

Influence of Amplitude and Starting Point on Accommodative Dynamics in Humans

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PURPOSE. The effects of amplitude and the starting point of an accommodative response on the dynamics of far-to-near (accommodation) and near-to-far (disaccommodation) focus were studied.

METHODS. Step responses were recorded with a dynamic optometer in nine 22- to 30-year-old subjects, under three conditions: (1) Fixed far: accommodative demands from 1 to 6 D were created by placing the far target at 6 m and the near target at various proximal distances. (2) Fixed near: accommodative demands from 1 to 5 D were created by placing the near target at 16.7 cm and the far target at various distal positions. (3) Fixed amplitude: far and near target positions were changed to create an accommodative demand of 1.5 D from starting positions of 1 to 4.5 D in 0.5-D steps. Each recorded response was fitted with an exponential function to calculate response amplitude, peak velocity, time constant, and starting point.

RESULTS. The relationship between starting point and amplitude of accommodation and disaccommodation was effectively manipulated in the three conditions. For accommodation and disaccommodation, peak velocity increased linearly with response starting point, whereas the peak velocity versus response amplitude relationship differed according to the condition. Similar amplitude responses were associated with a higher peak velocity and a smaller time constant at proximal starting points than at distal starting points. Low-amplitude responses were influenced by both starting point and amplitude.

CONCLUSIONS. The dynamics of accommodation and disaccommodation are strongly influenced by the starting point, but less so by amplitude. (*Invest Ophthalmol Vis Sci.* 2005;46:3463-3472) DOI:10.1167/iovs.04-1408

The act of focusing the eye on objects at different distances includes far-to-near (accommodation) and near-to-far (disaccommodation) focus. The dynamic characteristics of accommodative responses have been studied extensively,¹⁻⁸ but relatively few studies have been undertaken to address disaccommodation and to identify the differences in dynamics between accommodation and disaccommodation.⁹⁻¹¹ In a previous study in humans,⁹ differences between the dynamics of step accommodative and disaccommodative responses were

found, with disaccommodation occurring progressively faster than accommodation with increasing amplitude. In that study, accommodation started from a fixed far target position (6 m), but disaccommodation started from various near target positions. In other words, different amplitudes of accommodation were stimulated from the same starting point, but different amplitudes of disaccommodation were stimulated from various near starting points. It is possible that the differences between accommodative and disaccommodative dynamics are due to the difference in the starting point of a response.

Fisher^{12,13} suggested, based on a mathematical analysis, that the force of contraction of the ciliary muscle and the elastic properties of the lens capsule depend on the initial shape or configuration of the lens capsule/substance. In vitro studies of enucleated eye tissue suggest that the dynamics of accommodation and disaccommodation are dominated by the dynamics of the lens-ciliary body plant.^{12,14-18} These studies suggest that the passive, mechanical structures involved in accommodation may be rate limiting.¹³⁻¹⁷ The efficiency and the dynamics of these mechanical structures may be influenced by the starting configurations¹² and the elastic properties^{3,11,16,17} of the tissues. In vivo, the starting configuration of the accommodative tissues can be manipulated by changing the starting point of an accommodative response.^{3,11} Shirachi et al.³ showed that accommodation is faster in the far (1-4 D) than in the near (5-8 D) range, and disaccommodation is faster in the near (8-5 D) than in the far (4-1 D) range. Beers and Van Der Heijde¹¹ reported that time constants of accommodation are larger in the far range than in the near range and that time constants of disaccommodation are similar for both ranges. Although the results of these two studies do not directly agree, both suggest that the starting point of a response influences the dynamics of accommodation and disaccommodation.

Theoretical models have been proposed for the mechanism and dynamics of the accommodative system.¹⁹⁻²³ These models suggest that neural mechanisms, such as the firing rate of the midbrain neurons, are among the main determinants of the speed of accommodation.^{20,24,25} The basis for neural correlates is that the firing rate of the neurons is correlated with peak velocity and that firing rate increases linearly with amplitude.²⁴ Such a neural basis has been demonstrated for saccadic and vergence eye movements²⁶⁻²⁸ in the form of linear main sequence plots, where peak velocity is plotted against amplitude.²⁶ In the theoretical models of accommodation, it is implicitly assumed that peak velocity increases with amplitude of accommodation.^{19,20} Studies of humans have shown that peak velocity increases with amplitude of accommodation for low amplitudes (<3 D).^{5,29,30} However, in a previous study, it was shown that peak velocity increases at low amplitudes (<2 D) and saturates at higher amplitudes of accommodation, but increases linearly over the entire range of disaccommodative amplitudes.⁹ The assumption of the theoretical models of accommodation (i.e., that peak velocity increases with amplitude over a wide range of amplitudes) is not consistently upheld. Recently, a new pulse-step model of accommodation was proposed that accounts for the saturation of peak velocity at higher amplitudes of accommodation.²² Accommodation and disaccommodation also exhibit different dynamic characteris-

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tics,^{2,9-11} which precludes simple linear systems analysis.^{31,32} The theoretical models fail to consider the differences between accommodation and disaccommodation.

In the present study, accommodative and disaccommodative dynamics were examined over a wide range of amplitudes and starting points, in an attempt to reconcile prior, apparently contradictory, findings.^{3,11}

METHODS

Subjects

Nine subjects (ages 22–30 years; mean \pm SD, 24 ± 2.55) were recruited with informed consent in accordance with institutionally approved human subject protocols and under the tenets of the Declaration of Helsinki. The subjects were emmetropes ($+0.50$ to -0.50 D; $n = 4$) or myopes corrected with soft contact lenses (-2.00 to -4.25 D; $n = 5$) with visual acuity of at least 20/20 at distance. Each subject underwent a short optometric examination to ensure 20/20 distance Snellen visual acuity, no residual refractive error greater than ± 0.5 D as measured with a Hartinger coincidence refractometer, normal phoria (4Δ esophoria to 4Δ exophoria at 40 cm and 2Δ esophoria to 2Δ exophoria at distance), and normal near point of convergence (<8 cm). The screening procedure was followed by dynamic accommodation testing. The maximum accommodative amplitude of the subjects was measured objectively with a Hartinger coincidence refractometer during a push-up task. This was performed at the end of the dynamic experiment, to avoid inducing fatigue or influencing the experiment.

Dynamic Target Presentation

High-contrast, black-on-white, starlike targets were presented at far and near real distances. The far and near targets were alternately illuminated by ultrabright white LEDs fitted with individual rheostats. The targets were matched in luminance to 10 cd/m² on the white background by measurement through the optical system with a photometer (model LS100; Minolta, Osaka, Japan) held at the plane of the subject's eye. The far target at 6 m subtended 0.86° at the eye and the near target at 1 m subtended 1.66° . The target was spatially broadband, consisting of multiple spatial frequencies from 1 to 30 cyc/deg, with predominantly less than 9 cyc/deg, at 6 m. The angular size of the target increased approximately 1.5 times with each near target position or every diopter increase in accommodative demand. The switching of the LEDs that illuminated the targets was controlled by a computer. The duration of presentation of each target was randomly varied between 1.5 and 6 seconds with an instantaneous switch from one target to the other. A TTL voltage signal indicating the onset of the far and near stimuli was hardwired to the keyboard of a dynamic optometer (PowerRefractor; MultiChannel Systems, Rütlingen, Germany). The optometer recorded the far and near stimulus timing along with the refraction responses. The room lights were turned off after the subject was comfortably seated and stabilized in a head and chin rest. The far target, the near target, and the optometer were aligned with the subject's right eye, and the left eye was patched (Fig. 1A). Ten to 15 dynamic responses were recorded at each stimulus demand. The subjects were instructed to look at and focus on the target that was illuminated and to keep the target in clear focus. Practice sessions were provided so that the subjects were fully aware of the nature of the experiments.

Accommodative responses were recorded in three different conditions: fixed far, fixed near, and fixed amplitude (Fig. 1B). The fixed far condition was performed in one experimental session and the fixed near and fixed amplitude conditions were performed on a second session on a different day.

