THE SIGNIFICANCE
OF THE SHAPE OF THE LENS AND CAPSULAR ENERGY
CHANGES IN ACCOMMODATION

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SUMMARY

1. A method for the estimation of the energy released by the anterior part of the lens capsule during accommodation is described. This includes

(i) A determination of the pressure required to distend the capsule by a standard volume.

(ii) The calculation from the photographed lens profiles of the degree of capsular contraction which occurs when the lens changes from the un-accommodated to the accommodated form.

(iii) Capsular volume changes *in vitro* are then related to the surface area changes calculated for the lens *in vivo*.

2. A correlation exists between the stored capsular energy per unit area or surface tension and the accommodation power of different species. The human lens capsule releases 1170 ergs/cm^2 while the more spherical lenses of the cat and rabbit release 520 and 485 ergs/cm^2 respectively for a 10 % change in lens diameter. The amount of energy which can be stored depends on the degree of flatness of the lens and the volume of the anterior segment. The flatter the lens and the smaller the volume of the anterior segment, the greater the capsular surface tension.

3. The anterior surface of the human lens remains ellipsoidal throughout life. The changes of accommodation which occur in presbyopia may therefore be related to the lens profiles at various ages. It is found that a coefficient obtained by dividing the anterior volume of the lens by the 5th power of the equatorial radius of the lens modifies the degree of accommodation for a given change of lens diameter.

4. The loss of accommodation is proportional to the effective capsular surface energy until about the age of 45. The effective capsular surface energy can be defined as the energy which gives the same change in lens dioptric power per erg regardless of the lenticular profile changes which occur with age. It is obtained by multiplying capsular surface tension at a

given age by a ratio. This is obtained by dividing the profile coefficient mentioned in paragraph 3 of the given lens, by the profile coefficient of the reference lens aged 15 (0·068). The effective surface energy of the entire lens falls from 110 ergs at the age of 15 to 50 ergs at 60. Assuming that ciliary power remains unaltered 55 % of the loss of accommodation is accounted for solely by the fall in Young's Modulus of elasticity of the capsule and the changing shape of the lens with age.

INTRODUCTION

When Young's Modulus of elasticity of human lens capsule was found to have a value over 10 times as great as human aortic tissue (Fisher, 1969) it was thought that the accommodative power of the human lens may reside in the elastic strength of its capsule. To test this hypothesis, the elastic moduli of cat and rabbit lens capsules were determined: they are much lower than in man.

This seemed to confirm the idea that the human lens capsule could mould its lens more effectively than the capsule of animals which have less accommodation. The importance of the lens capsule in moulding the shape of the lens was stressed particularly by Fincham (1925) who considered that the lens substance had a purely passive role and was plastic in nature. Weale (1962) suggested that the lens substance had limited elastic properties of its own. A more precise idea of the function of the lens capsule in accommodation may be obtained by considering it as an elastic skin surrounding the lens cortex and free to slide upon it. It can thus be regarded as a surface which stores energy in the same way as the surface of a fluid and its effect measured in units similar to those of surface tension, namely, ergs per unit area (ergs/cm^2). However, this is not a perfect analogy since the surface tension of a pure fluid is independent of extension. In the case of the lens capsule, the force required to extend the capsule is proportional to the extension (Fisher, 1969).

The aim of the present experiments was to examine the relationship between the change in surface tension of the lens capsule during accommodation and the accommodative power of the lens. A linear relationship would be expected in each species, if similar amounts of energy are required to mould the lens substance which is assumed to be elastic, and sufficient ciliary power exists to return the lens to the unaccommodated state. In man as the lens capsule is 5–6 times thicker anteriorly than posteriorly (Salzmann, 1912), equal strains in these portions of the capsule would require forces proportional to their thickness. In a study of the distribution of fibres within the zonule Kaczurowski (1964) indicates that a much greater force is applied to the anterior capsule, since the zonular fibres passing

forwards are much thicker and more numerous than elsewhere. Moreover, the zonule is attached to the equator of the lens so that capsular movement across the equator and perpendicular to the zonule is likely to be small. These facts indicate that the strain in the anterior capsule is probably as great or greater than posteriorly. If this be so 5–6 times as much energy can be stored in the anterior capsule since 5–6 times as great a force will be required to stretch it. This is further confirmed by an observation of Fincham (1925) that 'Probably little moulding of the posterior portion of the lens occurs as the posterior polar radius of curvature hardly changes during accommodation'. In this investigation, therefore, only the profile of the anterior surface of the lens was considered. The increase in capsular surface tension (energy per unit area) can be calculated if determinations are made (*a*) of the force required to stretch the capsule by a given amount, and (*b*) of the degree of stretching of the capsule when the eye returns to the unaccommodated state. Two methods were employed to determine these values.

First, the force was measured by recording the pressure required to stretch the capsule by a given amount. This amount was estimated by noting the increase in volume of fluid which the capsule could enclose. Secondly, the degree of stretching was calculated from photographs of the profile of the lens.

METHODS

Material

Six specimens each of rabbit and cat capsules were examined by the method used for the thirty human lens capsules described in the previous paper (Fisher, 1969). From a different source, a further twenty-four human lenses were obtained for profile determinations, their post mortem ages being 24 hr or less.

Force of capsular distension

Characteristics of the capsule pressure chamber. The central part of the anterior capsule was distended into a portion of a sphere in the pressure–volume apparatus (Fisher, 1969). The volume of this spherical segment (*v*) and the pressure (*P*) required to change it by one microlitre was obtained using values from corrected pressure–volume curves previously described. Since only distension pressure was required the difficulties in the measurement of capsular thickness and Poisson's ratio, necessary for the evaluation of Young's Modulus of elasticity were not encountered.

Lens moulding pressure. Absolute values of the initial and final lens moulding pressures before and after accommodation could only be obtained by direct measurement upon the intact lens. At present this has not proved possible since the leakage consequent upon puncture of the capsule with a manometric needle has so far proved unavoidable.

However, above the age of 45 the final lens moulding pressure of the accommodated lens is probably about zero, since no residual capsular tension was found in six excised lens between the ages of 45 and 60. This lack of capsular tension was demonstrated in the following way. The capsule of the excised lens was carefully cut around the equator by the aid of an operating microscope. When the incision was completed no gaping of the capsule occurred. Furthermore, no change in shape of the lens could be demonstrated by serial photography of the lens profile (described later). In young lenses the residual tension of the

TABLE 1. Basic lens data for the calculation of energy values

Lens	Energy value E_a	$\delta V_p/2$	δV	Unaccommodated lens h_u	A_u	b_u	a_u	Accommodated lens h_a	R_m	A_a	b_a	a_a	p	V_u	vR	v	P
Human lenses																	
Neonatal	36	5·0	5·8	1·87	55·7	1·78	3·6	1·73	4·7	51·6	2·4	3·1	1·73	48·5	33·5	16·7	12·0
Age 15	108	7·7	11·3	1·95	79·6	1·82	4·5	1·77	6·5	72·6	2·3	4·0	1·36	77·0	23·6	10·1	29·0
Age 43	79	4·8	13·2	1·72	99·2	1·63	5·2	1·55	9·2	89·9	2·0	4·7	0·73	92·5	23·5	9·7	26·5
Age 65	47	2·3	16·5	1·83	111·9	1·81	5·4	1·64	9·7	100·0	2·2	4·9	0·28	110	15·0	5·0	20·0
Cat	75	1·8	35·8	4·40	210·0	3·44	7·0	4·15	7·6	198·0	4·0	6·5	0·094	352	14·7	4·7	17·2
Rabbit	65	2·2	23·6	4·49	178·0	3·49	6·25	4·28	6·3	169·5	4·1	5·75	0·187	284	15·9	6·1	21·0

Column descriptions:

- E_a — WORK DONE BY ANTERIOR PART OF CAPSULE (mm change in lens diameter (ergs))
- $\delta V_p/2$ — MEAN CAPSULAR MOULDING PRESSURE (mm Hg)
- δV — CHANGE IN VOLUME OF EQUIVALENT SPHERICAL SEGMENT (μl.)
- h_u — Depth of equivalent spherical segment (mm)
- A_u — Surface area of anterior part of lens (mm²)
- b_u — Distance of anterior pole from lens equator (mm)
- a_u — Radius of equator of the lens (mm)
- h_a — Depth of equivalent spherical segment (mm)
- R_m — Mean radius of curvature of anterior lens profile (mm)
- A_a — Surface area of anterior part of lens (mm²)
- b_a — Distance of anterior pole from lens equator (mm)
- a_a — Radius of equator of the lens (mm)
- p — CAPSULAR MOULDING PRESSURE PER UNIT CHANGE OF VOLUME (mm Hg/μl.)
- V_u — Volume of anterior segment of lens (mm³)
- vR — Volume × radius of curvature of capsule in apparatus (mm⁴)
- v — Volume of capsular segment in apparatus (mm³)
- P — Pressure per unit change of volume in apparatus (mm Hg/μl.)

