



Dynamics of the accommodation response to abrupt changes in target vergence as a function of age

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Abstract

The dynamic accommodation responses to small, abrupt changes in an accommodation stimulus were studied in two experiments. In the first, responses of 19 subjects with ages distributed between 18 and 49 years were measured for step stimuli of ± 1.05 D. In the second, responses to small step stimuli (± 0.75 , ± 1.75 D) were recorded for a group of six 'young' (mean age 22, range 16–26 years) and six 'old' (mean age 42, range 36–48 years) subjects. In both experiments, the low target vergences always lay within the accommodation range of all subjects. Whether the data were analysed in terms of simple reaction and response times, or in terms of the frequency response, no marked systematic changes with age were found in the dynamics of the response in either of the experiments. It is concluded that, for small stimuli within the amplitude of accommodation, the response dynamics over the adult age range studied remain remarkably constant, even though the amplitude progressively reduces with age as complete presbyopia is approached. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The process of presbyopia can be considered to begin in late childhood, since accommodation amplitudes are greatest at this time of life (Wold, 1967). Thereafter, the amplitude of accommodation decreases steadily until there is no functional accommodation at all after the age of about 50, although ocular depth-of-focus still allows adequate vision over a modest range of distances (e.g. Hamasaki, Ong, & Marg, 1956; Hofstetter, 1965; Ramsdale & Charman, 1989; Mordi & Ciuffreda, 1998). These changes in the clinically-important static amplitude of accommodation have been thoroughly studied and their fundamental characteristics have been reasonably well understood for a century or more (e.g. Donders, 1864; Duane, 1912). It appears that they are explicable within the broad framework of the basic accommodation mechanism originally proposed by Helmholtz (e.g. Glasser & Kaufman, 1999) and that a

major contributory factor is an increase with age in lens hardening, described as decreased elasticity and increased viscosity (e.g. Gullstrand, 1909; Fincham, 1937; Fisher, 1973; Glasser & Campbell, 1998, 1999). However, other age-dependent physiological and mechanical factors probably also play a role (see, e.g. Atchison, 1995; Gilmartin, 1995; Glasser & Kaufman, 1999, for reviews).

Much less attention has been devoted to the changes with age in the dynamic characteristics of accommodation, largely due to the difficulties of measuring the relatively short latencies and response times associated with abrupt changes in target distance. The increased lenticular hardness measured by Glasser and Campbell (1999) would be expected to limit both the amplitude and the rate at which the lens can respond to increased or decreased accommodative demand. Similarly changes with age in the ciliary body, the geometry of the zonular attachments and other factors (e.g. Atchison, 1995; Gilmartin, 1995; Glasser & Kaufman, 1999) would also be expected to affect both static and dynamic accommodation. Hence quantification of the

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changes with age in the dynamics of accommodation can help to improve understanding of the mechanisms of presbyopia.

Early studies using fairly crude reaction-time methods and step stimuli (Robertson, 1937; Allen, 1956) found that overall response times were longer for older subjects; a later experiment on much the same lines suggested that although far-to-near (FN) responses slowed with ageing, near-to-far (NF) responses did not (Temme & Morris, 1989). Sun et al. (1988), using an infra-red optometer and a stimulus change from 1 to 4 D (see also Sun & Stark, 1986), suggested that mean exponential time constants for the FN response increased from about 170 ms in youth to about 300 ms in the mid-forties, whereas, latency showed no change with age. Deterioration in accommodation dynamics with age was also found by Fukuda, Kanada and Saito (1990), Schaeffel, Wilhelm, and Zrenner (1993), Beers and van der Heijde (1996), using a variety of measurement techniques and conditions (see Table 1).

The conclusions of several of these studies depend heavily on the inclusion of one or two older subjects, whereas Schaeffel et al. (1993) have shown that there may be considerable inter-subject variation between the dynamics of different individuals of the same age. A further problem is that one of the stimuli often lay at the edge of, or beyond, the range of accommodation of the older subjects. Both sensory-optical and motor-plant factors will influence responses to these large stimuli. The longer response times recorded for older subjects may have arisen from an inability to reach a satisfactory level of focus to clear the image. Contrast reduction arising from the accommodative error would further reduce the accommodative response amplitude (Kotulak & Schor, 1987). In addition, any non-linear saturation effects near the upper limits of the accommodative range would change the dynamics of the accommodative response.

In an attempt to overcome some of these problems, Heron, Charman and Gray (1999) studied the dynamic responses to targets whose vergence changed sinusoidally with time at different temporal frequencies between 0.05 and 1.00 Hz. The stimulus amplitude and mean level always took the relatively modest values of 0.52 and 1.86 D, respectively, and the ages of the large group (19) of subjects were spread fairly uniformly between 18 and 49 years. Although subjects of similar ages often had substantially different accommodation dynamics (Schaeffel et al., 1993), the overall results showed only a small, gradual loss in accommodative gain with age at all temporal frequencies, while phase lag at any temporal frequency tended to increase slightly with age, particularly at higher frequencies. Results obtained with sinusoidally-changing stimuli can, however, be criticised in that the predictability of such stimuli may result in enhanced gain and diminished phase lags (Stark, 1968; Phillips, Shirachi, & Stark, 1972; Krishnan, Phillips, & Stark, 1973; Van der Wildt, Bouman, & Van der Kraats, 1974). Indeed, Charman and Heron (2000) have shown recently that the measured variation in phase lag with the temporal frequency of sinusoidal stimulus change is essentially linear in all studies of this type, implying that the lag arises from a simple, constant, time delay. Thus the phase lags obtained with predictable stimuli may tell us more about the training and alertness of the subjects than about the temporal abilities of the accommodation system.

For this reason responses to unpredictable stimuli may give a better indication of dynamic accommodation performance under real-life conditions. Heron et al. (1999) reported briefly on such data as a function of age and we first re-examine these to see if we can establish an age effect. We then describe further measurements of responses of groups of older and younger

Table 1
Summary of attempts to explore the changes in accommodation dynamics with age using step stimuli^a

Author	Method	Age range	Number of subjects	Stimulus	Latency change with age	Response time change with age
Allen (1956)	Reaction time	7–49	12	Variable	Total time increases with age (FN longer than NF)	
Sun et al. (1988)	Purkinje image optometer	13–46	6	1–4 D	None (325 ms)	Increase (FN) from about 100–200 ms
Temme and Morris (1989)	Reaction time	24–44	65	0.2–2.2 D	Total time increases FN but not NF	
Fukuda et al. (1990)	IR optometer	22–61	10	0.5–3.0 D	None?	Slower velocity with age
Schaeffel et al. (1993)	Photoretinoscopy	5–49	39	0–1, 2.5, 3.3, 4, 5 and 7.1 D		Decrease in maximum speed. NF faster than FN
Beers and van der Heijde (1996)	Ultrasound	15–55	20	0.6–1.6 D		Increase in both NF and FN (6–7 ms/year). NF faster than FN

^a FN represents far-to-near, NF near-to-far.

subjects to step stimuli in which the levels of stimulus involved all lay well within the steady-state range of accommodation of the subjects, although the constant magnitudes of step, which were used obviously represented a larger fraction of the amplitudes of the older subjects. The results have been analysed to explore the age dependence not only in terms of response latencies and stimulus times but also, through application of linear systems theory, in terms of the frequency-dependence of the gain and phase.

