 1.5 mm on one beak distance measurement.

Determination of spring constants. Length-tension (loading–unloading) curves for eye tissues are nonlinear, (and spring "constants" are not constants) but after a certain minimum load is reached the curves become linear when plotted on log–log scales. This minimum load may be needed to straighten out any structural fibers in the tissue, and corresponds to elongations (el.) of about 10%. It might also be related to tension inherent to all living tissues and a prerequisite for smooth muscle tonus and contraction. Ciliary muscle strips of 5×12 mm for example need a tension of 250–300 mg force for optimal contraction (van Alphen, 1961, 1976; van Alphen, Kern & Robinette, 1965) and such precontraction tensions also elongate the muscle by about 10%. We have used test results at and above 10% elongation, as we believe that loadings below 10% el. are below the physiologic range of interest. It is difficult to demonstrate this conclusively by experiments, because in dissecting specimens any original stretch is lost. However, since all incisions will gape it seems to be a reasonable assumption.

Length–tension curves were fitted in this load regime by a power law:

$$F = C\left(\frac{\Delta l}{l_0}\right)^A, \quad (\Delta l = l - l_0). \qquad (1)$$

Here F is the force, $\Delta l/l_0$ the relative extension and C and A are two parameters to be estimated.

The power parameter A was determined from the log–log plots by measuring the slope of each curve. The C's were found using the A's together with equation (1) and the measured load at 10% elongation. Those loads are the total loads applied over the 10 mm width of the beaks.

Since the relationship (1) between force and elongation is nonlinear, the concept of a spring constant is not uniquely defined. One possibility is to use S', where:

$$S' = \frac{F}{\Delta l} = \frac{C}{l_0}\left(\frac{\Delta l}{l_c}\right)^{A-1}. \qquad (2)$$

The total force is then $S' \times \Delta l/l_0$, where S' is the value at a given load and $\Delta l/l_0$ is the total elongation. For a mechanical model of accommodation of the eye, one is more likely to use a spring constant to predict, at a given load,

what additional change of length will result from a (presumed small) change of force. For this definition (tangent modulus) the spring constant is:

$$S = \mathrm{d}F/\mathrm{d}(\Delta l) = A\frac{C}{l_0}\left(\frac{\Delta l}{l_0}\right)^{A-1} = AS'. \quad (3)$$

For small changes in force about a given value, S is the appropriate spring constant. For large changes, it is necessary to resort to equation (2). It is the S' value which we report throughout as the spring constant. A Young's modulus could be obtained from either concept, by multiplying the appropriate spring constant by a length divided by the cross-sectional area. Mean values for l_0, A, S and C are given in Appendix II.

All of the values of spring constants reported here are based on 10% el. This is done because (a) the nonlinear portion of the curve (on a log–log plot) exists only for very small elongations, (b) for all but very small elongations, the log–log plots are linear up to at least 10% el. Therefore the 10% el. provides a valid comparison value, (c) upon unloading and repeated loading, the curves repeat themselves suggesting that even a 10% el. could be a valid extension of the physiologic range. However, it may well be that any single value of strain will not be in the physiologic range for all four structures we consider. To convert our spring constant to one appropriate for a given structure where the per cent elongation is p, say, the conversion is:

$$S_p = S_{10}(p/10)^{A-1}. \quad (4)$$

RESULTS

CLC specimens (n = 13). Loading and unloading the ciliary body–lens–ciliary body

An example of length–tension curves of CLC specimens is shown in Fig. 2. These curves are nonlinear and show hysteresis, since the descending branch is steeper than the ascending one; the hysteresis has not been included in the data or in the calculations. On loading, the lens gradually changes in shape from circular to ellipsoidal on frontal view; the load necessary to deform the lens is clearly higher in the older eye (Figs 3 and 4). Loading and unloading have been repeated occasionally as much as three times; the length–tension recordings as well as the photographs are found to be highly reproducible. On loading, the ciliary processes of the lens are being elongated and pulled away from

Table 1. Mean spring constants of CLC and CC; of CLC and ZLZ; and of ciliary muscle and choroid. Unit: dyne for 10% elongation

	S'	σ_{n-1}	n	Age
1. CLC	319	190		
			13	46.0
CC (lens removed)	154	75		
2. CLC	237	57		
			6	53.0
ZLZ (ciliary body cut)	142	38		
3. Ciliary muscle (m + eq)	283	237	17	46.2
meridional (m)	320	243	10	49.8
equatorial (eq)	230	235	7	41.1
4. Choroid (m + eq)	262	180	21	35.4
meridional (m)	255	208	10	32.2
equatorial (eq)	270	161	11	38.4

the lens periphery. The pupil also changes in shape from circular to ellipsoid and vice versa. The effect of the elasticity of the iris was ignored in the calculations.

CC specimens (n = 13)

After removal of the lens, length–tension curves of CC specimens are similar to those of CLC specimens, but ascending and descending limbs of the curves are steeper. The spring constants of CC specimens are expectedly lower than those of the corresponding CLC specimens (means in Table 1). The difference between means of 165 dynes should approach the spring constant of the lens (see below). Both CLC and CC length–tension curves are linear when using log–log coordinates at forces greater than 500 dynes (Fig. 6); at smaller forces the data deviate from the regression line, usually to the left, probably due to the uncertainty of the 0-point (see Discussion).

