Amplitude dependent accommodative dynamics in humans

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Abstract

Dynamics of accommodation (far-to-near focus) and disaccommodation (near-to-far focus) are described as a function of response amplitude. Accommodative responses to step stimuli of various amplitudes presented in real space were measured in eight 20–30 year old subjects. Responses were fitted with exponential functions to determine amplitude, time constant and peak velocity. Despite the intersubject variability, the results show that time constants of accommodation and peak velocity of disaccommodation increase with amplitude in all subjects. The dynamics of accommodation and disaccommodation are dependent on amplitude, but have different properties in each case.
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1. Introduction

Accommodation, in humans, has been studied extensively for more than a century and the static and dynamic aspects are fairly well understood and characterized. However, there is a paucity of literature on the dynamics of accommodation as a function of accommodative amplitude. Studying dynamics as a function of amplitude provides important information about dynamic behavior and have been considered powerful tools in understanding physiological systems (Bahill, Clark, & Stark, 1975).

There is an extensive literature on the amplitude dependent dynamics of eye movements, especially saccades, in the form of 'main sequence analysis' (see Bahill et al., 1975 for a review of literature; Van Opstal & Van Gisbergen, 1987). The 'main sequence' is a plot of peak velocity or time constant as a function of response amplitude, where peak velocity is the maximum velocity of a response and time constant is a mathematical representation of response time corresponding to the time taken to achieve 63% of the response (Shirachi et al., 1978). Main sequence plots give an idea of how the dynamic responses of a system change with increasing amplitude. The main sequence plot for saccades shows a strong relationship between peak velocity and amplitude (Bahill et al., 1975). This has been used to understand the neural generation and control of saccades, to describe the dynamics of the saccadic system and to identify abnormal saccades (Bahill et al., 1975). Similarly, main sequence of accommodation can be studied to understand normal accommodative dynamics and abnormal accommodation such as with presbyopia (Mordi, 1991).

Past studies on the age-related changes in accommodative (far-to-near focus) and disaccommodative (near-to-far focus) dynamics have provided equivocal results. Evidence for age-related changes in accommodative dynamics range from decrease in speed of both far-to-near and near-to-far accommodation (Beers & Van Der Heijde, 1996; Schaeffel, Wilhelm, & Zrenner, 1993), far-to-near accommodation only (Sun et al., 1988; Temme & Morris, 1989), near-to-far accommodation only (Heron & Winn, 1989) or to change in neither near-to-far nor far-to-near accommodation (Heron, Charman, & Gray, 1999; Heron, Charman, & Schor, 2001). Most of the differences may be due to methodological differences; however, studies that have measured similar parameters also show a lack of agreement (Heron & Winn, 1989; Heron et al., 1999, 2001). In addition, the well characterized age related decline in amplitude of accommodation (Duane, 1912) is

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an important confounding factor in studying aging changes in accommodative dynamics. This presents a potential confound when determining the appropriate amplitude to compare between young and old subjects. If maximum available amplitude is compared, then very different amplitudes may be compared in young and old subjects and if low amplitudes that are available to all subjects are compared, then different proportions of the available accommodation for young and old subjects are compared (Sun et al., 1988). This problem can possibly be overcome by studying accommodative dynamics over the full range of available amplitudes to obtain a "main sequence ratio" (the slope of main sequence plot) to compare between young and old and to identify possible age related changes in dynamics of accommodation.

Compared to the many studies on dynamics of eye movements, there are relatively few studies on accommodative dynamics in the form of main sequence analysis. In one such study, Ciuffreda and Kruger (1988), measured peak velocity of accommodation for amplitudes up to 3 D and showed that peak velocity of accommodation increased linearly with amplitude. Additionally, it was shown that different kinds of accommodation such as normal reflex, fast reflex and voluntary accommodation share the same linear relationship. This shows that irrespective of the accommodative effort, peak velocity and accommodation are linearly related (Ciuffreda & Kruger, 1988). In a recent study on anesthetized rhesus monkeys, it was shown that the peak velocity of centrally stimulated accommodation and disaccommodation increase linearly with amplitude over the full range of accommodation available (Vilupuru & Glasser, 2002). Furthermore, it was shown that peak velocity of disaccommodation is greater than peak velocity of accommodation (Vilupuru & Glasser, 2002). These studies indicate the benefits and utility of studying the amplitude dependent dynamics of accommodation, over a wide range of amplitudes.

The robust linear relationship observed between peak velocity and amplitude of centrally stimulated accommodation and disaccommodation in anesthetized rhesus monkeys has largely prompted the present study. It is of interest to determine if a similar linear relationship between peak velocity and amplitude exists in conscious humans accommodating voluntarily to real targets. It is of further interest to compare dynamics of centrally stimulated accommodation in anesthetized monkeys with voluntary accommodation in conscious humans, where, for the latter, all the cues to accommodation are intact.

The goal of this study was to generate main sequence plots of accommodation and disaccommodation in a group of young humans between the ages of 20 and 30 years to characterize the amplitude dependent dynamics of accommodation and disaccommodation.

2. Methods

2.1. Subjects

Eleven subjects between the ages of 20 and 30 years were recruited for the study according to institutionally approved human subject protocols. Subjects were either emmetropes (+0.50 D to −0.50 D) or myopes (range: −2.75 D to −5.75 D, mean: −4.68 ± 1.32 D) corrected with soft contact lenses.

2.2. Preliminary measures

Each subject was tested to ensure normal binocular vision, phoria and near point of convergence. Prior to dynamic accommodation testing, the following measurements were made. Refraction was measured in both eyes with a Hartinger coincidence refractometer. Subjective and objective amplitudes were measured to ensure normal accommodative amplitudes for the age group. Subjective near point of accommodation was determined with the push-up method. Amplitude of accommodation was measured objectively with the Hartinger coincidence refractometer, by placing increasing powered negative trial lenses in front of the left eye and measuring the consensual accommodative response in the right eye.

2.3. Dynamic accommodation experimental setup

2.3.1. Target presentation

Subjects alternately focused on two real targets placed at far and near. The targets were two high contrast 'H' letter targets printed on white paper and illuminated with white light emitting diodes. The far target was placed at 6 m and the near target was placed on a track and could be moved from 1 m (1 D) to 14 cm (7 D) from the subject's right eye (Fig. 1). Alignment of targets was achieved by having the subject look at the far target through the beam splitter while looking at the reflected image of the near target from the same beam splitter. The left eye was covered and the subject rotated the beam splitter until the two targets were aligned.