2. Experiment 1

2.1. Methods

These are described in detail in Heron et al. (1999) and will only be summarised here. Monocular accommodation to directly viewed targets was recorded using a modified Canon Auto Ref R1 infrared optometer (Pugh & Winn, 1988, 1989). Abrupt changes in target vergence between 2.38 and 1.33 D (distances of 0.42 and 0.75 m) and vice-versa were provided using two high-contrast, single-letter targets (6/9 Snellen equivalent). Each was mounted on a rotary solenoid and back lit by an electroluminescent panel to a luminance of 34 cd/m², so that the targets could be interchanged in less than 100 ms. Subjects were told to keep the target as clear as possible at all times. To minimise spurious noise and other movement artifacts, a headrest and bitebar were used to keep subjects in position relative to the optometer and target. The responses were sampled at 100 Hz. Since it is known that the accommodation response only extends up to a few hertz (e.g. Campbell & Westheimer, 1960; Krishnan et al., 1973; Kruger & Pola, 1986) the data were subsequently filtered to remove frequencies above about 10 Hz.

2.2. Subjects

Visually-normal subjects (19) with ages between 18 and 49 years were studied; all had amplitudes of accommodation, as measured using the standard push-up method (Atchison, Capper, & McCabe, 1994; Rosenfield & Cohen, 1996), which lay within normal limits for their age. Where present, any refractive error was corrected with a soft contact lens — no subject had astigmatism greater than 0.50 DC. The stimulus vergence range lay within the objective range of accommodation of all subjects. Mydriasis using two drops of 2.5% phenylephrine was necessary to keep recordings free of pupillary artefacts with some older subjects. It is known that phenylephrine may reduce slightly static amplitudes of accommodation (Mordi, Lyle, & Mousa, 1986a; Mordi, Tucker, & Charman, 1986b; Gimpel, Doughty, & Lyle, 1994). Our own preliminary experi-

ments suggested that, at the concentration used, the drug had little, if any, effect on dynamic responses to small steps, in agreement with the findings of a recent study by Culhane, Winn, and Gilmartin (1999), although the latter do find that phenylephrine may slightly enhance response dynamics at low and mid-temporal frequencies (up to about 0.3 Hz). Mordi et al. (1986b) found that at the higher concentration of 10%, response times were increased slightly.

2.3. Results

Accommodation responses displayed the fluctuations, finite reaction times or latencies, and response times which are characteristic of the accommodation system (see, Ciuffreda, 1991). As examples, Fig. 1 shows six typical NF and six FN step responses for a single subject (aged 37). It is evident that the traces show considerable individual variation in the mean levels immediately before and after the step. The amplitude of the fluctuations in accommodation is an appreciable fraction of the magnitude of the actual step response (see also, Phillips et al., 1972; Tucker & Charman, 1979; Sun & Stark, 1986; Takeda, Morabito, Xiao, Hashimoto, & Endo, 1996). The reduction in the power of the accommodation fluctuations with age has been discussed elsewhere (Fukuda et al., 1990; Heron & Schor, 1995; Toshida, Okuyama, & Tokoro, 1998), while Denieul (1982) has commented on the variation in their characteristics with the level of accommodation being exercised.

Fig. 1 shows, however, that in spite of the differences in detail between the individual responses, their basic temporal form is remarkably similar, the response being initiated and terminated at consistent time intervals after the stimulus has changed.

Fig. 2 shows the changes in far-to-near and near-to-far reaction and response times as a function of the age of the individual subjects. The reaction time or latency is the interval between the stimulus change and the start of the response, and the overall response time is that in which the accommodation is changing between its initial and final levels. These levels were determined by fitting lines of zero slope to the accommodation records -2 to 0 s before and $+2$ to $+4$ s after the stimulus change. The points at which the response started and finished were determined by eye from the response records; the response was assumed to start at the point where it just became systematically different from the starting level and to end when it just reached the final level.

Neither reaction nor response time appears to be a function of age. Three of the regression line slopes do not differ significantly from zero ($P > 0.2$) and the slope of the NF reaction times is marginally significant ($P < 0.05$).

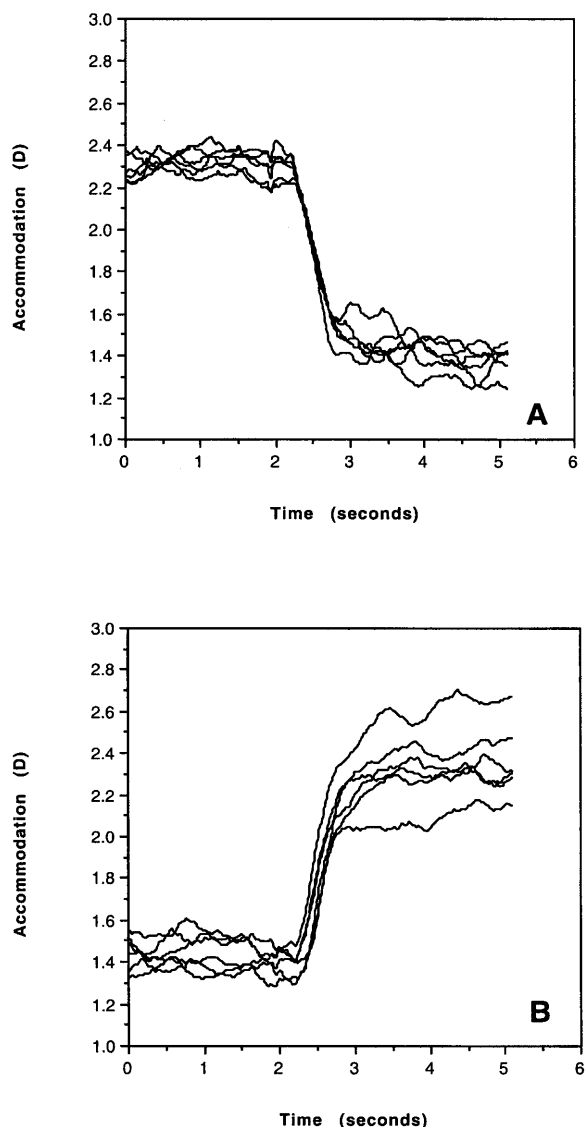


Fig. 1. Dynamic responses to individual 1.05 D step stimuli for a single subject (KO, aged 37 years) in experiment 1. The stimulus changes at 1.93 s along the timebase. Note the response variability and the noise associated with fluctuations in accommodation etc. A shows NF responses and B shows FN responses.

