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THE ELASTIC CONSTANTS OF THE HUMAN LENS

BY R. F. FISHER

From the Department of Physiological Optics, Institute of Ophthalmology, Judd Street, London WC1H 9QS

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SUMMARY

1. When the lens is spun around its antero-posterior polar axis in an apparatus designed for the purpose, high speed photography can be used to record its changing profile. By this method a variable radial centrifugal force can be applied to the lens which mimics the pull of the zonule.

2. If the lens is not stressed at its centre beyond 100 Nm^{-2} it behaves as a truly elastic body. When stressed beyond this limit visco-elastic strain is produced at its poles.

3. The human lens has isotropic elastic properties at the extremes of life, but at the other times Young's Modulus of Elasticity varies with the direction in which it is measured.

4. Young's Modulus of Elasticity of the lens varies with age, polar elasticity and equatorial elasticity, at birth being $0{\cdot}75 \times 10^3$ and $0{\cdot}85 \times 10^3$ Nm^{-2} respectively, while at 63 years of age both are equal to 3×10^3 Nm^{-2}.

5. A comparison of Young's Modulus of the young human lens with that of the rabbit and cat shows that the polar elasticity of the lenses of these animals was 5 times greater in the young rabbit, and 21 times greater in the adult cat. Equatorial elasticities of the rabbit and human lens were equal, while in the cat the equatorial elasticity was four times greater.

6. A mathematical model showing the lens substance possessing a nucleus of lower isotropic elasticity than that of the isotropic elastic cortex surrounding it, accounts for the difference between polar and equatorial elasticity of the intact adult lens.

7. The implications of these findings are discussed in relation to:

(i) accommodation and the rheological properties of the lens;

(ii) possible differences in the physical state of the lenticular proteins in the cortex and nucleus which may account for the senile variations in Young's Modulus of Elasticity in these regions of the lens;

(iii) the loss of accommodation due solely to an increase in Young's Modulus of Elasticity of the lens between the ages of 15 and 60. This would amount to 44 % of the total observed *in vivo*.

INTRODUCTION

Previous investigations of the stress/strain relation of the crystalline lens have shown without exception that it behaves as a rheological body (Fukuda, 1963; Kikkawa & Sato, 1963; Masakazu, Thomson & O'Neill, 1969). This means that when a force acts upon the lens it continues to deform it albeit at a decreasing rate, as long as the force is applied. Since this property has been found in the intact lens, an ever-increasing 'permanent set' would be expected to result from repeated or continuous forces acting solely through the zonule. In repeated accommodation a visco-elastic lens would, therefore, have to be subject to two opposing forces acting alternately and in different directions; for example, zonular tension radially and vitreous pressure axially. The theories of neither Helmholtz (1855) nor Tscherning (1904) admit of two such opposing forces acting independently on the lens and it is difficult to see how the anatomy of the human eye could produce an interplay of such forces. All the quantitative methods so far developed to study the elastic properties of the lens have entailed simple antero-posterior polar compressive techniques, as the accurate measurement of tensile radial forces acting through the zonule (Pau, 1951) seemed impracticable. However, if it can be shown that the lens is a truly elastic body when subject to radial forces the idea of a single set of forces acting through the zonule would not have to be modified.

This paper shows that the application of a physiological radial force to the lens can be achieved by spinning the lens about its antero-posterior axis; under these circumstances the lens exhibits simple elastic properties. The value of this spinning technique is illustrated in Fig. 1. When the lens

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Legend to Fig. 1

Fig. 1. Changes in the human lens following a compressive force or a centrifugal force of the same magnitude (comparison between lenses from a 26 yr old cadaver). Total force 1·5 g weight.

A. Effect of optical properties. The lenses were used to focus a point source of light while immersed in normal (0·9 %) saline, and the resulting image was photographed.

Note: the optical properties of the lens after spinning remains almost unchanged while the image produced by the paired lens after compression is a star figure. This is a three pointed star although the third limb indicated by a white arrow is only just visible.

B. Effect of lens fibre system. The lens fibre system is revealed by dark ground illumination and thick arrows point (upper left hand) to the commencement of anterior equatorial and (lower right hand) anterior apical fibres respectively. After spinning, the lens fibres appear little changed, whereas after compression separation of fibres occurs in the paired lens.

is compressed to decrease its thickness by a similar amount to that occurring naturally, its optical properties are destroyed as the fibre system is disrupted, whereas when it is spun no damage ensues. Fig. 2 shows that spinning of the lens is practicable and clear pictures of the lens can be obtained by high speed flash photography with little evidence of lens wobble. It is also possible to measure not only polar but also equatorial strains, and to relate the strains observed to a mathematical model of the lens.

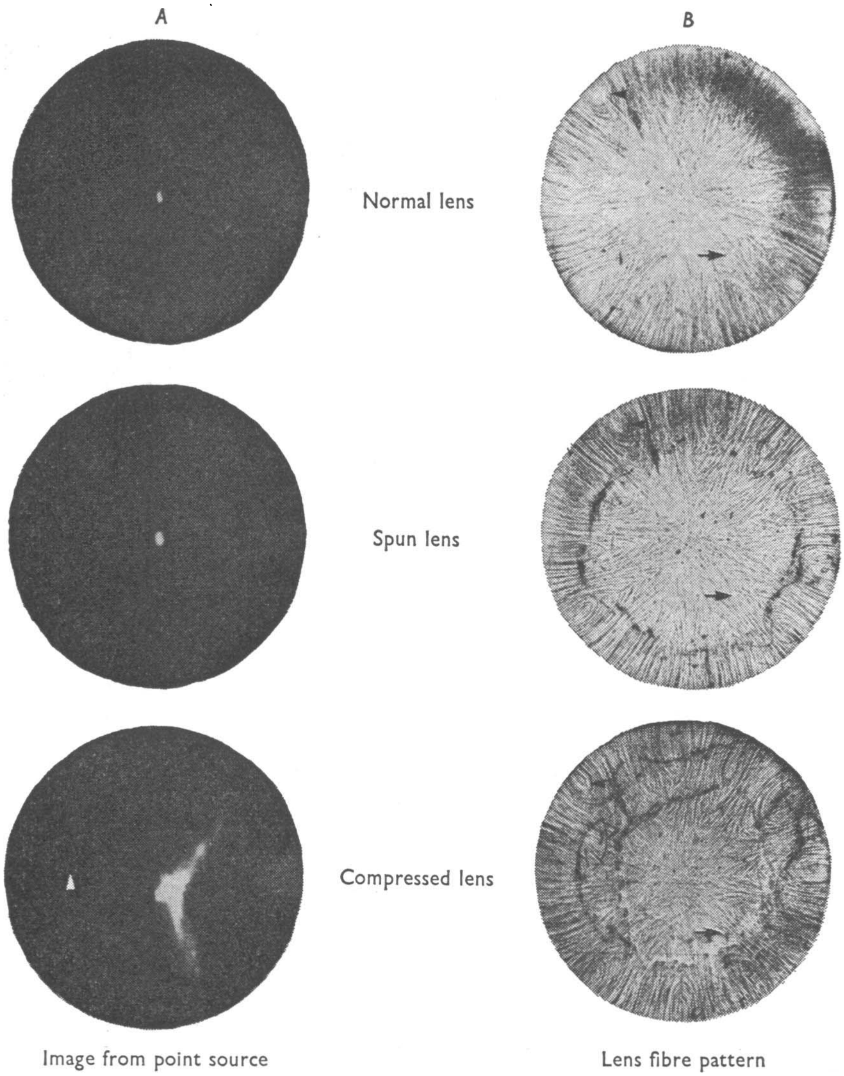

Fig. 1. For legend see opposite page.

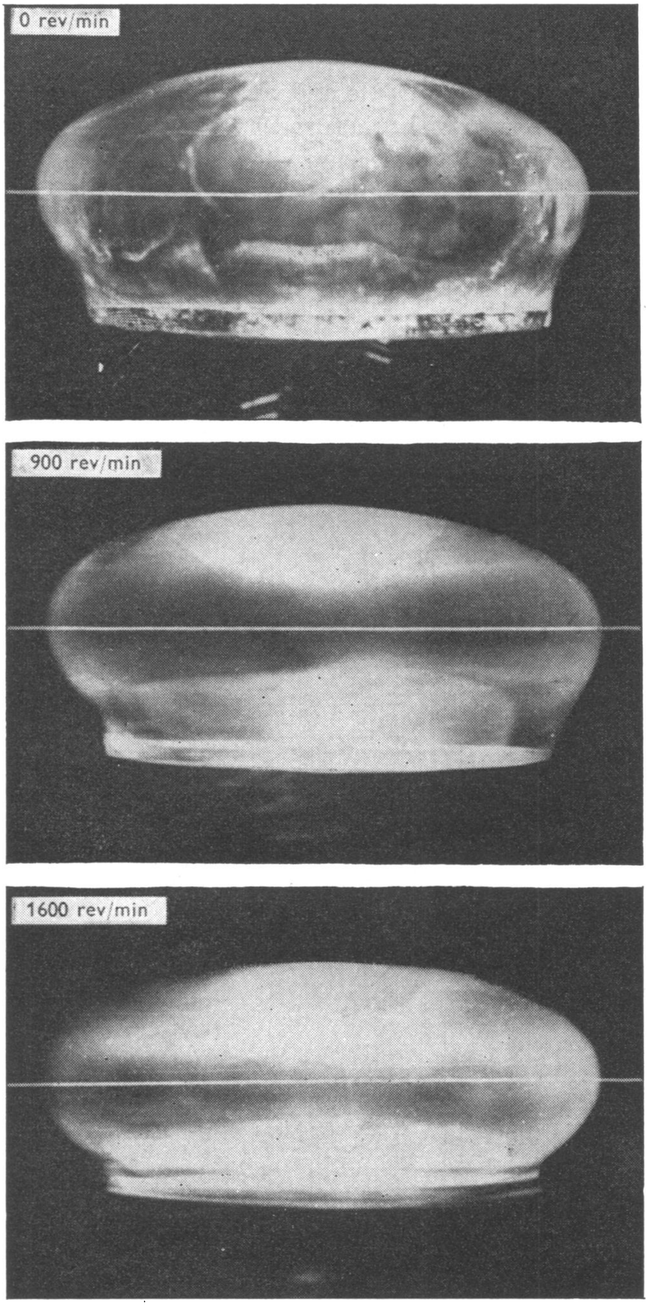

Fig. 2. For legend see opposite page.

METHODS

Lens preparation

Lenses were obtained from human cadavers not more than 24 hr after death, and in some cases as early as 8 hr after death. After the eye had been opened by a limbal incision so that the cornea could be removed, and the iris reflected, the lens was removed from the eye by cutting the zonule under magnification with microscissors. Most investigators have ruptured the zonule with a glass rod prior to removal of the lens but this method was abandoned as it was found to damage the peripheral lens fibres.

Storage experiments

All the lenses used were perfectly transparent at the time of testing, but to observe if storage of the lens within the eye adversely affected its elasticity, four pairs of rabbit lenses were tested. The elasticity of the lens of one eye was tested immediately after the animal had been killed and the other eye was removed and kept at 4° C for 48 hr. The lens was then removed from this eyeball, and its elasticity determined. Another four rabbits were used to determine the variation in elasticity between pairs of rabbit lenses. The variation in elasticity between fresh and stored lenses was found to be 10 %, and between paired fresh and fresh lenses 8 %. Thus errors induced by storage were little greater than normal elasticity variations.