During the experiment, the far and near targets were alternately illuminated for 2.5 s each, by a pulse generator. At any point in time, the subject binocularly viewed either the far or the near target and these were the only targets visible to the subject. An output from this pulse generator was fed into the computer that recorded the accommodative responses, to record the time of onset of the far and near stimuli. Both far and near targets had 100% contrast and had a luminance of 5 cd/m² on the background of the 'H' target. However, with an accommodative pupillary constriction, retinal illuminance would not be constant. The same near target
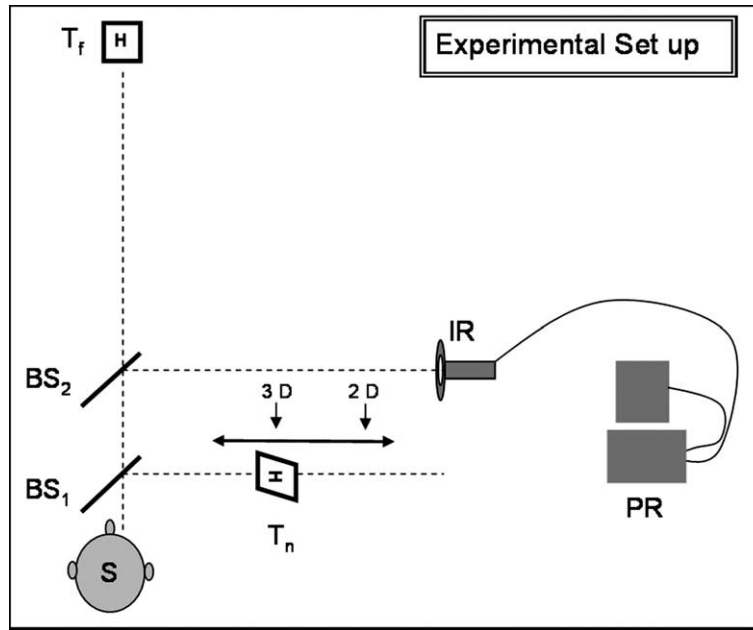
Fig. 1. The right eye of the subject (S) is aligned with the far target (T_f). The near target (T_n) is placed on an optical track and can be moved towards or away from subject to change target vergence. The far target, near target and infrared (IR) PowerRefractor (PR) camera are aligned with subject's right eye with help of two beam splitters (BS1 and BS2). The far and near target are illuminated alternately, the subject views them binocularly while the optometer measures refraction in the right eye continuously at 25 Hz.

was used at various distances, resulting in increasing angular subtense with decreasing distance. The angular size of the far target was changed to match the near targets. Therefore, though the angular subtense of the targets changed from one accommodative demand to the other, the angular subtense of far and near targets was constant for each accommodative demand. The angular size of one limb of the 'H' target was 1′ for 1 D, 2′ for 2 D etc.

The far target was fixed at 6 m and the near target was initially presented at 1 m. The far and near stimuli were alternately illuminated 10 times to get 10 accommodative and 10 disaccommodative responses. In subsequent trials, the near target was brought progressively closer to the subject to increase the near target vergence from 1 to 7 D in 1 D steps. The room lights were dimmed to try to maintain large pupil diameters and also to prevent other objects in the room from providing distracting stimuli (Owens, 1979; Rosenfield & Ciuffreda, 1991). Subjects viewed both the far and the near stimuli binocularly and were instructed to focus on whichever target was illuminated and to change focus when the illumination switched. Subjects were given a practice session to experience the task during which no data was collected. Verbal encouragement was provided to help the subjects concentrate on the stimulus during data collection. The goal of this experiment was to describe accommodative dynamics while preserving all the necessary cues to accommodation and so ample opportunity and encouragement was provided.

2.3.2. Measurement of accommodation

The PowerRefractor (MultiChannel systems, Germany), an infrared optometer, monitored the subject's refraction monocularly at 25 Hz while the subject concentrated on the stimuli. The far target, the near target and the camera of the PowerRefractor were aligned with the subject's right eye to ensure on axis refraction measurements (Fig. 1). The PowerRefractor software recorded the right eye refraction, pupil diameter and eye movements as well as time of onset of far and near stimuli.

The PowerRefractor consists of an infrared illumination source mounted on a knife-edge aperture in front of a CCD video camera. The infrared illumination source creates a vertical luminance gradient in the pupil of the eye and the PowerRefractor software records the slope of the vertical pupil luminance profile (see Choi et al., 2000; Gekeler, Schaeffel, Howland, & Wattam-Bell, 1997; Schaeffel et al., 1993; Wolffsohn, Hunt, & Gilmartin, 2002, for detailed descriptions of the PowerRefractor). The slope of the vertical pupil luminance profile was converted to refraction using a calibration function individually generated for each subject, as described by Schaeffel et al. (1993). The calibration procedure was performed prior to recording the accommodative responses. During the calibration procedure, the subject was asked to view the distance target with the left eye. A visible blocking, infrared pass filter (Kodak Wratten filter # 89B, high pass at 700 nm) was placed in front of the right eye, to prevent the right eye

from seeing the target while at the same time allowing the infrared optometer to measure refraction through the filter. Ophthalmic trial lenses (+6 to −6 in 2 D intervals) were placed in front of the right eye while the left eye viewed the distance target. The PowerRefractor standard calibration was set to a slope of one and an intercept of zero in the software. This constrained the PowerRefractor software to record the raw slope of the pupillary luminance profile. The effective refractive error created by holding the trial lens held in front of the eye was calculated, after compensating for the 1 m working distance of the PowerRefractor camera. This effective refractive error was plotted against slope of pupil luminance profile. A linear regression equation was fit to this data for each subject to generate an individual calibration function for each subject.

Fig. 2 shows a plot of effective refractive error versus slope of the vertical pupil luminance profile from all subjects. This combined data is fitted with a single regression line to demonstrate overall linearity, although individual regression equations were used for the data analysis. During the experiment, the PowerRefractor recorded the raw slope of the vertical pupil luminance profile. The measured slopes were subsequently converted to refraction using each subject's individual calibration function. The measured refractions were then converted to accommodation. Representative accommodative responses from one subject to 2, 4 and 6 D stimuli are shown in Fig. 3.