Fixed Far Condition. The far target was fixed at 6 m (~ 0 D), and the near target was first placed at 1 D and then brought progressively closer in 1-D steps to 6 D, in separate trials (Fig. 1B). In the fixed far condition, accommodation always started from the same fixed far target distance (6 m or ~ 0 D) and ended at different near target

distances. Disaccommodation started from different near distances according to the position of the near target and ended at the same far distance (6 m or ~ 0 D).

Fixed Near Condition. The near target was fixed at 6 D and the far target was first placed at 1 D and then brought progressively closer in 1-D steps to 5 D, in separate trials (Fig. 1B). In this fixed near condition, accommodation started from different far target distances and always ended at the same near target distance (16.7 cm, or 6 D). Disaccommodation always started from the fixed near target (16.7 cm, or 6 D) and ended at different far target distances.

Fixed Amplitude Condition. The difference in the accommodative demand between the far and near targets was fixed at 1.5 D. The far target was first placed at 1 D, and the near target was placed at 2.5 D (Fig. 1B). In subsequent trials, the far target was placed at 1.5 to 4.5 D in 0.5-D steps, and the near target was placed 1.5 D closer. In this paradigm, the amplitude was held constant; however, both the starting and ending points were changed.

In summary, stimulus amplitude was changed with the starting point for accommodation in the fixed near condition and for disaccommodation in the fixed far condition. Stimulus amplitude was changed independent of starting point in the fixed far condition for accommodation and in the fixed near condition for disaccommodation. Stimulus amplitude was held constant and starting and ending points were changed in the fixed amplitude condition.

To determine the influence of the order of presentation of the stimulus, the fixed near condition was repeated in a different experimental session on five of the original subjects (three emmetropes and two myopes). In this control experiment, the fixed near condition was first performed in the reverse order—that is, the 1-D stimulus amplitude [5–6 D] was presented first and the 5-D stimulus amplitude [1–6 D] was presented last. After this, the fixed near condition was presented in random order.

Measurement of Accommodation

Accommodation was measured with an infrared video optometer (PowerRefractor; MultiChannel Systems) that measures refraction, pupil diameter, and vergence binocularly at 25 Hz.^{9,33-36} The instrument was calibrated for each subject individually, as described previously.^{2,9} In all subjects, the linear calibration functions reached $r^2 > 0.9$, as described previously.⁹ The measured refractions were converted into accommodation by subtracting the measured refractions from zero (0), for further data analysis. It was necessary to know the actual starting refraction of each response, and therefore refractions were not simply subtracted from the baseline refraction.

Data Analysis

Fitting Exponential Functions. First-order exponential functions were used to fit accommodation (equation 1) and disaccommodation (equation 2), after removing latency, as described previously,⁹ to provide dynamic metrics that could be compared between the three conditions.

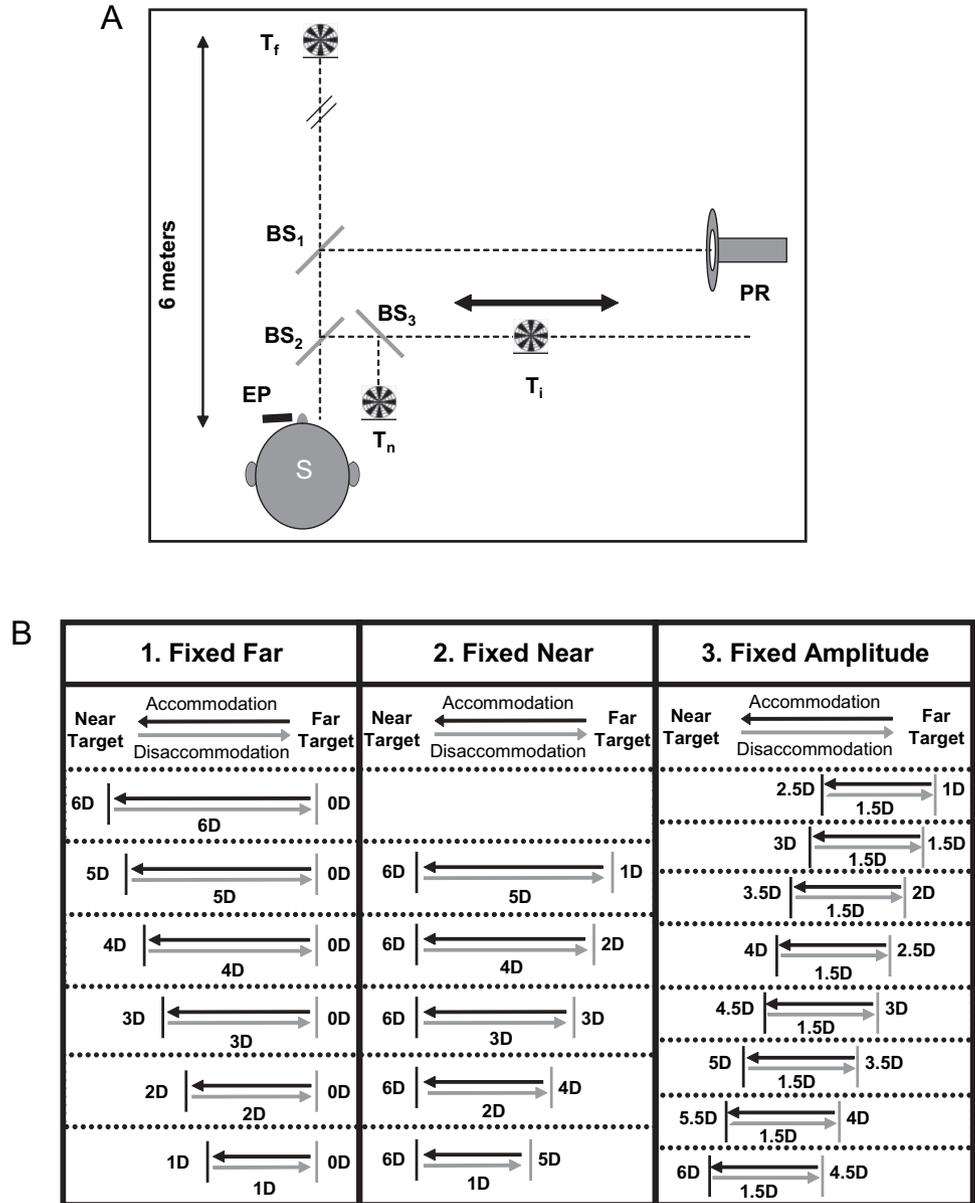
$$\text{Accommodation: } y = y_0 + a(1 - e^{-t/\tau}) \quad (1)$$

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

where y represents the response, y_0 represents the starting point, a represents the amplitude of the response, t represents time in seconds, and τ represents the time constant.

These exponential functions were fitted to the entire accommodative and disaccommodative responses (Fig. 2), with custom computer software using the Levenberg-Marquardt algorithm,³⁷ which iteratively found the best fit based on χ^2 reduction. The goodness of fit to each response was evaluated by examination of the residuals. Only fits with no systematic pattern and with no residuals greater than 1 D, considering the fluctuations of accommodation, were used in the final anal-

FIGURE 1. (A) Schematic of the experimental set up. The far (T_f), intermediate (T_i) and near (T_n) targets were aligned with the subject's (S) right eye with beam splitters BS_2 and BS_3 . The left eye was covered with an eye patch (EP). The optometer (PR; PowerRefractor; MultiChannel Systems, Rütlingen, Germany) camera was also aligned with the right eye of the subject with the beam splitter BS_1 . The positions of the far and near targets were fixed at 6 m (~ 0 D) and 16.7 cm (6 D), respectively, and the position of the intermediate target could be varied from 1 m (1 D) to 20 cm (5 D). Only two targets were used in each of the three conditions (B). The far and intermediate targets were used for the fixed far condition, and the near and intermediate targets were used for the fixed near and fixed amplitude conditions. (B) Schematic of the experimental paradigm. Accommodative and disaccommodative responses were measured under three conditions: fixed far, fixed near, and fixed amplitude. In the fixed far condition, the far target was placed at stimulus demands from 1 to 6 D in 1-D steps. In this condition, accommodation always started from the same far starting point (6 m) and disaccommodation started from various near distances. In the fixed near condition, the near target was fixed at 6 D, and the distal target was placed at stimulus demands from 1 to 5 D in 1-D steps. In this condition, accommodation started from various far target distances, and disaccommodation always started from the same near distance. In the fixed amplitude condition, the far and near targets were placed 1.5 D from each other to create a constant stimulus amplitude, while stimulating accommodation and disaccommodation at various starting and ending points.



ysis. Each fit was visually examined and if a steady state response was not achieved during the stimulus duration, then the fit was excluded from further data analysis.