Apparatus

The layout of the apparatus, which was designed to measure the strains and stresses produced in the lens by rotation is shown in Fig. 3. These strains at pole and equator were obtained by comparing photographs of the stationary and spinning lens, while lenticular stresses were calculated from the speed of rotation, density and size of the lens. The thickness of the stationary and spinning lens was also measured by means of a microscope with a ruled graticule in the eye piece. The speed of rotation of the lens was recorded by a tachometer accurate to ± 10 rev/min attached to a variable speed motor. Details of the apparatus were as follows.

(*a*) *Camera and electronic flash tube*

The lens profile was photographed at a distance of 50 mm by a 35 mm EDIXA single lens reflex camera with a 50 mm lens and extension bellows used at a stop of f. 16. The lens was illuminated by means of a 100 Joule electronic flash tube perpendicular to the optic axis of the camera, and placed centrally 300 mm above the anterior pole of the lens. The camera was focused on the centre of the lens equator. The film (Ilford F.P. 4) was developed in Ilford Microphen, fixed and washed in the normal manner.

Legend to Fig. 2

Fig. 2. Photographs of the stationary and spinning lens. The excised stationary (0 rev/min) lens shows an ellipsoidal profile. At a moderate speed of rotation (900 rev/min) an appreciable degree of reversible and therefore truly elastic flattening of the lens occurs. When high-speed rotation (1600 rev/min) is attempted a marked degree of incompletely reversible and therefore visco-elastic deformation is produced at the anterior pole of the lens. In contrast the equator (marked by a horizontal white line) still undergoes reversible and therefore simple elastic deformation.

(*b*) *The lens support*

The lens support served two purposes, namely (i) to prevent the lens either sagging into or outside the ring support, and (ii) to mimic the direction of stress within the lens substance by virtue of its weight and rotation, that produced by the zonule during accommodation. Apart from these considerations the support had to allow viewing of the posterior pole of the lens in motion.

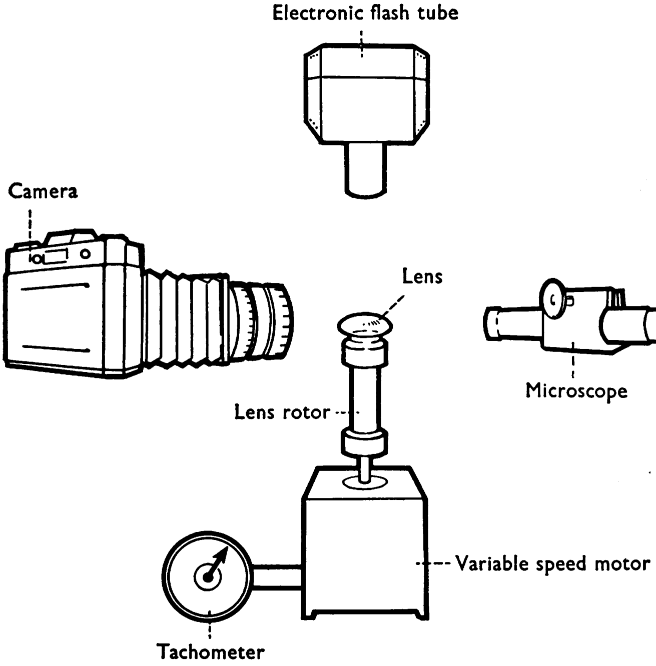

Fig. 3. Layout of apparatus for the measurement of changes in the profile of the lens at different speeds of rotation.

(i) *Changes in profile of the lens due to sagging when supported in air.* The shape of the lens when placed on the rotor was compared with its shape when immersed in saline as gross distortions might have occurred when the lens was not uniformly supported by fluid. This has been investigated previously (Fisher, 1969) and the radius and depth of the anterior segment of the lens supported successively in air and saline were found to agree respectively within ± 0·05 mm. This discrepancy was reduced by using different supports for lenses of different diameters. Five lenses ranging from neonatal to 60 yr old were compared by photography on the support in air and saline. The average of seven photographs for each lens taken in both media agreed to within ± 0·03 mm.

(ii) *Comparison of zonular pull with the stresses produced by spinning the lens.* The principles of design of the lens support are now discussed in some detail since the deviations of stress produced *in vitro* by weight and centrifugal force must simulate those produced *in vivo* by zonular pull if reliable values for the deformation in the complex lens fibre system are to be obtained. This was realized when the posterior polar strain of a lens was seen to increase by 50 % following inversion and spinning at the same speed. The direction of stress produced in the lens by the zonule had therefore to be ascertained.

The zonule acts on the lens probably chiefly through its principal fibres attached to the front and back of the lens capsule (Kaczurowski, 1964). The direction of pull of the anterior principal fibres subtending an angle and with the lens equator is shown diagrammatically in Fig. 4. Since the capsule is attached very loosely to the lens substance the zonule pulls along a line through the extremities of the zonular capsular attachment. The limits of the points of zonular attachment were taken as 1·0–1·5 mm from the equator of the lens (McCulloch, 1954). A line was drawn through these points to intersect one through the lens equator on the photographed profiles of ten lenses. The angle α of this intersection was then measured with a protractor and used in the design of the lens support.

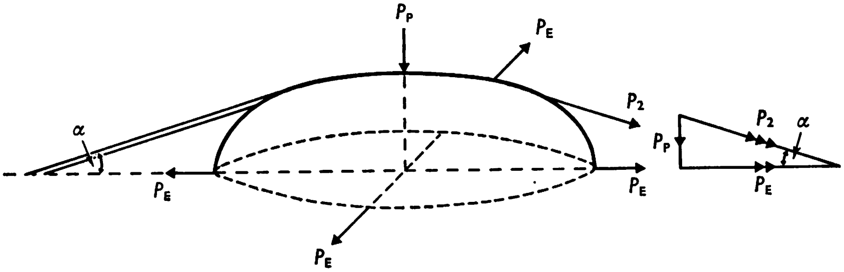

Fig. 4. Diagram showing forces produced in the anterior portion of the lens caused by the pull of the principal anterior zonular fibres. P_2 = force acting through zonular fibres, P_p = polar force, P_E = equatorial force, and α = angle of inclination of anterior zonule fibres to lens equator.

(For five young lenses (aged 4 months to 9 yr) $\alpha = 25{\cdot}4°$, S.D. ± 3·4° while for five older lenses (aged 10–65 yr) $\alpha = 19°$, S.D. ± 1·8°.)

When the lens was in air spinning on its support, two forces were acting through its centre, namely its own weight vertically downwards equivalent to the compressive anterior polar force of the zonule P_p, and a horizontal centrifugal force equivalent to the decompressive equatorial pull of the zonule P_E, shown in Fig. 4.

The horizontal component of these forces for different speeds of lens rotation, and the inclination to the equator of the lens of the resultant stress due to constant lens weight and variable rotational speed are shown in Fig. 5. Speeds of rotation between 1000 and 1500 rev/min produced the maximum reversible elastic deformation of the lens, and at these speeds the direction of stress at the centre of the spinning lens is very similar to that produced by the zonule (Fig. 5), the value of α lying between 33° and 18°.

(c) *The lens rotor*

This consisted of a light hollow central column with a heavy solid disk at its upper end. This disk had a central hole drilled to fit the uniform base diameter of differing lens supports selected for young and old lenses. It was balanced to reduce rotor vibration.

(d) *The microscope*

The thickness of the lenses was measured with a microscope containing a ruled graticule in the eye piece, reading to ± 0·02 mm. At high speeds the equatorial outline of the lens was blurred owing to variations in lens diameter, but the polar outline was clear and could be measured accurately.

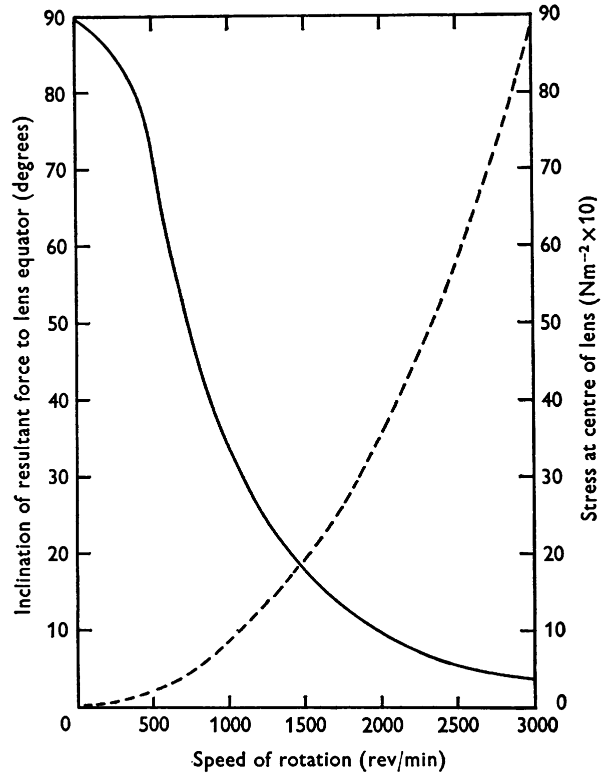

Fig. 5. Relationship between speed of rotation, centrifugal stress, and angle of inclination to the lens equator (α) of the stress compounded of spinning and gravity. — Inclination of resultant force in degrees. - - - - Stress (Nm^{-2}). (Dimensions of lens a_a = 4·25 mm, b_a = 2·2 mm. Mass of lens = 160 mg. Specific gravity of lens = 1·05.) *Note:* at speed of rotation employed (1000–1500 rev/min) α = 18–33°. Equatorial stress = 80–180 Nm^{-2} at centre of rotation of lens.

Procedure

(*a*) *Spinning the lens*

The excised lens was kept in warm saline (37 ± 1·0°) for about 20 min to reach the same temperature as the saline in the bath. It was then removed, and placed on the support by means of curved forceps. It was centred with the aid of two small marten's hair brushes, the centring being checked by manual rotation of the lens rotor. The stationary profile of the lens was then photographed seven times, differing angles of view being obtained by rotating the lens 15° before each photograph. The lens was then spun sufficiently long to obtain seven successive photographs and a measurement of thickness for a given rotor speed. This operation was completed in about 80 sec, and the lens returned to the warmed saline. After three such determinations at speeds of rotation increasing on each occasion by 250 rev/min the dimensions of the stationary lens were redetermined to see if a permanent set had been produced.

(*b*) *Measurement of photographs*

The photographs of the stationary or spinning lens were projected on to graph paper with a × 20 linear magnification and traced. Next, the position of the equator of the lens was found by the well-known technique of determining the normal to a point on a curve by reflexion of the curve in a mirror. Both ends of the equator were simultaneously determined with a large plane mirror placed perpendicularly to the surface of the graph paper and crossing each end of the lens profile. The reflecting surface of the mirror was directed towards the anterior pole of the lens and then moved about till the images of the profile at both ends of the trace were perpendicular to the surface of the mirror.

A line was drawn across the lens profile using the mirror as a ruler. The mirror was then turned round and its reflecting surface directed towards the posterior pole of the lens and the process repeated. The two lines drawn on the profile by this method were found to be some distance apart so a third line drawn equidistant between them was taken as the true equator of the lens. The uncertainty in regard to the position of the equator was not more than ± 0·02 mm.