capsule could be approximately assessed by the change in thickness of the lens which occurred with the previous procedure. In five lenses between the ages of 17 and 22 examined not longer than 8 hr after death, 0.13 ± 0.33 mm (s.d.) change in anterior thickness occurred. This represents only 27 % of the change (0.48 mm) during accommodation (Table 1, b_a 2.3, $b_u = 1.82$) and probably about the same percentage of the total change in moulding pressure (Appendix Eqns. (3.4) and (4.1)). The change in moulding pressure in the young lens during accommodation was about 15.4 mm Hg (mean pressure 7.7 mm, 15-year-old lens Table 1). Thus the final pressure in the accommodated lens was about 27 % of this value and under 4.0 mm Hg.
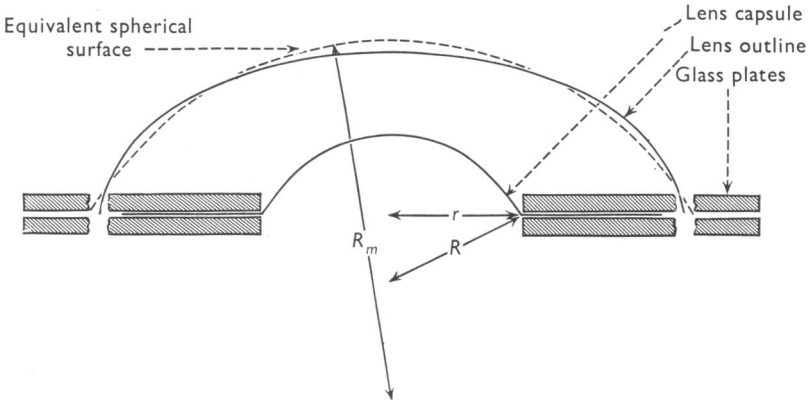

Fig. 1. Diagram showing the outline of the anterior lens surface superimposed upon the glass plates of the distension apparatus. The capsule in the apparatus surrounds an incompressible fluid which is allowed to change in volume, while the capsule in the *in vivo* lens surrounds incompressible fibres which alter in shape but not in volume. This change in shape is related to a volume change in an equivalent spherical segment of capsule having the same area as the anterior surface of the *in vivo* lens. R_m is the mean radius of curvature of the anterior lens surface. R is the radius of curvature of the capsule between the glass plates. r is the radius of curvature of the glass plate perforation (2 mm).

If therefore we assume that the moulding pressure in the accommodated lens is zero at all ages the role of the capsule in moulding the young lens, in terms of the amount of energy which can be stored, will be underestimated by about one third. Moreover, this assumption gives the lowest moulding pressure in the accommodated lens and the least amount of capsular energy which can be stored during accommodation, regardless of age.

To evaluate this lens moulding pressure the portion of capsule *in vitro* was considered to be representative of the entire anterior lenticular capsule *in vivo* (Fig. 1). Thus, if instead of only the central portion, the entire capsule were assumed to be in the distension chamber, the pressure (p) required to distend it by one microlitre could be calculated from Appendix Eqn. (1.2). The actual volume of the anterior portion of the lens (V_u) was much greater than the experimental spherical segment (v) and the calculated pressure required to effect the same volume change was in consequence much less. A typical value was 0.63 mm/Hg μl. ($P = 20$ mm Hg, $Rv = 15$, $R_m = 8$, $V_u = 80$).

Profile of the lens

The lens was placed upon a ring whose dimensions were such as to prevent the lens from sagging either into or outside the ring support. 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. Illumination of the lens was made 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 and the lens rotated through 15° after each photograph. The film (Ilford F.P. 3) was developed in Ilford Microphen, fixed and washed in the normal manner. The profiles were projected in an enlarger on to graph paper with a magnification of 20 diameters and then traced. The values for the radius (*a*) and depth (*b*) of the anterior segment of each lens were the average value of these seven profiles.

In order to check that no distortion of the lens occurred when it was freely supported in air, it was also photographed in saline in a rectangular calorimeter cell. The lens was rotated within the cell and photographed. As this technique was time consuming and difficult, only three lenses were checked in this way. The values for radius and depth whether photographed in air or saline agreed within $\pm 0 \cdot 05$ mm.

Extent of capsular distension

If the work done by the lens capsule in the living eye during accommodation was to be ascertained, the accompanying changes in capsular extension *in vivo* had to be related to the changes which were produced experimentally. Since the stretching of the lens capsule was recorded *in vitro* as a change in volume, the capsular extension *in vivo* had also to be expressed in terms of a volume change. Owing to its high water content and compact structure, the bulk modulus of the lens is probably very great. In accommodation, therefore, it is the area and not the volume of the lens which alters, and this causes some difficulty.

The mathematical determination of the parameters of a volume change system equivalent to the surface area variation of the lens *in vivo* is shown in Appendix Eqns. (2.2)–(3.4), and representative values of the parameters are given in Table 1. The steps involved in transforming area changes to volume changes were as follows

(i) The determination of changes in the area of the anterior lens surface during accommodation.

(ii) The calculation of the dimensions of a spherical segment of capsule with the same area and mean radius as the anterior surface of the lens.

Figure 2 illustrates these calculations graphically. The anterior surfaces of the unaccommodated and accommodated lens are shown and related to spherical segments of capsule. Although in practice the radius of curvature varies both *in vivo* and *in vitro* the mean radius of curvature of the anterior profile of the excised lens (R_m) is taken for the purpose of calculating volume changes. Since these experimental and accommodative changes in curvature are less than 12 %, this approximation is justified and the calculations are greatly simplified.

The area of the anterior surface of the lens

Accommodated lens. The excised lens was assumed to be fully accommodated. The anterior surface of the lens was found to have an ellipsoid profile (Fig. 3 *A*, *B*). From the radius of the lens equator and the distance of the equator from the anterior pole of the lens the area and volume of the anterior portion of the lens were obtained (Appendix Eqns. (2.2) and (1.1)).

Unaccommodated lens. It was assumed, first, that there was no change in lens volume, secondly, that the ellipsoidal profile was retained, and, thirdly, that the diameter of the unaccommodated human lens was 1 mm greater than the accommodated lens. The theoretical movement of the anterior pole of the lens for this change of diameter was about 0·45 mm and of the order found by Helmholtz (1855) and Fincham (1925). For the unaccommodated state, the distance of the anterior pole of the lens from its equator (b_u), together with its surface area (A_u), were calculated from Appendix Eqns. (2.5), (2.6) and (2.2) respectively. The values varied according to the age of the lens (see Table 1).

After the determination of the area and change in area of the anterior surface of the lens the area strain was readily deduced from the ratio of these volumes. This area strain had to be related to the pressure and volume changes which occurred experimentally (Appendix Eqns. (1.2), (3.3) and (3.4). These equations show, for example, that the area strain on a small spherical lens would be equivalent to a much larger volume change than the same area strain on a larger flattened lens. Fortunately, the anterior lens capsule even in this latter
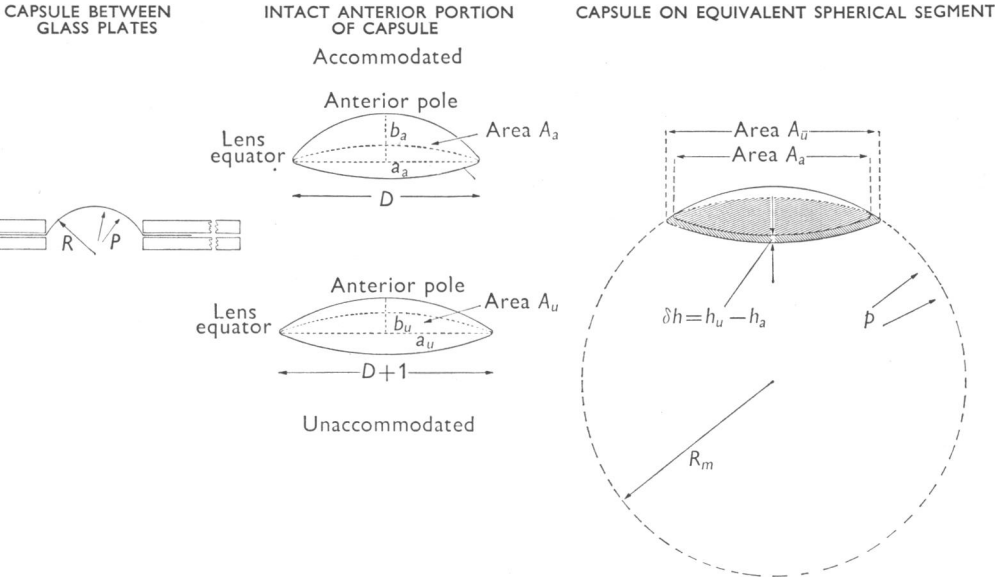
Fig. 2. Diagram showing relationship between the area of anterior lenticular surface during accommodation (A_u = area unaccommodated lens; A_a = area accommodated lens) and corresponding changes in an equivalent spherical segment of capsule. This spherical segment has the same radius as the mean radius of curvature (R_m) of the anterior lens profile. v = volume of capsule in glass plates. R = radius of capsule in glass plates. V_u = volume of anterior segment of lens. P = pressure in capsule in glass plates/μl. δV change in volume. p = pressure in equivalent spherical segment μl. change in volume. δh = difference in height of equivalent spherical segments. D = diameter of lens (mm). See Appendix for further details.