Comparing the Different Conditions. The exponential equations provided the response amplitudes (a), starting points (y_0), and time constants (τ). The peak velocity was obtained from the peak value of the first derivative of the fitted equations. To observe the trends present in the data, average values for each stimulus amplitude were plotted rather than each raw response. The response amplitude, response starting point, peak velocity, and time constant data were averaged for each stimulus in each condition for each subject. The mean data from each subject were further averaged to obtain a grand mean and standard error (SE) of each parameter for each stimulus amplitude in the different conditions. In subsequent figures, the data are shown as the mean \pm SEM for each stimulus condition. In some cases, the trends in the data were described with straight-line fits. To compare the straight-line fits to data from two different conditions, an F statistic was used. For this F statistic, the mean data from each subject were considered, rather than the grand mean, because the individual subject data provide a better estimate of variance than do the grand mean data.

RESULTS

The maximum objectively measured accommodative amplitude of the subjects ranged from 6.25 to 8.5 D (median, 7.25 D). Therefore, in all subjects, the largest stimulus amplitude (6 D) was within the individual maximum accommodative amplitudes. For accommodation, the proportion of dynamic responses included from each subject ranged from 41% to 69% (median, 58%) for the fixed far condition, 23% to 73% (median, 62%) for the fixed near condition, and 59% to 90% (median, 84%) for the fixed amplitude condition. For disaccommodation, the proportion of dynamic responses included from each subject ranged from 32% to 76% (median, 60%) for the fixed far condition, 45% to 66% (median, 55%) for the fixed near condition, and 54% to 91% (median, 76%) for the fixed amplitude condition. No differences between myopes and emmetropes were found in the percentage of data excluded. The responses that were included are those for which a clear start could be identified, for which exponential functions provided good fits and did not result in residuals greater than 1 D, and for which a steady state level at the end of the response was observed.

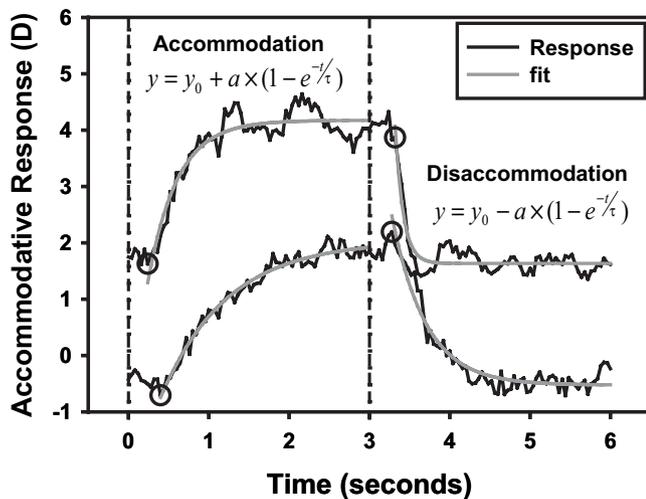


FIGURE 2. Two representative responses are shown for similar amplitude responses but with different starting points. *Black traces:* the responses; *gray lines:* exponential fits to the responses. The onset of responses (O) was identified by a custom computer algorithm. The exponential functions were fit to the data from the start of the response to the end of the stimulation period. The equations for the exponential fits to accommodation and disaccommodation are shown. *Dashed vertical lines:* the onset of the accommodative (at time 0 seconds) and disaccommodative (at time 3 seconds) stimuli. Latency is the time between stimulus onset and the start of a response (O). The exponential fit to individual responses provided response amplitude, starting point, peak velocity, and time constant.

Eye blinks occurring during the initial response precluded identification of the start of the response and resulted in the rejection of that response.

The influence of refractive error on the subject's responses was tested statistically with a three-factor ANOVA. The three factors considered were (1) refractive error with two levels (myopes and emmetropes); (2) condition, with two levels (fixed far and fixed near); and (3) stimulus amplitude with five levels (1, 2, 3, 4, and 5 D). Only fixed far and fixed near conditions were considered in this analysis, because similar amplitudes (1–5 D) were stimulated in only these two conditions. The dependent variables were response amplitude, peak velocity, and time constant. No significant interaction between refractive error and stimulus amplitude was found for response amplitude ($F_{4,77} = 0.56$, $P = 0.69$), peak velocity ($F_{4,77} = 0.15$, $P = 0.96$), or time constant ($F_{4,77} = 0.12$, $P = 0.98$). Similarly, no significant interaction between refractive error and condition was found for response amplitude ($F_{4,77} = 0.00$, $P = 0.97$), peak velocity ($F_{4,77} = 1.86$, $P = 0.18$), or time constant ($F_{4,77} = 0.11$, $P = 0.74$). Because refractive error did not influence the responses in this group of subjects, the data from emmetropic and myopic subjects were pooled in further data analyses.

Amplitude versus Starting Point

Stimulus response functions for amplitude and starting point of accommodation (Figs. 3A, 3C) and disaccommodation (Figs. 3B, 3D) for each condition were plotted. Similar stimulus amplitudes resulted in greater response amplitudes in the fixed near than in the fixed far condition (Figs. 3A, 3B).

The relationship between starting point and response amplitude was effectively manipulated for both accommodation and disaccommodation. In each of the three conditions, different relationships between response amplitude and response starting point were obtained. For accommodation (Fig. 3E), response starting point remained constant with response am-

plitude in the fixed far condition (slope = 0.01, $P = 0.47$), and response starting point decreased systematically with response amplitude in the fixed near condition (slope = -1.18 , $P < 0.05$). In the fixed amplitude condition, although the stimulus amplitude was 1.5 D, a range of accommodative response amplitudes (1.29–2.06 D) was recorded. The response amplitude increased with response starting point in this condition (slope = 2.88, $P < 0.05$). In the case of disaccommodation (Fig. 3F), response amplitude increased systematically with response starting point in the fixed far condition (slope = 1.02, $P < 0.05$). In the fixed near condition, response starting point remained relatively constant with response amplitude (slope = -0.16 , $P = 0.10$). In the fixed amplitude condition, a range of disaccommodative response amplitudes (1.21–1.86 D) was obtained and the response amplitude increased with response starting point (slope = 4.47, $P < 0.05$).

Peak Velocity of Accommodation

The different conditions resulted in characteristic trends in the dynamics of the accommodative responses (Fig. 4). Individual data from four representative subjects (Figs. 4A, 4B) and averaged data from all nine subjects (Figs. 4C–F) are shown. In the fixed far condition, peak velocity increased at low response amplitudes (≤ 2 D) and saturated at higher response amplitudes, as shown previously.⁹ In the fixed near condition, peak velocity decreased linearly with response amplitude ($y = -2.78x + 20.41$; $P < 0.05$). In the fixed amplitude condition, peak velocity increased linearly with response amplitude ($y = 10.84x - 7.63$; $P < 0.05$). Similar low-amplitude responses (≤ 3 D) were associated with very different peak velocities, depending on the condition. For example, in the fixed far condition a response amplitude of 1.94 ± 0.11 D (SEM) was associated with a peak velocity of 7.54 ± 1.39 D/s and in the fixed near condition a response amplitude of 1.85 ± 0.14 D was associated with a peak velocity of 14.74 ± 1.53 D/s. At higher response amplitudes, the peak velocities from the fixed far and fixed near conditions converged as the conditions became similar (Fig. 1B).