Removal of the lens from *loaded* CLC preparations causes a fall in tension. Cutting the top zonules from three loaded CLC specimen caused a mean 58% fall of transducer force; and cutting the remaining zonules produced a further mean fall of 18% for a total mean fall of 76% ($n = 3$). When the whole lens is excised, at loads varying between 2.5 and 6.7 g, mean tension falls 77% ($n = 17$); and when the fall in tension is plotted against the load, a line going through origin at a slope of 0.77 proves to be an excellent fit. There is an effect of age since most lenses older than 45 yr are above, and younger lenses are below the regression line, but due to the high correlation ($r = 0.81$) its effect must be moderate. Since the ZLZ spring carries 77% of the load, the 2 CC springs in parallel will carry 23%.
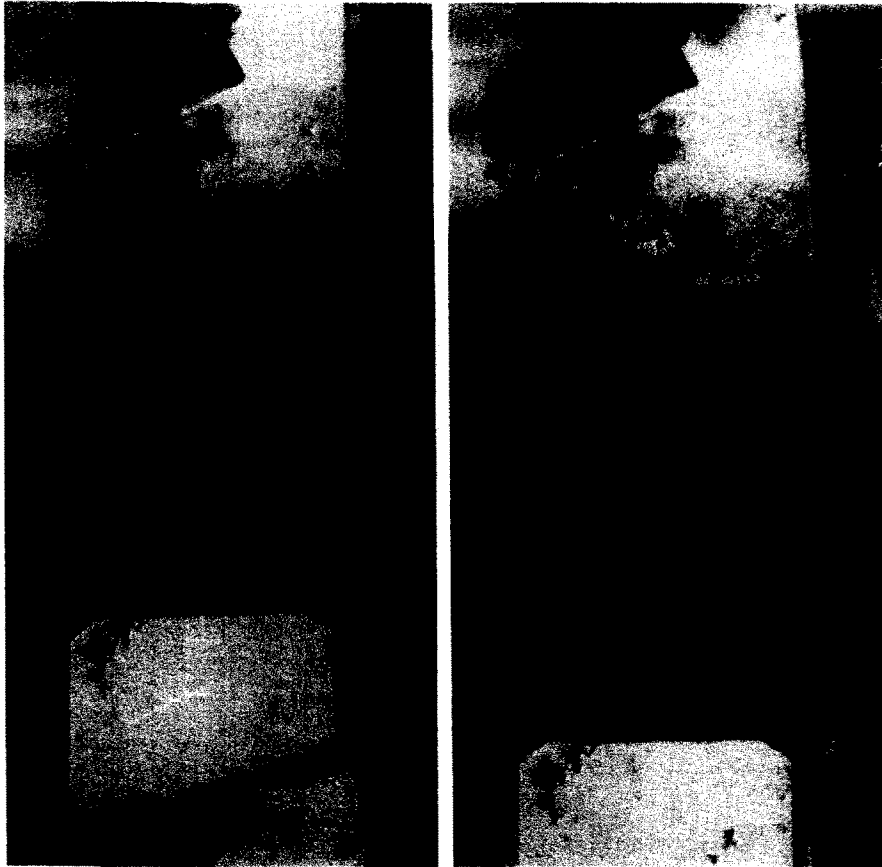
Fig. 3. Uniaxial loading of a CLC specimen (43-yr-old eye) showing ellipsoidal deformation of lens and pupil and elongation of the ciliary processes. Note the near radial direction of these processes.
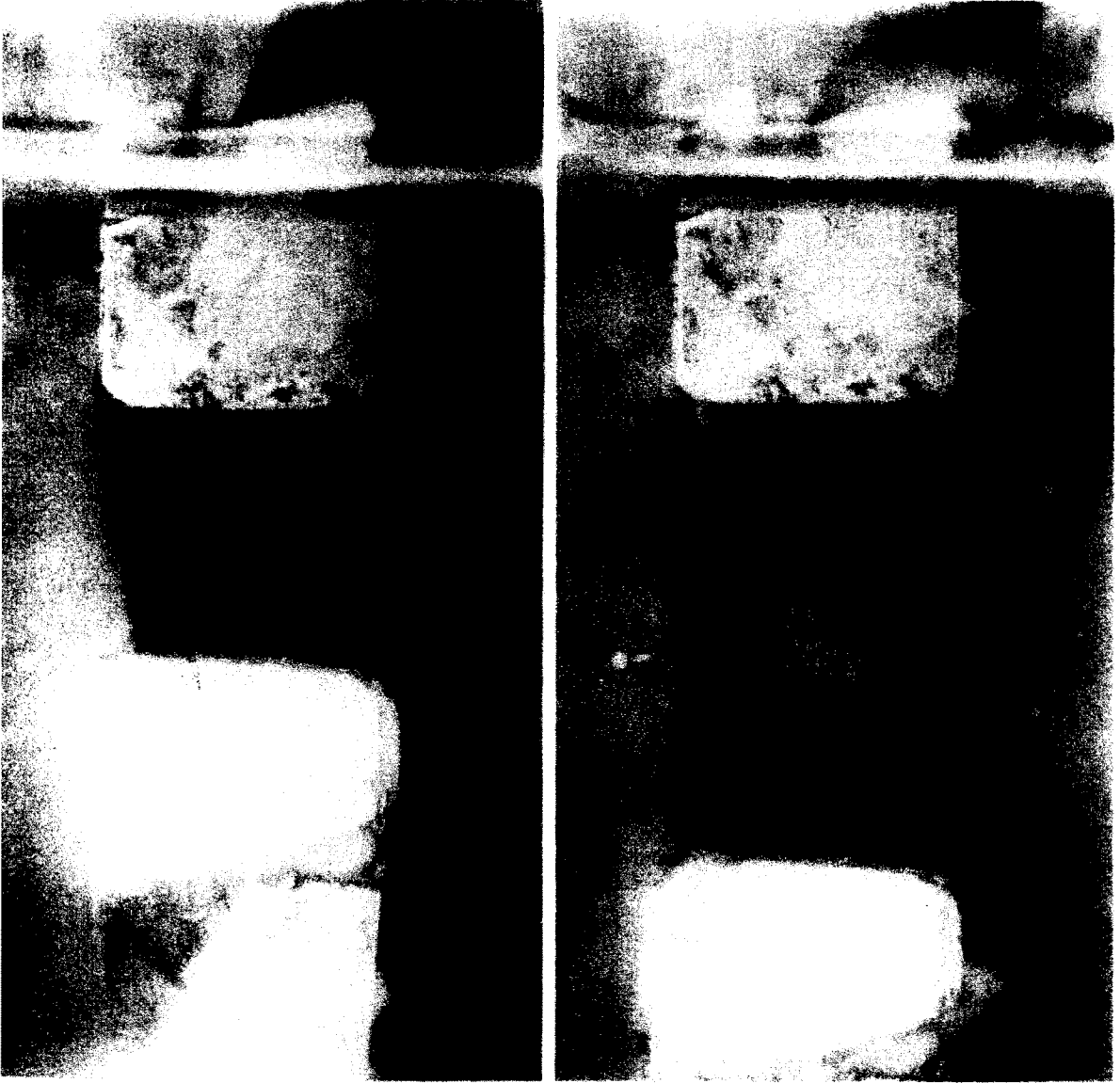
Fig. 4. Uniaxial loading of a CLC specimen (1-day-old eye). Compared to Fig. 3 there is much greater deformation of the lens at one-third the force.
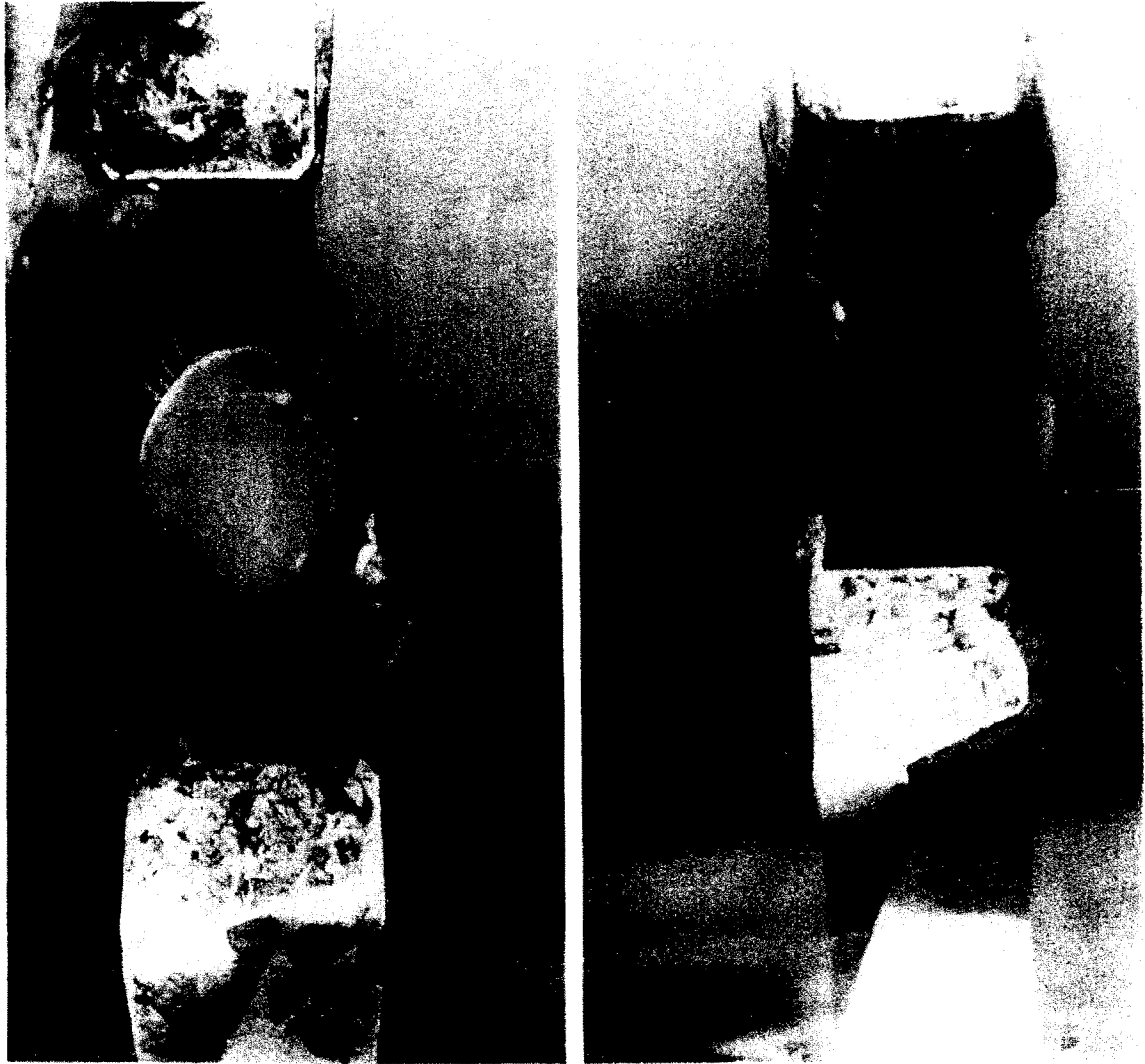
Fig. 5. Left: uniaxial loading of a ZLZ specimen (38-yr-old eye), showing large deformation of the lens. Since the ciliary body has been cut at 3 and at 9 o'clock, the force on the lens is transmitted solely by the zonules. Right: CC specimen—the specimen of Fig. 3 after removal of the lens and uniaxial loading.
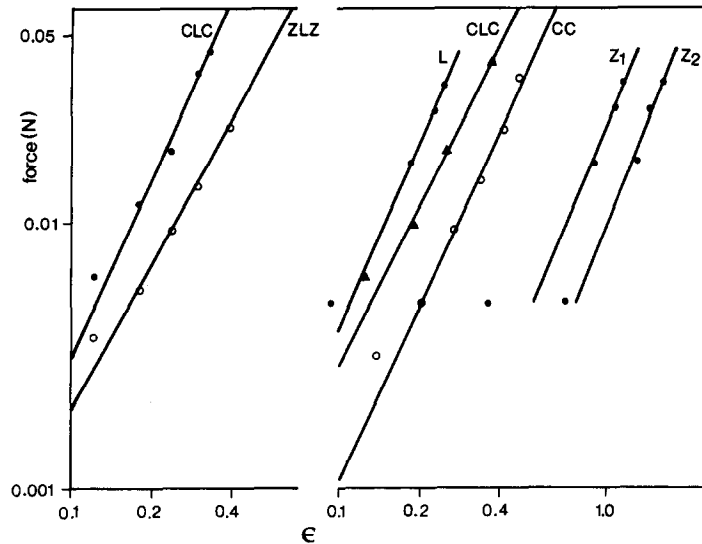
Fig. 6. Relations between log(force) and log(relative elongation) are linear at forces greater than 0.005 N (500 mg). Left: CLC before and ZLZ after cutting the ciliary body. Right: CLC, lens (L) and zonules (Z_1, Z_2) before and (CC) after removal of the lens. Regression lines of CLC, ZLZ and CLC, CC are obtained from whole preparations; those of L, Z_1 and Z_2 from measurements in CLC or ZLZ preparations.