2.3.3. Analysis

Ten accommodative and disaccommodative responses, at each stimulus amplitude, were recorded for each subject. Accommodative and disaccommodative
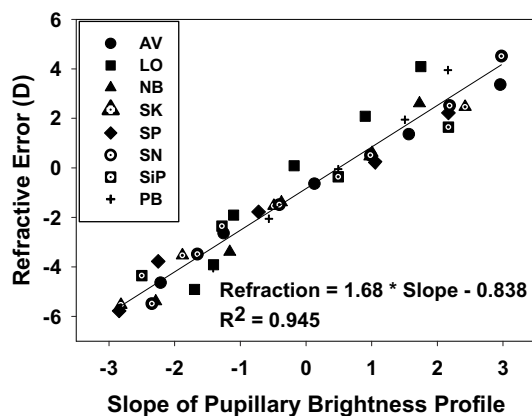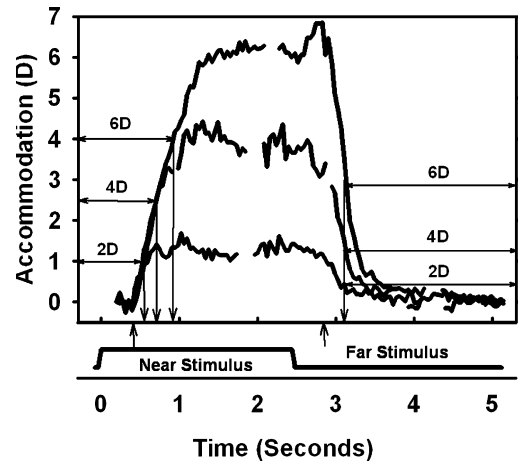

Fig. 3. Accommodative responses to 2, 4 and 6 D stimuli are shown. The solid line at the bottom of the graph shows the time course of the near and far targets, stimulating accommodation and disaccommodation respectively. Near stimuli were presented at time '0' for 2.5 s, at 50, 25 and 17 cm for accommodative demands of 2, 4 and 6 D respectively and far stimuli were presented at time 2.5 s to elicit disaccommodation from various accommodated states (see Section 2). Horizontal drop lines are at 63% of amplitude (Y-axis) and vertical drop lines show the time constant (X-axis) for each amplitude of accommodation and disaccommodation (see Section 2). Upward pointing arrows, beneath the X-axis, indicate the start of the accommodative and disaccommodative responses. Time constants of accommodation (0.11, 0.26 and 0.47 s) increase with amplitude, (2, 4 and 6 D) and time constants of disaccommodation (0.24, 0.24 and 0.25 s) are similar for different amplitudes (2, 4 and 6 D).

responses were extracted based on the events recorded during the experiment that identified onset of far and near stimuli. Each response was analyzed individually as described below to obtain peak velocities and time constants of accommodation and disaccommodation.

2.3.4. Step 1: removing latency

There is some latency between the onset of a stimulus and the initiation of an accommodative response. In order to fit exponential functions to accommodative responses, it is necessary to know when the accommodative response is initiated and to remove the data recorded during the latency period. To do this, an algorithm was developed similar to that described by Schor, Lott, Pope, and Graham (1999). The algorithm searched for three consecutive increasing data values, followed by four consecutive data values in which no two consecutive decreases occurred. When these criteria were met, the first data point in the sequence was recorded as the start of the response. The inverse algorithm was used to determine the start of the disaccommodative response. The performance of the algorithm was rigorously inspected based on the performance on the data from three subjects and was found to reliably determine the onset of accommodative and disaccommodative responses.

Fig. 2. Photorefraction calibration curves for each subject are plotted with a different symbol. Individual calibration functions were obtained for each subject by fitting the data for each subject with a linear regression equation (not shown). A linear equation is fitted (line shown) to the cumulative data to demonstrate the overall linear relation between refraction and slope of pupil brightness profile.

2.3.5. Step 2: fitting exponential functions

Each accommodative and disaccommodative trace was fitted with an exponential function (Beers & Van Der Heijde, 1994, 1996; Yamada & Ukai, 1997) that closely follows the responses (Fig. 4A and B). The exponential equations used to fit accommodation (Eq. (1)) and disaccommodation (Eq. (2)) responses were:

$$\text{Accommodation}: y = y_0 + a \times (1 - e^{-t/\tau}) \tag{1}$$

$$\text{Disaccommodation}: y = y_0 - a \times (1 - e^{-t/\tau}) \tag{2}$$

where "y" represents accommodation, "y_0" represents the initial value of accommodation, "a" represents the amplitude of the accommodative response, "t" represents time in seconds and "τ" represents time constant.

The exponential functions were fitted to the data from the entire accommodative and disaccommodative responses using SigmaPlot (SPSS Science), which iteratively found the best fit based on least squares weighting. The goodness of fit of each regression equation was evaluated by examination of the residuals. The refraction traces typically had a 0.5 D noise similar to the values reported in the past (Campbell, Robson, & Westheimer, 1959; Charman & Heron, 1988). Accommodative fluctuations with rms ranging from 0.05 to 0.4 D are reported in the literature (Charman & Heron, 1988). At high accommodative amplitudes, a small pupil size of less than 4 mm caused increased variability in the traces due to instrument artifacts. Considering fluctuations of accommodation, only fits with no systematic pattern in the residual plot and with no residuals greater than 1 D were used in the final analysis.

2.3.6. Step 3: parameters obtained

The exponential equations fitted to the data were used to obtain three parameters: (1) amplitude (a) and (2) time constant (τ), obtained directly from the fitted functions and (3) peak velocity (V_{max}), obtained by finding the peak value of the first derivative of the functions. The derivatives of equations (1) and (2) are:

$$\text{Accommodation}: \frac{\partial y}{\partial t} = \frac{a e^{-t/\tau}}{\tau} \tag{3}$$

$$\text{Disaccommodation}: \frac{\partial y}{\partial t} = \frac{-a e^{-t/\tau}}{\tau} \tag{4}$$

An exponential function starts with a high velocity and continues with an exponentially decreasing velocity. Therefore, peak velocity is the first value of the derivative of an exponential function. When the first derivative of Eqs. (3) and (4) were solved for $t = 0$, amplitude, time constant and peak velocity are related by:

$$V_{max} = a \times \tau \tag{5}$$

where V_{max} is peak velocity, a is amplitude and τ is the time constant.

3. Results

The photorefraction calibration functions for all subjects are shown cumulatively in Fig. 2. Individual calibration functions were linear over the range tested (r^2 ranged from 0.959 to 0.995). Although, individual calibration functions were used for analysis, a cumulative equation is shown in Fig. 2.