The position of the anterior pole of the lens was determined by projection of a line from the mid-point of the equator and perpendicular to it, to intersect the profile of the lens. The point of intersection was taken as the anterior pole of the lens, and the distance between the mid-point of the equator and the anterior pole as the distance of the anterior pole of the lens from the equatorial plane.

(*c*) *Determination of the density of the lens*

The appendix shows that the density of the lens substance had to be known, and this required mass and volume measurements. The lens was lightly dried with filter paper and weighed on a spring balance (accurate to ± 0·5 mg), while the volume was found by displacement, the lens being placed in a small graduated cylinder (5 ml., accurate to ± 0·5 ml.).

(*d*) *Analysis of errors*

(i) *Measurements*. An estimate of the accuracy of measurement of the lens profile was obtained by photographing a metal ball of known dimensions (6·0 mm) placed on the lens support instead of the lens. The radius of the ball by direct measurement or photography agreed to within ± 0·01 mm.

(ii) *Fluctuation in lens temperature*. As the lens was spun in air and not in a water-bath of constant temperature, differences in strain due to the change in temperature for a given speed of spinning were determined. Five lenses were spun at room temperature (19° C) in air (1000 rev/min) and the strains measured as described. The lenses were then warmed in a water-bath at 37° C for 20 min, spun in air at the same speed and the strains measured again. It was found that irrespective of age the average increase in strain was 0·03 mm S.D. ± 0·01 mm for the 18° rise in temperature before spinning.

A stationary lens at 37° C as judged by a simple calorimeter experiment takes about 10 min to cool in air to room temperature. Therefore the underestimate of strain due to cooling while it was spinning for 80 sec was probably much less than this. Furthermore since every lens was spun for the same period any underestimate of strain was constant. Spinning the lens in a constant temperature water-bath was impracticable as the immersed weight of the lens was insufficient to allow stable spinning to occur.

(iii) *Sampling errors*. When the lens was spun each photograph was taken at a random moment. Since the dimensions of the lens depend on seven profile measurements the effect of random sampling of photographs on the lens size had to be ascertained. A stationary lens was photographed 49 times at different angles of view and its size estimated separately from seven randomly chosen photographs. The seven values of lens size had a S.D. of ± 0·014 mm. As the change in dimensions of the lens due to spinning at 1000 rev/min are about 0·20 mm in the young lens and 0·06 at the age of 60, the S.D. of the sampling error is 7 and 23 % respectively.

(iv) *Lens wobble.* This could produce errors in the values of both stress and strain. If rapidly alternating stress was produced by lens wobble, damage to the lens fibre system and a permanent set ensued. Fortunately this was self evident since the lens flew off the rotor and had to be jettisoned. In fact the yield point of the young lens was shown very distinctly by its sudden instability on the lens rotor when spinning at a speed well below that of an older lens with a higher yield point.

If the lens was tilted its thickness could change with the angle of view apart from any deformation. However, this change in thickness is only about 0·02 mm for a 10° inclination of the lens equator to the spinning axis. This small change occurs because the ellipsoidal profile varies little in depth near the anterior pole of the lens. In practice an inclination of this magnitude could not occur since a 5° inclination caused the lens to fly off the rotor.

(v) *Stress distribution.* The exact distribution of stress within the complex system of lens fibres due to zonular tension is unknown. In spinning the lens the maximum stress occurred in the nucleus of the lens. Stresses within the substance of the lens decreased in proportion to the difference between the square of the lenticular radius and the square of the distance from the axis of rotation. The strain changes due to spinning therefore occurred to a much greater extent in the nucleus than the peripheral cortex, but this appears also to be the case in the living eye (Patnaik, 1967).

(*e*) *Calculation of Young's Modulus of Elasticity*

Young's Modulus of Elasticity was calculated for both the polar and equatorial regions of the lens. The lens was considered to be comprised of an infinite number of elementary disks spinning parallel to the lens equator (Fig. 15).

Owing to the smooth elliptical outline of the lens the azimuthal variation of the radius is continuous and in consequence the hoop and radial stresses are almost the same in parts of each adjacent disk equidistant from the axis of rotation. Therefore to prevent relative movement between disks only minor shear stress acting on the surfaces of each disk would be required. These shear stresses could therefore be neglected. Since the lens contains a great deal of water (66 %) its bulk modulus is high and Poisson's ratio of each disk can be assumed to be 0·5.

Young's Modulus of polar Elasticity was calculated from Appendix eqn. (3·6):

$$E_{\mathrm{P}} = \tfrac{7}{24} a_{\mathrm{a}}^2 b_{\mathrm{a}} \rho \omega^2 / \delta b .$$

Young's Modulus of equatorial Elasticity was calculated from Appendix eqn. (2·2):

$$E_{\mathrm{E}} = a_{\mathrm{a}}^3 \rho \omega^2 / 8\delta a,$$

where

E_{P} = Young's Modulus of polar Elasticity (Nm^{-2}),
E_{E} = Young Modulus of equatorial Elasticity (Nm^{-2}),
a_{a} = equatorial radius of accommodated lens (m),
b_{a} = perpendicular distance of anterior pole from the equatorial plane of accommodated lens (m),
δa = increase in equatorial radius of the lens due to rotation (m),
δb = decrease in distance of anterior pole from the equatorial plane of the lens due to rotation (m),
ρ = density of lens substance ($\mathrm{kg\ m}^{-3}$),
ω = speed of rotation of the lens ($\mathrm{rad\ s}^{-1}$).

(*f*) *Model of the lens fibre system*

When the polar and equatorial elasticities of the lens were calculated from the preceding formulae they differed throughout the non-presbyopic period of life. This could be explained in two ways: either the lens was composed of identical fibres each of which possessed different longitudinal and transverse elastic properties, or else the lens consisted of an elastic centre surrounded by a shell of differing elasticity.

If the latter held, then the shell would have to be thinner at the pole than at the equator for the composite body to behave like the spinning lens.

The anatomical structure of the human lens in cross-section shows precisely these differences between cortical thickness at the pole and equator of the lens respectively (Bellows, 1944). In addition, the lens shows a cortex and nucleus of differing refractive indices, so that it is reasonable to suppose that the elasticities of these regions are also dissimilar. Accordingly, a mathematical model was devised (Appendices 4 and 5) in which the lens had an isotropic elastic nucleus surrounded by a cortex with a different isotropic elasticity.

It must be remembered that lens fibres are laid down in the outer surface of the lens substance continuously throughout life, but the model of the lens does not take into account the probable gradual change in Young's Modulus of Elasticity of each successive fibre layer. Such a model, however, enables us to estimate the mean changes in elasticity of nucleus and cortex throughout life. The nucleus is spherical (Fig. 16) with a radius equal to the anterior polar depth of the lens (b_a). Thus the cortex does not extend to the anterior pole of the model. Since the centrifugal forces at the polar region of the lens are very small and the cortex is thin, the model still satisfactorily represents the apical strain of the spinning lens, and the strain calculations are greatly simplified.

The strain at the nuclear pole and equator could not be measured during spinning, and had to be calculated from the observed external strains in the entire lens. It was assumed that the ratio of polar and equatorial strains of the nucleus was equal to the ratio of the strains measured on the surface of the lens. Fortunately this is almost true in the human lens since polar and equatorial elasticities do not differ greatly.

Young's Modulus of nuclear Elasticity was calculated from Appendix eqn. (4·9):

$$E_N = E_P^2/E_E.$$

Young's Modulus of cortical Elasticity was calculated from Appendix eqn. (5·8):

$$E_C = E_E + 7\lambda_n^2(E_E - E_P),$$

where

E_N = Young's Modulus of nuclear Elasticity (Nm^{-2}),
E_C = Young's Modulus of cortical Elasticity (Nm^{-2}),
E_P = Young's Modulus of polar Elasticity (Nm^{-2}),
E_E = Young's Modulus of equatorial Elasticity (Nm^{-2}),
b_a = perpendicular distance of anterior pole from the equatorial plane of the accommodated lens (m),
a_a = equatorial radius of accommodated lens (m),
λ_n = b_a/a_a = ratio of radius of nucleus to radius of lens.

RESULTS

Stress/strain curves

Stress/strain curves of typical adult human lenses obtained by measuring changes at the equator and poles are shown in Fig. 6. The equatorial strain (filled squares) in both cases was almost linear for spinning speeds exceeding 750 rev/min while no permanent set could be produced before the experiment was terminated by the lens flying off the rotor. The anterior pole of the lens behaved quite differently since the stress/strain curve (filled circles and open circles) showed irreversible thinning of the lens at about 1250 rev/min.

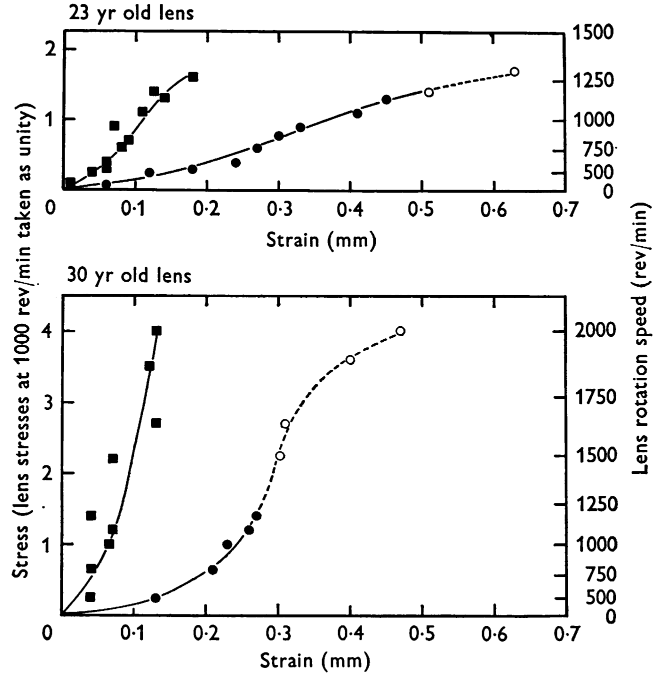

Fig. 6. Typical stress/strain curves for adult human lenses. Antero-posterior strain (change in lenticular thickness = δt mm; filled dots or circles). Equatorial strain (change in lenticular radius = δa mm; filled squares). Both strains plotted against centrifugal stress (1000 rev/min taken as unit of stress). ■–■–■– or ●–●–●– Reversible elastic strain, ○· · ·○· · ·○· · · irreversible visco-elastic strain. *Note*: corresponding speeds per unit of stress shown in rev/min on right-hand side.

In this region the strain curve resembled the S-shaped curve produced when stress is plotted against elongation for a piece of raw rubber stressed within and beyond the elastic limit (Treolar, 1967). The 23 yr old lens showed a change in axial thickness of between 0·4 and 0·5 mm before permanent set occurred. This change was very similar to that found by Fincham (1937) for two subjects aged 19 yrs when they were accommodating maximally (0·36 and 0·58 mm respectively). Thus a spinning speed of 1000 rev/min approached the maximum speed that could be used if a permanent set in lenticular thickness was to be avoided. This speed produced a maximum strain which increased the accuracy of measurement and, incidentally, simulated at the pole of the lens the accommodative changes observed *in vivo*.