case does not differ greatly from the profile and dimensions of a segment of a sphere (Fig. 1) (drawn to scale). The important dimensions of this segment were the radius of curvature (R_m) of the sphere of which it forms part and its depth (h). The former was equal to the mean radius of the curvature of the anterior lens profile calculated from Appendix Eqn. (2.3), and the latter was obtained from Appendix Eqn. (3.1) and (3.2). The segment was assumed to have the same surface area as the anterior portion of the lens. The difference in depth of two segments of the same radii of curvature representing the accommodated and unaccommodated lenses was about 0·2 mm. From this difference in depth the change in volume of the equivalent segment was obtained from Appendix Eqn. (3.4) (see Table 1).

Energy stored in the lens capsule

When the lens accommodates, the stretched capsule contracts, as the zonule relaxes: work is performed on the lens. Although a small amount of this energy may be dissipated in stretching the zonule or in heat, it will be shown later that almost all of it must be utilized in generating sufficient force to deform the lens. Since the force of contraction and the change
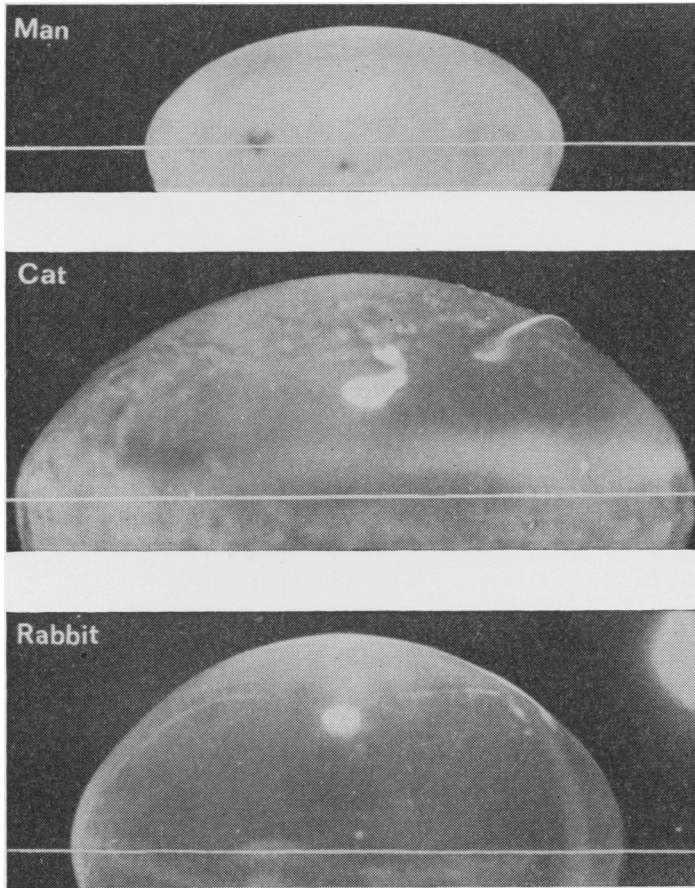

Fig. 3. *A.* Photographs of typical anterior lens profiles of man (aged 15), cat and rabbit with a line shown through each lens equator.
B. Traces of previous photographs with scale in mm below. Superimposed on each profile are plotted points at 0·5 mm increments in lens radius of the elliptic equation $(4x^2/D^2)+(y^2/b^2) = 1$. D = diameter of lens equator (mm). b = distance of anterior pole from equator (mm). V = anterior lens volume (mm^3) calculated from equation $\frac{1}{6}\pi D^2 b$. t = average thickness of capsule (μ).

in volume of an equivalent system have been calculated the work done can be determined from Appendix Eqn. (4.5). As pressure and volume strain were shown in the previous paper to be linear the work performed was half the product of volume and change in pressure.

Capsular 'surface tension' was obtained by dividing the total work done on the lens substance by the area of its anterior surface. To normalize the lens diameter in the different species the change in energy due to a 10 % increase in lens diameter was also calculated.
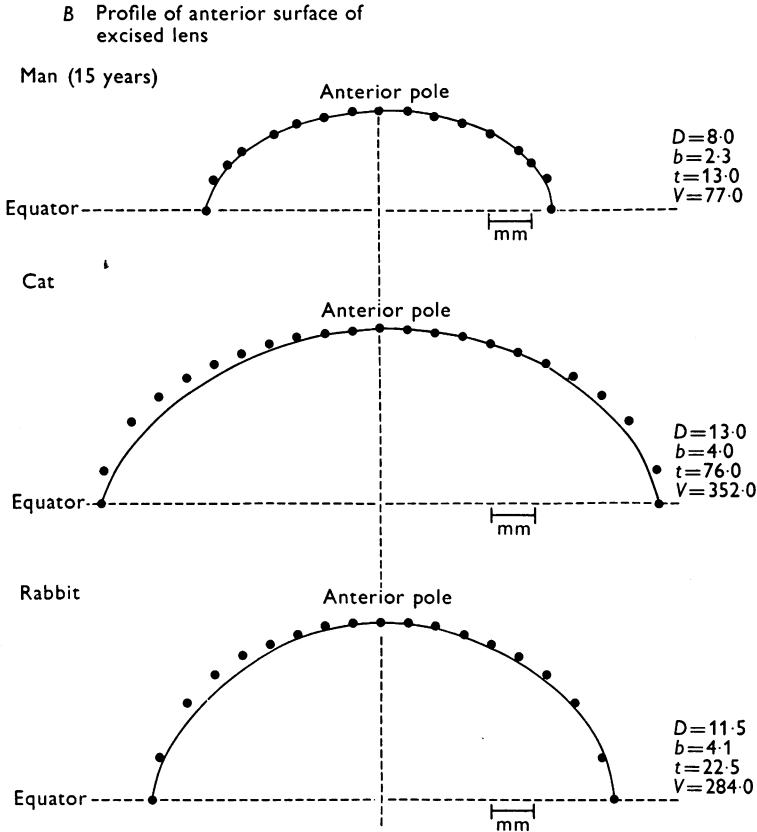

B   Profile of anterior surface of
    excised lens

Man (15 years)

Anterior pole

D=8·0
b=2·3
t=13·0
V=77·0

Equator

mm

Cat

Anterior pole

D=13·0
b=4·0
t=76·0
V=352·0

Equator

mm

Rabbit

Anterior pole

D=11·5
b=4·1
t=22·5
V=284·0

Equator

mm

Fig. 3 B. For legend see opposite page.

RESULTS

Comparison of lens profiles. Photographs and traces of profiles of human, rabbit and cat lens are shown in Fig. 3A, B. It will be noted that the human lens profile is fitted almost exactly to the equation of an ellipse where major and minor axes have values corresponding to the radius (*a*) and anterior polar thickness, (*b*) of the lens. In contrast, the cat and rabbit lenses are flattened at the periphery. The elliptical shape of the profile of the human lens was determined in ten cases for varying ages and never found to differ from the basic figure by more than ± 0·05 mm. No evidence of the conoid shape described by Tscherning (1904) and Fincham (1937) could be detected.

