Accommodation as a function of age and the linearity of the response dynamics

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Abstract

The changes with age in the accommodation responses to dynamic stimuli can reveal useful information on the factors underlying presbyopia development. Analysis of the monocular accommodation responses of 19 normal observers (ages 18–49 years) to stimuli whose vergence varied sinusoidally with time at different temporal frequencies (peak-to-peak stimulus 1.33–2.38 D, at 0.05–1.00 Hz) showed that at all ages both the gain and phase of the response were essentially linear functions of the temporal frequency. Extrapolation of least-squares, regression line fits to the gain data for each subject gave the gain at zero frequency, G_0, and the cut-off frequency, f_c, at which the gain fell to zero. G_0 reduced with age but f_c remained essentially constant at about 1.7 Hz, up to at least the age of about 40. The magnitude of the response to step stimuli covering the same stimulus range was well correlated with the value of G_0. The linear changes in phase lag with temporal frequency corresponded to simple time delays t_d. The time lag varied from close to zero for the youngest subjects to about 0.5 s for the subjects in their late forties. There was substantial variation between the responses of subjects of similar age: those subjects with high values of G_0 also tended to have low values of t_d, both effects probably being due to the superior ability of some individuals to predict the sinusoidal changes in the accommodation stimulus. Comparison of theoretical step responses, derived by applying linear theory to the parameters obtained from the results for the sinusoidal stimuli, with the actual responses to unpredictable steps for the same subjects supports the view that prediction effects and other possible factors make linear theory inapplicable to this type of data. The results are discussed in the context of current ideas on the development of presbyopia: it is suggested that the constancy of f_c with age is the result of the ciliary body maintaining its efficiency, whereas the fall in G_0 and increase in t_d result from increases in lens rigidity.
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Keywords: Accommodation; Age; Dynamics; Gain; Phase; Presbyopia

1. Introduction

In spite of more than two centuries of increasingly intensive study, many aspects of accommodation and its changes with age remain imperfectly understood. In particular, debate continues on the relative importance of changes in the different components of the accommodative system for the development of presbyopia (e.g., Atchison, 1995; Gilmartin, 1995; Glasser & Campbell, 1998, 1999; Kaufman, 1992; Koretz, Cook, & Kaufman, 1997; Pierscionek & Weale, 1995). A fuller understanding of these factors is important if surgical techniques such as the use accommodating intraocular lenses are to be successfully developed to restore accommodation to the ageing eye (Charman, 2004; Glasser, 1999).

The decline in the steady-state amplitude in accommodation with age has been recognised and quantified for more than a century (e.g., Donders, 1864; Duane, 1912). However, age changes in dynamic accommodation have received much less attention, even though they

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might provide valuable insights into the possible contributions to presbyopia of different parts of the accommodative mechanism. The relatively few recent studies that have been carried out have largely concentrated on responses to abrupt step changes in target vergence, occurring randomly in time (e.g., Heron, Charman, & Schor, 2001; Mordi & Ciuffreda, 2004; Schaeffel, Wilhelm, & Zrenner, 1993; Sun et al., 1987). These have produced somewhat variable results, with some authors claiming marked changes in one or more aspects of the response dynamics and others finding little change up to the age of 40. Some of this confusion may have arisen because of the differing sizes of the step changes used, which in some cases exceeded the amplitude of accommodation of the subjects. To avoid problems caused by possible saturation of the response, it would be useful to have more data on the responses to small steps. Information on the corresponding responses to small-amplitude, sinusoidally changing stimuli would also be valuable, since the predictability of these stimuli means that any changes in the responses with age would be expected to be dominated by mechanical changes in the accommodation plant, rather than by possible age-dependent changes in reaction time.

The main aim of the present study was therefore to acquire and analyse data on the dynamic accommodation responses to sinusoidal and step changes in target vergence for a group of adult subjects of differing ages, in an attempt to further explore the nature of presbyopic change. An additional aim was to determine the extent to which the data could be fitted within the framework of linear systems theory (see, e.g., Toates, 1975).

2. Methods

Nineteen subjects, aged between 18 and 49 years of age were used. All had normal distance and near acuities and no visual abnormalities. Any refractive error, if present, was corrected by a soft contact lens. Their subjective amplitudes of accommodation were normal for their ages.

Accommodation responses to a real-space stimulus consisting of a high-contrast Snellen letter (limb width 1.09 mm, white-light luminance 36 cd/m^2) were measured using an open-view, dynamic infra-red optometer (Canon Auto Ref R1, modified for dynamic recording at a sampling frequency of 100 Hz). This instrument requires a minimum pupil size of 3 mm (Pugh & Winn, 1988, 1989). Although recording was possible with natural pupils for the younger subjects, mydriasis was required for the majority of the older subjects. This was achieved using two drops of 2.5% phenylephrine and was used on the subjects who were aged 35, 37, 40, 41, 42, 45, 46, and 49, although it was not needed with the 43 or 44 year-old subjects.

The dynamic stimuli involved two types of temporal stimulus change. In the sinusoidal stimuli, the target, attached to the pen support of an X–Y plotter, was moved sinusoidally in position with time along the line of sight of the subject's observing eye, the other eye being occluded. The Canon instrument allowed the target to be viewed directly. The limiting target distances from the observing eye were 0.42 and 0.75 m, corresponding to vergences of 2.38 and 1.33 D, i.e., the range of target movement lay well within the range of accommodation of all the subjects (the subjective amplitude of the oldest subject was 3.75 D and his objective amplitude, as measured by the infra-red optometer, also exceeded the 1.05 D stimulus range). The frequency of oscillation was varied between 0.05 and 1.0 Hz, the 11 frequencies tested being presented in random order to the subjects, whose task was to keep the target as clear as possible. The laboratory illumination was such that subjects were aware of the spatial environment around the targets, and the movement of the targets was accompanied by movement noise which gave further cues to target change to supplement the visual information.

A step stimulus was also used, with abrupt near-to-far and far-to-near changes between similar letter stimuli placed at vergences of 1.33 and 2.38 D, these values being at the extremes of the range covered by the sinusoidal stimuli. The steps were all of the same magnitude but occurred randomly in time, so that they could not be predicted. Fuller details of the experimental methods are given elsewhere (Heron, Charman, & Gray, 1999, 2002; Heron et al., 2001).