Peak velocity increased with the response starting point of accommodation (Figs. 4B, 4D). The three conditions resulted in similar trends in the response starting point versus peak velocity relationship. Peak velocity increased linearly with response starting point in the fixed near ($y = 2.29x + 8.50$; $P < 0.05$) and fixed amplitude ($y = 3.71x + 6.43$; $P < 0.05$), conditions and the two relationships were not significantly different ($F_{2,112} = 0.60$, $P = 0.55$).

Time Constant of Accommodation

Time constants of accommodation increased linearly with response amplitude in both the fixed far ($y = 0.11x + 0.20$; $P < 0.05$) and fixed near ($y = 0.16x - 0.18$, $P < 0.05$) conditions and the two relationships were significantly different ($F_{2,92} = 18.73$, $P < 0.05$; Fig. 4E). In the fixed amplitude condition, time constants decreased linearly with response amplitude ($y = -0.13x + 0.42$, $P < 0.05$). For similar response amplitudes, the time constants were larger in the fixed far than in the fixed near condition. The fixed far and fixed near curves approached each other at higher response amplitudes as the conditions became similar.

In the fixed far condition, a wide range of time constants were obtained for the same response starting point (Fig. 4F). Time constants decreased linearly with increasing response starting point in the fixed near ($y = -0.14x + 0.53$, $P < 0.05$) and in the fixed amplitude ($y = -0.04x + 0.25$, $P < 0.05$) conditions, and the two relationships were significantly different ($F_{2,112} = 47.28$, $P < 0.05$). Time constants in the fixed amplitude condition were generally smaller than those in the

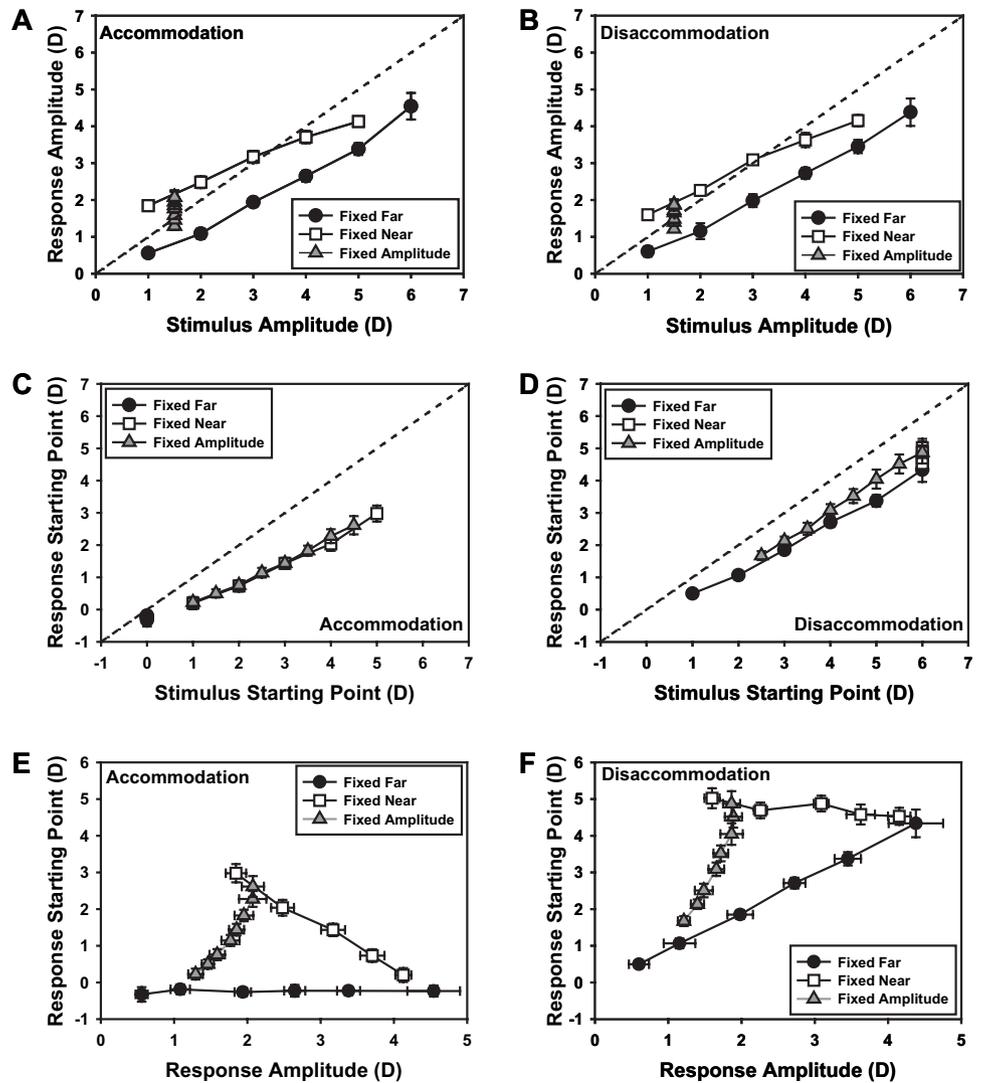


FIGURE 3. Stimulus-response functions for amplitude of accommodation (A) and disaccommodation (B) and for starting point of accommodation (C) and disaccommodation (D) are shown for the three conditions. Error bars, \pm SEM. For accommodation and disaccommodation, the response amplitude showed differences between conditions, but the response starting points were similar between conditions. The response amplitude was greater at proximal starting points than at distal starting points. The response starting point is plotted against response amplitude of accommodation (E) and disaccommodation (F) for the three conditions. The relationship between response starting point and response amplitude was different between the three conditions for accommodation and disaccommodation.

fixed near condition, because at similar distal stimulus starting points, response amplitudes were smaller in the fixed amplitude than in the fixed near condition (see Fig. 1B). Based on the exponential fits, time constants depend on peak velocity and response amplitude,⁹ and so they are harder to understand as a function of response starting point when response amplitude and peak velocity vary according to a particular condition. The time constant data are provided to enable a comparison of the dynamics of similar response amplitudes from different response starting points.

Peak Velocity of Disaccommodation

The different conditions resulted in characteristic trends in the dynamics of the disaccommodative responses (Fig. 5). Individual data from four representative subjects (Figs. 5A, 5B) and averaged data (Figs. 5C-F) are shown. Peak velocity increased linearly with response amplitude of disaccommodation in the fixed far ($y = 4.40x + 0.12, P < 0.05$) and fixed amplitude ($y = 13.28x - 9.78, P < 0.05$) conditions (Fig. 5C). The linear relationships were significantly different from each other ($F_{2,121} = 29.61, P < 0.05, P < 0.05$). Peak velocity increased at low response amplitudes and saturated at higher response amplitudes in the fixed near condition. Most of the peak velocities from the fixed near and fixed amplitude conditions lay outside the 95% confidence intervals for the fixed far data

(Fig. 5C, shaded area). For similar low response amplitudes (≤ 3 D), the peak velocities were significantly different between the conditions. For example, in the fixed far condition a response amplitude of 1.98 ± 0.17 D (SEM) was associated with a peak velocity of 7.45 ± 0.98 D/S and in the fixed near condition a response amplitude of 2.26 ± 0.09 D was associated with a peak velocity of 18.54 ± 1.78 D/S. At higher response amplitudes, the fixed far and fixed near conditions became similar (Fig. 1B).