It is obviously possible that, although the durations of the responses do not change with age, their magnitudes do. Fig. 3A shows that there may be a weak effect of this type, particularly for some of the over 40-year-old subjects (see also Heron et al., 1999, figure 10). The slope of the regression line is marginally significant ($P = 0.05$). The diminished magnitude of response for the older subjects has a corresponding effect on the mean response velocities, as obtained by dividing the response magnitudes by the response times (Fig. 3B and C), but the effects again lack statistical significance ($P > 0.1$). Evidently the impact of age across the age range of the adult subjects (18–49 years) on these response parameters for unpredictable step stimuli is small.

3. Experiment 2

This experiment was carried out in a further attempt to demonstrate convincingly age changes in the response, under conditions where the stimuli levels lay within the objective amplitude of the subjects. Rather than using a range of subject ages, the performance of a group of ‘young’ subjects was compared with that of an ‘old’ group.

3.1. Methods

3.1.1. Apparatus and procedures

Monocular response data were obtained with an SRI optometer (Cornsweet & Crane, 1970; Crane & Steele, 1978; Heron & Schor, 1995). The stimulus was a single, high-contrast, 6/9 Snellen letter viewed through the SRI’s Badal stimulus system, which keeps the target subtense constant with changes in vergence. Stimulus luminance was 50 cd/m². Step changes in stimulus vergence were either 0.25–1.00/1.00–0.25 or 0.25–2.00/2.00–0.25 D. As in experiment 1, the stimulus levels were kept low so as to be within the amplitude of accommodation of all the subjects. Four FN and four NF changes between each pair of stimulus levels were recorded from each subject. Each trial lasted 40 s, step changes occurring regularly at 10-s intervals, a long enough time to ensure that the response stabilised to its new level before the next change occurred and to make it difficult for the subject to predict the exact moment of change. The actual change in stimulus took 15 ms to complete, a negligible duration in comparison to the accommodation response times. The optometer output was sampled at 40 Hz. Subjects were told to keep the target as clear as possible at all times. A headrest and bitebar were used to keep subjects in position relative to the optometer and target and hence minimise spurious noise and other movement artefacts.

3.1.2. Subjects

Two groups of six subjects were used, classified as ‘young’ (mean age 22 years, range 16–26) and ‘old’ (mean age 42 years, range 36–48). All had no visual pathology or binocular vision problems; they were either emmetropic or were made so by introducing appropriate correcting lenses into the optometer’s optical system. To improve the signal-to-noise ratio, all pupils were dilated prior to recording using two drops of 2.5% phenylephrine. Amplitudes of accommodation were measured before and after the recording using the standard push-up method (Atchison et al., 1994; Rosenfield & Cohen, 1996). Average amplitudes without dilation and using a natural pupil were 9.4 ± 2.9 D for the younger group and 4.2 ± 1.8 D for the older group. Individual subjects were checked to ensure that they were capable of producing a monotonically

increasing response to increases in stimulus vergence over the range studied, i.e. that the stimuli lay on the approximately linear region of the individual's response/stimulus curve.

3.2. Results

Measurements of these reaction and response times are shown in Table 2, data for both step sizes having been pooled for the groups of young and old observers.

It can be seen that any differences between the young and old groups are small. As in experiment 1, no differences reach statistical significance ($P > 0.1$).

4. Discussion

The results of the present study, using small stimulus increments lying well within the amplitude of accommodation of the subjects, while agreeing with many of the results of previous authors show some important differences.

4.1. Reaction and response times

The reaction times (latencies) of about 350 ms in experiment 1 and 450 ms in experiment 2 were similar

to earlier data (e.g. Campbell & Westheimer, 1960, 370 ms; Phillips et al., 1972, 380 ms; Smithline, 1974, 380 ms; Tucker & Charman, 1979, 320 ms; Mordi et al., 1986b, 450 ms; Sun et al., 1988, 410 ms; Heron & Winn, 1989, 350 ms). Like Sun et al. (1988), the present study finds no evidence for any extension in accommodation reaction time with age over the time interval considered. This is not surprising, since other reaction times tend to show few changes between the ages of 20 and 50 (e.g. Weale, 1982), although they rise in later life.

Neither experiment 1 nor experiment 2 produced any evidence for statistically-significant differences in response times with age. The values recorded, about 550 ms in experiment 1 and 740 ms in experiment 2, are again typical of those found in the literature (Campbell & Westheimer, 1960, 600 ms; Tucker & Charman, 1979, 800 ms; Ibi, 1997, 700–900 ms). It may be that the slightly longer reaction and response times found in experiment 2 reflect the fact that subjects have greater difficulty in responding to internal, Badal type stimulus vergence than to external 'real' stimuli (Ibi, 1997)

Experiments 1 and 2 thus concur in showing that, when small step stimuli lying within the amplitude of accommodation are used, changes in response latency and duration with age are, if they exist at all, difficult to detect against the background of fluctuation noise and