3. Results

Fig. 1 gives examples of the dynamic responses to sinusoidal target oscillation for two subjects of different ages. The most obvious effects are reductions in the response amplitude and increases in phase lags with frequency and age. These trends will be discussed more fully below.

Several of such sinusoidal records, each of which lasted 10.24 s, were analysed for each subject and frequency to yield estimates of the mean gain (i.e., the mean of the peak-to-peak responses divided by 1.05 D, the peak-to-peak stimulus) and phase (i.e., the mean time lag, t_L, between each peak or trough in the response in relation to those of the stimulus, divided by the period of the sinusoidal stimulus and multiplied by 360°) of the response of the subject at that temporal frequency. Means and standard deviations were based on at least 10 cycles of target movement. In deriving the data, corrections were made for the mechanical characteristics of the X–Y plotter used to drive the accommodation stimulus: it was found that these introduced a slight loss in amplitude and an increasing phase lag in the stimulus
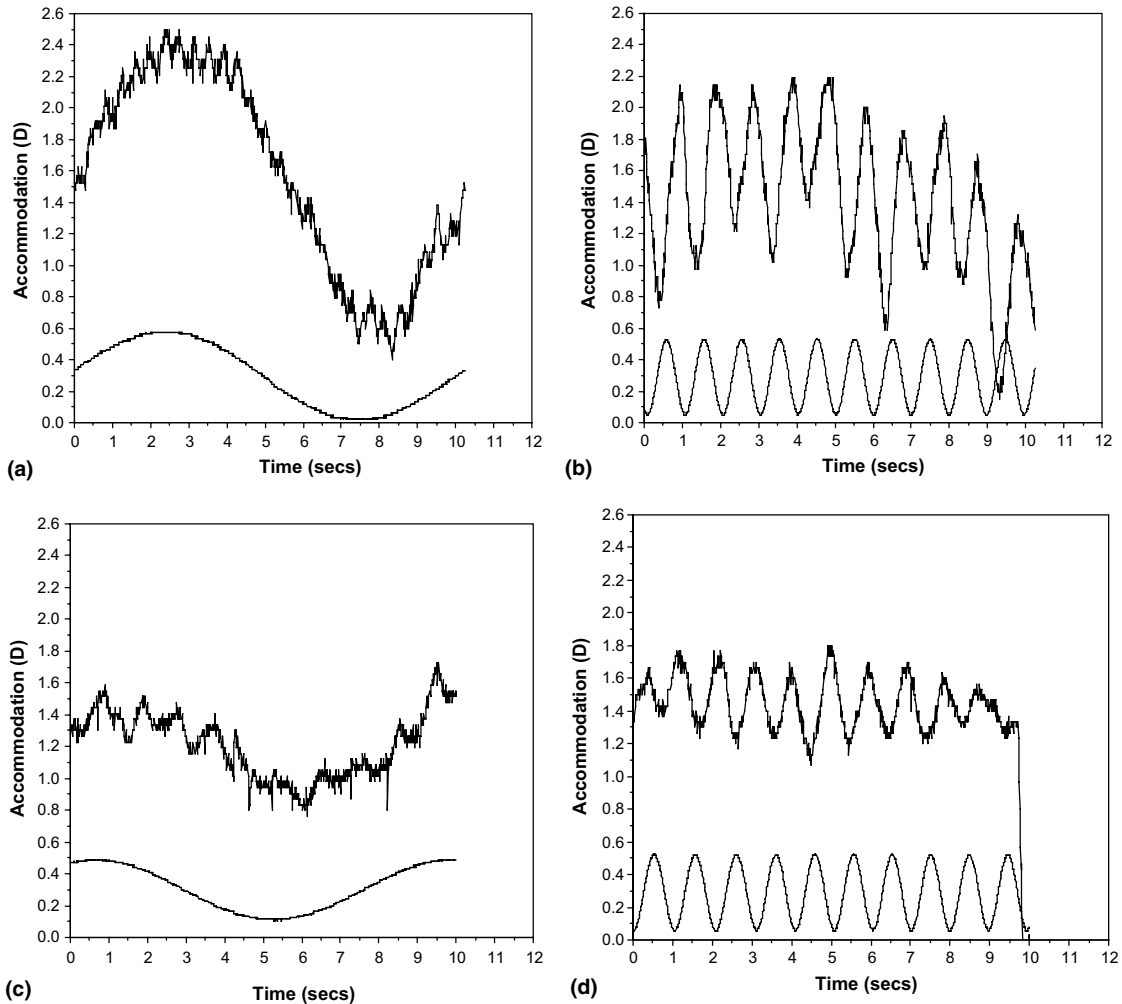
Fig. 1. Examples of responses at 0.1 and 1.0 Hz for 21 (a and b) and 41 (c and d) year-old subjects. To avoid overlap, the lower curves (in grey) indicate the time course, but not the absolute values, of the sinusoidally-changing stimuli (the true extreme values were 1.33 and 2.38 D). Note the obvious presence of accommodation fluctuations in the 0.1 Hz records.

at higher temporal frequencies, with a consequent effect upon the estimated gain and phase of the response. There were no effects below 0.8 Hz but at 1.0 Hz the amplitude of the dioptric stimulus variation fell by a factor of 0.86 and the plotter phase lagged by 62° with respect to the driving signal. This correction was omitted in the previous analyses of Heron et al. (1999, 2002), so that the present results are more valid than those in the earlier papers.

When each individual subject accommodated to the stimuli whose vergence varied sinusoidally with time, both the gain and the phase lag were found to vary essentially linearly as a function of the temporal frequency of the stimulus: the gain fell with frequency while the phase lag increased. The intercepts of the phase plots for all subjects lay close to the origin. Examples are shown in Fig. 2. The characteristics of these linear plots varied systematically with age.

Table 1 gives, for all the 19 subjects, the equations of the regression line fits, and R^2 and p values for gain and

phase plots of the type shown in Fig. 2. Note that the regression fits are generally good for all except the youngest of the phase plots but that the reliability of the regressions becomes poorer for the gain data of the older subjects, when the slope values approach zero. The y-intercept values are reasonably close to zero for all the phase regression equations, the larger departures (up to 40°) occurring for older (39 years+) subjects.

Responses to unpredictable step stimuli showed the usual reaction time, defined as the time interval between the known instant of stimulus change and the initiation of a systematic response change, and response time, defined as the interval between the initiation of the response and the time at which the response just reached its new steady-state level. Responses for each subject were analysed in terms of these parameters.