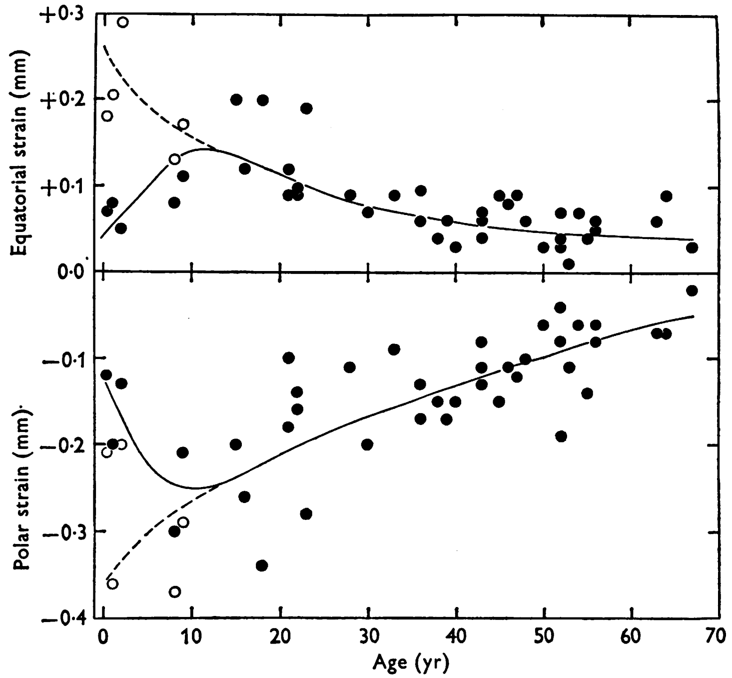

Fig. 7. Lenticular strains and age at a constant speed of lens rotation (1000 rev/min) ($N = 40$). *Note*: anterior polar strain (δb) and equatorial strain (δa) read off at 1000 rev/min from plotted strain curve of each lens. ● Actual strain values (mm). ○ Expected strain values if lenses between 0 and 10 yr old had dimensions of a standard 15 yr old lens ($a_a = 4{\cdot}25$ mm, $b_a = 2{\cdot}2$ mm).

Senile changes in lenticular strain at constant speed of rotation (1000 *rev/min*)

The increase in radius (δa) and the decrease in anterior polar thickness (δb) for forty human lenses are shown in Fig. 7. The strain values at 1000 rev/min were obtained from strain curves of each lens. Between birth and 10 yr of age strains were smaller than in the young adult because the centrifugal stresses produced by spinning them were also smaller. To decide whether the maximum and minimum of both these curves were caused by juvenile lens growth or by a reduction in Young's Modulus of Elasticity, strain values were calculated for these young lenses as if they had the same dimensions as a standard sized lens aged 15 yr ($a_a = 4{\cdot}25$ mm, $b_a = 2{\cdot}2$ mm). These are shown by a dashed curve with open circles. Given this correction, there was a continuous senile decrease in strain which was highly significant both for polar strain ($\delta r = -0{\cdot}45$, $P < 0{\cdot}01$) and equatorial strain ($r = +0{\cdot}38$, $P < 0{\cdot}015$). This correlation with age occurs despite the fact that for lenses above 15 yr of age the continuous growth of the lens increases the centrifugal stresses for a given speed of spinning, enhances the strains produced, and thus partially masks the decrease in the strain due to ageing. Both strain curves show, first, that the deflexion in advanced age is one third that of the deflexion obtained at 15 yr for the same speed of rotation, and secondly, variations in strain between lenses in the older age group often differ by 100 %. The latter finding gives a possible explanation for the known variations in onset of presbyopia in emmetropic eyes (Duke-Elder, 1954).

Young's Modulus of polar and equatorial Elasticity

The senile variation in polar elasticity and equatorial elasticities for forty human lenses are shown in Figs. 8 and 9 respectively. At birth, Young's Modulus of Elasticity is about $0{\cdot}7$–$0{\cdot}9 \times 10^3$ Nm^{-2} and at the age

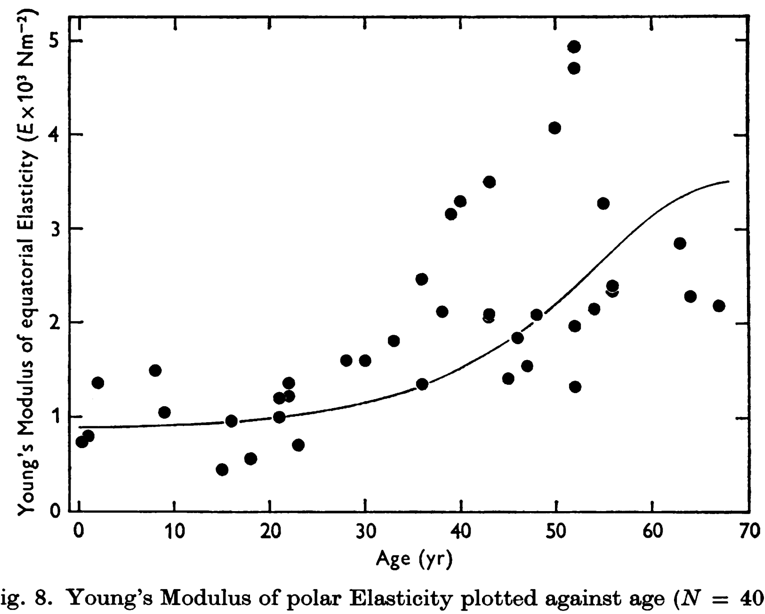

Fig. 8. Young's Modulus of polar Elasticity plotted against age ($N = 40$). Young's Modulus of Elasticity E_p (Nm^{-2}) calculated from $E_p = 3200a_a^2b_a\rho/\delta b$ (see text) where: a_a = radius of accommodated lens (m), b_a = perpendicular distance of anterior pole from equatorial plane of accommodated lens (m). ρ = density of lens substance (kg m^{-3}), δb = change in b_a due to spinning at 1000 rev/min (m).

of 60, 3×10^3 Nm^{-2} for both moduli. In both cases the senile changes in elasticity are highly significant, for polar elasticity ($r = +0{\cdot}72, P < 0{\cdot}001$), and for equatorial elasticity ($r = +0{\cdot}63$, $P < 0{\cdot}001$). There is a considerable scatter of values in the older lenses which is due to (i) difficulties in the measurement of small strains (discussed under Methods), (ii) natural variations in the ageing and elastic properties of the lenses and (iii) small differences in strain causing apparently large changes in elasticity since this varies inversely with the strain measurements.

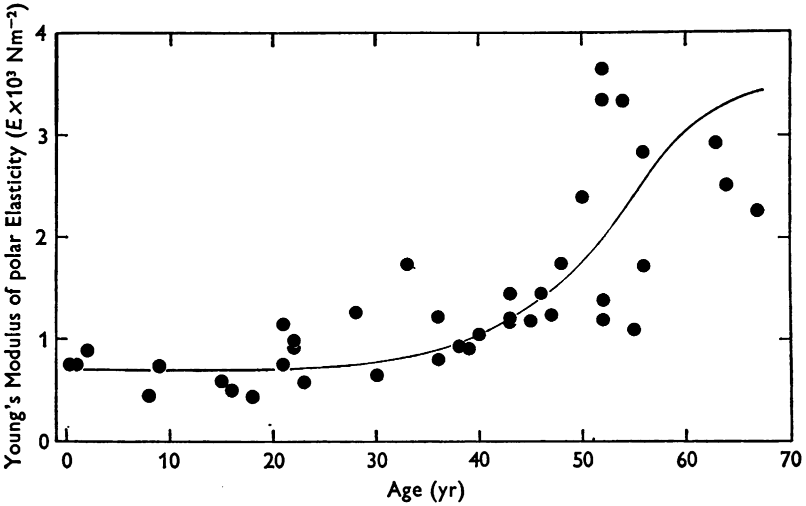

Fig. 9. Young's Modulus of equatorial Elasticity plotted against age ($N = 40$). Young's Modulus of equatorial Elasticity E_E (Nm^{-2}) calculated from $E_E = 1373 a_a^3 \rho / \delta a$ (see text), where a_a = radius of accommodated lens (m), ρ = density of lens substance (kg m^{-3}), δa = change in radius (a_a) due to spinning lens at 1000 rev/min (m).

DISCUSSION

The present results show that under conditions of physiological radial stress the human lens obeys Hooke's Law. Since, however, Young's Modulus of Elasticity varies with the direction of stress, this method has revealed the inadequacy of a simple elasticity value to describe the complex elastic properties of the lens. This complexity of lenticular strains under spinning and capsular stress is illustrated in Fig. 10, where changes in lens profiles of a 21 yr old human lens are magnified.

The profile of the spinning lens

On the right in Fig. 10 are shown (continuous lines) profile changes with a tenfold linear magnification in (A) the capsulated and (C) the decapsulated lens spinning at 1000 rev/min. The strains expected in a simple isotropic elastic body spinning at the same speed, and of the same dimensions and equatorial elasticity as the actual lens is shown by interrupted lines. The differences in strain between actual and theoretical cases is

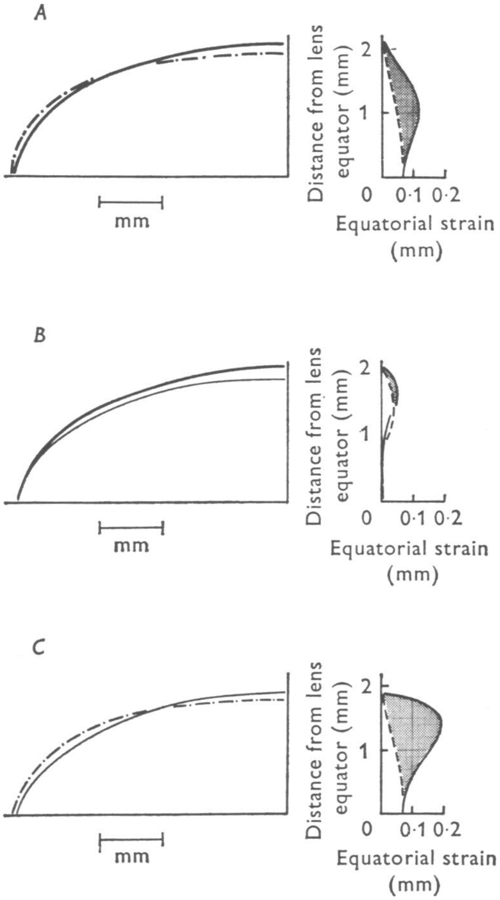

Fig. 10. The profile of spinning and decapsulated lenses: human lens (lenses of a 21 yr old cadaver). Left: profile drawn to scale. Right: horizontal changes in profile × 10; vertical distance above equator × 1. —actual profile; - - - - theoretical profile; ■ differences in profile. *A*, changes in profile between capsulated stationary and spinning lens (1000 rev/min); *B*, changes in profile following decapsulation of a stationary lens; *C*, changes in profile between *decapsulated* stationary and spinning lens (1000 rev/min).

(*a*) The theoretical profiles for *A* and *C* represent horizontal changes of radius in an isotropic elastic lens of the same dimensions, Young's Modulus of equatorial Elasticity, and spinning speed as the actual lens.