CLC and ZLZ (zonula–lens–zonula) specimens (n = 6)

After cutting the ciliary body horizontally at 9 and 3 o'clock, length–tension curves on loading and unloading are flatter than before cuts, but the deformation of the lens is similar to the deformation seen in CLC specimens (see Fig. 5). Each ZLZ specimen has a lower spring constant than the original CLC (mean values are given in Table 1). The mean ZLZ value of 142 dynes for 10% elongation is rather close to the estimated ZLZ value resulting from $S'_{CLC} - S'_{CC} = S'_{ZLZ} = 319 - 154 = 165$. Since each pair (CLC–CC) of data is from the same specimen, these values are strictly comparable.

ZLZ specimens (n = 16)

To make a clean estimate of the elasticity of lens and zonules, and to reduce the risk of zonular rupture, another series of ZLZ specimen was run without preliminary loading of the original CLC.

Elasticity of the lens

When the ciliary body has been cut at 3 and 9 o'clock, traction on the lens at 12 and 6 o'clock is transmitted solely by the zonula fibers. When the vertical elongation of the lens $(l - l_0)/l_0$ of ZLZ specimen is plotted against force (N), regression lines are nonlinear; semi-log plots tend to linearity, and log–log plots are linear above forces of 500 dynes. An example is shown in Fig. 6. Data below

500 dynes usually deviate from linearity. The data for all specimens combined are plotted in Fig. 7 together with the corresponding
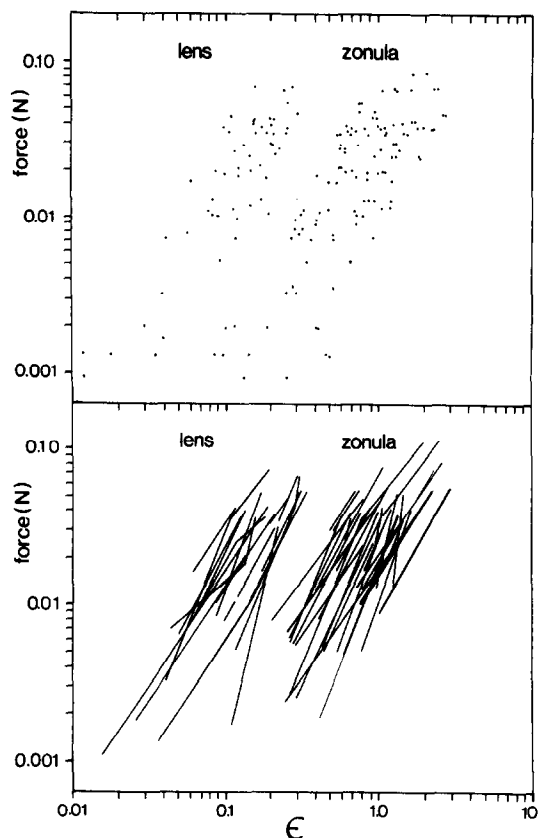

Fig. 7. Top: scattergram of log relative elongation $(l - l_0)/l_0$ of lens and zonula fibers of 16 ZLZ specimen. Bottom: best fit regression lines for each of the 16 specimens.

Table 2. Spring constants (S') and age for lens and zonules. Unit: dyne for 10% elongation

Age (yr):	0–1		2–39			40–70			0–70		
Spring constant mean age and n	$S' \pm \sigma_{n-1}$	n	$S' \pm \sigma_{n-1}$	Mean age	n	$S' \pm \sigma_{n-1}$	Mean age	n	$S' \pm \sigma_{n-1}$	Mean age	n
Lens alone, equat.	—	0	1230 ± 650	18.1	8	3650 ± 2270	49.2	9	2510 ± 2080	34.6	17
Lens alone, polar	—	0	1350 ± 800	27.3	3	2540 ± 240	48.0	2	1824 ± 677	35.6	5
Lens in ZLZ	—	0	1200 ± 730	16.5	4	1670 ± 1260	52.5	12	1560 ± 1150	43.5	16
Zon. in ZLZ	—	0	380 ± 320	16.5	8	650 ± 850	52.5	24	580 ± 750	43.5	32
Lens in CLC1[a]	490 ± 270[b]	7	1810 ± 1060	25.4	11	3550 ± 1620	49.5	20	2480 ± 1510	26.1[c]	38
Zon. in CLC[a]	460 ± 390[b]	14	900 ± 950	25.4	22	780 ± 940	49.5	40	760 ± 935	26.1[c]	76

[a]S'-values corrected for CC springs. [b]Ages: 1–3 days, $n = 5$; 1 yr, $n = 2$. [c]Mean age becomes 32.0 when excluding the seven items of age 0–1 yr in the first column.

regression lines. The regression lines were fitted by eye. The mean l_0 value of the lens is 9.26 mm ± 1.12 (SD).

Elasticity of the zonula fibers

In Fig. 6 the elongation of the upper (Z_1) and lower (Z_2) zonula fibers is plotted against force on a log–log scale for the same reasons as mentioned under elasticity of the lens; again deviations from linearity are present at forces below 500 mg. The regression lines of Z_1 and Z_2 are shown in Fig. 7. They were fitted by eye. The mean l_0 value for Z_1 is 2.7 mm; for Z_2 it is 3.0 mm. The slopes for Z_1 and Z_2 are nearly identical and have a correlation coefficient of 0.96; P_f values [force (N) required for 10% elongation] are also highly correlated ($r = 0.78$). There is no correlation between slopes nor between P_f values of lens and zonules. Spring constants are shown in Table 2.

Force and elongation of lens and zonules

Mean regression lines for lens and zonules in the ZLZ sample of Fig. 7, were determined by calculating the mean relative elongation at two levels of force: 0.01 and 0.1 N. We preferred this method since force is well defined while elongation is not; it not only depends on the stiffness of the specimen but also on age, hours after death and other (unknown) variables. The resulting mean regression lines have slopes and P_f values as shown in Table 4.

From these mean regression lines it follows that, at a load of 0.01 N, the mean elongation of the zonules (64%) is 6.7 × greater than that of the lens (9.5%); and the mean force required for 10% elongation of the lens (1.125 g) is 21.6 × greater than for 10% elongation of the zonules (0.052 g).