Properties of the lens capsule in man, the cat and the rabbit. Table 2 summarizes the properties of these species in regard to thickness, Young's Modulus of elasticity and the energy required to increase the area of 1 cm² of flat capsule by 10 %. It may be noted that despite the widely different values of Young's Modulus the energy required to increase this area of capsule by 10 % is approximately constant. In the cat, for example, the

TABLE 2. Comparative values of capsular energy under varying
conditions for man, cat and rabbit

	Man	Cat	Rabbit
Mean thickness of anterior part of capsule (10^{-3} mm)	12·0	76·0	22·5
Young's Modulus of elasticity (dyn/cm²)	5×10^7	$0·9 \times 10^7$	$2·5 \times 10^7$
Energy to increase the area of 1 cm² of flat capsule by 10 % (ergs)	300	342	281
Energy required to increase the equatorial diameter of the lens by 1 mm (ergs)	115	75	65
Energy stored per unit area in anterior part of capsule for 1 mm increase in equatorial diameter of the lens (ergs/cm²)	1300	360	370
Energy stored per unit area in anterior part of capsule when lens is normalized for a 10 % increase in equatorial diameter	1170	520	485
Amplitude of accommodation in dioptres	12	2	0 to 1

modulus elasticity is about 1/5 of that found in man but since the anterior lens capsule is over 6 times as thick the energy required to stretch it is increased slightly. When, however, the capsules of these species are compared *in situ* on their respective lenses the change in capsular surface tension for an increase in lens diameter of 1 mm in each case is quite different. Then the human lens capsule is computed to store three times as much energy per unit area as the other lens capsules.

Change in energy during accommodation of the human lens capsule. Representative calculations of lens capsule energy are shown in Table 1, while Fig. 4 illustrates graphically changes in stored energy as a function of age. The points plotted are for the anterior portion of thirty human lens capsules. E_G is the increase in stored capsular energy when the equator of the excised lens becomes 1 mm greater in diameter. It will be seen that the energy curve rises rapidly in infancy owing to lens flattening and the increase in thickness of the capsule. After the age of 15 capsular energy falls mainly due to the fall with age of Young's Modulus of elasticity. The decrease in energy after the age of 60 is enhanced because not only does Young's Modulus continue to decline but the lens capsule also becomes slightly thinner.
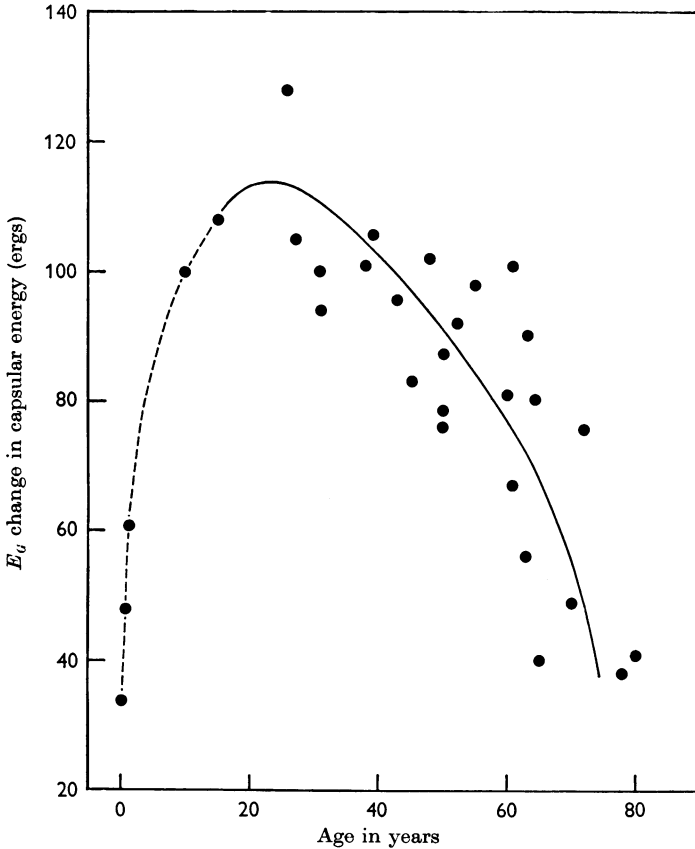
Fig. 4. Age and accommodation energy changes in thirty human anterior lens capsules. E_G = increase in energy stored in the capsule when the equator of the excised lens increases by 1 mm in diameter. Rapid rise of energy in infancy due to lens flattening and capsular thickening. Decline in adult life due to decrease in Young's Modulus of elasticity. Lens flattening and capsular thickening initially slightly reduce the rate of fall. Scatter greater than for Young's Modulus values since shape of lens and capsular thickness are additional variables. The experimental energy values are for a capsule rigidly clamped at its margin between glass plates. The capsule of the lens *in vivo* is free to move at the lens equator so that the values are about $0.25E_G$ for the intact lens (see text). Continuous curve, adult flattened lens; interrupted curve, juvenile spherical lens.

DISCUSSION

Weale (1962) suggested that deformation of the lens by external forces acting through the zonule was reversed by the internal stresses set up in the lens after the external force has ceased to act. The role of the capsule has been thought to be paramount in shaping the lens (Tscherning, 1904; Fincham, 1925). If, therefore, the energy required to change the shape of

the lens in accommodation is stored in its capsule, it should vary with the change in surface area of the capsule, its thickness and the value of Young's Modulus of elasticity. When these factors were taken into account and compared in the cat, rabbit and man, the energy required to change the surface area of 1 cm² of the capsule by 10 % was found to be approximately the same (Table 2). This comparison was made assuming that the capsule was stretched upon a flat surface. The accommodative powers of these species is well known, being about 12 dioptres in man (Duane, 1922), 2 dioptres in the cat (Ripps, Breinin & Baum, 1961), and under 1 dioptre in the rabbit (Fincham, 1925). There is thus no apparent correlation between constant capsular energy and the widely varying accommodative power of the lenses examined. These variations in accommodative power could possibly be explained by differences in the rigidity of the lens substance or defective ciliary power. Itoi, Ito & Kaneko (1965) have shown, however, that the lenses of the rabbit and man have approximately similar dynamic, visco-elastic properties when the whole lens is examined. The main reason for the very poor accommodation of the rabbit is probably a weak ciliary muscle, but Ripps et al. (1961) have shown that the cat has a well-developed ciliary muscle despite its poor accommodation. A factor common to both these lenses is the small degree of capsular stress and stretching which occurs if the lens diameters are assumed to change in the same way as human lenses. Only a small amount of stored capsular energy would therefore be available to deform the lens again to its accommodated state. The lenses of the cat and rabbit are much more spherical than the human lens (Fig. 3A, B), and the relevance of this fact to capsular surface tension or stored energy will now be discussed.

Lens profile and capsular energy

The effect of lens shape upon capsular surface tension can be best appreciated by considering a series of lenses differing in degree of flattening but possessing capsules of similar properties. These theoretical lenses have all the same increase in equatorial diameter and the ratio (K_E) of their capsular surface tension to the surface tension of a spherical lens of the same diameter is plotted against the degree of lens flattening (b/r) (Fig. 5). The lenses of different species with the same degree of flattening are indicated by vertical lines. The graph shows that the human lens appears to store about twice as much energy as the lenses of the cat or rabbit solely by virtue of its shape. When differences of diameter, radius of curvature of lens profiles, surface area and capsular properties are taken into account the capsular surface tension of the human lens is about 3 times as great as in these animals. If an allowance is also made for the differences in lens diameter between species, the lenticular energy values are in the same

order as the respective accommodative powers (Table 2). Rabl (1900) noted that 'primates have the flattest and smallest lenses of all species and this correlates with their high accommodative power'.

Lens profile and lens moulding pressure

The ability of the capsule to mould the lens depends not only on surface tension but also upon the pressure which it exerts perpendicular to its surface, i.e. the lens moulding pressure. Like the capsular surface tension,
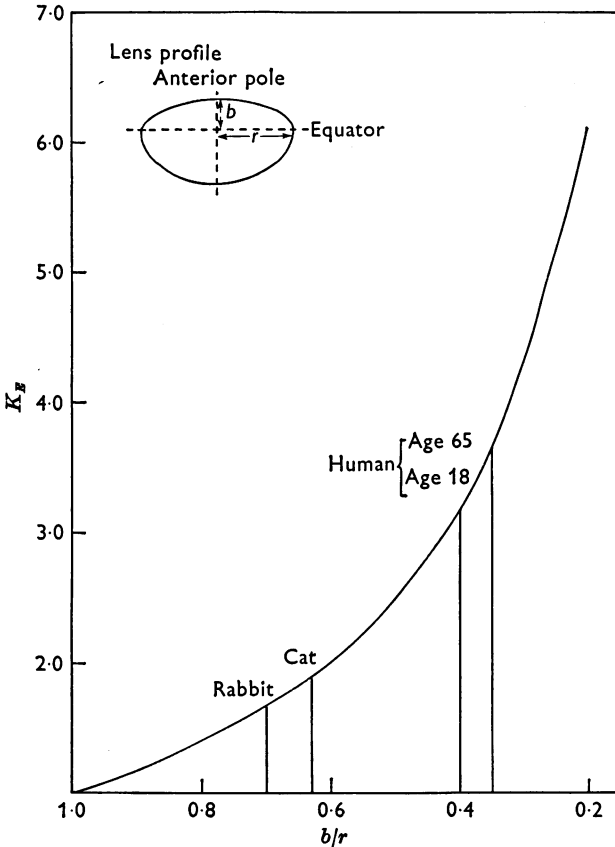