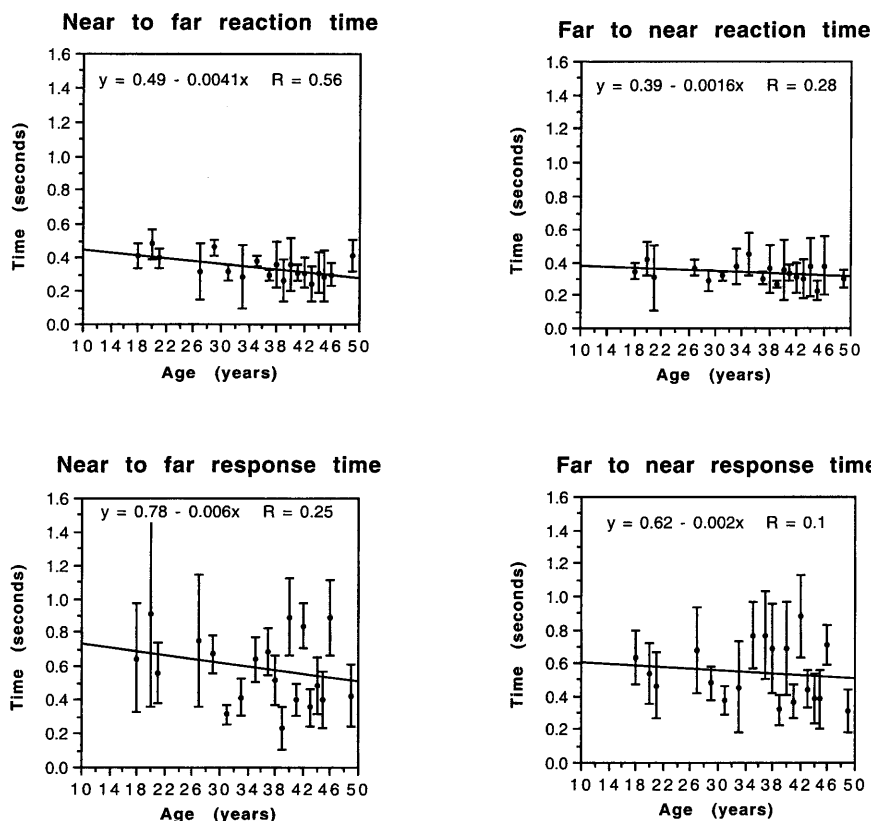


Fig. 2. NF and FN reaction and response times as a function of age in experiment 1.

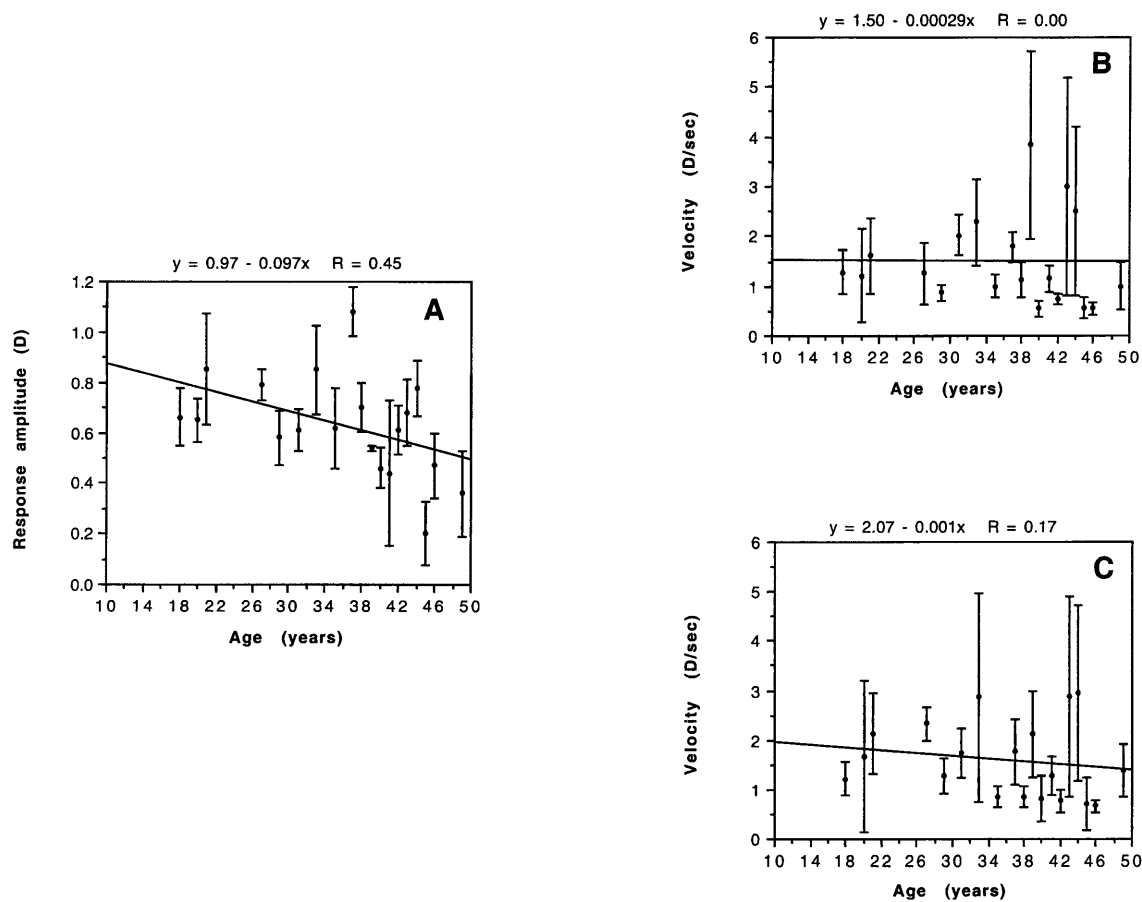


Fig. 3. (A) Response magnitude for the 1.05 D stimulus change in experiment 1, as a function of age. The data have been fitted with a regression line but might be better represented as being reasonably constant up to the age of about 40 and then declining rapidly. Mean response velocities are also shown for NF stimuli (B) and FN stimuli (C) as obtained by dividing the response magnitudes by the total response times.

individual response variation. The normal fluctuations in accommodation (e.g. Charman & Heron, 1988; Winn & Gilmartin, 1992) have a magnitude, which is an appreciable fraction of the response change for the relatively small steps in target vergence used (Fig. 1). Thus subtle age-dependent changes in the form of the response may be difficult to detect. How, then, can we refine the comparison?

4.2. Overall form of step responses

It is straightforward to reduce the effects of fluctuation noise by appropriate averaging of the original digital data across trials. Averaging can be carried out using the times at which the stimulus changed as reference points. Nevertheless, this process is not without its ambiguities. If, for example, the individual latency varies, due perhaps to variations in the subject's ability to anticipate the stimulus change (e.g. Phillips et al., 1972; Van der Wildt et al., 1974), but the response time remains the same, averaging of individual records will extend the apparent overall response time. Moreover, since many factors can contribute to slowing of accom-

modation (inattention, distraction, lack of effort, and fatigue), Sun et al. (1988) have argued that only the fastest responses should be considered to represent the limiting abilities of the system. However, this approach too has its problems, since random noise fluctuations or accommodative microfluctuations can, depending upon their phase with respect to the step response, either effectively enhance or degrade the apparent speed of any single response. This is particularly the case when the change in stimulus level is small, resulting in a relatively poor signal-to-noise ratio, as in the present case.