(*b*) Theoretical profile for *B* based on the assumption that the decapsulated lens retains its ellipsoidal shape.

shown by a shaded area. Since this is present whether the lens is capsulated or not it shows that a much greater degree of strain unexpectedly occurs above the equator. In the spinning decapsulated lens (*C*) the horizontal strain near the anterior pole, when due allowance has been made for vertical strains, is over twice as great as that observed at the equator and is, furthermore, irreversible even at 1000 rev/min. At the equator the theoretical and actual strains coincide since Young's Moduli of Elasticity for both lenses are equal. Moreover, since at the equator spinning stress is maximal the greatest strain takes place at this point in the theoretical lens.

A profile similar to that of the decapsulated lens can also be produced in the normal lens by spinning it at excessive speeds to produce irreversible strains thus showing that the capsule protects the underlying cortical fibres from damage at low speeds of rotation.

The large strain in the spinning lens some distance above the equator can be explained by a nucleus of low elasticity giving insufficient support to the cortex in this region. Since the radial strain at the equator is always smaller than elsewhere, always within the elastic range at high spinning speeds, and independent of the presence or absence of the capsule (compare *A* and *C*) it would seem that the equator of the cortex must be much more resistant to stress than its poles. A probable reason for this is the number of interlocking fibre junctions at suture lines (Wanko & Gavin, 1961).

The height of the plane parallel to the lens equator at which maximum strain occurs may be explained as follows. A spinning solid disk has only half the hoop stress due to centrifugal forces as a disk of similar radius possessing a small central hole. Thus two such disks of elementary thickness can be imagined spinning parallel to the lens equator. The first disk lies just above the apex of the lens nucleus and the second just below. The second disk contains at its centre a portion of the nucleus, and if the cortex of this second disk is not firmly bonded to the nucleus it virtually possesses a central hole, and hoop stress in it is twice as great as in the first disk. Thus there is a large radial strain immediately below the level of the apex of the nucleus. Furthermore, since radial strain decreases on approach to the stress resistant equator, the ratio of the distance of the plane of maximum radial strain (the plane of the second disk) from the lens equator, divided by the anterior polar depth of the lens, should be approximately equal to the ratio of the sagittal thickness of the nucleus and lens respectively, assuming that the internal structure of the lens is symmetrical. To test this hypothesis eight capsulated lenses between the ages of 26 and 38 yr were spun at 2000 rev/min to disrupt the lens. The ratio of the distance of the point of maximum strain from the equator to the anterior polar depth of the lens was found to be 0·83 while Gallati (1923) found a value of 0·75–0·8 for the ratio of nuclear to lenticular thickness for lenses of this age group. The good agreement of these ratios confirms both the explanation of the peculiar biscuit shape of the lens when spun at very high speeds (Fig. 11), and that the nucleus has a lower elasticity than the cortex in the first half of adult life.

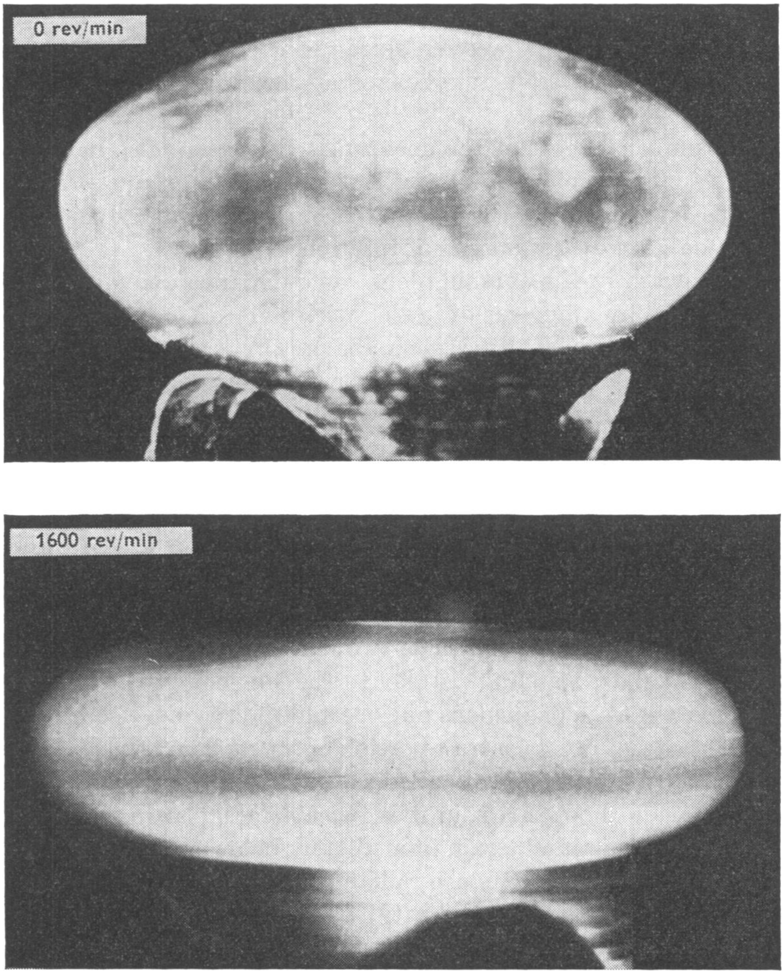

Fig. 11. Profile of a young adult human lens (26 yr old), stationary and spinning at 1600 rev/min. The lower photograph shows the form the lens assumes when elastic failure of the cortex has occurred owing to pressure from a nucleus of lower elasticity than that of the cortex.

The profile of the decapsulated lens

Fig. 10*B* shows the effect of carefully removing the capsule of a 21 yr old lens. The theoretical profile was obtained by making the radius and anterior polar depth of the capsulated and decapsulated lenses in turn the respective major and minor axes of an ellipse. The very small shaded and unshaded areas show that horizontal strains near the anterior pole of the lens are at first slightly greater, and then slightly smaller than theory would require. The apparent lack of change of equatorial radius in the decapsulated lens is due to the removal of the capsule. This reduces the increase of radius but exaggerates the decrease in polar depth at the anterior pole. However, since the capsule varies only about 0·01 mm in thickness between pole and equator the profile of the lens substance is in practice uniformly smaller in outline compared with that of a lens surrounded by an entirely unstretched capsule.

Although it cannot be assumed that the pull of the zonule changes the shape of the lens by removing all capsular stretching forces from the lens substance as does decapsulation, it would seem that the lens fibre substance is unlikely to be locally modified by the capsule, and decapsulation merely changes the anterior surface of the lens substance from one almost ellipsoidal profile to another.

Comparison of polar and equatorial elasticities in man, cat and rabbit

Table 1 shows the values of Young's Modulus of polar and equatorial Elasticities and their ratio for man, cat and rabbit. Large differences occur in Young's Modulus of polar Elasticity, the value of the adult cat lens being 21 times, and that of the young rabbit lens 5 times greater than that of the human lens. In other words, the human lens is much more easily compressed by the same force than the lenses of these animals. This fact together with the low capsular energy of the cat capsule (Fisher, 1969) makes an accommodation change in the shape of the lens in this animal impossible on mechanical grounds. A similar argument applies to the rabbit lens, and in neither case would one expect a change in lenticular shape following extirpation. Hartridge & Yamada (1922) found an increase of about 14·0D of accommodation in the cat lens following its removal from the eye but recently Vakkur & Bishop (1963) found that a small negative rather than positive dioptric power change in the lens occurs following excision. O'Neill & Brodkey (1969) have shown that the small amount of accommodation which occurs in the cat *in vivo* (1·75D) is due solely to lens movement and not to any change in lens form. As the shape of the cat lens does not change during accommodation a comparison of the ratio of polar to equatorial elasticity with the same ratio in the human lens does not further an understanding of accommodation in man. The low value of this ratio in the human lens must therefore be explained solely in terms of human lenticular accommodative changes.

The value of elasticity ratio in man of less than unity means that similar capsular compressive forces acting on the anterior pole of the lens when the lens flattens, or on the lens equator when the lens accommodates cause a much greater strain at the pole than the equator. If the lens is to change from one ellipsoidal profile to another, polar strain must be twice as great as equatorial strain (Appendix eqn. (6·1)). For this to occur with similar intra-lenticular stresses at the pole and the equator during accommodation, the ratio of polar elasticity to equatorial elasticity would have to be 0·5.

TABLE 1. Young's Modulus of Elasticity of the excised lenses of various species

	Man	Cat	Rabbit
Young's Modulus of polar Elasticity ($Nm^{-2} \times 10^{-3}$)	0·80	17·0	4·2
Young's Modulus of equatorial Elasticity ($Nm^{-2} \times 10^{-3}$)	1·3	4·8	1·3
Ratio of polar to equatorial Elasticity	0·62	3·55	3·23

Note: (*a*) Man, values from elasticity curve (Figs. 8 and 9) age 35.
(*b*) Cat, values average of three pairs of lenses, animals 1–2 yr old.
(*c*) Rabbit, values average of four pairs of lenses, animals 3–6 months old.

Thus the elastic properties of the human lens go a long way to satisfy this condition (elasticity ratio 0·7–0·62 during accommodative life). The additional polar strain required to flatten the lens into its unaccommodated ellipsoidal shape may be due to the pull of the zonule stretching the capsule further and so stressing the anterior pole of the lens more than the equator. As the anterior surface of the human lens has been shown to have an ellipsoidal profile (Fisher, 1969), the change to a more oblate ellipsoidal profile in the unaccommodated lens is very probable because of the low polar equatorial elasticity ratio.

Changes with age in the elasticity ratio (E_P/E_E) of the human lens

Fig. 12 shows the best fitting polynomial of the senile variation of the elasticity ratio. At birth the lens has nearly equal polar and equatorial elasticities, while at 63 the equality is precise. This isotropic elasticity at birth is probably due to the lens consisting almost entirely of nucleus. At the age of 30 when the elasticity ratio is minimal the differences in elasticity between pole and equator are maximal. Thereafter the difference drops until by late adult life the lens has isotropic elastic properties, while in old age the polar elasticity rises above that of the equator. The probable changes in the elasticity of nucleus and cortex which cause these complicated variations in the elasticity observed at the pole and equator of the lens are clarified by a study of a simple lens model (Appendices 4 and 5).

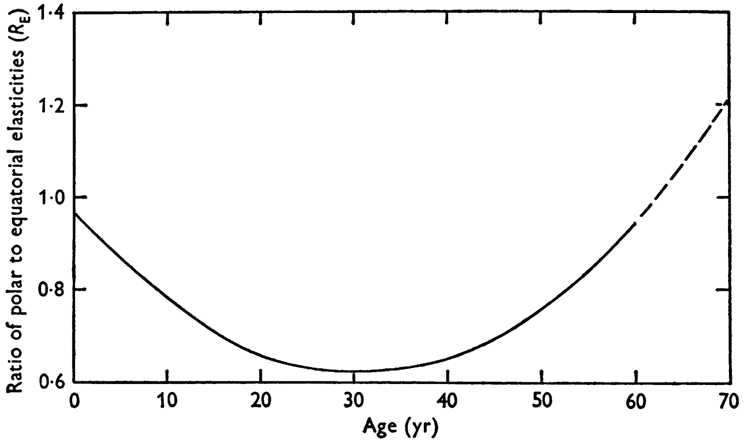

Fig. 12. Changes in the ratio of Young's Modulus of polar to equatorial Elasticity of the human lens with age (forty lenses shown in Figs. 8 and 9). Best-fitting polynomial $E_P/E_E = a + bA + cA^2$, where $E_P/E_E = R_E$ = elasticity ratio; A = age of lens in years; $a = 0{\cdot}97$; $b = -2{\cdot}32 \times 10^{-2}$; $c = 3{\cdot}75 \times 10^{-4}$. *Note*: (*a*) variance ratio = 4·53 and lies between the 1 % and 5 % critical values, (*b*) - - - extrapolated values.