Fig. 5. Theoretical curve to illustrate the effect of lens shape on the energy released by the anterior lens capsule during accommodation. K_E is the ratio of the energies released by a flattened lens, with a degree of flattening represented by the coefficient b/r to that of a spherical lens of similar radius. The capsule of the spherical and flattened lens have the same thickness and elastic properties. The limiting value of $K_E = 14\cdot8$ when $b/r = 0$. Vertical lines indicate the position of b/r coefficients of various species. Despite the increase in thickness of the human lens with age, the distance of the anterior pole from the lenticular equatorial plane (b) shows little change. The radius (r) increases with age so that the coefficient (b/r) becomes less.

this moulding pressure also depends on the shape of the lens. If the lens were a flat disk the capsule would not exert any pressure perpendicular to its plane surface and the apical moulding pressure would be zero. Any equatorial moulding pressure acting perpendicular to its cylindrical surface would only increase the thickness of this hypothetical disk-shaped lens. The flat capsule, however, stores the maximum amount of energy, which is 14·8 times as great as a spherical lens of the same diameter
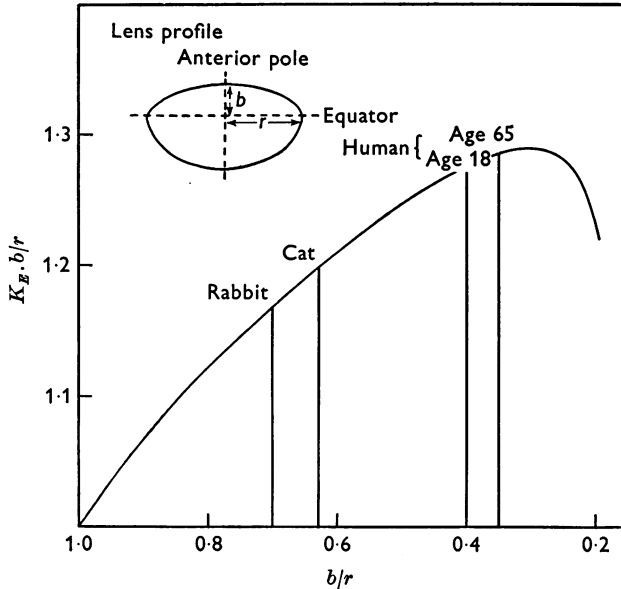

Fig. 6. Theoretical curve to illustrate the effect of lens shape on the capsular moulding pressure. The factor $K_E.b/r$ varies in a similar fashion to the moulding pressure (see text). The limiting value of $K_E.b/r = 0$ when $b/r = 0$. Vertical lines indicate the b/r coefficients of various species.

($K_E = 14·8$). In the human lens where the equatorial moulding pressure can influence lens curvature as well as lens thickness, its importance is much less than apical moulding pressure; this is because when lens moulding pressure is at a maximum the zonule of the unaccommodated lens opposes the equatorial moulding pressure. The moulding pressure thus depends on two variables: first, the stored energy which increases as the lens flattens and, secondly, the resultant pressure acting perpendicularly to the capsule, and decreasing as the lens flattens. This second factor varies in the same way as the ratio of the thickness of the anterior portion of the lens (b) to its radius (r), the degree of flattening (b/r), since this ratio is also zero when the lens is flat. Accordingly, the product $K_E.b/r$ is a rough indication of the magnitude of apical lens moulding pressure. Figure

6 illustrates this relationship and vertical lines again indicate the lenses of different species.

The variation in $K_E.b/r$ in the species examined is not very great but the flat human lens has a coefficient nearest the maximum value of this product. This degree of flattening of the human lens thus allows the capsule to exert its most effective apical moulding pressure.

The change in human capsular energy with age

The flattening of the lens from birth to the age of 15 increases the energy which can be stored in the lens capsule. From the age of 16 the flattening of the anterior portion of the lens continues with a slow increase in volume. This further flattening of the lens should increase the amount of stored energy between 18 and 65 by about 25 % (Fig. 5), but the marked fall in Young's Modulus of elasticity with age has a much greater effect and the energy falls by about 40 % (Fig. 4).

The energy values given in Fig. 2 are maximal, since the lens capsule was clamped rigidly between glass plates. In the living eye the capsule at the lens equator is probably free to move since tent-like elevations are produced by the insertion of the zonule (Duke-Elder, 1961). If, therefore, in the intact capsule stretching occurs equally on either side of the lens equator, only half the stretching need occur in the anterior capsule for a given increase in lens diameter. As a consequence of this the anterior capsular moulding pressure would be half as great and the energy stored in the anterior capsule only one quarter of that observed experimentally. This fact does not invalidate the subsequent discussion regarding the change in energy values with age since the 'fixed or free' equatorial attachment of the capsule is similar for lenses of every age.

Lens profile and curvature changes

Tscherning was unable to show an increased thickness of the lens during accommodation and suggested that the lens shape was altered by the pressure of the vitreous. This theory was modified by Fincham (1937) who showed that Helmholtz (1855) was correct in stating that the lens increased in thickness. Fincham supposed that it was impossible to account for the small change in diameter of the lens associated with its marked increase in central curvature without assuming that it became 'conoid'. These objections are without foundation since the properties of an ellipsoid surface fulfil the requirements found in the human eye. The average change in curvature of the anterior surface of the lens through a 3 mm pupil varies from 12 to 7·6 mm with a movement of 0·5 mm in the periphery of the lens. These values are almost exactly those found by Fincham (1937). Furthermore, the excised lens is in a more accommodative 'conoid'

form than the lens *in situ*, since it has been shown that when the zonule is released it still has some residual tension (Helmholtz, 1855; von Pflugk, 1932).

Lens profile changes and accommodation

Since the profile of the anterior lens surface has been shown to be an ellipse and there are negligible changes in the posterior surface during accommodation (Helmholtz, 1855; Fincham, 1937), it can be shown from Appendix Eqn. (5.4) that

$$\delta D = \frac{-6(\mu - 1)}{\pi} \frac{V_u}{a_u^5} \, \delta a_u \times 10^{-3},$$

where δD = amplitude of accommodation in dioptres, μ = the mean refractive index of the lens in aqueous (1·07) (μ = 1·42 for air (white light)), V_u = volume of anterior segment of lens (mm^3), a_u = radius of unaccommodative lens (mm), and δa_u = change in radius of lens during accommodation.

Fincham (1937) showed that in one case a forward movement of 0·66 mm during accommodation occurred in the central part of the lens and produced a subjective accommodative change of 8 dioptres. This change in a 19-year-old lens (a_a = 4·2, b_a = 2·4) causes an increase of 0·73 mm in the radius of the lens if the profile remains ellipsoid. From the above equation this would give an accommodative change of about 7 dioptres.

According to Wagstaff (1966), when accommodation is measured by an objective method the true accommodation is about 2 dioptres less than the subjective value, so this equation gives a dioptric change of about the correct order. Fincham's view that a conoid surface of the lens is necessary to explain its high accommodative power is thus invalid. The equation also predicts that changes in the anterior volume and radius of the lens markedly influence accommodation and also that accommodation is proportional to the change in lens diameter. These factors are discussed under presbyopia.

The change of tension in the zonule during accommodation

Since this work was completed, O'Neill & Doyle (1968) have calculated the hoop stress in the capsule or the tension in the zonule which would be required to produce a conoid shape in the accommodated lens as suggested by Fincham (1925). The values for the elastic properties of the capsule (Young's Modulus 6×10^7 dyn/cm^2, Poisson's ratio 0·5) used in their calculations were very similar to those found experimentally and described in the previous paper (Fisher, 1969).

On the assumption that the conoid form of the lens is produced during accommodation when the lens decreases in diameter by one mm, these

authors found that the minimal change in zonular tension would be 1·257 g/mm of lens circumference. By the present experimental method, it was found that the minimal change in energy is 28 ergs (Fig. 4, 20-year-old lens) and this would produce in a lens 9·0 mm in diameter a change in zonular tension only about 1/30 as great (0·04 g/mm of lens circumference).