There was little evidence for significant changes in either reaction or response times with age (see Heron et al., 2001) the mean reaction times being 0.34 ± 0.10 s (far-to-near) and 0.35 ± 0.10 s (near-to-far). Mean
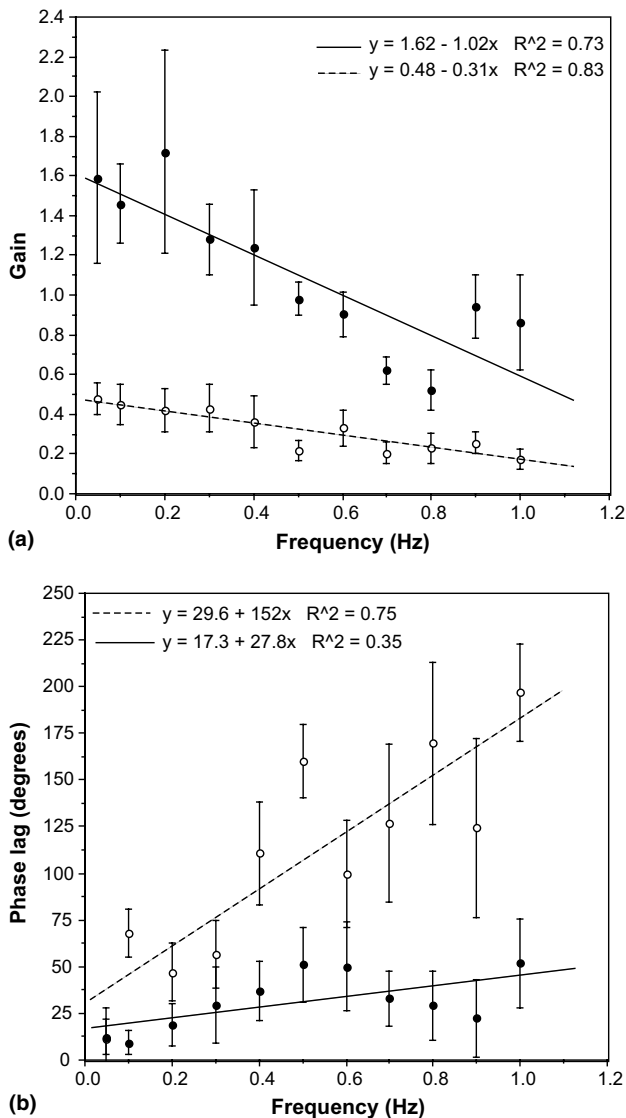
Fig. 2. Examples of changes in (a) gain and (b) phase with frequency for two subjects aged 21 (full lines, filled symbols) and 41 years (dashed lines, open symbols). The straight lines are least-squares linear regression fits to the data. Error bars represent standard deviations.

response times were $0.53 \pm 0.18\,\text{s}$ (far-to-near) and $0.56 \pm 0.24\,\text{s}$ (near-to-far). The differences between near-to-far and far-to-near times were not significant (Heron et al., 1999, 2001). The magnitude of the step response reduced with age, with some indication that most of the decline occurred after the age of 40 (Heron et al., 1999, 2001).

4. Discussion

Assuming that it is valid to extrapolate the straight-line fits of the type shown in Fig. 2(a), obtained for data measured in the frequency band 0.05–1.0 Hz, we can find their intercepts with the axes. According to linear

systems theory (Toates, 1975), the gain at zero frequency, G_0, ought to relate to the magnitude of the steady-state response to a step stimulus (i.e., the peak-to-trough response change for a sinusoidal stimulus of very low spatial frequency should equal that for a step stimulus between the same dioptric limits, although their temporal profiles will differ). There is evidently also a cut-off frequency, f_c, at which the gain falls to zero and beyond which no response occurs. Linear increases in phase lag with temporal frequency, of the type shown in Fig. 2(b), correspond closely to simple, frequency-independent, time delays, t_d s, between corresponding peaks of the stimulus and response (Campbell & Westheimer, 1960; Charman & Heron, 2000). With such delays, the slope of the straight-line plot of phase lag in degrees against frequency in Hertz is simply $360\,t_d$.

Fig. 3 shows the variation with the age of the individual subject in the values of (a) gain at zero frequency, G_0, (b) cut-off frequency, f_c Hz, and (c) time delay, t_d s. The values have been derived from the least-squares fits (Table 1) to data of the type illustrated in Fig. 2. Evidently, although dynamic response characteristics show some decline with age, the system remains reasonably active until well into the forties, retaining substantial low-frequency gain with little change in cut-off frequency (Fig. 3(a) and (b)).

In interpreting these findings, we note first, following many others (e.g., Stark, 1968, pp. 185–230; van der Wildt, Bouman, & van der Kraats, 1974), that a stimulus whose vergence varies sinusoidally with time is entirely predictable and favours a strong voluntary component or prediction operator in the accommodation response. In the present experiment, the regularly changing blur cues were heavily reinforced by target subtense, proximity, aural and other cues. This situation helps the subject to anticipate the movement of the target and to minimise the phase lags in the response: this ability is unlikely to diminish systematically over the age range studied, although it may vary with the individual. In contrast, the response to an unpredictable step or other stimulus always shows a reaction time or latency: as noted earlier, reaction times showed no significant changes with age, implying that neural responses were unimpaired. It is likely, then, that the observed general increases with age in the phase lags of the frequency characteristics of the response to sinusoidal stimuli (Table 1 and Fig. 3(c)), and the increases in t_d, are caused primarily by the changing mechanical limitations of the accommodation system, such as the visco-elastic properties of the lens, rather than by neural factors (e.g., Glasser & Campbell, 1999). Part of the scatter of the data may, however, be caused by variations between the predictive abilities of subjects of similar age, as discussed more fully below.