Peak velocity of disaccommodation increased linearly with response starting point in the fixed far ($y = 4.33x + 0.63; P < 0.05$) and fixed amplitude ($y = 2.92x + 2.32; P < 0.05$) conditions (Fig. 5D) and the two linear relationships were significantly different ($F_{2,121} = 14.26; P < 0.05$). In the fixed near condition, only a restricted range of response starting points resulted, and so no trends were evident. Most of the data from the different conditions fell within the 95% confidence intervals for the fixed far data (Fig. 5D, shaded area). However, one mean from the fixed near condition (Fig. 5D, arrow) and the data for higher response starting points in the fixed amplitude condition had lower peak velocities compared with the fixed far data. The one mean from the fixed near condition was recorded for the lowest response amplitude in that condition (1.60 D). The differences among the different conditions suggest that response amplitude has some influence

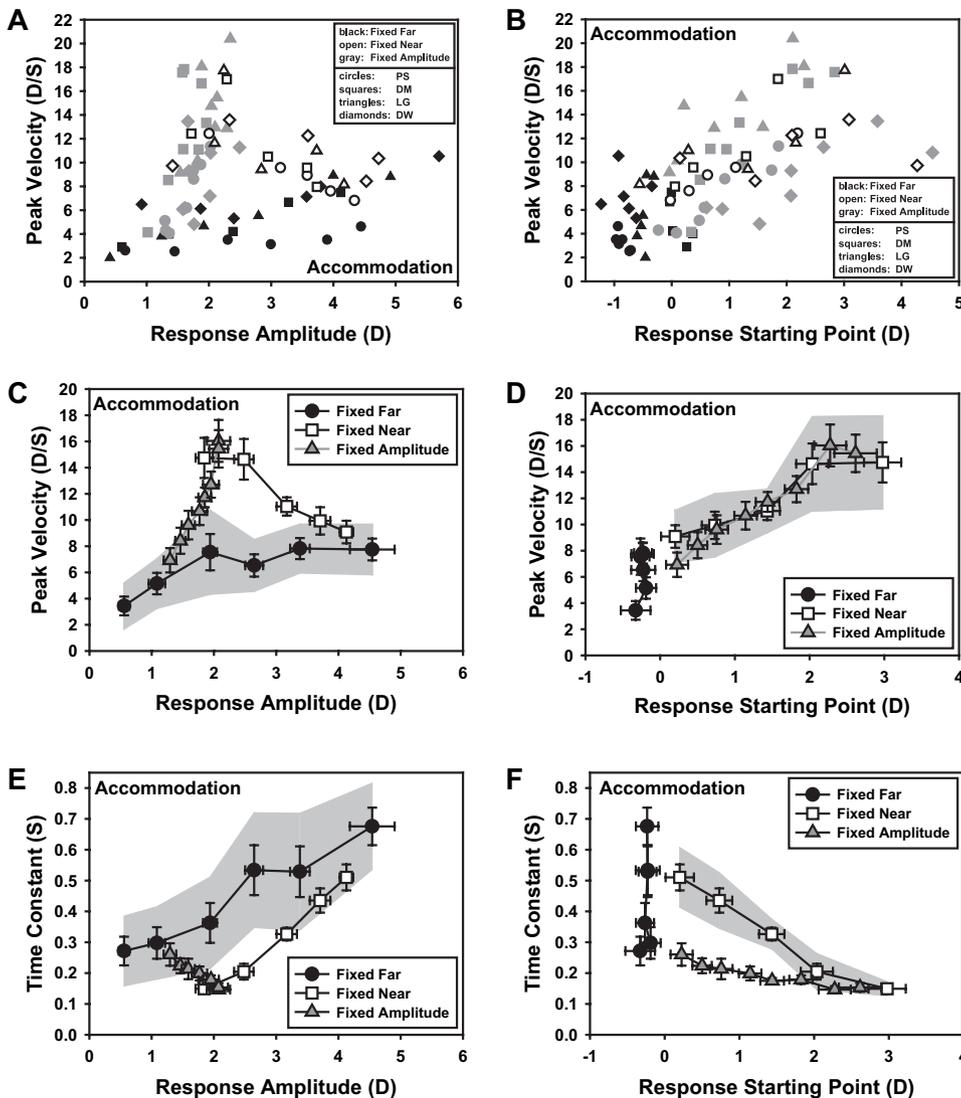


FIGURE 4. Peak velocity is plotted against response amplitude (A) and response starting point (B) of accommodation for fixed far, fixed near, and fixed amplitude conditions. Data from four representative subjects in terms of refractive error and age are shown. PS is a 24-year-old emmetrope. DM is a 23-year-old emmetrope; LG is a 25-year-old -4.25 -D myope; and DW is a 30-year-old -3.5 -D myope. To visualize trends between conditions, mean peak velocities are plotted against mean response amplitudes (C) and response starting points (D) for each stimulus in the three conditions for accommodation. Similarly, mean time constants are plotted against mean response amplitudes (E) and response starting points (F). Error bars, \pm SEM; shaded area surrounding the fixed far (C, E) and fixed near (D, F) data represent the 95% CI for the y-axis data. Peak velocity exhibited different relationships with response amplitude (A, C) in the three conditions and cumulatively, peak velocity increased with response starting point (B, D). Time constants exhibited different relationships with response amplitude (E) and response starting point (F) in the three conditions. Similar amplitude responses had higher peak velocity and lower time constants at proximal starting points than at distal starting points (compare fixed far and fixed near data in C, E).

on the disaccommodative dynamics although response starting point strongly influences the dynamics.

Time Constant of Disaccommodation

The time constants recorded for similar amplitude disaccommodative responses were larger in the fixed far condition than in the fixed near and fixed amplitude conditions (Fig. 5E). As response amplitude increased, the fixed far and fixed near conditions began to resemble each other, and so the curves tended to converge. Also, time constants recorded for similar response starting points were larger in the fixed far compared to fixed near and fixed amplitude conditions. As with accommodation, by virtue of the exponential fits used, time constants as a function of response starting point (Fig. 5F) are mathematically related to the amplitude and peak velocity of a response.

Fixed Near Control Experiment

For accommodation, the random order fixed near condition produced results similar to that shown in Figure 4C, in that peak velocity decreased with response amplitude (Fig. 6A). However, when the stimuli were presented in a reverse order, peak velocity was invariant with response amplitude (Fig. 6A). The peak velocities for the smallest response amplitudes were still greater than the peak velocity for the smallest response

amplitude in the original fixed far condition (Fig. 6A, shaded area). For disaccommodation, the peak velocity versus response amplitude relationships from the three repetitions of the fixed near condition were not systematically different. In all three repetitions, peak velocity increased at low amplitudes and saturated at higher amplitudes of disaccommodation.

DISCUSSION

Characteristics of the Stimulus

It has been suggested that restricting the cues available for accommodation can affect the response characteristics.^{30,38} Therefore real targets were used, and the subjects were also provided practice sessions so that they could become familiar with the experiment and provide robust responses. The subjects were aware of the target distances at each stimulus demand, although the target durations were randomized. In previous experiments⁹ and in the present experiment, response amplitude and dynamics were compared for various stimulus durations for a 5-D stimulus amplitude. No relationship was found between the dynamics or amplitude of the responses and the trial number or the stimulus duration, including the response to the shortest stimulus duration of 1.5 seconds. The level of luminance of the targets was well beyond the threshold