Generally, subjects found the focusing task easy to perform and complied well. At high amplitudes subjects showed strong pupil constriction and so accommodation could not be measured in some subjects, due to inability of PowerRefractor to measure through pupils smaller than about 3.5 mm. Therefore, out of 11 subjects tested, only those subjects in whom accommodation could be measured for at least five different stimulus amplitudes were included in the analysis ($n = 8$). Fig. 5 shows the stimulus response functions for the eight subjects. Some subjects showed relatively linear 1:1 stimulus response functions while others showed an increasing lag of accommodation with amplitude as they approach the maximum amplitude.
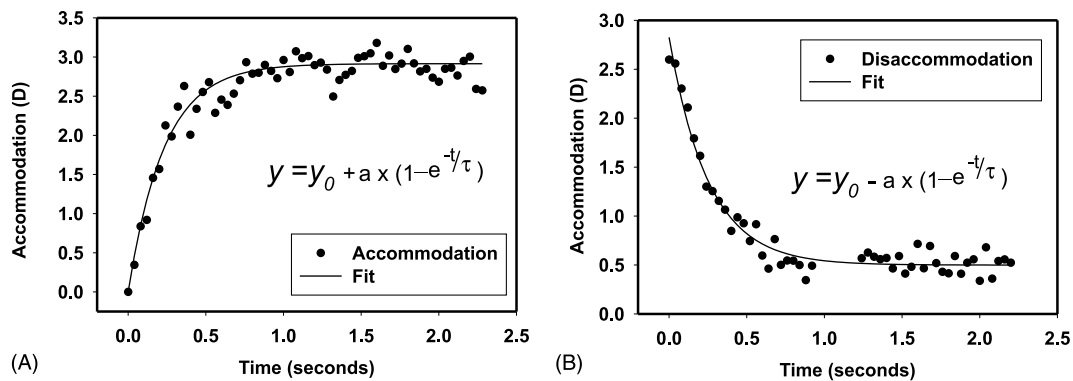

Fig. 4. Individual accommodative (A) and disaccommodative traces (B), (symbols), are fitted with functions (solid lines) using Eqs. (1) and (2), after removing latency (see text).
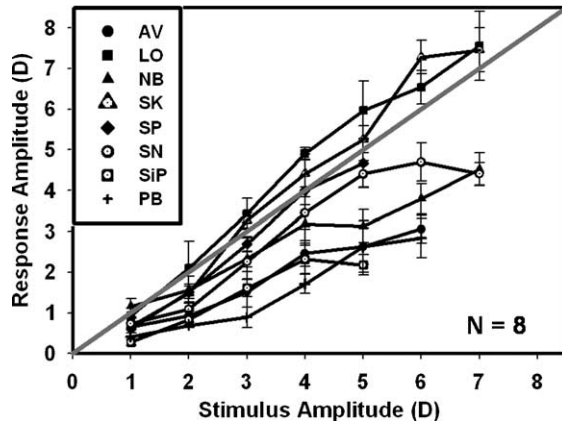
Fig. 5. The mean ± SD of relative changes in accommodation are plotted against stimulus amplitude to obtain the stimulus–response function for each subject, represented in different symbols. The diagonal gray line represents the 1:1 line. In five out of the eight subjects, it can be observed that lag of accommodation increases with stimulus amplitude. The two over-accommodators (subjects Sk and LO) were experienced subjects regularly involved in accommodation experiments. Subject PB with 3.5 D under accommodation for 6 D distance reported that the target was clear and did not report any difficulty with the experiment.

The main results of this study are the relationships between the dynamic parameters peak velocity, time constant and amplitude of accommodation and disaccommodation. Amplitude for accommodation is the difference in refraction from baseline to the maximum amplitude achieved. Amplitude for disaccommodation is the difference in refraction from the end of the accommodative response (when the eye is still accommodated) to baseline (after the eye is no longer accommodated). These amplitudes may differ if there is some drift in refraction while the eye is accommodated. In Fig. 6, peak velocity and time constants for each response are plotted against amplitude of accommodation (6A and C) and disaccommodation (6B and D), as scatter plot, with a different symbol for each subject. Linear regression equations are fit to the data in (B) and (C). The solid curves in (A) and (D) are theoretical relationships explained below.

3.1. Peak velocity

Peak velocity is plotted as a function of accommodative amplitude in Fig. 6A. The data shows substantial intersubject variability and shows no clear trend. However, at low amplitudes, lower peak velocities were recorded than at the higher amplitudes. ANOVA analysis considering peak velocities for 1 D amplitude bins showed significant differences ($p < 0.05$). Post-hoc tests showed, in general, that peak velocities for the low amplitude response bins were lower than for the higher amplitude response bins. For example, peak velocities for the 0–1 D bin were lower than for the higher am-

plitude bins (3–4, 4–5, 5–6, 7–8, 8–9 D but not 1–2, 2–3 or 6–7 D) with $p < 0.05$.

Fig. 6B shows peak velocity plotted against amplitude of disaccommodation. Peak velocity of disaccommodation increases linearly with amplitude ($r^2 = 0.68$; $p < 0.0001$). In this graph, the linear regression equation is fit to the cumulative data and the slope provides the main sequence ratio (MSR) (Bahill et al., 1975) of 4.18 s^{-1} for all subjects. MSRs of individual subjects were similar [mean MSR = 4.37 s^{-1} ± 1.39 (SD)].

3.2. Time constants

When time constants are plotted against accommodative amplitude (Fig. 6C), it can be seen that time constants increase linearly with amplitude of accommodation ($r^2 = 0.37$; $p < 0.0001$). Here too, there is considerable interindividual variability, although unlike the peak velocity data the trends are more consistent for any given individual (range of r^2: 0.52–0.93).

Time constants plotted against amplitude of disaccommodation (Fig. 6D), show no obvious relationship. However at low amplitudes, lower time constants were recorded than at higher amplitudes. ANOVA analysis considering time constants for 1 D amplitude bins showed significant differences ($p < 0.05$). Post-hoc tests showed that time constants for the 0–1 D bin were lower than for the higher amplitude bins (2–3 and 4–5 D but not for any other bins) with $p < 0.05$.

3.3. Prediction of trends

Peak velocity and time constants (Fig. 6) were obtained from fitting functions (1) and (2) to the raw accommodative responses. Relatively few of the low amplitude responses were adequately fit by functions (1) and (2), resulting in a paucity of data and larger variability at low amplitudes. To better understand the nonlinear trends, theoretical relationships between peak velocity and amplitude for accommodation (Fig. 6A) and time constants and amplitude for disaccommodation (Fig. 6D) were determined. For accommodation, the cumulative linear regression of time constant versus amplitude (Fig. 6C) was used to calculate time constants for each amplitude. Peak velocity at each amplitude was then calculated from Eq. (5) and is graphed as a solid curve in Fig. 6A. Similarly, for disaccommodation, the cumulative linear regression of peak velocity versus amplitude (Fig. 6D) was used to calculate peak velocity at each amplitude. Time constant at each amplitude was then calculated from Eq. (5) and is graphed as a solid curve in Fig. 6D.