Prediction may also enhance the amplitude of the sinusoidal response and is almost certainly responsible for

Table 1
Regression line equations and R^2 values for the variation of gain and phase as a function of frequency for each subject

Age (years)	Gain/frequency	R squared	p	Phase/frequency	R squared	p
18	$y = 1.06 − 0.50x$	0.68	0.002	$y = 21.7 + 6.5x$	0.01	0.76
20	$y = 1.01 − 0.50x$	0.85	0.0001	$y = 7.9 + 37.7x$	0.53	0.01
21	$y = 1.62 − 1.02x$	0.73	0.0009	$y = 17.3 + 27.8x$	0.35	0.05
27	$y = 1.08 − 0.70x$	0.82	0.0001	$y = 2.3 + 78.1x$	0.86	0.0001
29	$y = 0.67 − 0.36x$	0.45	0.023	$y = 5.4 + 78.1x$	0.85	0.0001
31	$y = 0.86 − 0.51x$	0.91	0.0001	$y = −6.3 + 78.6x$	0.77	0.0004
33	$y = 1.42 − 1.12x$	0.89	0.0001	$y = 9.4 + 42.8x$	0.83	0.0001
35	$y = 0.79 − 0.63x$	0.79	0.0002	$y = 6.2 + 101.9x$	0.88	0.0001
37	$y = 1.69 − 0.94x$	0.92	0.0001	$y = 13.4 + 44.2x$	0.57	0.007
38	$y = 0.72 − 0.47x$	0.8	0.0002	$y = 0.74 + 57.5$	0.7	0.0013
39	$y = 0.53 − 0.22x$	0.63	0.0035	$y = 53 + 94.8x$	0.77	0.004
40	$y = 0.53 − 0.20x$	0.42	0.03	$y = 22.0 + 74.5x$	0.91	0.0001
41	$y = 0.48 − 0.31x$	0.83	0.0001	$y = 29.6 + 152.4x$	0.75	0.0005
42	$y = 0.56 − 0.13x$	0.14	0.26	$y = 0.18 + 226.6x$	0.85	0.0001
43	$y = 0.82 − 0.15x$	0.15	0.24	$y = 16.4 + 71.8x$	0.75	0.0006
44	$y = 0.92 − 0.64x$	0.95	0.0001	$y = 4.0 + 89.7x$	0.73	0.0008
45	$y = 0.28 + 0.07x$	0.1	0.37	$y = −29.6 + 240.5x$	0.78	0.0007
46	$y = 0.63 − 0.25x$	0.33	0.06	$y = 11.1 + 140.6x$	0.86	0.0001
49	$y = 0.38 + 0.02x$	0.002	0.9	$y = −32.7 + 278.3x$	0.82	0.0001

R is the Pearson product moment correlation coefficient and p is the probability.

the finding that G_0 exceeds unity for many subjects (Fig. 3(a)).

One interesting feature of data of this type is the extent to which they support or contradict the concept that accommodation acts as (or can be reasonably well approximated by) a simple linear system, in which responses to any form of stimulus can be predicted from a knowledge of the responses to sinusoidal stimuli using linear systems theory.

4.1. Gain at zero frequency, G_0

Considering first G_0, the gain at zero frequency (Fig. 3(a)), this exceeds unity for many of the younger subjects, presumably because of over-strong voluntary input associated with the ability to predict the repetitive stimulus. As age increases, G_0 appears to fall, and must collapse to zero when complete presbyopia is reached. Although in Fig. 3(a) a straight line has been fitted to the data, the fit is rather poor, with considerable individual variation in the results for subjects of similar age (see also Schaeffel et al., 1993).

As noted earlier, if linear theory held, the individual values of G_0 should predict the magnitude of the subject's corresponding response to a step stimulus. Fig. 4 plots for each subject the experimentally-measured relative response to an unpredictable step stimulus with the same overall magnitude as the peak-to-trough change in the sinusoidal stimuli (the relative response is the response change divided by the stimulus change) against the corresponding values of G_0: the subject's age is indicated at each datum point. In comparison with the very scattered gain/age plot of Fig. 3(a), the data points of Fig. 4 follow a much more systematic trend, suggesting

that both G_0 and step response amplitude are related to the accommodative abilities of the individual, rather than simply to calendar age. Note that although in general the points nearer the origin (i.e., with less active accommodation) refer to older subjects and those further away to younger subjects, there are many exceptions to this and, indeed, that the "best" accommodator is aged 37 years.

Rather than following a one-to-one straight-line relationship, most of the points fall below this line. There is some suggestion that the trend of the points may be non-linear and be quite well fitted by a quadratic equation. The straight line and quadratic regression equations are:

$$y = 0.46x + 0.23 \quad (R^2 = 0.83, \ p = 0.0001)$$

$$y = −0.21x^2 + 0.89x + 0.05 \quad (R^2 = 0.86, \ p = 0.0001)$$

where y is the relative step response, x the value of G_0, and R is the Pearson product moment correlation coefficient. It is reasonable to suggest that most of the points in Fig. 4 fall below the line of unit slope because of the effect of prediction on G_0. As noted earlier, with the plentiful additional non-blur cues available in the experiment, prediction and voluntary effort help to enhance the responses to regular sinusoidal stimuli and hence to increase the value of G_0, an effect which is absent with unpredictable step stimuli. Many younger subjects achieve values of G_0 in excess of unity, whereas no subject over-accommodates for a step response: thus the step response predicted from the responses to sinusoidal change is too high. A linear relationship with a slope less than unity would imply that the enhancement of the gain due to prediction was a constant proportion of the sinusoidal responses of all subjects, irrespective of
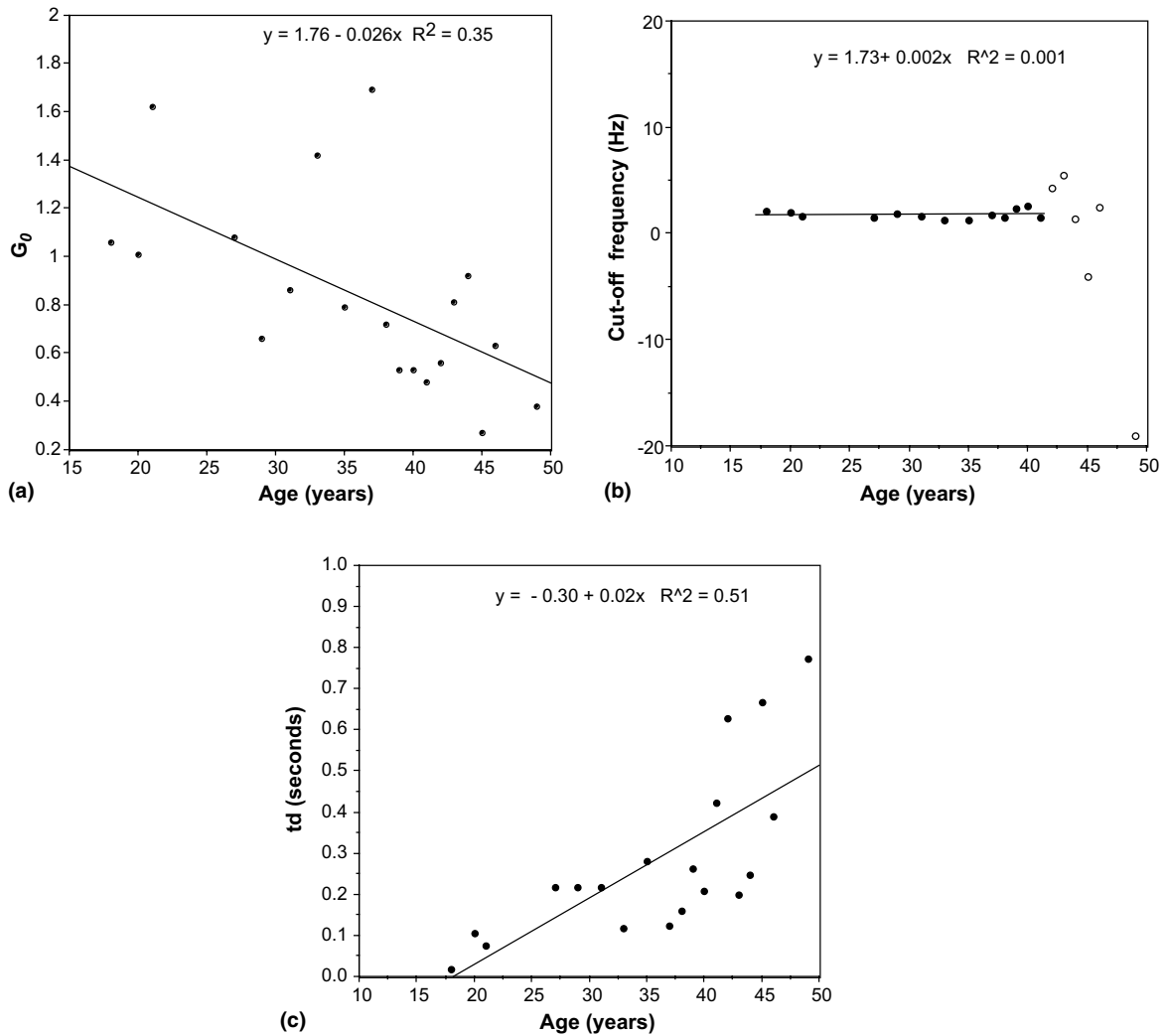
Fig. 3. Variation with subject age in (a) the gain at zero frequency G_0, (b) the cut-off frequency, f_c Hz, and (c) the time lag, t_d s, as derived from plots of the type illustrated in Fig. 2. Least-squares regression line fits are also shown. The *p*-values for the regression lines are 0.007, 0.91 and 0.0006 for (a), (b) and (c) respectively. In (b) the least-squares regression line has been fitted over the limited age range 18–41 years, since the low slope of the gain/frequency lines for the older subjects (see Fig. 2(a)) makes the *x*-intercept very unreliable.

their age or accommodative efficiency. A non-linear relationship would be expected if prediction was more effective among the younger, better accommodators and was of lesser importance for those who were poor accommodators due to age or other factors. Irrespective of whether the relationship is linear or quadratic, the fact that G_0 exceeds the relative step response for almost all subjects suggests that prediction must have helped all of them to improve their sinusoidal responses to some extent.

4.2. Cut-off frequency, f_c

Although G_0 falls with age, the cut-off frequency at which the gain falls to zero, f_c, appears to be robust against age change (at around 1.7 Hz) up to at least the early forties (Fig. 3(b)). Thereafter the estimates of f_c become unreliable due to the large uncertainties in

the intercept associated with the relatively low slopes of the gain/frequency curves for the older subjects (Table 1): when the slopes approach zero, any uncertainties in slope cause large variations in intercept, this being the explanation for the high negative cut-off frequencies derived for the 45 and 49 year old subjects. If we ignore the data for the six oldest subjects, the regression line over the age range 18–41 years is

$$y = 1.73 + 0.002x \quad (R^2 = 0.001, \ p = 0.91)$$

where y is the value of f_c in Hz and x is the age in years. The slope in this regression equation is very low and f_c is essentially independent of age. The mean value of f_c for subjects in the age range 18–41 inclusive is 1.79 ± 0.42 Hz.

The important feature here is that although the amplitudes of accommodation of the subjects were steadily declining with age in accordance with classical
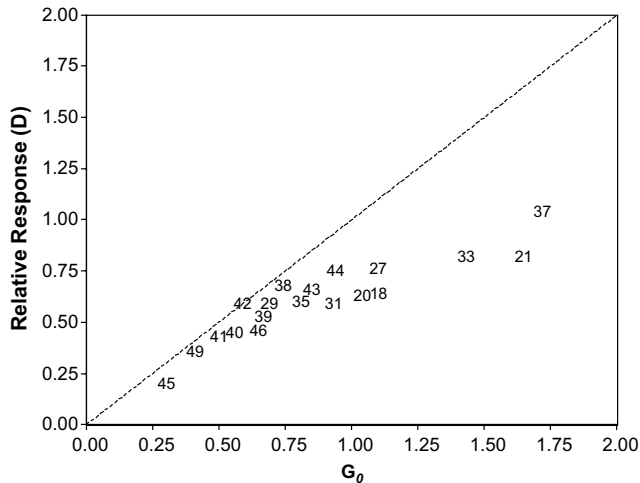
Fig. 4. Magnitude of the relative response to a random step stimulus as a function of the corresponding gain at zero frequency, G_0, for sinusoidal stimuli, plotted for each of the 19 subjects of differing ages. Each point is labeled with the age of the subject. The dashed line is a one-to-one relationship.

data (e.g., Donders, 1864; Duane, 1912), the frequency bandwidth of their dynamic response was essentially unaffected.