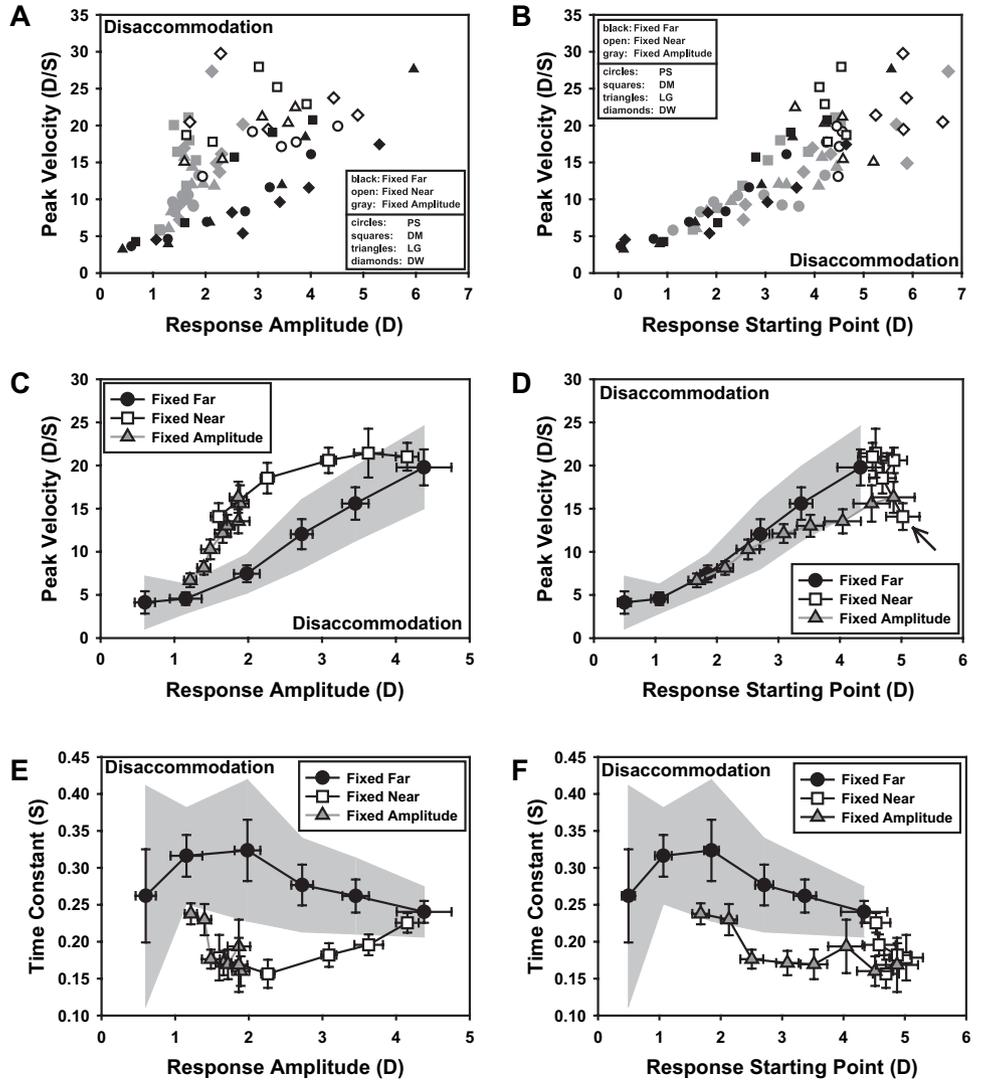


FIGURE 5. Peak velocity is plotted against response amplitude (A) and response starting point (B) of disaccommodation for fixed far, fixed near, and fixed amplitude conditions. Mean peak velocities are plotted against mean response amplitudes (C) and response starting points (D) for each stimulus in the three conditions for disaccommodation. Similarly, mean time constants are plotted against mean response amplitudes (E) and response starting points (F). Error bars, \pm SEM; shaded area surrounding fixed far data represents the 95% CI for the y-axis data. The peak velocity exhibits different relationships with response amplitude (A, C) in the three conditions, and the peak velocity generally increases with response starting point (B, D). (D, arrow) Low-amplitude response from the fixed near condition with a peak velocity lower than the other responses from that condition. Time constants exhibit different relationships with response amplitude (E) and response starting point (F) in the three conditions. Similar amplitude responses have higher peak velocities and lower time constants at proximal starting points than at distal starting points (compare fixed far and fixed near data in C, E).

luminance (~ 0.51 cd/m²) required to produce robust accommodative responses³⁹ and was similar to luminance levels used in previous studies of dynamic accommodation.^{9,40-42}

Use of Exponential Functions to Fit Accommodative Responses

The optometer (PowerRefractor; MultiChannel Systems) measures at 25 Hz. This relatively low sampling frequency would result in considerable noise if the response velocity were calculated by a successive two-point difference method that can be used with higher frequency signals.³⁰ Therefore, the dynamic metrics of peak velocity and time constant were obtained by fitting analytical exponential functions to the data. Accommodative responses have been fitted with first-order exponential functions in the past.^{9-11,43,44} It has recently been shown that the second-order characteristics of the accommodative response, such as peak acceleration, time to peak acceleration, and duration of acceleration, offer important new insights into accommodative dynamics.³⁰ The first-order approximation of the accommodative responses inferred by fitting exponential functions in the present study precludes analysis of second-order characteristics. Nevertheless, exponential functions fit to the responses from all three conditions provide dynamic parameters that exhibit key differences and allow quantitative comparisons of the responses from the different conditions.

Amplitude versus Starting Point

The response amplitude and starting point in all three conditions showed a classical lag of accommodation at higher stimulus levels^{2,9,45} (Figs. 3A, 3C). Similar stimulus amplitudes produced larger response amplitudes in the fixed near compared to the fixed far condition (Figs. 3A, 3B). A constant stimulus amplitude in the fixed amplitude condition resulted in larger response amplitudes at more proximal starting points. These two findings could be related to the characteristics of the accommodative stimulus-response function. It is possible that as the stimulus starting point moved from the lead zone to the linear zone in the stimulus-response function, where a lag of accommodation exists, an increase in accommodative response amplitude with accommodative demand resulted. It is also possible that changes in the depth of focus of the eye as a function of the accommodative state could have resulted in the differences in the gain of the accommodative system as a function of starting point. The differences between the stimulus amplitude and the response amplitude dictate that response rather than stimulus be considered when describing dynamics of accommodation, as was done in the present study.

In the fixed near condition, as the stimulus starting point became more proximal, there was a lag of accommodation with respect to the stimulus starting level. Consequently, the retinal blur may have been greater than the stimulus amplitude.

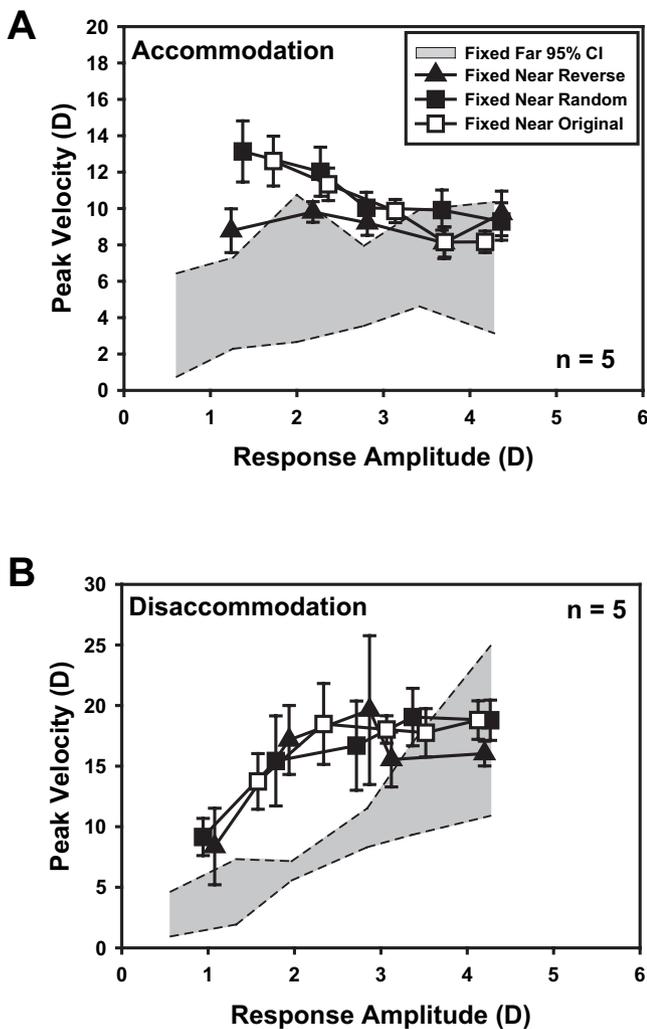


FIGURE 6. The results from the fixed near condition presented in reverse order and then in random order of stimulus amplitudes are shown for accommodation (A) and disaccommodation (B). Data are from five of the original nine subjects. Error bars, \pm SEM. Horizontal error bars have been omitted for clarity. For accommodation, the data from the randomized experiment are similar to the original fixed near condition, whereas the data from the reversed experiment are different from the original and the randomized fixed near conditions. Peak velocities for the lowest response amplitudes of accommodation are still higher than the 95% CI for similar amplitude responses from the fixed far condition (*shaded area*). The three repetitions of the fixed near condition produced very similar dynamics of disaccommodation (B).