Earlier, we roughly estimated from Fig. 7 the forces required for 10% elongation of lens and zonules by drawing lines through the center and

Table 3. Pearson and Spearman rank correlation coefficients between age and spring constants (S') and between age and log S' for L(ens), Z(onules), choroid and ciliary M(uscle)

Tissue	Correlation:	Pearson			Spearman	
		r	p	n	r	p
L alone	Age–S'	0.73	0.001*	17	0.72	0.001*
L alone	Age–log S'	0.75	0.001*	17		
L in ZLZ	Age–S'	0.04	0.895	16	0.30	0.149
L in ZLZ	Age–log S'	0.04	0.906	16		
Z_1 in ZLZ	Age–S'	0.05	0.872	16	−0.08	0.397
Z_2 in ZLZ	Age–log S'	0.02	0.937	16	−0.13	0.328
L in CLC	Age–S'	0.69	0.000*	38	0.66	0.000*
L in CLC	Age–log S'	0.73	0.000*	38		
Z_1 in CLC	Age–S'	0.23	0.176	38	0.18	0.153
Z_2 in CLC	Age–log S'	0.19	0.265	38	0.14	0.207
Choroid	Age–S'	0.58	0.006*	21	0.59	0.002*
Choroid	Age–log S'	0.67	0.001*	21		
Ciliary M	Age–S'	0.40	0.141	17	0.49	0.023*
Ciliary M	Age–log S'	0.33	0.238	17		

r: Correlation coefficient; p: probability; * significant.
In all specimens, Z_1 refers to zonules at 12 o'clock and Z_2 to zonules at 6 o'clock.
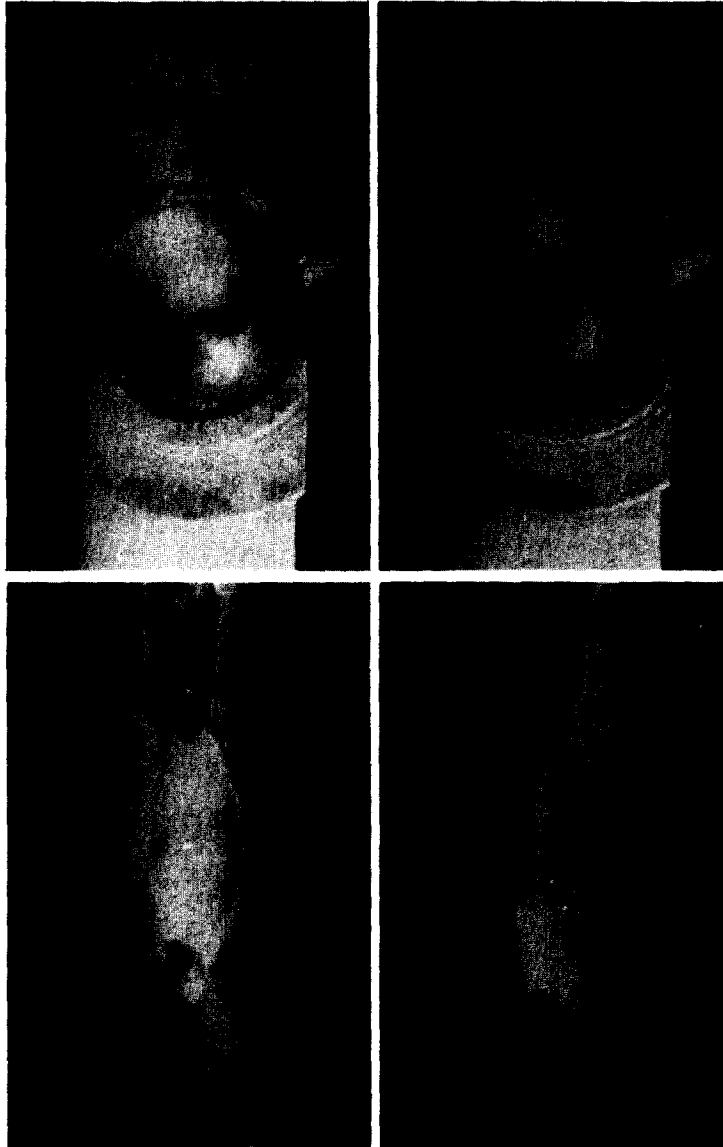
Fig. 8. Direct loading of the lens at the equator. Front view: lens deformation from circle to ellipse (upper). Side view: both anterior and posterior surfaces of the lens flatten on loading. Posterior surfaces are on the right.

Fig. 9. Uniaxial loading of a 5 mm wide choroidal strip after cutting the sclera horizontally (upper); and loading of a 5 mm wide ciliary muscle strip, excised in a frontal plane, parallel to the limbus (lower). The vessels of the ciliary processes are perpendicular to the (vertical) direction of force and will not be stretched on loading. Strips on the left are unloaded; strips on the right are loaded at 2.5 g force.

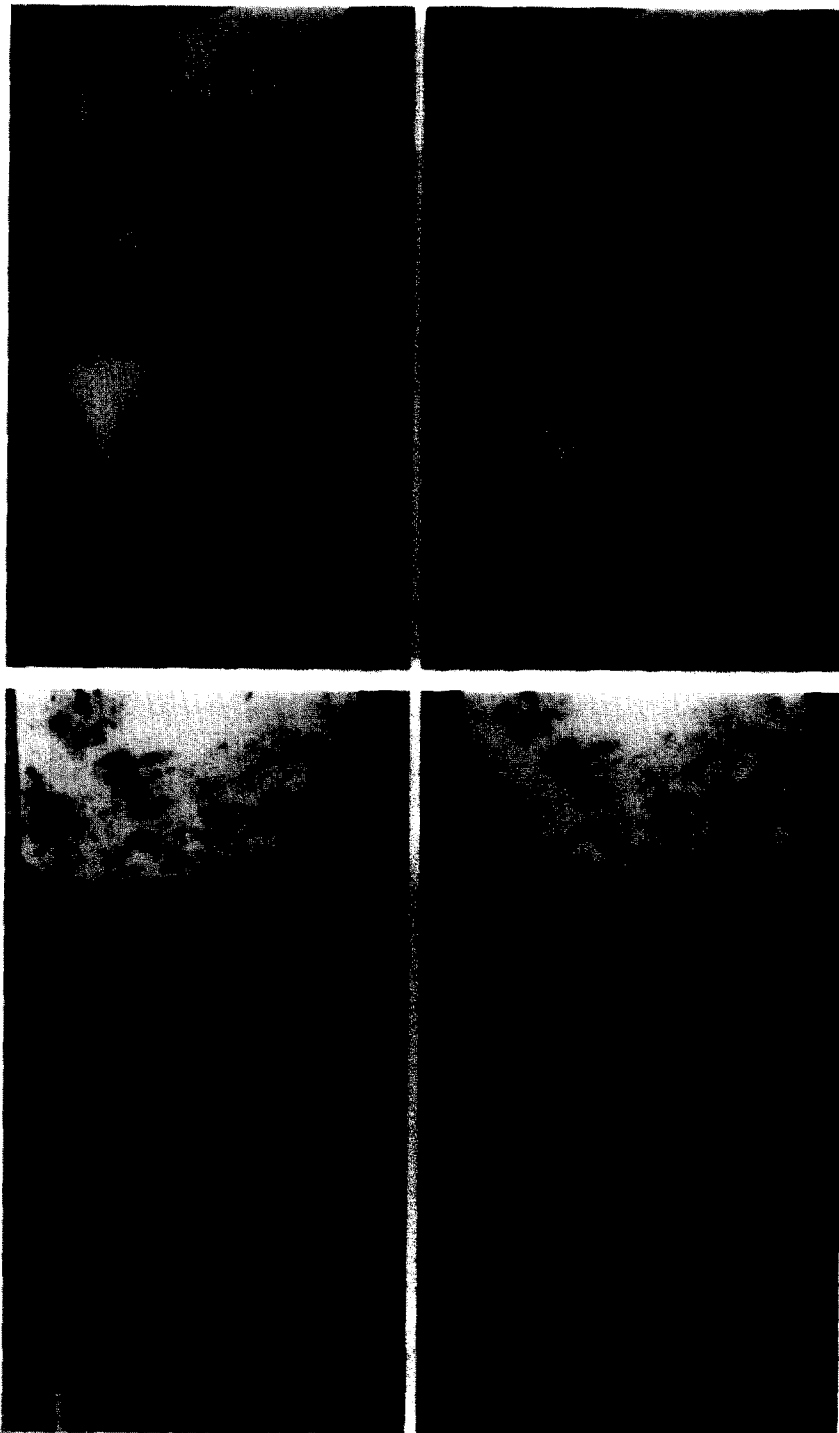Table 4. Slopes and P_f (N) at 10% elongation of mean regression lines of 16 ZLZ specimen

	Slope	P_f (N)
Lens	1.93	0.011
Z_1	1.60	0.00051
Z_2	1.60	0.000475

the boundaries of the field. We found that the force required for 10% elongation of the lens at the mean and at the extremes is 20× greater than for the zonula fibers. It was also found that at a force of 1 g (~0.01 N) the elongation of the zonules is ~7× that of the lens at the mean and 6× at the extremes. Results of other methods are essentially the same; but with most of the variance in elongation they are second choice to the one employed.