Table 2
Experiment 2^a

	Young	Old
Reaction time (NF)	0.48 ± 0.15	0.42 ± 0.17
Reaction time (FN)	0.49 ± 0.16	0.41 ± 0.17
Response time (NF)	0.57 ± 0.27	0.72 ± 0.39
Response time (FN)	0.83 ± 0.47	0.84 ± 0.61

^a Mean latencies (reaction) and response times, in seconds, based on individual responses. Data for both step sizes have been pooled to give two categories, NF and FN. Errors indicated are S.D.

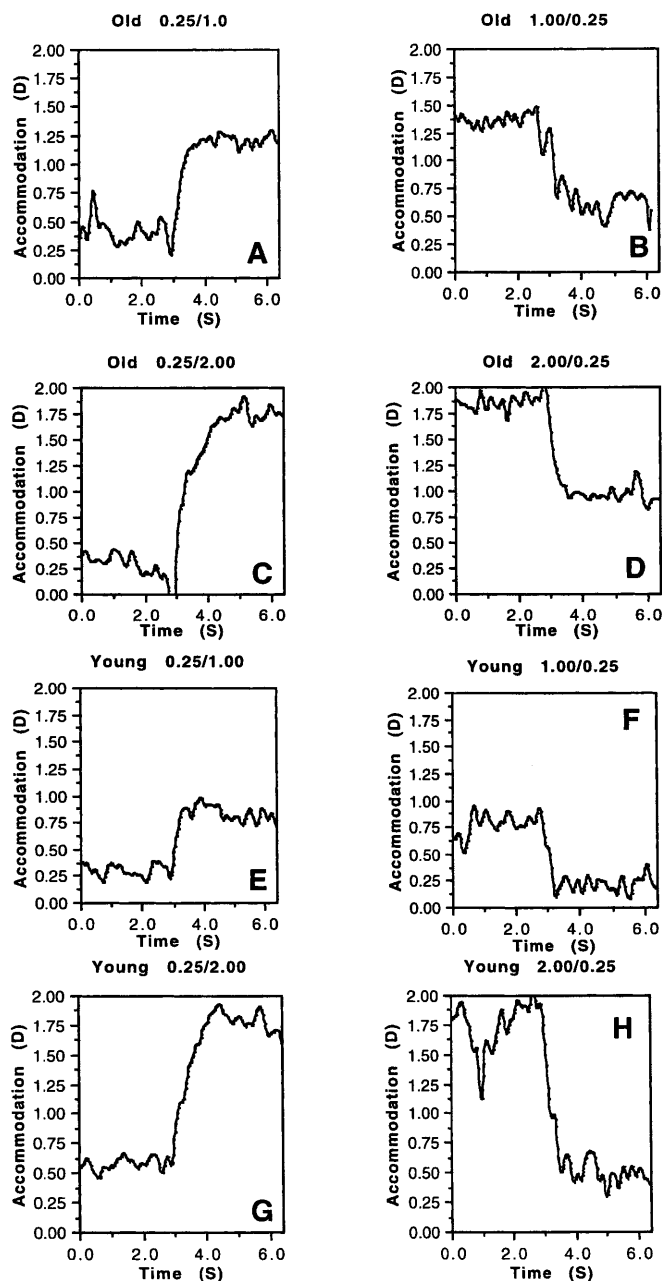


Fig. 4. Average step responses to the stimulus changes indicated for the old (A–D) and young (E–H) age groups.

Thus, in an attempt to give a realistic picture of ‘typical’ mean responses, all responses for a given age group and condition in experiment 2, which were not degraded by blinks or other artefacts were averaged. The mean responses were then filtered to remove content at frequencies above 7 Hz.

The mean step responses at this stage for the various conditions of experiment 2 are illustrated in Fig. 4 — the stimulus changes occur at 2.5 s along the abscissae. Note that, as might be expected from the fact that the slope of the typical steady-state response/stimulus curve is generally less than unity (Ciuffreda, 1991), the total

changes in response are generally smaller than the changes in stimulus. The differences between the mean ‘steady state’ responses of the young and old groups to each of the three stimulus levels (0.25, 1.00 and 2.00 D) are not significant (see Heron & Schor, 1995).

Although qualitatively the differences between corresponding young and old response curves in Fig. 4 appear to be only minor, it could be argued that they may be difficult to appreciate because of the presence of residual noise and the differing ‘steady state’ response levels (i.e. lags of accommodation) in the two subject groups. Any differences in response dynamics can be better appreciated by plotting the responses in relative terms in which the upper and lower mean steady-state levels are normalised as 1.0 and 0, respectively. A comparison is made on this basis in Fig. 5, the data having been further smoothed to reduce higher-frequency noise. Although there are differences between the pairs of curves, with the young response being faster in three of the four cases, the differences are small and of doubtful statistical or practical significance.

It is of interest that, for both young and old groups, relaxation (NF) appears to take place more rapidly than accommodation (FN). This can be appreciated more readily if one of the relative step responses is inverted for direct comparison (Fig. 6).

Although the initial response dynamics are comparable, the latter parts of the response appear to be slower in the FN case than in the NF in both age groups. The fact that the time course of the FN response is somewhat slower is in accord with the response times of Table 2, although the effect is not statistically significant. Early evidence for such an effect was also equivocal, with some finding shorter NF times (e.g. Allen, 1956; Campbell & Westheimer, 1960) and some shorter FN (e.g. Tucker & Charman, 1979; Heron & Winn, 1989), while Shirachi et al. (1978) found different results at different target distances. This disagreement continues. Temme and Morris (1989) suggest that FN is faster in young subjects and NF in older; this is also suggested in the data of Beers and van der Heijde (1994, 1996), although it is not obvious in the results of Fukuda et al. (1990). Schaeffel et al. (1993) find that NF tends to be faster at all ages. In part, these disagreements may derive from differences in the methods used to assess the speed of response, e.g. average velocity, maximal velocity, overall duration of the response change etc. In Fig. 6, for example, maximal velocities as evidenced by the maximal slopes of the step responses (Table 3) are similar, although the overall response durations appear a little longer for FN. Beers and van der Heijde (1996) have argued that in the FN case, the time constant for the response is dominated by the viscous and elastic properties of the lens, whereas in the NF case the properties of the zonule, ciliary body and