In the fixed far condition for accommodation, retinal blur would most likely be proportional to the stimulus amplitude. Therefore, although the responses were averaged for each stimulus condition, there could have been differences in the magnitude of retinal blur, apparent stimulus amplitudes, and therefore also response amplitudes, which could have influenced the dynamics. The saturation of peak velocity at higher response amplitudes in the fixed far condition (Fig. 4C), however, suggests that peak velocity is not simply directly proportional to the magnitude of blur.

The response starting point at the 6-m (~ 0 D) stimulus represents the distance refraction. The subjects could have been 0.50 D under- or overcorrected, or the baseline, distance refraction could have been influenced by the experimental setup. Therefore, the raw distance refraction values were used as the response starting point for a 0-D stimulus. The Power-

Refractor and some other infrared optometers have been shown to have a slight hyperopic bias.⁴⁶⁻⁴⁹ Previous studies on the PowerRefractor have reported overestimation of hyperopic refractive errors from 0.41 to 0.60 D.^{46,49} This overestimation of hyperopic refractive errors was not corrected in the present study, and the response starting points with the 6-m (~ 0 D) stimulus are therefore shown as negative numbers in Figures 2, 3, 4, and 5.

Factors Influencing Dynamics of Accommodation and Disaccommodation

Cumulatively, the three conditions provided peak velocities and time constants for amplitudes associated with different starting points and vice versa. The differences in the relationship between response starting point and response amplitude among the three conditions allows a comparison of peak velocities for similar response amplitudes associated with different response starting points and for similar response starting points associated with different response amplitudes. In this analysis, if peak velocity for a particular response amplitude from different conditions is similar, it shows a lack of influence from response starting point. If similar response starting points from different conditions have similar peak velocities, a lack of influence from response amplitude can be inferred.

For accommodation and disaccommodation, the relationship between peak velocity and amplitude was different among the three conditions (Figs. 4C, 5C). Peak velocity is linearly related to the response starting point (Figs. 4D, 5D). No systematic differences among the three conditions in the peak velocity versus response starting point relationships were found. From a fixed starting point, peak velocity was found to increase at low response amplitudes and saturate at higher response amplitudes (fixed far in Fig. 4C, and fixed near in Fig. 5C). In general, dynamics of accommodative and disaccommodative responses were strongly influenced by starting point and less so by amplitude. The peak velocity of accommodation and disaccommodation was higher at proximal starting points.

In the fixed near condition, peak velocity of accommodation decreased with response amplitude. This is an interesting trend that, to our knowledge, has never been reported or suggested to occur. The fixed near and fixed amplitude conditions were tested on a different day from the fixed far condition. In the second experimental session, the fixed near condition was first tested followed by the fixed amplitude condition. In the fixed near condition, the largest stimulus amplitude was presented first and the smallest stimulus amplitude was presented last. Higher peak velocities for smaller response amplitudes are contrary to what might be expected to be caused by fatiguing. Furthermore, repeated accommodative responses can be elicited with little evidence of fatigue.⁵⁰ Thus, it is unlikely that fatigue explains the results obtained in the present study.

It is still of concern that practice or training effects related to the order of presentation could have influenced the results. It has been reported that the dynamics of accommodation can be enhanced through training,⁵¹⁻⁵³ suggesting that the accommodative dynamics are modifiable. The difference between the original and the reverse order of presentation of the fixed near condition (Fig. 6A) suggests that training or other factors related to the order of presentation may have modified the dynamics of accommodation. However, the results of the randomized and reverse-order control experiment still concur with the finding that similar-amplitude accommodative and disaccommodative responses are faster from a proximal than a distal starting point (Fig. 6). It was found that the reversed and random order produced different results for accommodation (Fig. 6A), but not for disaccommodation (Fig. 6B). It will be

worthwhile in future studies to explore the effects of training and the plasticity of accommodative dynamics.

Comparison with Previous Studies

Two prior studies have explored the influence of starting point or operating range on accommodative dynamics^{3,11}; however, both studies describe dynamics in terms of time constants only. Time constants are an indicator of response duration, and they depend on the speed (velocity) as well as the amplitude of a response. Peak velocity is the maximum velocity of a response and occurs very early in a response.^{5,26} Peak velocity occurs during the visually open-loop period of accommodation and can, in general, be considered a good indicator of the first-order dynamics of accommodation.^{5,20}

Shirachi et al.³ report that time constants for similar accommodative stimulus amplitudes are smaller when acting in the far range than in the near range. Beers et al.,¹¹ report that for a high amplitude (4-D stimulus amplitude), the time constants of accommodation were smaller at the near than at the far range. The results from the present study agree with those of Beers et al., in that the time constants for similar response accommodative amplitudes were smaller at proximal starting points than at distal starting points. However, both the previous studies do not provide any information about the response amplitudes. This information is important, because time constants are related to response amplitudes,⁹ and differences in response amplitudes obtained at far range and near range will confound any results based on time constants. In the present study, when response amplitude rather than stimulus amplitude was considered, smaller time constants were recorded at proximal starting points than at distal starting points for similar-amplitude responses, in agreement with Beers et al.¹¹

The two previous studies also report data on disaccommodation. Shirachi et al.³ reported that disaccommodation is faster when acting at a near than at a far range. Beers et al.¹¹ showed that time constants of disaccommodation are independent of stimulus amplitude at far and near range and that the dynamics of disaccommodation are similar at far range and near range. The present study concurs with Shirachi et al.³ and showed that disaccommodation was influenced by response starting point and that it was faster at near than at far range (Fig. 5). Again, as mentioned before for accommodation, a difference in response amplitude for the same stimulus amplitude may confound the comparison of time constants.

Yamada and Ukai⁴⁴ showed that the peak velocities of disaccommodative responses are similar for various amplitude responses from a common starting point. It was suggested that disaccommodative responses, regardless of the amplitude, are directed toward the resting position of accommodation along a common trajectory and are stopped along their path to attain the desired intermediate steady state levels. The present study showed a similar result, in that disaccommodative responses from a common starting point had similar peak velocities over a range of amplitudes (fixed near condition in Fig. 5C) and that peak velocity of disaccommodation increased linearly with response starting point (Fig. 5D). For accommodation, Yamada and Ukai did not find a common trajectory for various amplitude responses. They found that similar amplitude accommodative responses from a proximal starting point have smaller time constants, but did not discuss this aspect further. In the present study it was found that peak velocity of accommodative responses from a common starting point increased with amplitude at low amplitudes (~2 D) and saturated thereafter (fixed far condition in Fig. 4C) in accordance with prior results.⁹ This suggests that at low amplitudes, there is no common trajectory in the accommodative responses, but that a common trajectory can be achieved at higher accommodative

amplitudes. Peak velocity of accommodative responses also increased linearly with response starting point.

Biomechanical Basis for Accommodative and Disaccommodative Dynamics

In primates, accommodation occurs by the contraction of the ciliary muscle and movement of the apex of the muscle toward the lens equator, causing the zonular fibers to relax and the lens capsule to mold the lens substance into an accommodated state.^{54,55} Disaccommodation occurs by the movement of the ciliary muscle away from the lens equator, exerting an active pull on the zonular fibers, lens capsule, and lens substance.⁵⁴ It is plausible that the dynamics of accommodation are dictated by the passive resistance of the lens substance,¹⁷ capsular molding force,¹⁶ and force of ciliary muscle contraction. However, disaccommodation may be a more active process through the active pulling of the zonular fibers by elastic forces such as the choroid and posterior zonular fibers¹¹ during ciliary muscle relaxation.^{13,56} The velocity of ciliary muscle relaxation with disaccommodation⁵⁷ could be directly translated into velocity of lens changes and therefore to the change in refraction with disaccommodation. The influence of starting point on accommodative and disaccommodative dynamics, as shown in the current study, indicates the existence of a nonlinearity in the system. The ciliary muscle and the capsular molding forces may be influenced by the starting configuration of the ciliary muscle,¹³ configuration of the insertion of zonular fibers in the lens capsule, or the configuration of the lens.¹² This effect of starting configuration on the ciliary muscle and lens-molding forces could result in the starting point influencing accommodative and disaccommodative dynamics, as seen in this and previous studies.