Changes in Young's Modulus of Elasticity of the lens model

The changes in the profile of the spinning lens (Fig. 10) show that at a constant spinning speed (1000 rev/min) the equatorial strain is not influenced by the presence or absence of the capsule, while polar strain falls about 20 % if the capsule is removed. This small effect of the capsule on polar strain is ignored in calculations involving the proposed lens model (see Methods). Since, however, the equatorial strain of the spinning capsulated lens is a true measure of the restrictive effect of the cortical fibres on the lens nucleus, it is possible to ignore the pressure of the capsule while the lens is spinning and to calculate separately mean elasticity values of both nuclear and cortical lens fibre substance (Appendices eqns. (4·9) and (5·8)). Fig. 13 shows the best fitting polynomials for Young's Modulus of nuclear and cortical Elasticity.

Young's Modulus of nuclear Elasticity

The constant value of Young's Modulus of nuclear Elasticity before the age of 40 and the rise thereafter probably follows the change in moisture

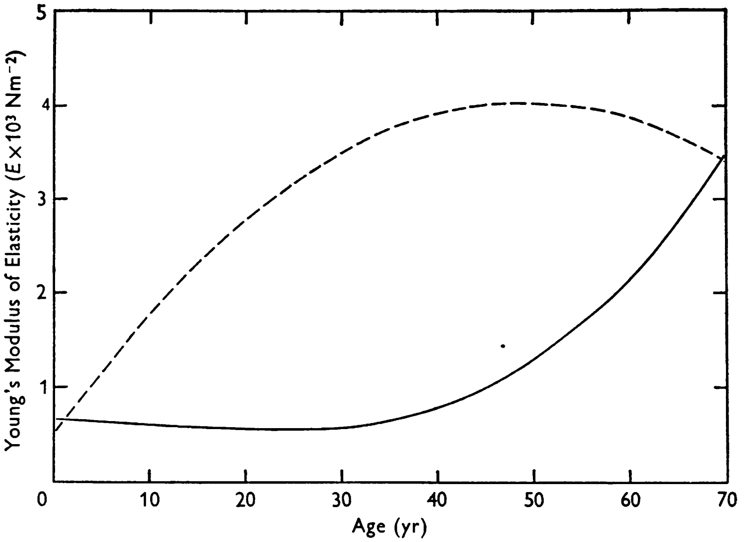

Fig. 13. Senile changes in Young's Modulus of nuclear and lenticular Elasticities predicted from the lens model.

—— *Young's Modulus of nuclear Elasticity.* Best-fitting polynomial for forty human lenses (Figs. 8 and 9).

$$E_N = a_n + b_n A + c_n A^2 + d_n A^3,$$

where E_N = Young's Modulus of nuclear Elasticity (Nm^{-2}) and A = patient's age in years.

Constants:

$$a_n = 0\cdot640, \quad b_n = -3\cdot529\times10^{-3},$$
$$c_n = 4\cdot286\times10^{-4}, \quad d_n = 1\cdot518\times10^{-5}.$$

Significance of changes in Young's Modulus of nuclear Elasticity with age:

$$r = 0\cdot595, \quad P < 0\cdot001,$$

variance ratio 14·3 in excess of 0·1 % critical point.

- - - - - - *Young's Modulus of cortical Elasticity.* Best-fitting polynomial for forty human lenses (Figs. 8 and 9).

$$E_c = a_c + b_c A + c_c A^2,$$

where E_c = Young's Modulus of cortical Elasticity (Nm^{-2}) and A = patient's age in years.

Constants:

$$a_c = 0\cdot46, \quad b_c = 1\cdot45\times10^{-1}, \quad c_c = -1\cdot484\times10^{-3}.$$

Significance of changes in Young's Modulus of cortical Elasticity with age:

$$r = 0\cdot43, \quad P < 0\cdot005,$$

variance ratio 5·83 in excess of 1 % critical point.

Note: $E_N = E_p^2/E_E$ and $E_c = E_E + 7\lambda_n^2(E_E - E_p)$ (see text) where E_p = Young's Modulus of polar Elasticity (Nm^{-2}), E_E = Young's Modulus of equatorial Elasticity (Nm^{-2}), $\lambda_n = b_a/a_a$, where b_a = anterior polar depth of lens (mm), a_a = equatorial radius of lens (mm).

content of the nucleus. Mean values for this quantity (Bellows, 1944) show a slight fall (2 %) from birth to the age of 40, whereas between 40 and 50 yrs of age the fall is much greater (6 %), while Lebensohn (1936) showed that the nucleus is the least hydrated portion of the lens. Since protein in the lens nucleus contains less than 66 % water further dehydration is likely to induce crystallization.

Crystallization in long chain molecules such as protein or raw rubber causes a rapid rise in Young's Modulus of Elasticity. In raw rubber, for example, a 25 % increase in crystallization was found to cause a one hundredfold increase in Young's Modulus of Elasticity (Leitner, 1955). But the exact senile variation of the moisture content of the human lens nucleus and its relation to the elasticity modulus requires more study.

The best fit curve in Fig. 13 for nuclear elasticity shows that very large values would be expected in old age while cortical elasticity remains constant or even falls. These predicted values of elasticity could not be measured accurately because of the small strains involved (see Methods). However, the type of elastic failure following the spinning of a lens at high speed in the older age group produces a verification of the 'hard' or high elasticity modulus of the ageing lenticular nucleus. Such a lens spun beyond its elastic limit is shown in Fig. 14. Failure in this case occurred in the cortex which yielded and produced a ridge on the unyielding nucleus. Only about one out of ten lenses had a nucleus of sufficiently high Young's Modulus of nuclear Elasticity to show this effect. Nevertheless, this experiment well illustrated the differences between the elasticity moduli of cortex and nucleus predicted by the mathematical lens model.

Young's Modulus of cortical Elasticity

Fig. 13 shows that there is a continuous rise in Young's Modulus of cortical Elasticity until about 50 yrs of age. Its subsequent decrease may be due to sampling errors in a population of ageing lenses of constant elasticity.

The continuous rise of Young's Modulus of cortical Elasticity during the first 30 yr of life, when changes in the moisture content of the lens are probably very small, requires an explanation different from that given for the rapid rise in Young's Modulus of nuclear Elasticity after 40 yr of age. Such a rise could be caused by a senile shift in the proportion of long to short chain protein molecules within the cortical lens fibres. This would require to be in favour of proteins of smaller chain length since Young's Modulus of Elasticity is approximately inversely proportional to mean chain length (Treolar, 1967).

François & Rabaey (1957) found that following electrophoresis the Anlage of cortical proteins of a 14-month-old human lens differed considerably from that of a lens of 25, but later in a 42 yr old lens the change in protein fractions was small. Thus continuous changes in the constituent concentrations of cortical lens protein fractions occur within the first 30 yr of life. In addition, the electrophoretic patterns show that the main trend was towards a higher percentage of proteins with lower molecular weight and therefore shorter chain length (François, Rabaey & Wieme, 1955).

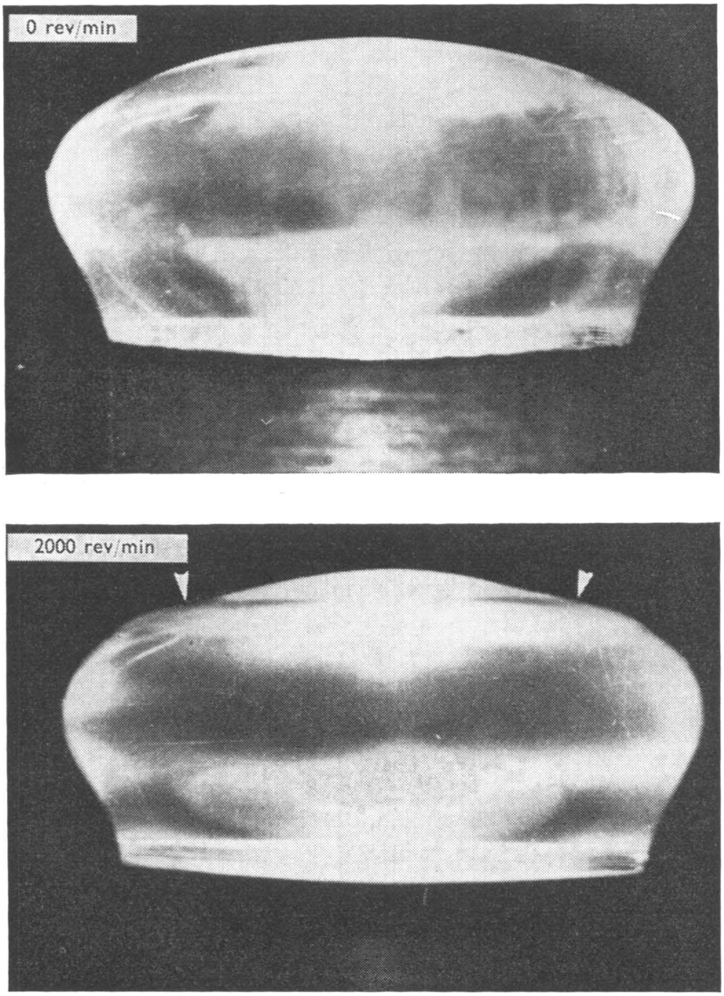

Fig. 14. Profile of an old adult human lens (67 yr of age) at rest and spinning at 2000 rev/min. The second profile shows the form the lens assumes when elastic failure of the cortex has occurred around a nucleus with a Young's Modulus of Elasticity higher than that of the cortex. *Note*: arrow shows point of failure of the cortex.

Since moisture loss and subsequent protein crystallization are unlikely, the rapid rise in Young's Modulus of cortical Elasticity would require either (*a*) an increasing synthesis of lower molecular weight protein during each addition of cortical fibres to the growing lens or (*b*) senile increase in the recurrence of cross-linkages between adjacent protein molecules. This would also reduce the mean chain length.

The change in concentration of the various cortical lens proteins as age advances favours the former hypothesis but further determinations both electrophoretic and elastic, preferably on isolated cortical fibres of the same lens, are required to establish the exact relationship between this changing pattern of cortical protein synthesis and the rising value of Young's Modulus of Elasticity.

Young's Modulus of lenticular Elasticity and accommodation

Figs. 8 and 9 show that Young's Modulus of polar Elasticity is, at the age of 15, $0{\cdot}7 \times 10^3$ (Nm^{-2}) and $0{\cdot}9 \times 10^3$ (Nm^{-2}) for equatorial elasticity; at the age of 60, both equal 3×10^3 (Nm^{-2}). The effect of an increase in Young's Modulus of Elasticity of the lens is estimated most easily on the assumption that it is an isotropic elastic body. Fig. 12 shows that at 60 yr of age the ratio of polar and equatorial elasticities is 0·98 and therefore the condition is satisfied. At 15 yr of age this ratio is only 0·7 with a mean value of $0{\cdot}8 \times 10^3$ (Nm^{-2}); this differs by only 10 % from either polar or equatorial elasticity and the assumption of isotropicity introduces no great error.