It is interesting to note that a cut-off frequency of around 1.7 Hz is lower than that of the upper limit of the frequency content of the "steady-state" microfluctuations in accommodation of the eye (see, e.g., Charman & Heron, 1988; Winn, 2000, for reviews), which appears to extend up to at least 5 Hz (e.g., Campbell, Westheimer, & Robson, 1958; Kotulak & Schor, 1986; Winn & Gilmartin, 1992). If f_c represents the upper frequency limit for a visual-stimulus-driven, true lenticular response, i.e., a stimulus-driven shape change, this may support the concept that at least part of the frequency spectrum of the fluctuations is due to random "noise" in the system. Campbell (1960) was able to demonstrate that there is a high degree of correlation between the phase and amplitude of the major fluctuations of the two eyes, suggesting that at least the low-frequency components of the fluctuations have a common neural origin, this being confirmed by others (Clark & Crane, 1978; Heron & Winn, 1989; Heron, Winn, Pugh, & Eadie, 1989). However, correlation between high-frequency components has not yet been reliably demonstrated, except insofar as they are affected by the arterial pulse (Winn, Pugh, Gilmartin, & Owens, 1990). It is possible that small axial and transverse lens movements contribute to the fluctuations, as well as true changes in lens power. It is observed that, in the young, the amplitude of the fluctuations increases at all frequencies as mean accommodation level is increased (Denieul, 1982; Kotulak & Schor, 1986; Krueger, 1978). This may be because the slacker zonule then allows greater lens movement than when greater zonular tension is applied for distance vision and the lens is more constrained. The finding (Toshida, Okuyama, & Tokoro, 1998) that measured high-frequency fluctuations do not increase with accommodative effort for older (>40 years) subjects, even though the ciliary body is still active and can still reduce the zonular tension, argues against the "lens movement" hypothesis, however, and a general reduction in fluctuations with age has been reported (Heron & Schor, 1995; Mordi & Ciuffreda, 2004; Toshida et al., 1998).

4.3. Time delays, t_d

It can be seen (Fig. 3(c)) that the time delays, t_d, derived from the linear change in phase shift with frequency, increase with age, from a value close to zero at about the age of 20 to approaching 0.4 s at 40 years. It is again important to emphasise that this time delay is not a classical response latency or reaction time, since the sinusoidal stimulus change was entirely predictable, with strong combined blur, size and audible cues. In principle, there would appear to be no reason why the ability to predict the movement of the sinusoidal stimulus should diminish systematically over the age range studied. Thus the progressive increase in t_d with age appears to be due mainly to increasing delays associated with the changes in the visco-elastic properties of the accommodative plant (Glasser & Campbell, 1999), rather than to neural effects.

Differences in the ability of some individuals to anticipate the stimulus changes must play some role in the results however. This is illustrated by Fig. 5, which plots the individual values of t_d against the corresponding values of G_0, the gain at zero frequency. It is striking that, whatever their ages, all those subjects with high gains have low values of t_d, suggesting that these individuals are skilled at using prediction to both maximise gain and minimise phase lags. If we set these "good predictors" to one side, most of the subjects have time delays between about 0.2 and 0.4 s, which would be quite compatible with the time constants for the step response data, where reaction times remained constant with age at about 0.35 s. Nevertheless there is evidently a group of older subjects who, in spite of the possibility of using prediction, have time delays to sinusoidal stimuli in excess of 0.6 s, suggesting that a real increase in time delay with age must be present. This is more specifically illustrated in Fig. 6, where the mean of the near-to-far and far-to-near reaction times for step stimuli is plotted against the corresponding value of t_d for each subject. While there is no systematic increase in the step reaction times with age, the values of t_d tend to be greater for the older subjects (see also Fig. 3(c)).

One feature of the phase results appears puzzling. Why are substantial phase lags to sinusoidal change, rising to 180° at 1 Hz (i.e., a value of $t_d \geqslant 0.5$ s) for the
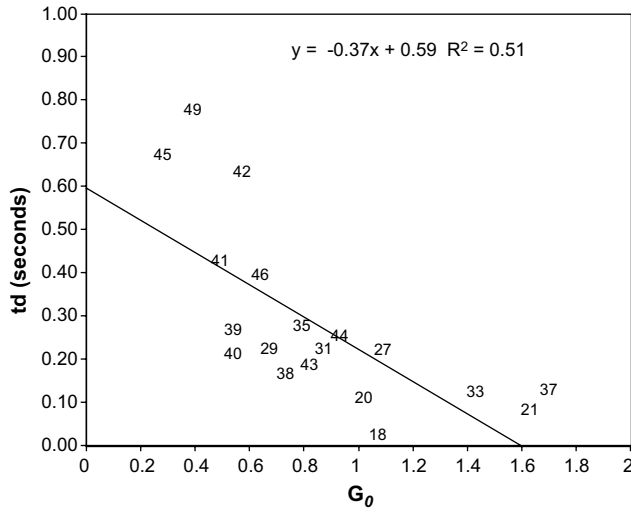
Fig. 5. Time delay, t_d s, as a function of gain G_0 for individual subjects. Data points are shown as the ages of the corresponding subjects. The regression line is $y = -0.37x + 0.59$, $R^2 = 0.51$, $p = 0.0007$.

oldest subjects, tolerated (see, e.g., Fig. 2(b))? It might be thought that, with a lag of 180°, an active response would create a worse time-averaged retinal image than would occur if the response was maintained at a steady mean level. This question is, however, complicated by depth-of-focus effects which may give image clarity for an adequate fraction of each cycle even in the presence of a large phase error and by subject-dependent mismatches between the mean values of the stimulus and response. Since most of the older subjects had their pupils dilated and all pupils had diameters in excess of 3 mm, it is unlikely that the older subjects had a larger depth-of-focus than their younger counterparts.
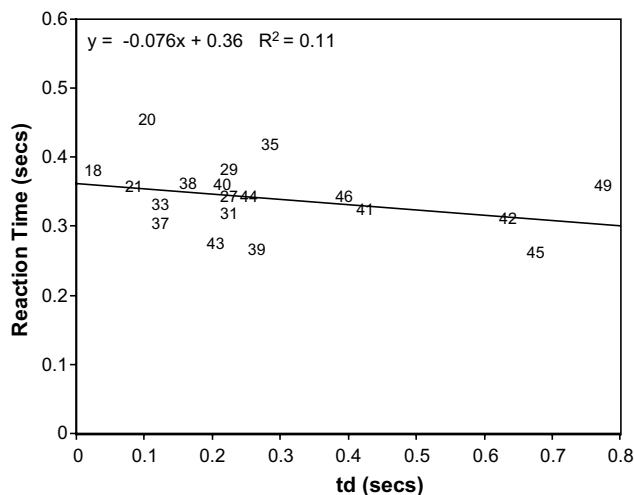

Fig. 6. Mean of the reaction times to near-to-far and far-to-near step stimuli as a function of the corresponding value of the time delay, t_d, derived from sinusoidal stimuli, for each subject. Numbers indicate the ages in years of the individual subjects. The regression line is $y = 0.076x + 0.36$, $R^2 = 0.11$, $p = 0.17$.