CLC specimens (n = 38)

Since in the ZLZ group the sample size is small ($n = 16$) and only 4 samples are younger than 40, a larger sample ($n = 38$) was extracted from available data on CLC specimen. To correct for the presence of CC springs, in parallel with lens and zonules, 23% was subtracted from the spring constants shown in Table 2. There is a marked effect of age on the zonules except for the first year of life. The spring constants of lens and zonules in the first year are almost the same; at age 25, the lens/zonule quotient doubles and at age 50 it quadruples. For the ZLZ specimen this quotient is lower and about 2.5 at age 53.

Subdividing the 16 ZLZ specimen in age groups <40 ($n = 4$) and >40 ($n = 12$) did not show significant effects of age on mean elongation of L and Z at a force of 0.01 N nor of the mean force required for 10% elongation, possibly due to the small sample size of the younger group. A similar analysis was done for 36 CLC specimen.* The results are shown in Table 5. For the lens there clearly is an effect of age. For the zonules, the effect of age is limited to age 0.3 and the two older groups; the difference between the two older groups is not significant due to large standard deviations. The effect of age is magnified for the ratios between lens and zonules. At age 50 the force required for 10% elongation of the lens is 14× that of the zonules against 2.5× at age 0.3; and the elongation of the lens at 0.01 N force is 7× that of the zonules at age 50 against 2.5 at age 0.3.

*Two were omitted because of an extreme c or A value.

Direct lens loadings

Length–tension curves of equatorial and polar traction recordings of the lens often have sigmoidal shapes on both ascending and descending legs. The correct zero point will be at the bending point, because before this point the ellipsoid-shaped lens with horizontal axis is obviously compressed. Past the bending point, with the long axis vertically, it is evidently stressed in tension. By increasing chart speed, the bending point could be defined in the experiment with reasonable accuracy. The sigmoid shape of the loading curves is presumably the result of glueing the capsule to the beaks. It may alter the Poisson contraction and modify the spring constants. Also, capsule may separate from lens substance (von Sallmann, 1952).

When the lens is loaded at the equator ($n = 17$) length-tension relations are nonlinear but linear on log–log scales. Spring constants for 10% el. are shown in Table 2; they triple in value at mean age 49 compared to mean age 18.

Polar loads ($n = 5$) of 10 g increase mean lens thickness by 0.69 mm and reduce its mean diameter by 0.25 mm. The 48-yr-old lenses are significantly stiffer than the 26-yr-old lenses but in this very small sample the spring constants do not even double (Table 2).

Loading ciliary muscle and choroid (Fig. 8)

Length–tension curves are nonlinear but linear with log–log coordinates. Spring constants are shown in Table 1. These constants have almost the same magnitude (about 270 dynes/10% el.) for both choroid and ciliary muscle, and they increase with age, i.e. both choroid and ciliary muscle become stiffer (see correlations, Table 3).

The long ciliary muscle in 3 specimens measured 5.8, 6.6 and 7.4 mm. The other seven specimens were all longer than 7.4 mm, with a mean of 11.7 ± 3.8 mm. Hence, these "ciliary

Table 5. Elongation of lens and zonules in CLC specimen

n	Age (yr)	L	Z	L/Z
Force[a] (N) required for 10% elongation				
7	0.3	0.003 N	0.0012 N	2.5
11	25.4	0.016 N	0.0022 N	7
18	49.9	0.034 N	0.0024 N	14
Elongation (%) at 0.01 N force[b]				
7	0.3	18%	48%	2.5
11	25.4	8%	38%	5
18	49.9	4%	28%	7

[a]Corrected and [b]not corrected for CC springs.

muscles" contain choroid. The equatorial ciliary muscle strips are longer than the longitudinal. The mean length is 17.0 ± 7.7 mm ($n = 7$). These strips do not contain choroid but include the pars plicata. Since its vessels run perpendicular to the direction of force they will not affect the elasticity of the strip.

Choroidal specimen cut in two different directions have almost the same spring constants, contrary to expectation from previous experiments (van Alphen, 1986). Power law relations and age dependency fully confirm our earlier findings (Graebel & van Alphen, 1977).

Deformation of the lens

A measure of the ellipsoid deformation (and of the "elasticity" of the lens) is the length (L) over the width (W) of the lens; and for a given deformation more force is needed when age advances (Table 6). Side views of the lens during loading show flattening of anterior and posterior lens surfaces, an increase in length of the lens and a decrease in thickness (Fig. 9). Since L/W increases with force the frontal area of the ellipse should increase. Indeed, uniaxial stress increases the surface of the front of the lens, as measured on enlarged photographs. The surface area of the side of the lens also does increase. If, on loading, lens volume is to remain constant, the area of the cross section of the lens (in the third dimension) should decrease. However no pictures were taken along the loading axis.

Rupture of zonula fibers

When the specimen is stressed and zonula fibers rupture, they do so at either 12 or 6 o'clock, and sometimes at both. The corresponding part of the lens equator flattens, and tension no longer goes up and may fall. Most zonular fibers rupture at stresses of approx. 6 g in eyes above 40 years of age, but eyes of 1 day to 14 yr may withstand forces of over 10 g. Hence, zonular rupture is related to age whereas zonular elasticity after the first year of age (and probably the first decade) is not.

Correlations with age

Since the distribution of S' with age is frequently nonGaussian and the regression nonlinear, the nonparametric Spearman rank test was included to evaluate the results. Table 3 shows significant correlation coefficients between spring constants of lens and age (except for ZLZ specimen). Correlations between spring con-

stants of zonules and age are not significant. This confirms Fisher's finding (1986) that the elasticity of the zonules is not affected by age. Spring constants of Z_1 and Z_2 are strongly correlated in both CLC and ZLZ specimen but spring constants of L are significantly correlated only with those of Z_1 in the CLC group (not shown in Table 3).

We also show that choroid and ciliary muscle get significantly stiffer with age which might still be another factor in the etiology of presbyopia.

DISCUSSION

Stress–strain

Nonlinear stress–strain relations are the rule in biology and from this work it appears that lens, zonules, choroid and ciliary muscle are no exception. Fisher (1971) found slightly sigmoid but near linear relations between force and deformation of the spinning human lens (his Fig. 16, Ref. 14) because he applied relatively small forces. At small forces stress–strain relations will also be linear on arithmetical plots.

Physiological forces do not guarantee linearity; length–tension relations of arterial strips are nonlinear within physiological limits. Stress–strain relations of CLC, ZLZ, lens, zonulae, ciliary muscle and choroid specimens are all nonlinear, but log stress vs log strain is linear above forces of 500 dynes. Deviations from linearity at forces below 500 dynes are probably due to the fact that biological tissues are always under tension, and that *in vivo*, zero stress and zero strain do not exist.

When loading the lens, in the manner we have employed, not all of the zonules participate equally in the amount of force carried or in the elongation. Zonules running from the center of the beak to the lens, at 12 o'clock, will experience more elongation than those at the outer ends of the beaks, running to 11 and 1 o'clock of the lens (as well as 5 and 7) and presumably therefore will carry smaller loads. Because of the nonlinear nature of equation (1), it is difficult to

Table 6. Ellipsoid deformation of the lens at 2 loads and various ages

Age	L/W at 1.5 g	L/W at 6 g	n
1–3 days	1.35–1.5	1.73	4
4–10 yr	1.21	1.51	3
18 yr	1.11	1.30	1
37–40 yr	1-09	1.20	3
50 yr	1.04	1.12	1

L/W ratio of length L over width W (= transverse diameter).

make an exact determination of this effect. However an estimate can be made by considering that both initial length and change of length are related to distances in the direction of pull by the cosine of the angle between them. Thus the angular dependency cancels out in this part of equation (1). Integration over the total angle of the force per zonula times the cosine of the angle (to get force in the direction of pull) gives the pull exerted on the specimen. Since the total included angle used in the tests is roughly 60 deg, the net result is that essentially no correction of the data need be made for the complicated geometry of the specimen.