The theoretical relationships suggests that peak velocities of accommodation (Fig. 6A) and time constants of disaccommodation (Fig. 6D) tend to increase at lower amplitudes and saturate at higher amplitudes. These
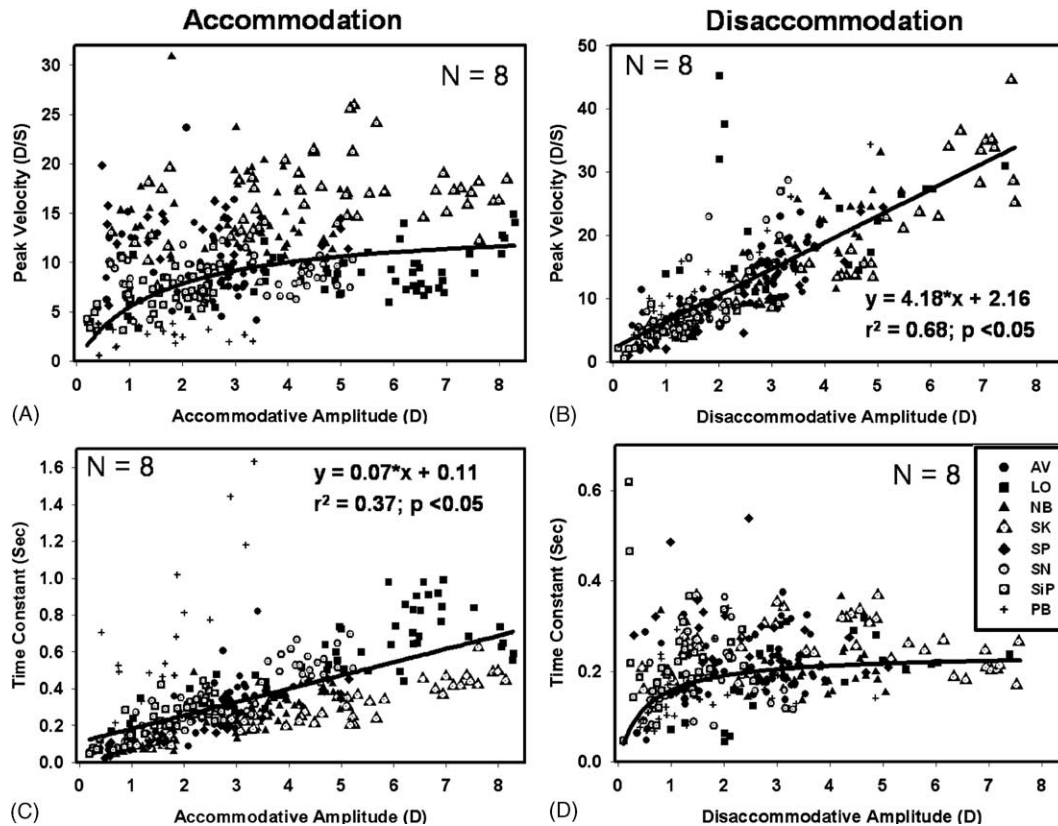
Fig. 6. In all the graphs, each subject is represented by a different symbol and the symbol for a subject is the same in all graphs. (A) Peak velocities of accommodation plotted against response amplitudes show that peak velocities are scattered with a trend of increasing peak velocity at low amplitudes and saturation at higher amplitudes. (B) Peak velocities of disaccommodation plotted against response amplitudes show that peak velocities increase linearly with amplitude and that peak velocities are similar between subjects. (C) Time constants of accommodation plotted against response amplitudes show that time constants increase with amplitude. (D) Time constants of disaccommodation plotted against response amplitudes show that time constants increase at low amplitudes and saturate at higher amplitudes. Different scales are used in each graph.

theoretical curves provide reasonable predictions of the actual data, within the large interindividual variability observed.

4. Discussion

4.1. Use of the PowerRefractor

The PowerRefractor is, as far as the authors are aware, the only available optometer that dynamically records binocular accommodation, pupil diameter and vergence, with an open field of view. It has been used previously for studies of refractive error (Choi et al., 2000; Gekeler et al., 1997) and static and dynamic accommodation (Schaeffel et al., 1993). In the present study, the PowerRefractor was used to measure accommodation in one eye and monitor eye movements to ensure that near and far targets were aligned and the measured eye did not undergo significant eye movements during accommodation. Pupil diameter, although recorded, was not considered further.

While the generalized PowerRefractor calibration function has been shown to be accurate and sufficient for population screening and refraction measurements (Choi et al., 2000; Gekeler et al., 1997; Schaeffel et al., 1993), we used individual calibrations functions (Fig. 2) to ensure accurate measurements of accommodation over a wide range of amplitudes for each individual subject.

4.2. Accommodative latency

The algorithm used to detect the onset of accommodative and disaccommodative responses showed latencies in the range 200–500 ms, in agreement with past studies (Ciuffreda, 1991; Heron & Winn, 1989; Heron et al., 2001; Schor et al., 1999; Shirachi et al., 1978). At very low amplitudes (less than 1 D) or when blinks occurred during a trial, it was not possible to objectively determine the start of an accommodative response. In such cases, these accommodative responses were excluded from further analysis. This resulted in a disproportionate loss of low amplitude (less than 1 D) data.

This was considered acceptable because one of the goals of this study was to undertake an objective analysis and so only those traces that could be objectively analyzed by the algorithm were considered.

4.3. Accommodative responses

The stimulus and presentation paradigm used was chosen in an attempt to elicit a predictable, measurable and appropriate accommodative response to each stimulus amplitude. Our intention was to elicit accommodative responses covering as wide a range of accommodative amplitudes as possible, but several subjects showed low maximum accommodative amplitudes for their ages. Other studies using objective optometers have recorded higher amplitudes of 8–10 D (Shirachi et al., 1978; Yamada & Ukai, 1997). The low amplitudes we recorded could be due to actual low amplitudes in our subjects, variations in individual subjects responses to the same target conditions, large targets at higher accommodative demands or less effort exerted. It has previously been suggested that these are possible causes for low amplitudes being recorded (Ciuffreda, 1991; Stark & Atchison, 1994). The stimulus response curves for some subjects show that response amplitudes were still increasing at the highest stimulus amplitudes. It is possible that higher amplitudes would have been elicited from these subjects if still higher stimulus amplitudes had been used.