It is perhaps possible that, for the older subjects, the response might be more heavily influenced by a combination of prediction factors, such as the changing subtense of the real-space targets and the auditory cues provided by the noise made when the target moved over the platten of the X–Y plotter used to provide the motion, with true blur cues only playing a minor role. Accommodation responses can be enhanced by cross-modal coupling from auditory information (e.g., Kitagawa & Ichihara, 2002). On the other hand, the observed regular changes in phase lag with frequency and age, with no evidence for any abrupt changes in regression slopes or t_d values at any particular age, make it difficult to believe that the younger and older subjects use fundamentally different cues to guide their dynamic accommodation responses.

4.4. Form of step response

We found that, for step stimuli, reaction and response times (about 0.35 and 0.55 s respectively) showed no significant changes with age (Heron et al., 1999, 2001). These values are similar to those found by other authors (Campbell & Westheimer, 1960; Heron & Winn, 1989; Tucker & Charman, 1979). Others have also found little change with age in the reaction time (Sun et al., 1988), although Mordi and Ciuffreda (2004) using a larger subject group found a small increase, from about 0.34 to 0.41 s between the ages of 22 and 42 years. A near-zero change in the reaction time to step stimuli is probably to be expected, since other reaction times remain essentially constant over the age range 20–50 years (Weale, 1982). Some other recent studies (Heron et al., 2001; Mordi & Ciuffreda, 2004) have also concluded that response times are essentially invariant with age up to the early forties, although an increase was found in the small-scale study of Sun et al. (1988), which involved only six subjects of different ages, and in the indirect ultrasonic measurements of Beers and van der Heijde (1996).

The observation that the amplitude of the step response declined with age, even though both the stimulus levels lay within the objective amplitude of all the subjects, reflects the reduction in the slope of the response/stimulus curve that occurs with age, particularly after about 40 (Kalsi, Heron, & Charman, 2001; Mordi & Ciuffreda, 1998; Ramsdale & Charman, 1989). This reduction in slope appears to reflect an adaptive change in the accommodation system to make best use of the available objective amplitude and the ocular depth-of-focus (Kalsi et al., 2001; Ramsdale & Charman, 1989).

Using linear systems theory and the various parameters derived from the sinusoidal data, we can predict the overall form of the expected response to an abrupt step stimulus. Charman and Heron (2000) showed that, for a linear system, a linear change in gain with temporal fre-

quency implies a step response of the form $S(t) = \int_{-\infty}^{t} \sin c^2(\pi f_c t)\,dt$, where t s is the time and f_c the cut-off frequency (Hz).

The overall magnitude of the step response will be G_0 multiplied by the stimulus magnitude. The basic response will be delayed by t_d and will take the form $S(t)$. If f_c is constant with age, so also will be the temporal shape of the step response.

Fig. 7 shows (a) theoretical near-to-far and far-to-near step responses for our "best" accommodator (KO, age 37, $G_0 = 1.69$; $t_d = 0.123$ s; $f_c = 1.80$ Hz) predicted on this basis and (b) some of her corresponding experimental results for step stimuli. In both (a) and (b) the responses have been normalised in terms of the change in target vergence (1.05 D). It is clear that, although the theoretical and observed step responses are qualitatively similar, linear theory, using parameters

derived from responses to sinusoidally-varying stimuli, yields unrealistic predictions for many important details of the step response. As noted earlier, this subject's high value of G_0, caused by the predictability of the sinusoidal stimuli, leads to the theoretical expectation of an excessively large step response: in contrast, for real steps the difference between the steady-state response levels on either side of the step will never exceed the stimulus change (i.e., the "gain" will never exceed unity), although there may be occasional initial overshoots (Campbell & Westheimer, 1960). Again prediction of sinusoidal changes, by reducing phase lags and hence the value of t_d, leads to the theoretical step response occurring at an earlier time than the real responses (indeed, as can be seen from Fig. 7(a), predicted accommodation starts to change before the step stimulus change occurs). Lastly the observed
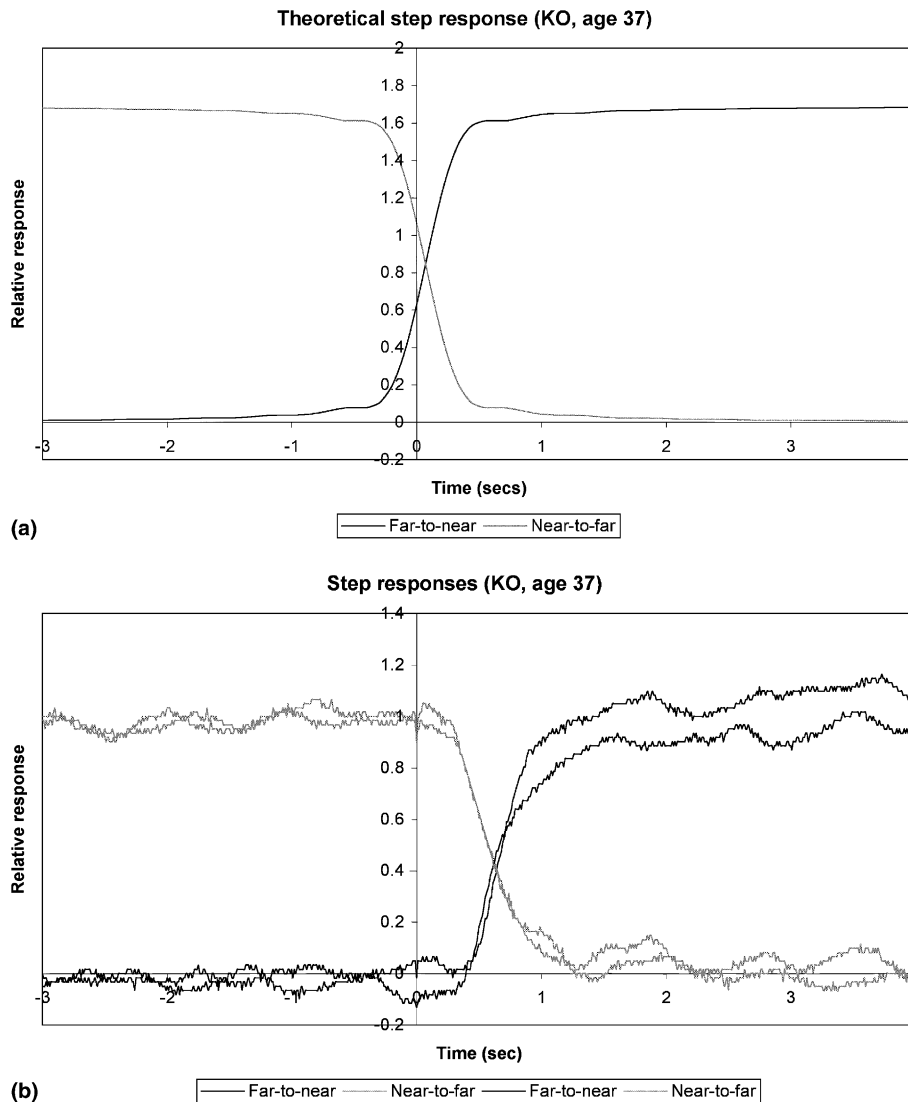