The mean value of 230 dynes/10% el. for equatorial ciliary muscle strips is low compared to values of 154 for CC strips as shown in (1) Table 1. It should have a value of $2 \times 154 = 308$ dynes, since CC specimens equal two equatorial ciliary muscle strips in parallel. On the other hand, a value of 154 is rather high compared to the value of 95 resulting from (2), Table 1: $S'_{CLC} - S'_{ZLZ} = S'_{CC} = 237 - 142 = 95$. (Since the structures are in parallel, they will have the same change of length. Since their A's and l_0's are approximately the same, it is reasonable to assume that their spring constants may be subtracted.) Higher mean age (53 vs 41) in (2) may be one reason for the discrepancy and the small sample size ($n = 6$) may be another; also there is additional ciliary body tissue at 12 and 6 o'clock which is absent between two single ciliary muscle strips.

There is considerable variation between S' for "L alone", L in ZLZ and L in CLC as shown in Table 2. The "L alone" is difficult to compare with L in ZLZ and L in CLC because the method employed is entirely different for "L alone" compared to the two others. Still, S' for L in CLC is much greater than S' for L in ZLZ despite a 23% correction for the presence of CC springs in the CLC preparation. Now it follows from Table 1 that on removal of the ZLZ spring in 13 CLC preparations, the CC spring carries 48% of the load; and when the ciliary body is cut the ZLZ spring carries 60%; here 40% is lost by cutting the CC springs. If we correct by 48% instead of 23% (by multiplying the 23% corrected CLC values for L in CLC by $0.48/0.77 = 0.6234$) we find rather close values for the spring constants of L in ZLZ and L in CLC (means differ by a factor 1.17) as well as for the spring constants of Z in ZLZ and Z in CLC (means differ by a factor of 0.88).

It is quite possible that by removing the lens from the loaded CLC specimen, the fall in tension of 77% is exaggerated by the fact that the specimen is under tension. Moreover, the specimen lengthens on removal of the lens which seemingly potentiates the fall in tension. Both factors may contribute to greatly underestimate the magnitude of the CC springs. On the other hand, mechanical factors, due to glueing the lens to the holder, may have caused over-estimation of S' of "L alone" specimens.

Forces and pressures

We will outline here a simplified calculation (based on the law of Laplace) of the approximate forces that operate in the eye when the lens is focused for far (nAcc) and for near (Acc). For far, the ciliary muscle is relaxed and the capsules are under maximal choroidal tension to flatten the lens. If the ciliary muscle is totally relaxed, choroidal tension depends on the difference between IOP and pressure in the suprachoroidal space (SPSC). This pressure is 1.5 mm Hg lower than IOP in cats (van Alphen, 1961) and 3.7 mm Hg in cynomolgus monkeys (Emi, Pederson & Carol, 1989). If the SCSP in humans were of the same magnitude as in the monkey the tangential force on the choroid per unit length would be $F_{ch} = 0.5pr = 0.5 \times 3.7 \times 133.33 \times 0.01175 = 2.89$ N/m ~ 3 N/m (in which $p = 3.7 \times 133.33$ N/m² and r, the mean radius for choroid equals 11.75 mm). If we ignore angles, the force on the capsules in the nonaccommodated (nAcc) eye will be:

$$F_{ch} = F_{antC} + F_{postC} = 3 \text{ N/m};$$

where F_{antC} and F_{postC} are the forces on anterior and posterior capsules respectively. By applying the law of Laplace to the lens capsules of the nAcc eye we find: $F_{antC} = 0.8$ (LP $-$ IOP) for a radius of curvature $= 12$ mm (LP: lens pressure) and $F_{postC} = 0.4$ (LP $-$ VP) for a radius of curvature $= 6$ mm (VP: vitreous pressure). For IOP $= 20$ mm Hg we find 3 LP $=$ VP $+ 47.5$. Because a force balance gives only one equation for two unknowns, we varied VP and calculated LP, F_{antC} and F_{postC} while keeping F_{ch} and IOP constant. The results are shown in Table 7.

Similarly, for the Acc eye we write:

$$0.4 \text{ (LP} - \text{IOP)} + 0.4 \text{ (LP} - \text{VP)} = 0.5 \text{ N/m};$$

assuming radii of curvature of 6 mm and a choroidal force of 0.5 N/m (and not zero, since only extreme accommodation will cause zero tension of the zonules and capsules, and may

Table 7. Pressures and forces in the accommodated and nonaccommodated eye

	Pressure (mm Hg)			Forces (N/m)	
	IOP	VP	LP	F_{antC}	F_{postC}
nAcc	20	20	22.5	2.00	1.00
	20	21	22.83	2.26	0.732
	20	22	23.17	2.54	0.468
	20	23	23.5	2.80	0.200
	20	24	23.83	3.06	−0.68
Acc	16	16	16.625	0.25	0.25
	16	17	17.125	0.45	0.05
	16	18	17.625	0.65	−0.15
	16	19	18.125	0.85	−0.35
	16	20	18.625	1.05	−0.55

allow the lens to fall forward). Acc will also cause a sustained fall in IOP of 3–4 mm Hg. At IOP = 16 we find 2 LP = VP + 17.25. Again, we varied VP and LP and calculated F_{antC} and F_{postC} while keeping F_{ch} and IOP constant. Results are shown in Table 7.

Negative capsular forces in the table mean that the force is compressive; zero force would mean that the capsule is slack. Hence, LP must be >IOP and >VP or capsule is curved in the opposite direction. Therefore, in our example, VP should be between 20 and 23 mm Hg (nAcc) and between 16 and 17 (Acc) with LP up to 2.5 mm Hg higher than VP (nAcc) and up to 0.6 mm Hg (Acc). This differs greatly from the estimate given by O'Neill and Doyle (1968) of 24 mm Hg for the increment in lens pressure when the lens returns to the unaccommodated state.

A possible explanation for the curvature of the posterior zonules is that they are supported by the hyaloid membrane (Hm) which roughly has the shape of the top of a torus. If Z and H are the tensions per unit length in zonules and Hm, and r is the local radius of the Hm, then the pressure difference $\Delta p = VP - IOP = (Z + H)/r$. Since Z is about 3 N/m and r is of the order of 10 mm, Δp would be of the order of 2 mm Hg if H were zero. However, it is likely that the Hm is in fact compressed by the zonules, implying that H is negative, so that Δp is actually smaller than this estimate.

Spinning the lens and accommodation

Fisher (1971) determined the Young's modulus (E) of elasticity of human lenses by spinning the lenses around the anterior-posterior polar axis and comparing his experiments with a linear elastic model. This method would be close to the ideal if the lens properties were homogeneous, which they of course are

not. Additionally, centrifugal forces do not really mimic capsular forces in accommodation. Moreover, lens content rather than lens capsule will determine the shape of the spinning lens, while of course the reverse is true in accommodation. Finally, spinning the lens might disrupt lens fiber anatomy. Five lenses, centrifuged at 1000 rpm, and 5 noncentrifuged fellow control lenses, were examined with a SEM by B. Willekens. The ages ranged from 56 to 80 yr. Before centrifugation all lenses were clear on transillumination except for spoke-like opacities at the equator. All five centrifuged lenses showed pronounced varicose swellings of the equatorial lens fibers close to the cataractous changes, presumably indicating that the fibers were leaking. Varicose changes were absent in the controls.

Changes in position and curvature of the posterior lens surface, as shown by Purkinje images, are both minimal compared to the changes of the anterior lens surface.

The posterior pole was supposed to stay put during accommodation until Coleman in 1970 determined ultrasonically, in 25 students, that it moves backward. (But is it certain that the velocity of ultrasound waves is not affected by increased thickness of the lens nucleus?) However, Koretz, Kaufman and Handelman (1988) found the location of the posterior surface essentially unchanged in 100 subjects. The posterior curvature was also supposed to show very little change during accommodation. But Brown showed in 1973, with slitlamp photography, that its curvature might increase although the magnitude is unknown (and may be zero) since the rays pass through the lens. The flattening of the posterior capsule of the spinning lens was not emphasized until Fisher's publication of 1982 in which he showed flattening of the posterior pole to be slightly less than the anterior pole. We confirmed that on spinning the lens, both capsules flatten and total lens thickness decreases, no matter whether spun with posterior or anterior surface down $(n = 6)$.