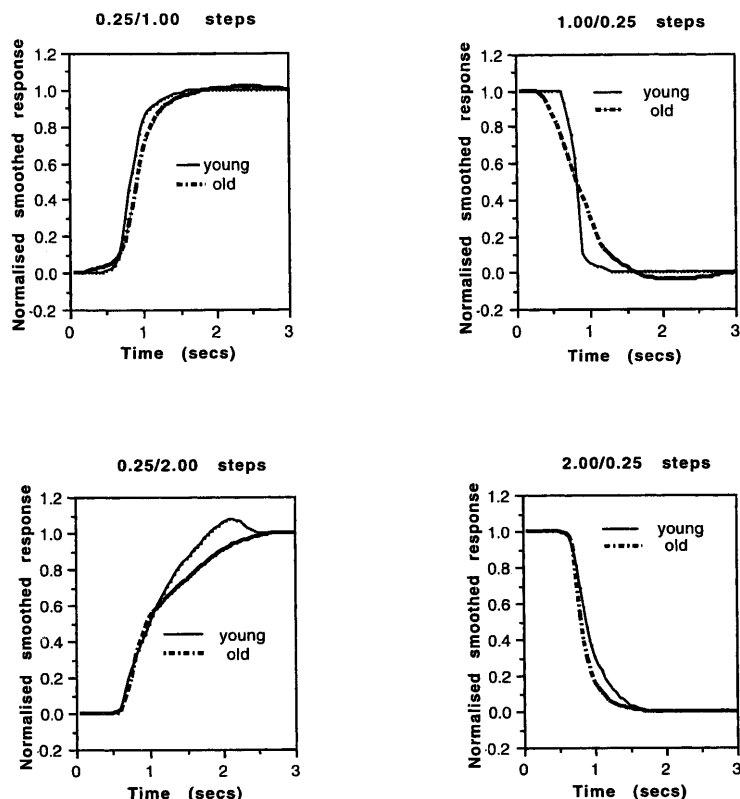


Fig. 5. Comparison of normalised, smoothed step-response profiles for young and old subjects. In each case the results have been normalised so that the response to the lower stimulus is zero and that to the upper stimulus is unity.

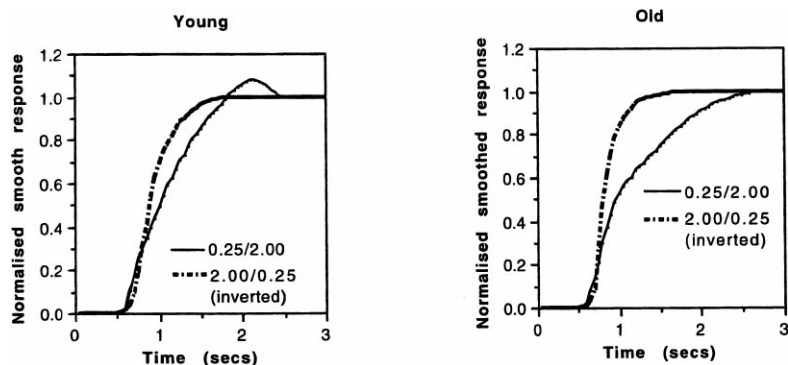


Fig. 6. Normalised responses of old and young subjects to both directions of stimulus change between 0.25 and 2.00 D. The NF responses are shown inverted to allow direct comparison of their temporal profile with the FN responses.

Table 3
Experiment 2^a

Step (dioptries)	Mean velocity (D/s) (young)	Peak velocity (D/s) (young)	Mean velocity (D/s) (old)	Peak velocity (D/s) (old)
0.25–1.00	1.2 ± 0.7	1.8 ± 1.0	1.1 ± 0.7	1.9 ± 0.9
1.00–0.25	1.8 ± 0.9	3.1 ± 1.0	0.7 ± 0.5	1.0 ± 0.6
0.25–2.00	1.0 ± 0.7	2.1 ± 1.1	1.0 ± 0.6	2.9 ± 1.6
2.00–0.25	1.9 ± 0.9	3.5 ± 0.8	1.8 ± 0.9	3.7 ± 0.9

^a Mean response velocity (i.e. total dioptric response change/response duration) and maximal response velocity as deduced from the mean step responses for young and old subjects. The mean velocity is defined over the interval 10–90% of the total step response. Errors indicated are S.D.

choroid also come into play. In Fig. 6, the NF characteristics appear faster than the FN in both age groups, but the latter part of the FN response may be more sluggish in the older group. This would accord with the indirect findings of Temme and Morris (1989) and may suggest, then, that the slower FN responses are a manifestation of the decline with age in the elastic properties of the lens and its capsule found by Fisher (1969a,b, 1971, 1973), allied, perhaps, to an increase in lens viscosity (Glasser & Campbell, 1999). The similarity in the basic NF characteristics could imply that in this case, as argued by Beers and van der Heijde (1996), the spring constant of the zonule and choroid becomes important and this only increases slightly with age. It may be remarked that any differences between FN and NF response characteristics could be at least partly associated with central, rather than plant, mechanisms; if central mechanisms began to exert less effort as near focus was approached this could extend the associated response time.

It is also worth noting that the response to the larger step appears, in general, to be of longer duration than that to the smaller step (see also Heron, 1972; Heron & Winn, 1989; Tucker & Charman, 1979; Hung & Ciuffreda, 1988; Schaeffel et al., 1993). However, it must again be emphasised that any differences between the two age groups in their response dynamics are minor for both the larger ± 1.75 D steps and the smaller ± 0.75 D steps.

4.3. Frequency analysis

In a linear system, the gain and phase as a function of temporal frequency can be deduced from the step response by first differentiating the latter to obtain the impulse response, and then taking its Fourier transform. This approach has been applied to accommodation dynamics by Krueger (1973) and Van der Wildt et al. (1974).

There is, however, a substantial amount of experimental evidence to suggest that the accommodation system cannot be considered to be linear (Stark, Takahashi, & Zames, 1965; O'Neill, Sanathanan, & Brodkey, 1969; Shirachi et al., 1978; Charman & Heron, 2000). As discussed previously, the dynamics appear to vary with stimulus magnitude, direction and other factors.

In spite of these reservations, it is of interest to compute the gain and phase curves from step responses using the assumption of linearity, and to determine the extent to which the results agree with those obtained using sinusoidally-varying stimuli. Any effects of non-linearity might be expected to be less significant with small stimuli and at present the Fourier approach represents the only way of relating the two types of study.