4.4. Peak velocities

In prior studies, peak velocity of accommodation was found to increase linearly with amplitude in monkeys and in humans (Ciuffreda & Kruger, 1988; Vilupuru & Glasser, 2002). In the present study, peak velocity showed a high degree of variability and showed no clear change with amplitude (Fig. 6A). In anesthetized monkeys, accommodation was elicited by electrically stimulating the Edinger–Westphal neurons (Vilupuru & Glasser, 2002). In the present study, accommodation was stimulated by presenting visual stimuli to conscious humans. This difference could be due to differences between anesthetized versus awake subjects, electrical stimulation versus blur stimulation of accommodation, or because of the absence versus the presence of visual feedback.

The previous study on humans in which accommodative responses from as low as 0.1 up to 3 D was measured, showed that peak velocity of accommodation increased linearly with amplitude (Ciuffreda & Kruger, 1988). The relatively few low amplitude (less than 1 D) data in the present study precludes direct comparison of the two studies. However, the present study shows no linear increase with amplitude when higher amplitudes are considered.

A higher degree of variability is seen in the human data than in the monkey data of Vilupuru and Glasser (2002). This is not surprising because in the monkey studies the accommodative responses can be rigorously controlled and greater individual variation is expected from conscious humans. The substantial variability in the peak velocities of accommodation as seen in Fig. 6A, has also been observed in previous studies of accommodative dynamics (Ciuffreda & Kruger, 1988; Schaeffel et al., 1993). For disaccommodation (near-to-far focus) there is a more systematic linear relation between peak velocity and amplitude in all subjects (Fig. 6B). This is in agreement with the disaccommodation results from the anesthetized monkeys (Vilupuru & Glasser, 2002).

4.5. Time constants

One of the findings of this study is the increase in time constants with increasing accommodative amplitudes but similar time constants for various disaccommodative amplitudes. This can also be seen in the raw accommodative traces to 2, 4 and 6 D stimuli (Fig. 3). Fig. 6C shows that time constants increase with amplitude in all subjects, although with considerable interindividual variability. To compare the relationship for all subjects, normalized time constants were plotted against normalized amplitude in Fig. 7. The amplitude dependent increase in time constants is comparable with results from a study by Shirachi et al. (1978), in which it was shown that accommodative responses of similar amplitudes have longer time constants at close range than at far range. This suggests that there is a range dependent slowing down of dynamics that could potentially further slow down the large amplitude responses in the present study. Beers and Van Der Heijde (1994) have also shown that time constants of accommodative changes in lens
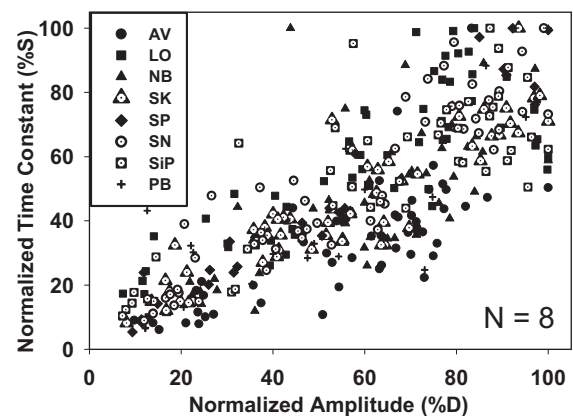

Fig. 7. Normalized time constants (%s) plotted as a function of normalized amplitude (%D) for accommodation. Time constants and amplitudes were normalized with respect to the maximum measured time constants and amplitudes respectively, in each subject. Individual subjects are represented by different symbols.

thickness measured with A-scan ultrasound, for far-to-near accommodation, increase with increasing stimulus amplitudes for 1, 2 and 4 D.

Time constants of disaccommodation (Fig. 6D) appear to be independent of amplitude. Previous studies suggest that time constants for disaccommodation are independent of stimulus amplitude for amplitudes greater than 2 D (Yamada & Ukai, 1997) and 1 D (Beers & Van Der Heijde, 1994), although neither of these studies measured responses at lower amplitudes. Yamada and Ukai (1997) found no relationship between time constants and stimulus amplitude of disaccommodation and concluded that the dynamics of disaccommodation are independent of amplitude and that the amount of defocus was not used as an error signal in the control system of disaccommodation. However, peak velocity of disaccommodation increases with amplitude (Fig. 6B), and so the dynamics of disaccommodation are not independent of amplitude, although time constants may be so for amplitudes greater than 1 D.

4.6. Relationship between amplitude, peak velocity and time constant

The three parameters considered were amplitude (a), peak velocity (V_{max}) and time constants (τ). Eqs. (1) and (2) that were fitted to the accommodative and disaccommodative responses relate the maximum accommodative state (a) to the time constant (τ). The derivatives of these functions provide the peak velocity. Thus, accommodative amplitude, time constant and peak velocity are all necessarily related. Eq. (5) shows that the relationship between peak velocity and time constant is amplitude dependent. In order to understand the relationship between the three parameters, one parameter, namely amplitude, was fixed and the relationship between peak velocities and time constants was examined. The data of time constants and peak velocities were sorted by response amplitude and separated in 1 D response amplitude bins 0–1; 1–2 and 2–3 D, etc. For each 1 D bin, peak velocities were plotted against time constants (Fig. 8A and B). From Eq. (5), peak velocities were calculated for time constants spanning a similar range to those found for various amplitudes. The values of time constants and peak velocities thus generated were plotted as solid lines for accommodative amplitudes of 1.5 D, 2.5 D, etc., up to 7.5 D (solid lines in Fig. 8A and B). This provides a family of curves that vary systematically as a function of amplitude and show the relationship between time constants and peak velocity as a function of amplitude. This means, for instance, that for a disaccommodative amplitude of 2–2.9 D, a velocity of 45 D/s is possible with a time constant of 0.05 s. This family of curves demonstrates how time constants and peak velocity vary as a function of amplitude.