Taking the previous value of zonular tension to produce a conoid lens (1·257 g/mm) the total force exerted by the ciliary body on the entire lens would be about 32 g weight. The dimensions of the base of the ciliary body are 5·4 mm wide and 24·0 mm in diameter (Duke-Elder, 1961). Therefore the total force exerted on this area of the globe by a normal intraocular pressure of 20 mm Hg would be about 11 g weight. Thus before the ciliary body could exert sufficient force to cause a conoid shape in the lens the globe would have become indented in the region of the ciliary body.

The maximum hoop stress for the conoid shape is given as 12·3 Newtons/metre; this stress for a capsule $20\,\mu$ thick (Salzmann, 1912) would result in a hoop stress of $6·25 \times 10^7$ dyn/cm². Fisher (1969) showed that even in the young capsule the ultimate stress was only about one third of this value ($2·3 \times 10^7$ dyn/cm²).

The forces required to mould the lens into a conoid shape are therefore much greater than the ciliary body or capsule can exert.

The present value (0·04 g/mm lens circumference) giving a value of 1 g weight for the tension in the entire zonule is further confirmed by the work of Kikkawa & Sato (1963). These authors showed that a compressive force of about 2·0 g weight on the entire lens was required to produce a strain of about 0·5 mm. Their technique, which involved applying a cup to the lens, unfortunately caused some damage to the lens films, and resulted in a non-elastic deformation. Nevertheless, the forces required to produce similar antero-posterior or radial strains are of the same order.

Thus not only have the present observations and measurements failed to show a 'conoid' form to the accommodated lens, but also the physiological moulding forces shaping the lens have been shown to be only about 3 % of the magnitude required to produce this profile.

Presbyopia

Changes with age in the volume and diameter of the lens

In Fig. 7 the volume of the anterior lens segment divided by the 5th power of the radius of the lens (V_u/a_u^5) is plotted against age. The points are divisible in two distinct groups. Those representing lenses from 0 to 10 years and those from 15 to 75 years. The former represent the rapid fall in (V_u/a_u^5) values as the neonatal lens changes from an almost spherical shape to the flattened adult lens. The latter group represents a slow decrease in (V_u/a_u^5) caused by the greater effect of increasing lens diameter compared

with a small increase in volume. The value of this coefficient is 0·068 at 15 years and decreases to 0·043 at 60. For the same alteration in the diameter of the lens equator at these two ages the older lens will be 36 % less accommodated.
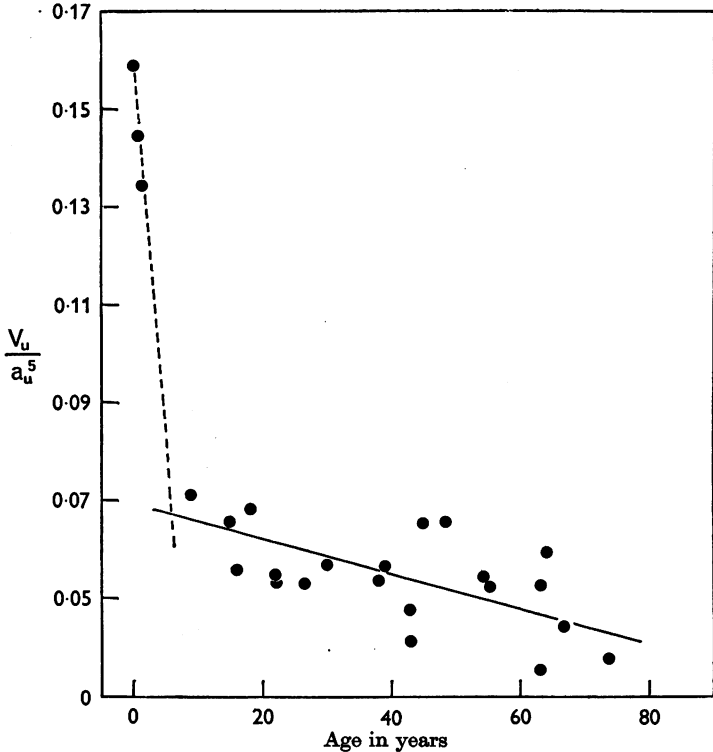

Fig. 7. Age and the influence of lens shape on accommodative amplitude for twenty-four human lenses. For a given change of equatorial diameter the infant spherical lens shows a much greater change in dioptric power than the adult flattened lens. The coefficient V_u/a_u^5 introduces a correction for the progressive flattening of the ageing lens when changes in dioptric power and lens diameter are related. The interrupted line indicates the rapid decrease of this coefficient until the age of 10 (juvenile spherical lens), and thereafter the continuous line shows its slow decrease throughout life (adult flattened lens). V_u is the anterior volume of the lens (mm³). a_u is the radius of the unaccommodated lens (mm).

Changes with age in the amplitude of movement of the lens equator

The amplitude of movement of the lens equator (δa_u) tends to be reduced as age advances by the growth of the lens and the fall in the ability of the capsule to mould the lens substance. Other factors producing this effect are the change in power of the ciliary muscle, the change in zonular elasticity and the increase in the resistance of the lens substance. These factors will now be considered.

Growth of the lens. Weale (1962) pointed out that the movement of the lens equator may be reduced by the growth of the lens. Figure 8 shows the change in radius of the lens which amounts to about 0·4 mm between the ages of 15 and 60. If the range of movement of the ciliary muscle in youth is about 0·73 mm (previous section) then a decrease by this amount would reduce the range of action of the ciliary muscle by 55 % if no compensation
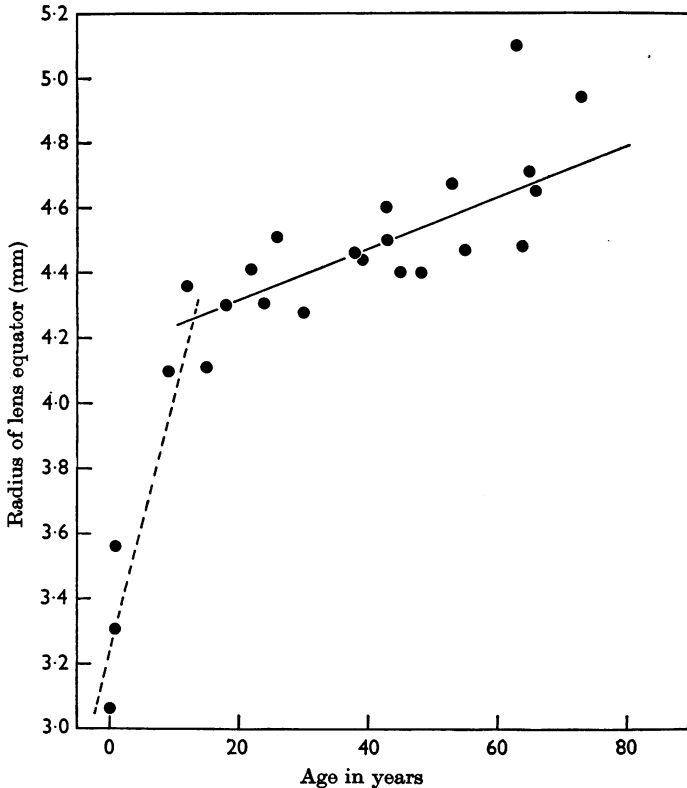

Fig. 8. Age and increase in the equatorial radius of the lens (mm) for twenty-four human lenses. The interrupted line indicates the rapid growth of the lens and the increase in its equatorial radius until the age of 10 (juvenile spherical lens) and thereafter the continuous line shows the slow increase throughout life (adult flattened lens).

in activity occurred. Since the change in accommodation is proportional to the change in radius of the lens equator there would be a similar loss of accommodation from lens growth alone.

Capsular surface tension. As the capsular surface tension of the lens falls, owing to a decrease in Young's Modulus of elasticity with age, the movement of the lens equator also decreases. This change in diameter is directly proportional to the surface energy of the lens capsule, if the resistance of

the lens fibres and energy losses (zonular stretching, heat loss) remains constant and the force acts radially around the lens (Appendix Eqn. (6.3)). The surface energy between 15 and 60 years falls from 110 to 80 ergs. The loss in accommodation from this factor alone would be 28 %.

Effective capsular energy of the lens. As the lens becomes older it becomes flatter and although this enhances the energy which can be stored (Fig. 5) it decreases the change in dioptric power for the same increase of equatorial diameter. Since the stored capsular energy is proportional to equatorial strain it is less able to alter the dioptric power of the ageing lens. The variation between energy and dioptric power can be adjusted by multiplying the energy values for a particular age by the factor shown in Fig. 7.