If during accommodation the curvature of the posterior surface of the lens barely changes. It means that the forces on the lens cannot be radial, since either spinning the lens or unaxial stress flattens both anterior and posterior surfaces.

Fisher (1983) showed that vitreous is not necessary for accommodation. He did not show that the eye is able to accommodate without pressure and that is the point that Coleman

(1970) is making. It is the young eye (below age 35) with near zero pressure that is of interest because an eye without pressure, with or without vitreous, is presumably unable to accommodate since the zonula fibers will be slack (van Alphen, 1963). But zonula support requires a pressure gradient which so far has not been demonstrated. Also, it is hard to see how such a gradient would allow the posterior capsule in the celebrated Graves (1925)–Fincham (1937) case to markedly relax and bulge posteriorly during accommodation, "displaying folds and receding from the anterior capsule, which relaxes only slightly".

When Fisher believes that it is the capsule plus the inherent structure of the lens substance that moulds the anterior surface of the lens into the accommodated shape we certainly agree, since there is nothing else to affect its shape; but then the same mechanism should maintain an almost constant curvature of the posterior surface for both far and near vision. This mechanism has yet to be unraveled.

Young's moduli are presented in Table A1, Appendix I. A comparison with Fisher's moduli, obtained by entirely different methods, suggests an approximate range of Young's moduli for lens capsule, lens substance and zonules. We also add here moduli for choroid and ciliary muscle. The figures suggests that lens capsule has the same stiffness as the zonules; both are three magnitudes stiffer than lens substance and choroid.

Mechanical modelling of accommodation

Our goal is to utilize the above force-elongation relations in a mathematical model which includes all of the tissues involved in accommodation. To accomplish this, a thorough understanding of the role of each element in the total structure is necessary. It would seem that at present not all of the necessary information is available. There still is a question as to whether there is a difference in pressure between aqueous and vitreous. The "hydraulic" theories of Tscherning (1904) and Coleman (1970) require that there be a difference, and so does a support hypothesis of posterior zonules to explain its curved course; but experimental measurements show this difference to be slight, and perhaps insignificant. The pressure in the lens has yet to be measured. Questions as to whether or where zonules are anchored to the pars plicata of the ciliary body must also be resolved. A recent, well docu-

mented, model by Wyatt (1988) postulates a zonular connection between the lens and the region of the scleral spur; we are not sure that conclusive evidence for such a connection exists. Wyatt (1988) clearly points out that the three dimensionality of the eye is an important consideration in any mechanical modelling. This has been considered in models of the lens, and was referred to earlier by Graebel and van Alphen (1977), but otherwise has been ignored in discussions by others. The role of the capsule versus cortex of the lens differs considerably in the models of O'Neill and Doyle (1968) and Koretz and Handelman (1982); and an analysis of the posterior capsule and whether it does or does not change its curvature during accommodation has yet to be established. Brown (1973) and Koretz et al. (1987) believe that curvature increases, but are unable to correct for refraction by the lens.

REFERENCES

van Alphen, G. W. H. M. (1961). On emmetropia and ametropia. *Ophthalmologica (Suppl.)*, *142*, 1–92.

van Alphen, G. W. H. M. (1963). The structural changes in miosis and mydriasis of the monkey eye. *Archives of Ophthalmology*, *69*, 802–814.

van Alphen, G. W. H. M. (1976). The adrenergic receptors of the intraocular muscles of the human eye. *Investigative Ophthalmology*, *15*, 502–505.

van Alphen, G. W. H. M. (1978). A correlation matrix of optical elements and age of the human eye. *Experimental Eye Research*, *26*, 573–579.

van Alphen, G. W. H. M. (1979). Scanning electron microscopy of the monkey eye in miosis and mydriasis. *Experimental Eye Research*, *29*, 511–526.

van Alphen, G. W. H. M. (1986). Choroidal stress and emmetropization. *Vision Research*, *26*, 723–734.

van Alphen, G. W. H. M., Kern, R. & Robinette, S. L. (1965). Adrenergic receptors of the intraocular muscles. *Archives of Ophthalmology*, *74*, 253–259.

Brown, N. (1973). The change in shape and internal form of the lens of the eye on accommodation. *Experimental Eye Research*, *15*, 441–459.

Coleman, D. J. (1970). Unified model for accommodative mechanism. *American Journal of Ophthalmology*, *69(6)*, 1063–1079.

Emi, K., Pederson, J. E. & Carol, B. T. (1989). Hydrostatic pressure of the suprachoroidal space. *Investigative Ophthalmology and Visual Science*, *30*, 233–238.

Fincham, E. F. (1937). The mechanism of accommodation. *British Journal of Ophthalmology (Monograph Suppl.)*, 8, 1–80.

Fisher, R. F. (1969a). Elastic constants of the human lens capsule. *Journal of Physiology, London*, 201, 1–19.

Fisher, R. F. (1969b). The significance of the shape of the lens and capsular energy changes in accommodation. *Journal of Physiology, London*, 201, 21–47.

Fisher, R. F. (1971). The elastic constants of the human lens. *Journal of Physiology, London*, 212, 147–180.

Fisher, R. F. (1977). The force of contraction of the human ciliary muscle during accommodation. *Journal of Physiology, London*, 270, 51–74.

Fisher, R. F. (1982). The vitreous and lens in accommodation. *Transactions of the Ophthalmological Society, U.K.*, 102, 318–322.

Fisher, R. F. (1983). Is the vitreous necessary for accommodation in man? *British Journal of Ophthalmology*, 67, 206.

Fisher, R. F. (1986). The ciliary body in accommodation. *Transactions of the Ophthalmological Society, U.K.*, 105, 208–219.

Graebel, W. P. & van Alphen, G. W. H. M. (1977). The elasticity of sclera and choroid of the human eye, and its implications on scleral rigidity and accommodation. *Journal of Biomechanical Engineering*, 99, 203–208.

Graves, B. (1925). The response of the lens capsules in the act of accommodation. *American Ophthalmological Society*, 23, 184–198.

Helmholtz, H. von (1856). *Handbuch der physiologischen Optik*. Leipzig: Voss.

Koretz, J. F. & Handelman, G. H. (1982). Model of the accommodative mechanism in the human eye. *Vision Research*, 22, 917–927.

Koretz, J. F., Bertasso, A. M., Neider, M. W., Gabelt, B. T. & Kaufman, P. L. (1987). Slit-lamp studies of the rhesus monkey eye: II. Changes in crystalline lens shape, thickness and position during accommodation and aging. *Experimental Eye Research*, 45, 317–320.

Koretz, J. F., Kaufman, P. L. & Handelman, G. H. (1988). Aging of the human accommodative mechanism: Changes in lens dynamics. *8th ICER Abstracts*.

O'Neill, W. D. & Doyle, J. M. (1968). A thin shell deformation analysis of the human lens. *Vision Research*, 8, 193–206.

Salzmann, M. (1900). Thickness of lens capsule listed by Eisler in Die Linse, *Kurzes Handbuch der Ophthalmologie, Erster Band* (p. 175). Berlin: Springer (1930).

Streeten, B. W. (1982). Zonular apparatus. In Jakobiec, A. F. (Ed.), *Ocular anatomy*, (pp. 331–353). Philadelphia: Harper & Row.

Tscherning, M. (1904). Le mécanisme de l'accommodation. *Annales d'Oculist, Paris*, 131, 168–179.

Von Smallmann, L. (1952). Experimental studies on early lens changes after Roentgen irradiation. *Archives of Ophthalmology*, 47, 305–320.

Wyatt, H. (1988). Some aspects of the mechanics of accommodation. *Vision Research*, 28, 75–86.

APPENDIX I

Provisional Young's moduli at 10% elongation were calculated to allow a comparison with Fisher's figures. We present these figures *with all proper reserve* since they include assumptions of homogeneity, isotropy and linearity, and neglect complications of transverse effects in nonlinear elastic tissues. (Transverse effects are similar to Poisson effects in linearly elastic materials.)