Fig. 7. (a) Theoretical relative responses to abrupt changes in stimulus vergence for subject KO (age 37), as derived by linear theory from the characteristics of her responses to sinusoidally-varying accommodation stimuli (see text). (b) Experimentally-measured responses for the same subject to random step stimuli. Far-to-near responses are shown in black, near-to-far in grey.

response lacks the predicted symmetry about its midpoint: the change in response when it is initiated is much more rapid than that when it terminates. Other limitations of linear systems theory as applied to accommodation have been discussed by Charman and Heron (2000).

4.5. Origins of the observed changes in response dynamics with age

What do these results imply regarding the age-dependent changes in the accommodative mechanism? As noted earlier, the near-zero change in the reaction time to step stimuli is probably to be expected, since other reaction times remain essentially constant over the age range 20–50 years (Weale, 1982). This raises the puzzling question, however, as to why, when the step response time shows little change with age and the sinusoidal stimuli are completely predictable, the phase lags for the sinusoidal responses, and t_d, increase markedly with age, leading to the failure of linear theory to adequately predict the step responses (Fig. 7). As noted by Heron et al. (2002) it may be that regular, repetitive stimuli lead to lens hysteresis effects which are not present with widely-spaced, step stimuli.

In view of the known ability of the ciliary body to maintain its efficiency with age (Fisher, 1977; Strenk et al., 1999; Swegmark, 1969) in spite of some changes in geometry and structure (Pardue & Sivak, 2000), it appears reasonable to invoke change in the visco-elastic properties of the lens and its capsule as the prime explanation for the loss in amplitude of both the sinusoidal and step responses with age (e.g., Fisher, 1969, 1971; Glasser & Campbell, 1998, 1999; Glasser & Kaufman, 1999). The exact effects may, however, be complicated by the evidence (Chen & O'Leary, 2002; Kalsi et al., 2001; Mordi & Ciuffreda, 1998; Ramsdale & Charman, 1989) that the accommodative control system may change with age in such a way as to make optimal use of the available combination of ocular power change and depth-of-focus: this may favour a reduced response amplitude within the available amplitude of accommodation of older subjects, particularly after the age of 40 (Kalsi et al., 2001). A further complication is obviously the voluntary component of accommodation, which appears to vary markedly between individuals of similar age (see, e.g., Fig. 3(a), and 4) and which is also dependent upon attentional factors (Francis, Jiang, Owens, & Tyrell, 2003).

One particularly interesting feature of the results is the apparent stability with age of the cut-off frequency, f_c, beyond which no response to sinusoidal stimuli occurs. Some caution must, of course, be exercised in interpreting this result, since it depends on the extrapolation of straight-line fits over the frequency range 0.05–1.0 Hz to an intercept at around 1.7 Hz. Nevertheless, if the result is accepted at its face value it may be

that this stability is associated with an element of the system which is itself reasonably stable with age, such as the ciliary body, rather than the lens, with its marked changes with age in both bulk and elasticity. Thus the cut-off frequency could be due to the characteristics of the ciliary body (and perhaps to neural limitations), while the increase in phase lags and t_d could originate in the age-dependent lenticular and capsular changes.

Scheimpflug imaging studies (Dubbelmann, van der Heijde, Weeber, & Vrensen, 2003; Koretz, Cook, & Kaufman, 2002) suggest that, with relaxed accommodation, it is primarily the lens cortex that increases in thickness with age, while the nucleus shows only a slight thickening. In contrast, at fixed age, accommodation causes a marked increase in nuclear thickness but only minor changes in the thickness of the anterior and posterior cortex (although the curvatures of the cortical surfaces change). Moffat, Atchison, and Pope (2002) suggest, on the basis of magnetic resonance microimaging, that the nuclear refractive index may fall with age and that this is due to a decrease in soluble lens crystallins in the nucleus. It may be, then, that the observed changes in response to periodic stimuli, in particular the increase in phase lags and t_d, are caused primarily by hysteresis effects in the lens cortex rather than the nucleus. As was suggested earlier, the constancy of the cut-off frequency f_c may be due to the continued vigour of the activity of the ciliary body.

Finally we note that it is important to remember that the same stimuli were employed with all subjects. Hence, even though the stimuli always lay within the available range of accommodation, the magnitude of the stimulus change represented a much bigger fraction of the smaller available amplitude of accommodation of the older subjects. Stimuli of this type obviously are more relevant to performance of everyday tasks but it would clearly be of interest to carry out similar studies using stimuli whose amplitude was scaled to the available objective amplitude of accommodation of the individual subject, although this might present signal-to-noise problems with older subjects. Alternatively, the stimuli might be scaled to produce constant response amplitude, since this allows a more reliable comparison to be made of rates of accommodation and disaccommodation at different ages (Vilupuru & Glasser, 2002).

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