This adjustment corrects for the loss of lenticular accommodation which occurs, and is greater than would be expected solely from the decline in capsular energy. A given amount of capsular energy thus becomes less effective in changing the dioptric power of the flattened ageing lens. This effective capsular energy of the lens can be defined therefore as the energy which gives the same change of dioptric power of the lens per erg regardless of the lenticular profile changes which occur with age. In order to calculate this effective capsular energy for lenses of different ages, a lens of a particular age must be employed as a reference lens profile. The initial reference shape in this series of lenses is the profile of a 15 year old lens since at this age the initial rapid growth of the lens ceases (Figs. 7 and 8). From Appendix Eqn. (6.4)

$$E_F = \frac{V_u}{a_u^5} \frac{a_{u_{15}}^5}{V_{u_{15}}^5} E_G = 14 \cdot 7 \frac{V_u}{a_u^5} E_G,$$

where E_F is the effective capsular energy of the lens; E_G is the change in capsular energy of the lens per mm increase in equatorial diameter; $V_{u_{15}}$, V_u is the volume of the anterior segment of the lens at 15 and a specified age; $a_{u_{15}}$, a_u is the radius of the lens at 15 and a specified age.

The fall in effective surface energy of the lens is from 110 to 50 ergs between the ages of 15 and 60, and the loss of accommodation from these combined factors is 55 %.

Accommodation and effective capsular energy. At the age of 15 the change in capsular energy due to 1 mm change in the equatorial diameter of the lens is about 110 ergs (Fig. 2). The effective capsular energy is also the same since this lens is made the standard for the comparison of other lens profiles. The amplitude of accommodation at this age is about 11·0 dioptres (Duane, 1922). If, therefore, the refractive index of the lens (Huggert, 1948), the range of action of the ciliary muscle and the resistance of the lens fibres remain constant throughout life, then the amplitude of accommodation is 0·1 dioptre/erg of effective capsular energy. Figure 9 illustrates the loss of accommodation due solely to the fall in Young's

Modulus of elasticity of the capsule modified by the individual profiles of twenty-four human lenses from birth to old age. The young lens shows a rapid rise in accommodative power in the first year or so of life. At the age of 60 about 5·0 dioptres of accommodation would still remain if these two factors were the sole cause of presbyopia.

Change in range and power of ciliary muscle. Unfortunately, no data for these values are extant. The range of movement of the lens may be increased by an increased action of the ciliary muscle or it may be decreased by a growth of ciliary processes (Weale, 1962) or zonular stretching. Thus,
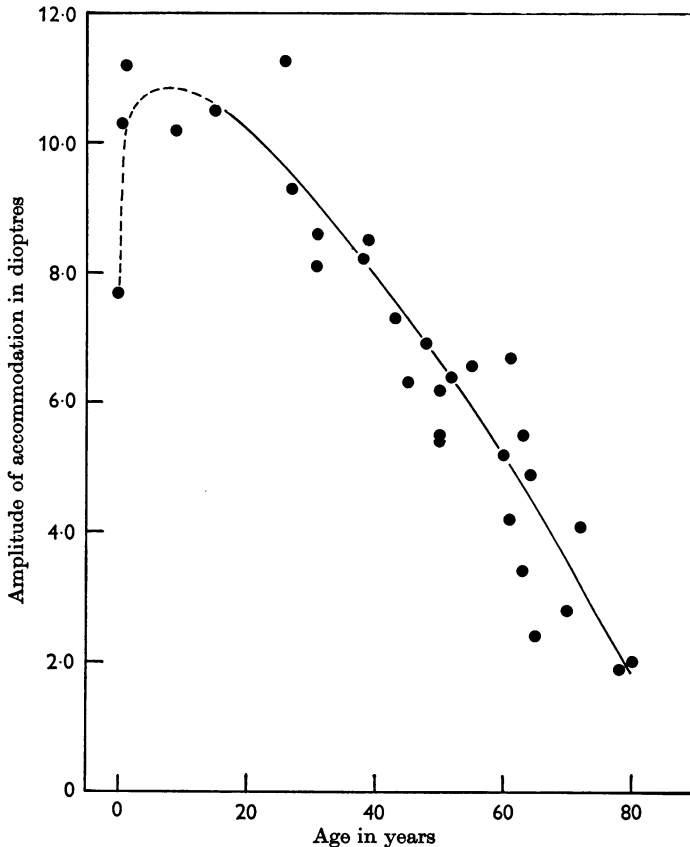

Fig. 9. Calculated variations in accommodation amplitude in thirty human lenses caused solely by age differences in the capsule and shape of the lens (- - - juvenile, —— adult). The refractive index, range of action of the ciliary muscle, and the resistance to deformation of the lens fibres are considered to remain constant while the amplitude of accommodation at 15 years is assumed to be 11·0 dioptres. Amplitude of accommodation (δD) calculated from $\delta D = 1·47\ V_u/a_u^5 . E_G$ (see text), where V_u = anterior volume of lens (mm³) and a_u = radius of unaccommodated lens (mm). E_G = increase of energy stored in the capsule of the excised lens when the lens equator increases by 1 mm in diameter (ergs).

if it is assumed that the range of movement of the ciliary muscle is decreased by lens growth, this factor together with the fall in effective capsular surface energy could account for all the loss in accommodation at the age of 60 without there being any corresponding increase in the resistance of the lens substance.

Resistance of lens substance. At present the Helmholtz–Fincham theory explains the onset of presbyopia in older subjects as being due to hardening of the substance of the lens but this still leaves unexplained the decreasing accommodative power below the age of 30, since young lenses are known to be soft. This early decrease in accommodation is more satisfactorily explained by the application of an external force applied to the lens as suggested by Tscherning (1904). It is seen from the previous discussion that the whole of the loss in accommodation could be accounted for by factors other than the increase in lens hardness. If the range of action of the ciliary muscle remains constant, however, at least 45 % of the loss of accommodation must be caused by lens hardening. If this lens hardening remains constant or increases uniformly there should be a linear relationship between the fall in effective capsular energy and the loss in accommodation. To test this hypothesis the accommodative power of the eye in dioptres for a given age was plotted against the known effective capsular energy (Fig. 10). The literature is not unanimous as regards the accommodative power at different ages; variations are attributable to the method used in the measurements and recently dynamic retinoscopy has shown that particularly in older age groups the accommodative power is less than previously supposed and, in fact, by about the age of 60 is zero (Hamasaki, Org & Munz, 1956; Wagstaff, 1966).

The accommodation is indeed proportional to the effective energy change in the lens at least until the age of 45, since the points plotted lie on or near a straight line as predicted by the theory (Fig. 10). As the exact change in lens diameter is unknown, the constant in Appendix Eqn. (6.4) is indeterminate. It follows from this that the absolute value of the slope of the line shown in Fig. 10 is also unknown. Two possibilities remain in regard to the resistance of the lens substance before the age of 45. Either the lens substance could be of constant resistance and the whole presbyopic change explained by the inability of the lens capsule to mould the lens, coupled with the decreasing range of ciliary muscle movement, or the increase in resistance of lens substance is approximately uniform until about the age of 45. This investigation has confirmed that, so far from being due to one factor, namely, hypothetical lenticular sclerosis, presbyopia can be attributed to at least three. They are (i) changes in Young's Modulus of elasticity of the capsule, (ii) change in lens shape owing to continuous growth, and (iii) increase in lens resistance or at least one other

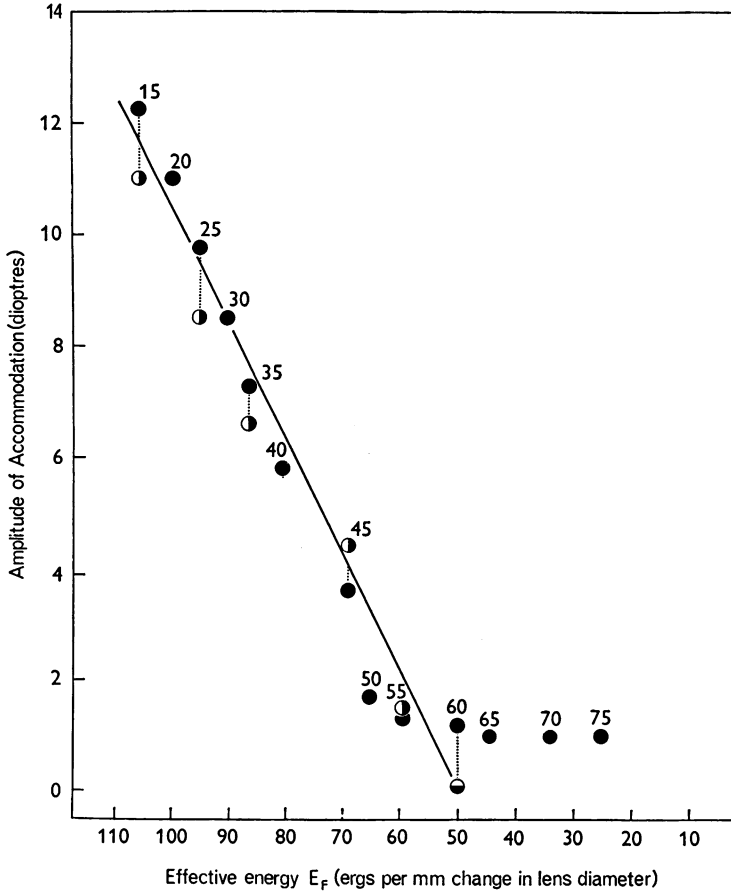factor. Experiments are in progress to test the alternative explanations under (iii).