We first consider the results for an individual subject and the question of whether averaging of responses

substantially affects the derived Bode plots. Using FN responses for the 37-year-old subject shown in Fig. 1B, we can calculate the corresponding mean step response (Fig. 7A). This allows us to calculate first the gain curves from the individual responses (Fig. 7B) and then the gain from the average step response. Fig. 7C confirms that the gain derived from the average step response (open symbols) is essentially identical to the mean of the gain curves derived from the individual step responses (filled symbols). This suggests that averaging the steps does not degrade significantly the response gradient and hence the associated gain curve. Note in Fig. 7C, whereas below about 2 Hz the steady fall in gain with temporal frequency mainly represents the true dynamic characteristics of the response, the roughly constant, small values above about 2 Hz probably reflect the spectrum of the accommodation fluctuations and other noise.

Fig. 8A gives the overall average result found for gain, as derived from the step responses of experiment 2. In deriving this result, the gains found from each of the four mean step responses for each age group in Fig. 4 have been averaged. The present gain results are broadly comparable to those of authors who used sinusoidal stimuli. Some of the observed discrepancies are caused by the assumption made by several authors that there is unit gain at zero temporal frequencies; this is equivalent to saying that the steady-state response/stimulus curve has unit slope, whereas in practice the latter is typically less than unity and varies with the subject and observing conditions (see Ciuffreda, 1991). The instructions given to the subjects will also influence the results (Van der Wildt et al., 1974). Note that Heron et al. (1999) found gains in excess of unity for young subjects, presumably due to the effects of anticipation with regularly-varying stimuli.

Although our step-derived gains at higher temporal frequencies are somewhat higher than many of the results with a sinusoidally-changing stimulus, they fail to approach the levels derived from step responses by Van der Wildt et al. (1974) (see dashed curve in Fig. 8A). This is possibly because the latter authors used only their fastest step responses, whereas, as noted earlier, we used all responses. In addition, Van der Wildt and his colleagues would appear to have assumed that the overall magnitude of the step response equalled that of the stimulus, leading to unit gain at zero frequency. Note that there is some indication that gains at higher frequencies tend to be slightly higher for our younger group of subjects, i.e. their accommodation system may be a little faster; the differences are small, however.

The mean phase data derived from experiment 2 are shown in Fig. 8B. Following the suggestion of Van der Wildt et al. (1974), the phase data have been corrected for the reaction times given in Table 2. The results

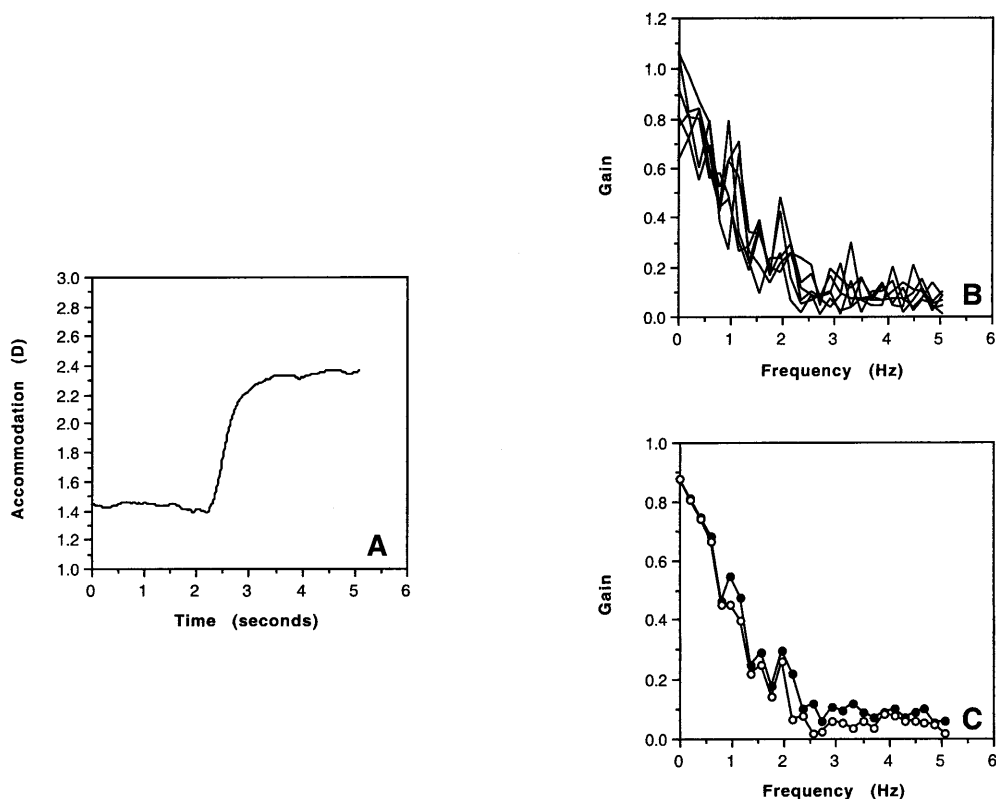


Fig. 7. Gain results derived from step responses for the subject whose data are illustrated in Fig. 1. (A) Mean of the FN step responses illustrated in Fig. 1B. (B) Individual gain curves derived from the individual step responses of Fig. 1B. (C) Mean gains derived from the mean step response of Fig. 7A (open symbols) and from the mean of the individual curves of Fig. 7B (filled symbols). There is little difference in the results below 2 Hz.

shown, therefore, nominally represent optimal anticipation for the step. The residual phase lags are higher than those derived from steps by Van der Wildt et al. (1974) (see dashed curve in Fig. 8B) which increase only modestly with temporal frequency. This may again be because we did not use only the fastest responses. While the present lags are broadly comparable with typical results for sinusoidally-changing stimuli, including those of Heron et al. (1999), the phase lags at frequencies up to 1 Hz are greater than those found by many investigators. This probably reflects the importance of anticipation in reducing phase lags when sinusoidal stimuli are used; even when the step-derived phase data are corrected for the reaction time, responses are delayed in comparison to those that can be achieved with regular sinusoidal stimuli. Van der Wildt et al. (1974) noted that, with such sinusoidal stimuli, phase lags can even be reduced to zero whenever a subject succeeds in following the stimulus very accurately.

Phase lags appear to be slightly greater for the older age group but the differences are of doubtful significance. Note that the quasi-linear relation between phase and temporal frequency that is evident in most of the data of Fig. 8B implies that most of the changes can be explained by a simple constant time delay (Campbell & Westheimer, 1960; Charman & Heron, 2000). In the

case of our step data, the phase lags of about $100^\circ/\text{Hz}$ correspond to time delays of about 300 ms, (see Table 2). This is evidently plausible in that the peak of the impulse response (i.e. the position of maximal response velocity) typically follows the initiation of the response by about this time interval.