The energy required to deform an elastic body is proportional to Young's Modulus of Elasticity and the square of the strain produced.

Then if

W = amount of energy per unit volume required to deform the lens,

E_L = Young's Modulus of lens Elasticity,

δa = change in equatorial radius of lens,

a_a = equatorial radius of lens (accommodated),

$$W \propto (\delta a/a_a)^2 . E_L.$$

In order to calculate solely the effect of the increase of Young's Modulus of Elasticity of the lens it is assumed that the available capsular energy and the lenticular volume remain constant between the ages of 15 and 60 yr. Thus

$$\frac{\delta a_{60}}{\delta a_{15}} = \frac{a_{a60}}{a_{a15}} \sqrt{\left(\frac{E_{L15}}{E_{L60}}\right)},$$

where

$$\delta a_{15} = 4{\cdot}25 \text{ mm}, \quad \delta a_{60} = 4{\cdot}60 \text{ mm}, \quad E_{L15} = 0{\cdot}8 \times 10^3 \text{ Nm}^{-2},$$
$$E_{L60} = 3 \times 10^3 \text{ Nm}^{-2}.$$

Hence the ratio of the changes in radius of lenses 60 and 15 yr old respectively is 0·56. If there were no change in shape or size of the lens with age the amplitude of accommodation throughout life would remain proportional to the change in radius of the lens (Fisher, 1969). On the above assumptions therefore accommodation is reduced in the same proportion as the change in radius. Thus the change in accommodation at 60 is 56 % of that at the age of 15, or the loss of accommodation due solely to an increase in lens substance elasticity is 44 %.

This estimate of the loss of accommodation due to a rise in Young's Modulus of the lens has to be modified once some of the above assumptions are abandoned and a decrease in energy from the capsule or ciliary body, or the change in shape of the lens with age is also introduced.

An assessment of the influence of these factors on accommodation forms the subject of a subsequent paper.

I would like to acknowledge the encouragement given to me by Dr R. A. Weale, the technical assistance and painstaking measurement of all the original photographs by Mrs B. Pettet, the method of photographing the lens fibre system, Fig. 1, by Dr John Mellerio, the computer programming by Mr Brian Augier, the expert manufacture of the spinning equipment by Mr G. R. Mould, and drawings Fig. 3 and Fig. 15 by Mr T. R. Tarrant.

APPENDIX

1. *Young's Modulus of equatorial and polar Elasticity*

From Fig. 15, when lens is spinning let:

ρ = density of lens substance (kg m^{-3}),

ω = speed of rotation of the lens (rad s^{-1}),

x = radius of elementary segment $ABCD$ (m),

x_a = radius of elementary disk (m),

δx = increase in radius of elementary segment (m),

$\delta\theta$ = angle subtended at axis of rotation by elementary segment $ABCD$ (rad),

y = perpendicular distance of elementary disk from the plane of the lens equator (m),

δy = thickness of elementary disk (m),

f_x = radial stress per unit area (Nm^{-2}),

f_c = circumferential stress per unit area (Nm^{-2}),

μ = peripheral radial strain in elementary disk,

$\delta\lambda$ = axial polar strain in elementary disk,

E_E = Young's Modulus of equatorial Elasticity (Nm^{-2}),

E_P = Young's Modulus of polar Elasticity (Nm^{-2}),

m = reciprocal of Poisson's ratio,

a_a = equatorial radius of the accommodated lens (m),

δa = increase in equatorial radius of the lens (m),

b_a = perpendicular distance of anterior pole from the equatorial plane of the lens (m),

δb = decrease in distance of anterior pole from the equatorial plane of the lens due to rotation (m).

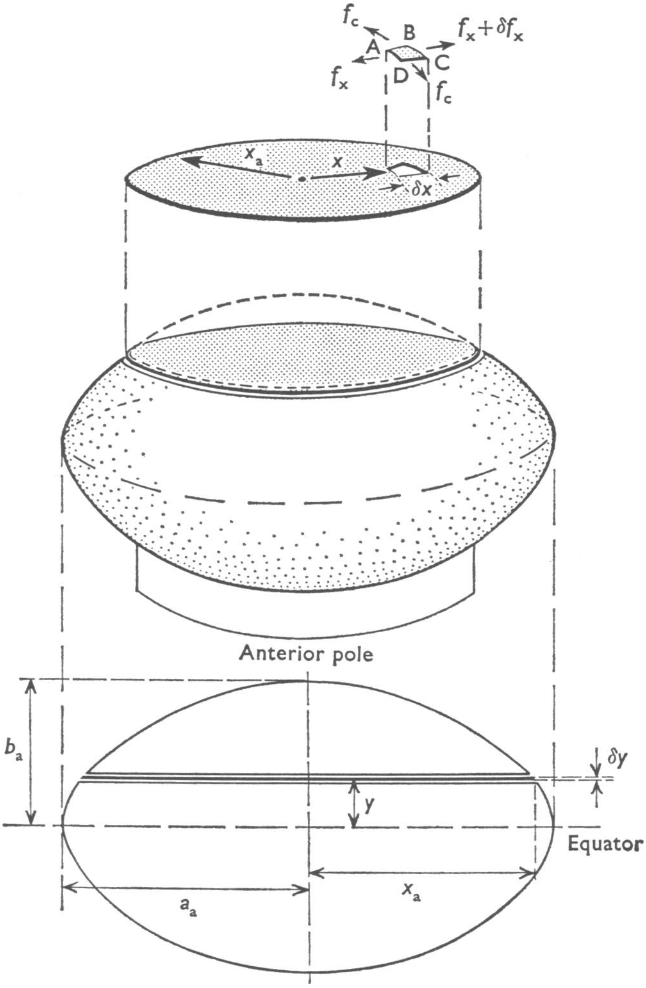

Fig. 15. Diagram showing forces acting on the spinning lens. The shaded area represents an elementary disk spinning about the anterior-posterior polar axis of the lens. The small segment *ABCD* is removed from the disk to show the forces acting upon its faces.

Values of stress in an elementary spinning disk (Fig. 15)

Consider a small element of the elementary disk *ABCD*. On the flat surface of the disk there is no normal induced stress and shear stresses are considered to be negligible (see Methods). Then the radial force on element *ABCD* due to rotation $= (\rho\omega^2 x) \times (\delta y) \times (x\delta\theta) \times (\delta x)$ (force on *AD* plus resolved forces on faces *AB* and *DC* minus force on *BC*)

$$= \left\{f_{\mathrm{x}} x\,\delta\theta + 2f_{\mathrm{c}}\,\delta x \sin\frac{\delta\theta}{2} - (f_{\mathrm{x}} + \delta f_{\mathrm{x}})(x+\delta x)\,\delta\theta\right\}\delta y.$$

In the limit $\delta x = 0$. Then

$$f_{\mathrm{c}} = f_{\mathrm{x}} + x\frac{\mathrm{d}(f_{\mathrm{x}})}{\mathrm{d}x} + \rho\omega^2 x^2. \qquad (1\cdot1)$$

Now since the radial strain tends to increase while centrifugal strain decreases,

$$\text{Circumferential strain} = \mu/x$$

$$= \frac{1}{E_{\mathrm{E}}}\left(f_{\mathrm{c}} - \frac{f_{\mathrm{x}}}{m}\right). \qquad (1\cdot2)$$

In a similar way

$$\text{Radial strain} = \mathrm{d}\mu/\mathrm{d}x$$

$$= \frac{1}{E_{\mathrm{E}}}\left(f_{\mathrm{x}} - \frac{f_{\mathrm{c}}}{m}\right). \qquad (1\cdot3)$$

Differentiating (1·2) and eliminating

$$f_{\mathrm{c}} - f_{\mathrm{x}} + \frac{m}{m+1}\,x\frac{\mathrm{d}(f_{\mathrm{c}})}{\mathrm{d}x} - \frac{1}{m+1}\,x\frac{\mathrm{d}(f_{\mathrm{x}})}{\mathrm{d}x} = 0.$$

Substituting the value $(f_{\mathrm{c}} - f_{\mathrm{x}})$ from (1·1), then

$$\frac{\mathrm{d}}{\mathrm{d}x}\left\{f_{\mathrm{c}} - f_{\mathrm{x}}\right\} + \frac{m+1}{m}\rho\omega^2 x = 0.$$

Thus

$$(f_{\mathrm{c}} + f_{\mathrm{x}}) = \kappa_1\frac{m+1}{2m}\rho\omega^2 x^2, \qquad (1\cdot4)$$

where κ_1 is a constant.

Substituting the value of f_{c} in (1·1)

$$2f_{\mathrm{x}} + x\frac{\mathrm{d}(f_{\mathrm{x}})}{\mathrm{d}x} + \rho\omega^{\mathrm{L}} x^2 = \kappa_1 - \frac{m+1}{2m}\rho\omega^2 x^2.$$

Multiplying each side by x and rearranging

$$\frac{\mathrm{d}}{\mathrm{d}x}(x^2 f_{\mathrm{x}}) = \kappa_1 x - \frac{3(m+1)}{8m}\rho\omega^2 x^3.$$

Thus

$$f_{\mathrm{x}} = \frac{\kappa_1}{2} + \frac{\kappa_2}{x^2} - \frac{3(m+1)}{8m}\rho\omega^2 x^2. \qquad (1\cdot5)$$

From (1·4)
$$f_c = \frac{\kappa_1}{2} - \frac{\kappa_2}{x^2} - \frac{m+3}{8m}\rho\omega^2x^2, \tag{1·6}$$
where κ_2 is a constant.

The values of κ_1 and κ_2 are obtained from the boundary conditions when $x = x_a$, then $f_x = 0$ and $x_a = 0, \mu = 0$. Thus

$$f_x = \frac{3m+1}{8m}\{x_a^2 - x^2\}\rho\omega^2, \tag{1·7}$$

$$f_c = \frac{1}{8m}\{(3m+1)x_a^2 - (m+3)x^2\}\rho\omega^2. \tag{1·8}$$

If there is no change in volume $m = 2$ (Poisson's ratio = 0·5). Then

$$f_x = \tfrac{7}{16}(x_a^2 - x^2)\rho\omega^2 \tag{1·9}$$

and
$$f_c = \tfrac{1}{16}(7x_a^2 - 5x^2)\rho\omega^2. \tag{1·10}$$

2. *Young's Modulus of equatorial Elasticity*

The total equatorial strain for a given speed from (1·3)

$$\int_0^{\delta_a} d\mu = \delta a = \frac{1}{E_E}\int_0^{a_a}\left(f_x - \frac{f_c}{m}\right)dx. \tag{2·1}$$

Thus from eqns. (1·9) and (1·10) and (2·1) substituting and integrating with respect to dx

$$E_E = a_a^3\rho\omega^2/8\delta a. \tag{2·2}$$

3. *Young's Modulus of polar Elasticity*

Maximum stress occurs at the centre of rotation of the lens where $x = 0$, and hoop and radial stresses are equal.