Fig. 10. Presbyopic changes in amplitude of accommodation and effective energy of the lens capsule. Effective energy $E_{F} = 14\cdot7\ V_u/A_u^5.E_G$ (see text, where V_u = anterior volume of lens (mm³) and a_u = radius of unaccommodated lens (mm). E_G = increase of anterior capsular energy stored in the excised lens when the lens equator increases by 1 mm in diameter. ● Duane's data; ◑ Brückner's data mean per decade); ◓ Hamasaki's data. Age in years (15 to 75).

APPENDIX

1. *Lens moulding pressure*

The relationship between the anterior part of the capsule on the lens and the portion under test in the apparatus can be diagrammed as in Fig. 1.

R = radius of curvature of capsule in apparatus (mm);

v = volume of segment of capsule in apparatus (mm³);

P = pressure required to distend capsule by one microlitre (mm Hg);

p = pressure required to distend equivalent spherical segment by one microlitre (mm Hg);

V_u = volume of anterior segment of lens (mm³);

a_u = equatorial radius of unaccommodated lens (mm);

b_u = distance of anterior pole from equator of lens (mm);

R_m = mean radius of curvature of anterior lens profile (mm).

Now the volume of half an ellipsoid is

$$V_u = \frac{2}{3}\ \pi b_u a_u^2 \tag{1.1}$$

from preceding paper

$$\delta V = \frac{3}{2}.Rv\left[\frac{1-\sigma}{t_m E}\right] \times \text{pressure.}$$

Thus if δV is 1 μl. in each case, the moulding pressure for the same capsule is

$$p = \frac{Rv}{R_m V_u}\ P. \tag{1.2}$$

2. *Area of anterior surface of the lens*

The relationship between the change in area of the anterior part of the capsule and the change in volume of an equivalent spherical segment of capsule can be diagrammed as in Fig. 2.

A_u and A_a = areas of anterior surface of unaccommodated and accommodated lens respectively;

a_u and a_a = equatorial radii of unaccommodated and accommodated lens respectively;

b_u and b_a = perpendicular distances of anterior pole from equatorial plane of lens;

h_u and h_a = depths of segments of an equivalent spherical segment of capsule with the same anterior surface area as the unaccommodated and accommodated lens respectively;

δV = change of volume in the equivalent spherical segment of capsule corresponding to the area changes of the anterior part of the capsule during accommodation.

For an ellipsoidal surface

If
$$c = \left(\frac{a}{b}\right)^2 \quad \text{and} \quad \alpha^2 = \frac{a^2}{c^2 - c}, \tag{2.1}$$

$$\text{area} = A = 2\pi\sqrt{(c^2 - c)}\left\{\frac{b}{2}\ \sqrt{(b^2 + \alpha^2)} + \frac{\alpha^2}{2}\ \sinh^{-1}\frac{b}{\alpha}\right\}. \tag{2.2}$$

Appropriate suffixes denote values for the accommodated and unaccommodated lens respectively.

For an ellipsoidal profile

R = radius of curvature at point x, y

$$R_m = \frac{1}{10} \sum_1^{10} R \tag{2.3}$$

where $$R = \{y^2 b_u^4 + x^2 a_u^4\}^{\frac{3}{2}} / b_u^4 a_u^4.$$

The radius of curvature is measured at 8 equidistant points along the y axis and also at points $y = 0$, $y = a_u$. x co-ordinates are obtained from the profile equation

$$\frac{y^2}{a_u^2} + \frac{x^2}{b_u^2} = 1. \tag{2.4}$$

If there is no change of volume and the ellipsoidal profile is retained during accommodation

$$a_u^2 b_u = a_a^2 b_a \tag{2.5}$$

where $$a_u = (a_a + 0 \cdot 5). \tag{2.6}$$

3. *Change of volume in equivalent spherical segment*

Area of equivalent segment is A_u and A_a respectively. From the properties of a segment of a sphere

$$A_u = 2R_m h_u, \tag{3.1}$$

$$A_a = 2R_m h_a, \tag{3.2}$$

$$V = \tfrac{1}{3}\pi h_u (3R_m - h_u). \tag{3.3}$$

Differentiating equation (3·3)

$$\delta V = \pi (2R_m h_u - h_u^2) \delta h \tag{3.4}$$

where $\delta h = h_u - h_a$.

4. *Energy stored in anterior portion of lens capsule when equatorial diameter of lens increases by 1 mm*

E_G = work done in ergs

Since pressure exerted by capsule is proportional to distension:

$$\left. \begin{array}{l} \text{final pressure increase} = p \cdot \delta V, \\ \text{mean pressure increase} = \tfrac{1}{2} p \cdot \delta V \end{array} \right\} \tag{4.1}$$

$$\begin{aligned} \text{work done} &= \tfrac{1}{2} p \cdot \delta V \times \delta V \\ &= \tfrac{1}{2} p \cdot \delta V^2. \end{aligned} \tag{4.3}$$

From Eqns. (1.2) and (4.3).

$$E_G = \frac{0 \cdot 618 Rv \, P \delta V}{R_m V_u}. \tag{4.5}$$

Note: 1 cm of mercury exerts a force of 12,360 dyn/cm² since a water–mercury manometer was used in the apparatus.

5. *Relationship between change in dioptric power and change in lens diameter*

D = dioptric power of lens (dioptres);

R_1 = radius of curvature of anterior lenticular surface (mm);

R_2 = radius of curvature of posterior lenticular surface (mm);

t = thickness of lens (mm);

μ = mean refractive index of lens in aqueous;

δa_u = change in equatorial radius of lens (mm);

then

$$D = (\mu - 1) \left(\frac{1}{R_1} - \frac{1}{R_2} - \frac{(\mu-1)t}{R_1 R_2} \right) \times 10^{-3}. \tag{5.1}$$

Now R_2 is almost constant in accommodation and t only changes by 0·5 mm; μ is also constant throughout life. $(\mu-1)t/R_2$ only changes by 3 % $\times 1/R_1$ during accommodation. Therefore

$$D = (\mu - 1) \left(\frac{1}{R_1} - k \right) \times 10^{-3} \tag{5.2}$$

where k is a constant.

From Appendix Eqns. (2·3) and (1·1)

$$R_1 = \frac{a_u^2}{b_u} \quad \text{and} \quad b_u = \frac{3V_u}{2\pi a_u^2}$$

so that

$$\frac{1}{R_1} = \frac{b_u}{a_u^2} = \frac{3V_u}{2\pi a_u^4}. \tag{5.3}$$

Combining equations (5·2) and (5·3) and differentiating with respect to a_u

$$\delta D = -6 \frac{(\mu - 1)}{\pi} \frac{V_u}{a_u^5} \delta a_u \times 10^{-3}. \tag{5.4}$$

6. *Work done by capsule on lens substance*

$\displaystyle\sum_{a_u}^{a_u + \delta_a} f_r =$ mean sum of radial forces of lens substance opposing the moulding pressure of the capsule (dyn);

r_c = range of action of ciliary muscle (mm);

E_G = energy stored in lens capsule per mm increase in equatorial diameter of lens (ergs).

Energy stored in lens capsule

$$= r_c . E_G. \tag{6.1}$$

Work done on lens substance when zonule relaxed

$$\sum_{a_u}^{a_u + \delta_a} f_r . \delta a_u \tag{6.2}$$

If energy stored in capsule is utilized in deforming lens substance, from (6.1) and (6.2)

$$\delta a_u = \frac{r_c}{\sum\limits_{a_u} f_r} E_G \tag{6.3}$$

Combining Eqns. (5·4) and (6·3) and allowing lens substance resistance and ciliary muscle range of action to be constant throughout life

$$\delta D = \frac{-6K}{\pi} (\mu - 1) \frac{V_u}{a_u^5} E_G \times 10^{-3} \tag{6.4}$$

where K is a constant.

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