4.4. General considerations

Overall, the important finding of this study is that, for small stimulus changes lying within the range for which the accommodative system is responsive, any differences between the dynamic characteristics of young and older, pre-presbyopic, adult subjects are small. Thus the results found with unpredictable step stimuli support those found with sinusoidally-changing stimuli (Heron et al., 1999).

Is the absence of age change in accommodation dynamics surprising? It should again be emphasised that our findings refer only to small stimulus changes.

We note first that several authors have demonstrated that, within the amplitude of accommodation, steady-state accommodation was also surprisingly robust against increase in age (Ramsdale & Charman, 1989; Mordi & Ciuffreda, 1998; Kalsi, Heron, & Charman, 2001). Up to the age of about 40 years, only minor

changes occur in slope of the static response/stimulus curve as measured over the stimulus range 0.5–2.5 D. The results of Fig. 3a are in accord with these findings; it is only after the age of 40 that the magnitude of the step response starts to show a marked decline.

Given the inhomogeneous nature of the lens, with the older nucleus being less elastic than the outer, younger, cortical layers, an apparently attractive explanation for our failure to find an age effect is that, with our stimuli,

differences in response speed with age were minimised by the fact that responses only necessitated changes in the more superficial cortical layers. On the other hand, the Scheimpflug slit-lamp observations of Koretz, Cook, and Kaufman (1997) suggest that accommodation involves nuclear, rather than cortical, changes in axial thickness, so that this explanation may not be tenable. There is, of course, little doubt that the classical view that lens hardening, described as decreased

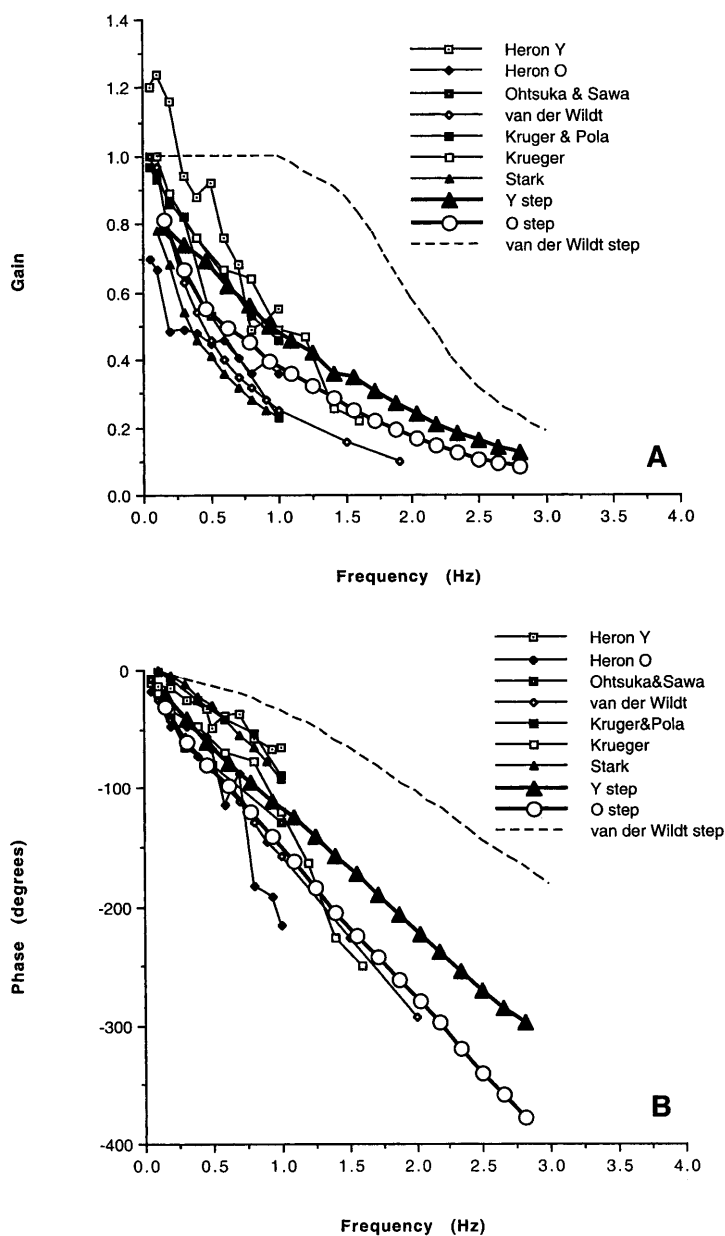


Fig. 8. Mean overall results from experiment 2 for gain and phase as a function of temporal frequency for young and old subjects in comparison to the results of different investigators using targets with sinusoidally-varying vergence and the results of Van der Wildt et al. (1974) derived from step responses (dashed line). The phases deduced from the present step data have been corrected for the effect of response latencies as given in Table 2. (A) Gain; (B) phase. The gain and phase data derived from experiment 2 are shown as filled triangles with bold line for young subjects (Y step) and in open circles with bold line for old subjects (O step). The sources of the other data displayed are: Stark (1968), Krueger (1973); Van der Wildt et al. (1974); Kruger and Pola (1986); Ohtsuka and Sawa (1997); Heron et al. (1999) [Heron Y (20-year-old subjects) and Heron O (45-year-old subjects)].

elasticity and increased viscosity, plays a significant role in the overall development of presbyopia is correct (Glasser & Campbell, 1998, 1999).

A further possible hypothesis derives from the recent observations by Strenk et al. (1999), using magnetic resonance imaging, that whereas ciliary muscle activity continues to occur even in advanced presbyopia, the diameter of the unaccommodated ciliary muscle ring decreases with age. This could suggest that the decline in amplitude of accommodation was at least partly associated with the reduced ring diameter, which would have the effect of reducing the maximal possible zonular tension and hence the attainable reduction in lens power from its maximally-accommodated state. On the other hand, such ciliary body changes would not necessarily affect the speed of accommodation within the effective amplitude, so that the dynamics of small accommodation changes would alter very little with age.

For larger stimulus changes, approaching the amplitude of accommodation, it would be expected that ageing effects would become much more obvious. Indeed when stimuli lie close to the limits of the accommodative range, response times to the final equilibrium level can extend over many minutes (Charman & Tucker, 1978).

5. Conclusion

It would appear that, provided that the stimulus changes lie within the slowly-diminishing amplitude of accommodation, the dynamic accommodation response shows only relatively minor changes between about 20 and about 40 years, just as the static response remains tolerably accurate within its increasingly limited range. Thus the system remains adequate for most everyday demands of vision until the amplitude falls below that required for typical reading or similar near tasks.

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