Thus from eqns. (1·9) or (1·10)

$$f_c = f_x = \tfrac{7}{16}x_a^2\rho\omega^2. \tag{3·1}$$

The change in thickness of an elementary disk at its centre is produced by the forces f_c and f_x acting at right angles and perpendicular to the strain.

$$\text{Thus strain} = \delta\lambda/\delta y. \tag{3·2}$$

In the limit $\delta y \to 0$

$$\frac{d\lambda}{dy} = \frac{1}{E_P}\left\{\frac{f_c}{m} + \frac{f_x}{m}\right\}.$$

Integrating with respect to $\mathrm{d}\lambda$ and $\mathrm{d}y$,

$$\int_0^{\delta b} \mathrm{d}\lambda = \delta b = \frac{1}{E_P}\int_0^{b_a}\left(\frac{f_x}{m}+\frac{f_c}{m}\right)\mathrm{d}y \tag{3·3}$$

if there is no change in lenticular volume and $m = 2$.

Thus from eqns. (3·1) and (3·3)

$$\delta b = \frac{7\rho\omega^2}{16E_P}\cdot\int_0^{b_a} x_a^2\,\mathrm{d}y. \tag{3·4}$$

Now if the anterior surface of the lens is an ellipsoid of revolution then

$$\frac{x_a^2}{a_a^2}+\frac{y^2}{b_a^2} = 1. \tag{3·5}$$

Thus from eqns. (3·4) and (3·5) integrating with respect to and rearranging

$$E_P = \tfrac{7}{24}\cdot a_a^2 b_a \rho\omega^2/\delta b. \tag{3·6}$$

4. *Young's Modulus of Elasticity of the nucleus of the lens model*

Young's Modulus of Elasticity of lens model

From Fig. 16 for the stationary lens:

E_N = Young's Modulus of Elasticity of the nucleus of the model (Nm^{-2}).
f_y = a polar stress acting on the nucleus of the model (Nm^{-2}),
f_x = equal equatorial stresses acting on the nucleus of the model at right angles to each other (Nm^{-2}),
e_y = polar strain of nucleus due to stress f_y,
e_x = equatorial strain of nucleus due to stress f_x,
e'_x = equatorial strain of nucleus if cortex were absent,
α = ratio of nuclear strain with a cortex, to nuclear strain if cortex of model were absent.

From Fig. 15 for the spinning lens:

δa = change in equatorial radius of the lens due to spinning (m),
$\delta a'$ = change in equatorial radius of the lens spinning at the same speed if the lens had an isotropic elastic modulus equal to that deduced from the strain observed at the anterior pole (m).

Since f_x acts on the nucleus in two horizontal directions at right angles and the nucleus has isometropic elasticity:

axial strains
$$e_y = \frac{f_y}{E_N}-\frac{2f_x}{mE_N}, \tag{4·1}$$

equatorial strain $$e_{\mathrm{X}} = \frac{f_{\mathrm{X}}}{E_{\mathrm{N}}} - \frac{f_{\mathrm{X}}+f_{\mathrm{Y}}}{mE_{\mathrm{N}}}, \tag{4·2}$$

if nucleus were free to expand $f_{\mathrm{X}} = 0$.

Thus from (4·2) $$e'x = -f_{\mathrm{Y}}/mE_{\mathrm{N}}. \tag{4·3}$$

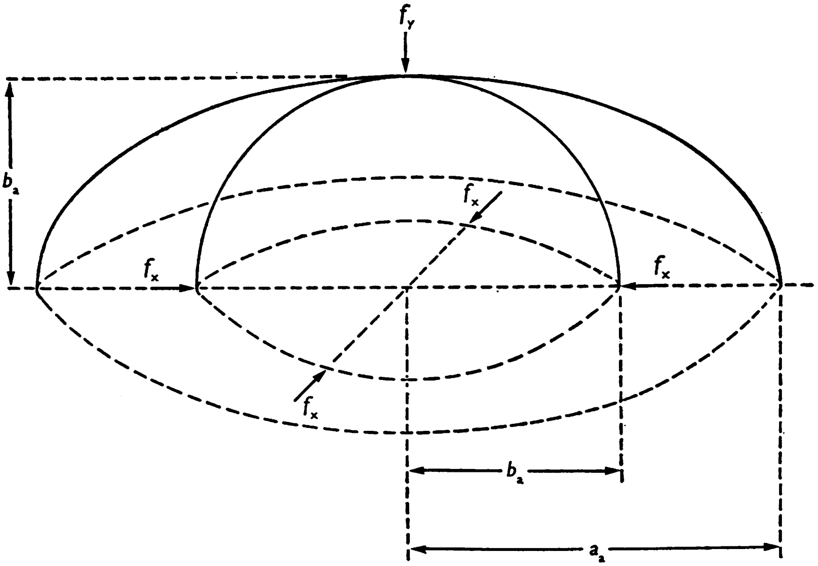

Fig. 16. Diagram of the lens model. The radius of the nucleus of the lens is made equal to the anterior polar depth of the lens (b_a), while the constraint of cortical fibres on the nucleus of the model is estimated from the observed external strains at the pole and equator when the lens is spinning.

Now $$\alpha = e_{\mathrm{X}}/e'x.$$

From (4·3) and (4·2)

$$f_{\mathrm{Y}} \cdot \frac{-\alpha}{mE_{\mathrm{N}}} = \frac{f_{\mathrm{X}}}{E_{\mathrm{N}}} - \frac{f_{\mathrm{X}}+f_{\mathrm{Y}}}{E_{\mathrm{N}}}, \tag{4·4}$$

or $$f_{\mathrm{X}} = \frac{1-\alpha}{m-1} \cdot f_y \tag{4·5}$$

From (4·1) and (4·5) allowing $m = 2$,

$$E_{\mathrm{N}} = \alpha f_{\mathrm{Y}}/e_{\mathrm{Y}}.$$

Now $f_{\mathrm{Y}}/e_{\mathrm{Y}}$ is the elasticity due to cortical constraint on the observed elasticity at the lens pole E_{P}. Thus

$$\alpha = f_{\mathrm{Y}}/e_{\mathrm{Y}} = \alpha E_{\mathrm{P}} = E_{\mathrm{N}}. \tag{4·6}$$

From the definitions of δa and $\delta a'$ and appendix eqn. (2·2)

$$\delta a/\delta a' = E_{\mathrm{P}}/E_{\mathrm{E}}. \tag{4·7}$$

Now $\delta a/\delta a'$ is derived from the observed effect of cortical fibre constraint on the external surface of the intact lens. Since E_{P} does not differ greatly from E_{E} this value is taken as representing the constraint of the cortex on the nucleus. Thus

$$\delta a/\delta a' = \alpha = E_{\mathrm{P}}/E_{\mathrm{E}}, \tag{4·8}$$

thus from (4·6) and (4·8)

$$E_{\mathrm{N}} = E_{\mathrm{P}}^2/E_{\mathrm{E}}. \tag{4·9}$$

5. *Young's Modulus of Elasticity of lens model cortex*

When the lens is spinning (Fig. 15) let:

E_{c} = Young's Modulus of Elasticity of cortex of the lens model (Nm^{-2});
f_{s} = radial stress in a solid disk at a radius (b_{a}) from axis of rotation (Nm^{-2});
f_{xs} = radial stress in a composite disk of nucleus and cortex at radius (b_{a}) from axis of rotation (Nm^{-2});
λ_{n} = ratio of radius of nucleus to the equatorial radius of the lens model ($b_{\mathrm{a}}/a_{\mathrm{a}}$);
δah = change in equatorial radius of a lens model consisting only of cortex with a hollow spherical centre radius (m).

Boundary conditions

The two extremes which have to be considered are a young adult lens with a nucleus of very low elasticity, and a lens of about 60 yr old when the nucleus and the cortex have similar elasticities. If no cohesive force exists between nucleus and cortex in the young lens, $f_{\mathrm{xs}} = 0$ and the disk at the equator has a central hole of radius b_{a}.

Thus when $f_{\mathrm{xs}} = 0$, $x = b_{\mathrm{a}}$ and also $x = a_{\mathrm{a}}$. From eqns. (1·5) and (1·6)

$$f_{\mathrm{x}} = \frac{1}{16}\left\{7a_{\mathrm{a}}^2 + 7b_{\mathrm{a}}^2 + \frac{7a_{\mathrm{a}}^2 b_{\mathrm{a}}^2}{x^2} - 7x^2\right\}\rho\omega^2, \tag{5·1}$$

$$f_{\mathrm{c}} = \frac{1}{16}\left\{7a_{\mathrm{a}}^2 + 7b_{\mathrm{a}}^2 + \frac{7a^2 b_{\mathrm{a}}^2}{x^2} - 5x^2\right\}\rho\omega^2. \tag{5·2}$$

Substituting boundary conditions and integrating as before

$$\delta a = \frac{a_{\mathrm{a}}^3}{8E_{\mathrm{c}}}(7\lambda_{\mathrm{n}}^2 + 1)\rho\omega^2, \quad \text{where} \quad \lambda_{\mathrm{n}} = b_{\mathrm{a}}/a_{\mathrm{a}}. \tag{5·3}$$

Now from (2·2)

$$\delta a = \frac{a_{\mathrm{a}}^3}{8E_{\mathrm{E}}}\rho\omega^2.$$

Thus if such a cortex without nuclear adhesion has the same strain as that observed in the actual lens. Then

$$\delta ah = \delta a \tag{5·4}$$

and

$$E_c = \Delta E_E, \quad \text{where} \quad \Delta = (7\lambda_n^2+1). \tag{5·5}$$

The boundary conditions of Δ are

$$\Delta = (7\lambda_n^2+1) \quad \text{when} \quad f_{xs} = 0$$

and

$$\Delta = 1 \quad \text{when} \quad f_{xs} = f_s.$$

Now f_{xs} depends on the absolute values of E_N and E_c and these are unknown, so for an approximate solution let f_{xs} be linearly related to Δ within the boundary conditions. Thus $\Delta = af_{xs}+b$ where a and b are constants.

From the boundary conditions

$$a = -7\lambda_n^2/f_s,$$

$$b = 7\lambda_n^2+1.$$

Thus

$$\Delta = 1+7\lambda_n^2(1-f_{xs}/f_s). \tag{5·6}$$

Now the force between the nucleus of the spinning model and its cortex f_{xs} is proportional to the apparent elasticity of the isotropic elastic sphere radius b_a. This apparent elasticity is measured at the anterior pole of the actual lens and is therefore E_P.

Thus $f_{xs} = kE_P$ where k is a constant when

$$f_{xs} = f_s, \quad E_P = E_E,$$

therefore

$$k = f_s/E_E,$$

thus

$$f_{xs}/f_s = E_P/E_E. \tag{5·7}$$

Combining eqns. (5·5), (5·6) and (5·7)

$$E_c = E_E+7\lambda_n^2(E_E-E_P). \tag{5·8}$$

6. *Changes in polar and equatorial strains of the lens for the profile to remain ellipsoidal*

If there is no change in the anterior volume of the lens for an ellipsoid of revolution the volume is

$$\tfrac{2}{3}\pi a_a^2 b_a = \tfrac{2}{3}\pi(a_a+\delta a)^2(b_a-\delta b).$$

Neglecting products of the second order

$$2a_a . b_a . \delta a = \delta b a_a^2,$$

or

$$2\times(\delta a/a_a) = \delta b/b_a. \tag{6·1}$$

Thus the polar strain equals double the equatorial strain.

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