Fig. 8A shows (1) for any given response amplitude there is a range of peak velocities and time constants that are recorded; (2) peak velocity holds a non-linear reciprocal relationship (or a log-linear relationship) with time constant; (3) for any given response amplitude, as peak velocity decreases time constant increases and vice versa; and (4) the curves become progressively more linear with increasing amplitude. Similar relationships are observed for disaccommodation (Fig. 8B). Although the relationship between the possible values is constrained, a given time constant can occur for a wide range of amplitudes just as a given peak velocity can occur for a wide range of amplitudes. The data show a series of parallel linear relationships when graphed on log–log scales, however crowding of the data tends to obscure the amplitude dependent relationship, so the data have been presented on linear scales.
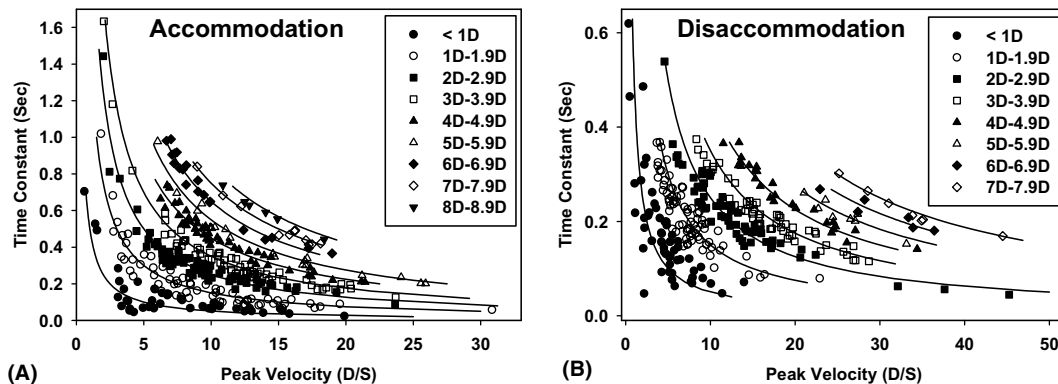

Fig. 8. Time constants plotted as a function of peak velocity for (A) accommodation and (B) disaccommodation. Data from all accommodative responses analyzed are separated into 1 D response amplitude bins. Alternating solid and open symbols are used for increasing amplitudes. The solid curves show calculated relationships between peak velocity and time constants for each 1 D interval (see text for full explanation). These curves were calculated for the ranges of time constants and peak velocities measured for each response amplitude. Peak velocities and time constants hold an amplitude dependent reciprocal non-linear relationship.

The relationship between time constants and peak velocities are of course defined by functions (1) and (2) used to fit the accommodative and disaccommodative responses. However, since these equations provide good fits to the physiological data, the equations also provide some information on the constraints that the accommodative system acts under. The family of curves demonstrates that the accommodative dynamics are amplitude dependent. While there is some limited range of possible time constants and peak velocities that occur for any given response amplitude, the range is dependent on the amplitude of the response. The data also shows that as amplitude increases, a given time constant is associated with an increasingly greater peak velocity.

4.7. Accommodation versus disaccommodation

The fundamental difference in the main sequence of accommodation and disaccommodation shown in this study is that for accommodation *time constants* increase with amplitude while for disaccommodation *peak velocity* increases with amplitude (Fig. 6C and B). From A-scan studies, Beers and Van Der Heijde (1994) also reported that time constants of accommodation increase with amplitude, but they did not analyze peak velocity of disaccommodation responses.

In the past it has been suggested that accommodation is significantly faster than disaccommodation (Heron & Winn, 1989) or that disaccommodation is faster than accommodation (Beers & Van Der Heijde, 1994; Heron et al., 2001; Schaeffel et al., 1993). The present study, in accordance with the rhesus monkey results (Vilupuru & Glasser, 2002), suggests that disaccommodation occurs progressively faster than accommodation, and this difference is greater with increasing amplitude (Fig. 6A–D).

It is of interest to explore the differences between accommodation and disaccommodation. The differences may be attributed to biomechanical factors (Beers & Van Der Heijde, 1994) or possibly to neurophysiological factors. Accommodation and disaccommodation are two fundamentally different processes from biomechanical and neurophysiological points of view.

4.7.1. Biomechanical factors

Biomechanically, the act of accommodation relies on contraction and movement of the ciliary muscle and the molding force of the capsule against the resistance of the lens substance (Fisher, 1969, 1977, 1986). Disaccommodation relies on the ciliary muscle being pulled back to the unaccommodated configuration and the stretching forces being transmitted through the zonular fibers and capsule to the lens substance (Fincham, 1937; Fisher, 1977; Glasser & Campbell, 1998; Glasser & Kaufman, 1999). The rate limiting step in each case could be ciliary muscle movement or the passive resistance of the lens substance. The difference in peak velocity for accommodation versus disaccommodation, could for example be explained by considering ciliary muscle movements. For accommodation, ciliary muscle contraction may occur at the same velocity regardless of amplitude, but velocity of movement for disaccommodation may increase for increasing amplitudes. A lens/capsular based explanation may suggest that ciliary muscle velocity increases with amplitude for both accommodation and disaccommodation, but the capsule molds the lens substance in a rate limited fashion during accommodation. However, with disaccommodation, since the ciliary muscle actively pulls on the lens and capsule through the zonule, the increased velocity of ciliary muscle movement with disaccommodation may cause disaccommodation peak velocity to increase with increasing amplitude.

In the present study, accommodation always started from a fixed far target distance (6 m) and went to various higher amplitudes, but disaccommodation started from various near target distances and went to a fixed far target distance. The forces exerted by the ciliary body, zonules and lens capsule have been shown to be influenced by the initial shape and geometry of the lens (Fisher, 1969, 1986). In this study accommodation always started from the same point and disaccommodation started from different points. Therefore it is possible that accommodation peak velocities did not change with amplitude since it had the same starting point and disaccommodation peak velocity varied because it started from various accommodated starting points.

4.7.2. Neurophysiological factors

Similarly, neurophysiologic factors may explain the differences between accommodation and disaccommodation. Vilupuru and Glasser (2002) showed that peak velocity of electrically stimulated accommodation increased linearly over the entire amplitude in anesthetized rhesus monkeys. However, the present study in conscious humans shows no systematic increase in peak velocity of accommodation. The accommodative plant of monkeys is very similar to humans in anatomy and response characteristics, except that monkeys may be capable of higher accommodative amplitudes (Smith & Harwerth, 1984). In the anesthetized monkeys, no neural feedback is required to achieve a particular accommodative response. On the other hand, visual feedback is important in awake behaving humans to determine when response matches demand. The neural feedback may include blur and contrast cues for example. These factors may provide some inherent limitation to the dynamics of accommodative responses, but may not be used when the eye is simply disaccommodating back to the far stimulus at or near the rest state of accommo-

dation. In other words, feedback may be involved for accurate accommodation, but may not be involved for disaccommodation to infinity.

4.8. Differences between monkey and human experiments

The monkey experiments showed different and more consistent results (Vilupuru & Glasser, 2002). This may be due in part to the rigorous control that can be imposed on the experimental conditions with anesthetized monkeys that are not possible in human behavioral experiments. More consistent accommodative responses are elicited with a regulated electrical stimulus in anesthetized monkeys compared to the voluntary accommodative responses in awake behaving humans. This raises questions as to the physiological significance of each of these experimental situations. Variations due to conscious factors in human behavioral experiments are important and relevant for understanding natural accommodation in humans. However dynamic studies of accommodation in humans will always be subject to the influence of consciousness and this may limit the conclusions that can be drawn about function of the plant. Similarly, while accommodation studies in anesthetized monkeys may provide information about the control of the physiological plant, they may not be truly representative of natural conscious voluntary accommodation.