1. Lens Substance

To calculate E for the lens at 10% elongation, we need to know the load and the area over which it is acting. The mean load is found from Table 2 at the indicated mean age. The cross sectional area was approximated by an ellipse (to be comparable with Fisher's E) and measures πab. Its major axis $2a$ is equal to l_0 shown in Appendix II; the minor axis $2b$ equals lens thickness which is found from the equation:

$$2b = 3.545 + 0.015 \times \text{age} + 0.002\, R$$

<div align="right">(van Alphen, 1978);</div>

in which age is significant at the 1% level and the ocular refraction R at the 5% level. Since R is unknown and since it happened to be a less significant factor than age it was ignored. The stress divided by the strain (10% or 0.1) equals E. The values for E, calculated for lens alone, lens in ZLZ and lens in CLC are shown in Table A1.

2. Lens Capsule

It was shown already in 1926 by Fincham, that the elasticity of lens capsule is far greater than of lens substance; this was confirmed by Fisher in 1960 and 1961. If we know the area of the capsule over which the load is acting we may approximate E for the capsule by ignoring the elasticity of the lens substance. Capsular area for anterior capsule was calculated from $1/2\, \pi k(a + b)$ in which a and b are the half axes and k the thickness of the anterior capsule, assumed to be equal everywhere, to the thickness at the anterior pole. A similar calculation was done for the much thinner posterior capsule. Values for k were taken from Salzmann (1900). Young's moduli for capsule, calculated as for lens substance are shown in Table 5. However, since capsular thickness increases from pole to equator (as clearly shown by Salzmann's data, 1900, confirmed by Fisher) a more realistic model for capsular area of the half ellipse is given by:

$$1/2\, \pi(k_1 + k_2)(a + b),$$

in which k_1 stands for polar thickness and k_2 for equatorial thickness. This produces a total capsular area which is about $\frac{1}{3}$ greater than by the first approach with corresponding $\frac{1}{3}$ smaller values for E.

3. Zonules

The larger bundles run through the valleys between ciliary processes from pars plana to the lens. They are triangular, ribbon-like or rod-like in monkey and man. In man, the flat ribbons measure 30–60 μm (Streeten, 1982, and others) and may be about 10 μm thick, judging from the increase in capsule thickness at the insertion of the zonule. A ribbon of 50–60 μm × 10 μm would have a cross-sectional area of 550 μm^2; the area of a rod of 30 μm in dia is 700 μm^2; and the area of a triangle of base 30, 400 μm^2. Also one beak comprises about 12 valleys and each valley contains six zonula bundles. Since the load for 10% elongation is 600 dynes, the stress would be: 600/12 × 6 × 550 dynes/μm^2, hence a mean value of $E = 1.5 \times 10^6$ N/m^2.

4. Choroid

Choroid thickness is 0.16 mm at least, which gives an E of 3.3×10^4 N/m^2 for a strip 5 mm wide at a mean load of 262 dynes. Since Coleman, 1970 found a thickness of 420 μm at the macula in the living human eye, the periphery might also be thicker but at the most 0.25 mm, which would result in an E of 2.1×10^4 N/m^{-2}.

5. Ciliary Muscle

Ciliary muscle with a maximal thickness of 0.5 mm from apex to base, (with the ciliary muscle midway between contraction and relaxation), gives an E of 1.2×10^4 N/m² for a 5 mm wide strip, at a mean load of 283 dynes.

The results for various tissues with their approximate ages are summarized in Table A1. Values for lens and lens capsule are in line with Fisher's 1971 and 1969 findings except that Fisher's E's for lens capsule decrease with age whereas our E's for capsule increase with age. We emphasize that our calculations for lens and lens capsule are based on cross-section area and force for 10% el. and such calculations would equally apply to a cylinder having the same cross-section area and the same height as the lens or lens capsule. Hence our values may be too high.

Fisher's E (1986) for zonules is half a magnitude lower than ours. Fisher's E for zonules was based on mean diameter and total number of zonular filaments, and the force of contraction of the ciliary muscle, which force was deduced "by comparing the changes in lens profile due to zonular tension and centrifugal force" (Fisher, 1977). Ours is based on the force required for 10% el. and mean cross-section area. The number of bundles, 6–10 per valley, as quoted by Streeten (1982) is probably too high and if the monkey (*Pacio cynocephalus*) is a guide the number is 5, two thicker zonules to the anterior capsule and three thinner ones to the posterior capsule (van Alphen, 1979 as counted and measured in the pictures but not quoted in the paper). For our calculations we used the lower figure of Streeten: 6 bundles per valley.

Table A1. Young's moduli (N/m² at 10% elongation) and age (mean age on abscissa corresponds with decimal points of the y-mods and is also given in parentheses)

	Age (yr)				
	0	20	40	60	80
Capsule x 10⁶					
L alone					
L in ZLZ		1.2 (18.1)		2.1 (49.2)	
L in CLC		1.0 (16.5)		1.0 (52.5)	
	0.7 (0.5)		1.1 (25.4)	2.0 (49.5)	
Fisher x 10⁶ (1969 a,b)	6 ('child')			3 (60)	1.5 (80)
Lens x 10³					
L alone		4.4 (18.1)		10.9 (49.2)	
L in ZLZ		4.8 (16.5)		5.2 (52.5)	
L in CLC	3.7 (0.5)		6.7 (25.4)	11.7 (49.5)	
Fisher x 10³ (1971)	0.8 (0)			3 (60)	
Zonules x 10⁶					
Z in ZLZ		1.0 (16.5)		1.5 (52.5)	
Z in CLC	1.2 (0.5)		2.3 (25.4)	2.0 (49.5)	
Fisher x 10⁵ (1986)			3.5 (30) (ages 15-45)		
Choroid x 10⁴			3.3 (35.4)		
Cil.M. x 10⁵			1.2 (46.2)		

APPENDIX II

Mean Values for ZLZ and CLC Specimen

n	Mean and SD	Age	L		P_f ×1600	S ×1000	C	Z_1		P_f ×1600	S ×1000	C	Z_2		P_f ×1600	S ×1000	C
			A	l_0				A	l_0				A	l_0			
			L in ZLZ					**Z_1 in ZLZ**					**Z_2 in ZLZ**				
4	$\bar{X}$	16.5	1.98	8.43	15.6	23.70	0.94	2.40	1.82	0.99	9.01	8.18	1.77	1.43	0.82	5.73	0.03
	σ_{n-1}	8.9	0.09	0.73	7.77	13.64	0.39	1.69	0.77	0.71	7.67	16.31	0.52	0.27	0.56	3.10	0.02
12	$\bar{X}$	52.5	1.97	8.31	20.8	27.47	4.53	1.91	2.36	1.52	8.00	3.78	1.62	2.51	1.43	5.94	0.04
	σ_{n-1}	7.0	1.03	2.82	16.4	19.89	7.89	0.87	1.73	2.07	9.74	8.72	0.61	2.22	1.87	5.77	0.04
			L in CLC					**Z_1 in CLC**					**Z_2 in CLC**				
7	$\bar{X}$	0.3	1.96	6.55	6.3	11.25	0.43	1.74	1.98	1.38	7.59	0.06	1.83	2.36	3.73	10.89	0.10
	σ_{n-1}	0.5	0.59	0.83	3.1	6.00	0.26	0.46	0.76	0.85	3.21	0.06	0.63	1.29	4.28	9.80	0.14
11	$\bar{X}$	25.3	1.81	8.70	33.1	38.75	1.45	1.51	2.20	5.45	16.21	0.09	1.71	2.13	3.56	12.41	0.61
	σ_{n-1}	13.5	0.45	0.44	20.3	17.33	1.21	0.60	0.99	5.39	12.69	0.13	0.78	1.01	5.08	10.25	1.92
20	$\bar{X}$	49.5	1.49	9.05	67.9	59.51	3.25	1.54	2.64	5.39	11.49	0.05	1.52	2.89	4.27	10.12	0.05
	σ_{n-1}	8.6	0.69	0.55	32.6	27.24	8.25	0.55	1.60	7.60	10.39	0.02	0.54	1.29	4.90	8.26	0.03

P_f, the force required for 10% elongation pertains to a beat width of 10 mm.
Units: age (yr); l_0 (mm); P_f and S (N); A and C, no dimension.