5. Conclusion

Accommodation and disaccommodation show amplitude dependent dynamics that differ from each other. During accommodation, time constants increase with amplitude and during disaccommodation, peak velocities increase with amplitude. Disaccommodation occurs progressively faster than accommodation with increasing amplitude.

Dynamics of accommodation and disaccommodation differ in their dependency on stimulus characteristics and also on the biomechanical and geometric forces acting on the plant. Important information about the mechanism and dynamics of accommodation can be obtained by comparing in vitro studies, controlled studies on animal models and behavioral experiments on humans.

The main sequence plots of accommodation and disaccommodation provide information about the dynamics of accommodation. These have allowed quantitative descriptions of accommodation and disaccommodation in young human subjects. Ultimately, responses from older subjects, may allow a better understanding of possible age-related changes in the dynamics of accommodation.

References

Bahill, T. A., Clark, M. R., & Stark, L. (1975). The main sequence, a tool for studying human eye movements. *Mathematical Biosciences, 24*, 191–204.

Beers, A. P. A., & Van Der Heijde, G. L. (1994). In vivo determination of the biomechanical properties of the component elements of the accommodation mechanism. *Vision Research, 34*, 2897–2905.

Beers, A. P. A., & Van Der Heijde, G. L. (1996). Age-related changes in the accommodation mechanism. *Optometry and Vision Science, 73*, 235–242.

Campbell, F. W., Robson, J. G., & Westheimer, G. (1959). Fluctuations of accommodation under steady viewing conditions. *Journal of Physiology, London, 145*, 579–594.

Charman, W. N., & Heron, G. (1988). Fluctuations in accommodation: a review. *Ophthalmic and Physiological Optics, 8*, 153–164.

Choi, M., Weiss, S., Schaeffel, F., Seidemann, A., Howland, H. C., Wilhelm, B., & Wilhelm, H. (2000). Laboratory, clinical, kindergarten test of a new eccentric infrared photorefractor (Powerrefractor). *Optometry and Vision Science, 77*(10), 537–548.

Ciuffreda, K. J. (1991). The Glenn A. Fry invited lecture. Accommodation to gratings and more naturalistic stimuli. *Optometry and Vision Science, 68*, 243–260.

Ciuffreda, K. J., & Kruger, P. B. (1988). Dynamics of human voluntary accommodation. *American Journal of Optometry and Physiological Optics, 65*, 365–370.

Duane, A. (1912). Normal values of the accommodation at all ages. *Journal of the American Medical Association, 59*, 1010–1013.

Fincham, E. F. (1937). The mechanism of accommodation. *British Journal of Ophthalmology Monograph, VIII*, 7–80.

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

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

Fisher, R. F. (1986). The ciliary body in accommodation. *Transactions of the Opthalmological Societies of the United Kingdom, 105*, 208–219.

Gekeler, F., Schaeffel, F., Howland, H. C., & Wattam-Bell, J. (1997). Measurement of astigmatism by automated infrared photoretinoscopy. *Optometry and Vision Science, 74*(7), 472–482.

Glasser, A., & Campbell, M. C. (1998). Presbyopia and the optical changes in the human crystalline lens with age. *Vision Research, 38*(2), 209–229.

Glasser, A., & Kaufman, P. L. (1999). The mechanism of accommodation in primates. *Ophthalmology, 106*(5), 863–872.

Heron, G., Charman, W. N., & Gray, L. S. (1999). Accommodation response and ageing. *Investigative Ophthalmology and Vision Science, 40*, 2872–2883.

Heron, G., Charman, W. N., & Schor, C. (2001). Dynamics of the accommodation response to abrupt changes in target vergence as a function of age. *Vision Research, 41*, 507–519.

Heron, G., & Winn, B. (1989). Binocular accommodation reaction and response times for normal observers. *Ophthalmology and Physiological Optics, 9*, 176–182.

Mordi, J. A. (1991). *Accommodation, aging and presbyopia.* Ph.D. thesis, SUNY State College of Optometry, New York, NY.

Owens, D. A. (1979). The Mandelbaum effect: evidence for an accommodative bias towards intermediate viewing distances. *Journal of the Optical Society of America, 69*, 646–652.

Rosenfield, M., & Ciuffreda, K. J. (1991). Accommodative responses to conflicting stimuli. *Journal of the Optical Society of America, 8*(2), 422–426.

Schaeffel, F., Wilhelm, H., & Zrenner, E. (1993). Inter-individual variability in the dynamics of natural accommodation in humans: Relation to age and refractive errors. *Journal of Physiology, 461*, 301–320.

Schor, C. M., Lott, L. A., Pope, D., & Graham, A. D. (1999). Saccades reduce latency and increase velocity of ocular accommodation. *Vision Research, 39*, 3769–3795.

Shirachi, D., Liu, J., Michael, L., Jang, J., Wong, J., & Stark, L. (1978). Accommodation dynamics 1. Range nonlinearity. *American Journal of Optometry and Physiological Optics, 55*, 631–641.

Smith, E. L., III, & Harwerth, R. S. (1984). Behavioral measurements of accommodative amplitude in rhesus monkeys. *Vision Research, 24*(12), 1821–1827.

Stark, L. R., & Atchison, D. A. (1994). Subject instructions and methods of target presentation in accommodation research. *Investigative Ophthalmology and Vision Science, 35*, 527–528.

Sun, F., Stark, L., Nguyen, A., Wong, J., Lakshminarayanan, V., & Mueller, E. (1988). Changes in accommodation with age: static and dynamic. *American Journal of Optometry and Physiological Optics, 65*, 492–498.

Temme, L. A., & Morris, A. (1989). Speed of accommodation and age. *Optometry and Vision Science, 66*, 106–112.

Van Opstal, A. J., & Van Gisbergen, J. A. M. (1987). Skewness of saccadic velocity profiles: a unifying parameter for normal and slow saccades. *Vision Research, 27*, 731–745.

Vilupuru, A. V., & Glasser, A. (2002). Dynamics accommodation in rhesus monkeys. *Vision Research, 42*, 125–141.

Wolffsohn, J. S., Hunt, O. A., & Gilmartin, B. (2002). Continuous measurement of accommodation in human factor applications. *Ophthalmic and Physiological Optics, 22*, 380–384.

Yamada, T., & Ukai, K. (1997). Amount of defocus is not used as an error signal in the control system of accommodation dynamics. *Ophthalmic Physiological Optics, 17*, 55–60.