An implication of the present study is that the theoretical models of the accommodative system should necessarily consider the differences between accommodation and disaccommodation, in terms of mechanism and dynamics. The differences seen in the response dynamics of accommodation and disaccommodation may preclude simple linear systems analysis of the accommodative system. Dynamic models of accommodation should necessarily consider the plant dynamics and their influence on the overall dynamics of the accommodative system. Necessary consideration should also be given to the amplitude and starting point of a response when modeling the dynamics of the accommodative system.

CONCLUSIONS

The dynamics of accommodation and disaccommodation are strongly influenced by the response starting point. Response amplitude also influences the dynamics, albeit not as strongly as does the response starting point. The influence of response amplitude or starting point on the dynamics also depends on the metrics used to characterize dynamics, such as the time constant or peak velocity. In general, accommodative and disaccommodative responses of similar amplitudes were faster at proximal response starting points than at distal response starting points.

References

1. Sun F, Stark L. Dynamics of accommodation: measurements for clinical application. *Exp Neurol*. 1986;91:71-79.
2. Schaeffel F, Wilhelm H, Zrenner E. Inter-individual variability in the dynamics of natural accommodation in humans: relation to age and refractive errors. *J Physiol*. 1993;461:301-320.
3. Shirachi D, Liu J, Lee M, Jang J, Wong J, Stark L. Accommodation dynamics I. Range nonlinearity. *Am J Optom Physiol Opt*. 1978; 55:631-641.

4. Heron G, Charman WN, Schor C. Dynamics of the accommodation response to abrupt changes in target vergence as a function of age. *Vision Res.* 2001;41:507-519.
5. Ciuffreda KJ, Kruger PB. Dynamics of human voluntary accommodation. *Am J Optom Physiol Opt.* 1988;65:365-370.
6. Campbell FW, Westheimer G. Dynamics of accommodative responses of the human eye. *J Physiol.* 1960;151:285-295.
7. Tucker J, Charman WN. Reaction and response times for accommodation. *Am J Optom Physiol Opt.* 1979;56:490-503.
8. Heron G, Winn B. Binocular accommodation reaction and response times for normal observers. *Ophthalmic Physiol Opt.* 1989;9:176-183.
9. Kasthurirangan S, Vilupuru AS, Glasser A. Amplitude dependent accommodative dynamics in humans. *Vision Res.* 2003;43:2945-2956.
10. Vilupuru AS, Glasser A. Dynamic accommodation in rhesus monkeys. *Vision Res.* 2002;42:125-141.
11. Beers APA, Van Der Heijde GL. In vivo determination of the biomechanical properties of the component elements of the accommodative mechanism. *Vision Res.* 1994;34:2897-2905.
12. Fisher RF. The significance of the shape of the lens and capsular energy changes in accommodation. *J Physiol.* 1969;201:21-47.
13. Fisher RF. The force of contraction of the human ciliary muscle during accommodation. *J Physiol.* 1977;270:51-74.
14. O'Neill WD, Brodkey JS. A nonlinear analysis of the mechanics of accommodation. *Vision Res.* 1970;10:375-391.
15. Ejiri M, Thompson HE, O'Neill WD. Dynamic visco-elastic properties of the lens. *Vision Res.* 1969;9:233-244.
16. Fisher RF. Elastic constants of the human lens capsule. *J Physiol.* 1969;201:1-19.
17. Fisher RF. The elastic constants of the human lens. *J Physiol.* 1971;212:147-180.
18. Fisher RF. The ciliary body in accommodation. *Trans Ophthalmol Soc UK.* 1986;105:208-219.
19. Schor CM, Alexander J, Cormack L, Stevenson S. Negative feedback control model of proximal convergence and accommodation. *Ophthalmic Physiol Opt.* 1992;12:307-318.
20. Hung GK, Ciuffreda KJ. Dual-mode behaviour in the human accommodation system. *Ophthalmic Physiol Opt.* 1988;8:327-332.
21. Ebenholtz SM, Citek K. Absence of adaptive plasticity after voluntary vergence and accommodation. *Vision Res.* 1995;35:2773-2783.
22. Schor CM, Bharadwaj SR. A pulse-step model of accommodation dynamics in the aging eye. *Vision Res.* 2005;45:1237-1254.
23. Khosroyani M, Hung GK. A dual-mode dynamic model of the human accommodation system. *Bull Math Biol.* 2002;64:285-299.
24. Gamlin PD, Zhang Y, Clendaniel RA, Mays LE. Behavior of identified Edinger-Westphal neurons during ocular accommodation. *J Neurophysiol.* 1994;72:2368-2382.
25. Schor CM, Lott LA, Pope D, Graham AD. Saccades reduce latency and increase velocity of ocular accommodation. *Vision Res.* 1999;39:3769-3795.
26. Bahill AT, Clark MR, Stark L. The Main Sequence, a tool for studying human eye movements. *Math Biosci.* 1975;24:191-204.
27. Hung GK, Zhu H, Ciuffreda KJ. Convergence and divergence exhibit different response characteristics to symmetric stimuli. *Vision Res.* 1997;37:1197-1205.
28. Hung GK, Ciuffreda KJ, Semmlow JL, Horng JL. Vergence eye movements under natural viewing conditions. *Invest Ophthalmol Vis Sci.* 1994;35:3486-3492.
29. Mordt JA, Ciuffreda KJ. Dynamic aspects of accommodation: age and presbyopia. *Vision Res.* 2004;44:591-601.
30. Bharadwaj SR, Schor CM. Acceleration characteristics of human ocular accommodation. *Vision Res.* 2005;45:17-28.
31. Charman WN, Heron G. On the linearity of accommodation dynamics. *Vision Res.* 2000;40:2057-2066.
32. Heron G, Charman WN. Accommodation as a function of age and the linearity of the response dynamics. *Vision Res.* 2004;44:3119-3130.
33. Seidemann A, Schaeffel F. An evaluation of the lag of accommodation using photorefractor. *Vision Res.* 2003;43:419-430.
34. Wolffsohn JS, Hunt OA, Gilmartin B. Continuous measurement of accommodation in human factor applications. *Ophthalmic Physiol Opt.* 2002;22:380-384.
35. Allen PM, Radhakrishnan H, O'Leary DJ. Repeatability and validity of the PowerRefractor and the Nidek AR600-A in an adult population with healthy eyes. *Optom Vis Sci.* 2003;80:245-251.
36. Hunt OA, Wolffsohn JS, Gilmartin B. Evaluation of the measurement of refractive error by the PowerRefractor: a remote, continuous and binocular measurement system of oculomotor function. *Br J Ophthalmol.* 2003;87:1504-1508.
37. Press WH, Teukolsky SA, Vetterling WT, Flannery BP. Modeling of data. *Numerical Recipes in C, The Art of Scientific Computing.* 2nd ed. Cambridge, UK: Cambridge University Press; 1997:656-706.
38. Stark LR, Atchison DA. Subject instructions and methods of target presentation in accommodation research. *Invest Ophthalmol Vis Sci.* 1994;35:528-537.
39. Johnson CA. Effects of luminance and stimulus distance on accommodation and visual resolution. *J Opt Soc Am.* 1976;66:138-142.
40. Schor CM, Kotulak JC. Dynamic interactions between accommodation and convergence are velocity sensitive. *Vision Res.* 1986;26:927-942.
41. Charman WN, Heron G. Fluctuations in accommodation: a review. *Ophthalmic Physiol Opt.* 1988;8:153-164.
42. Gray LS, Winn B, Gilmartin B. Effect of target luminance on microfluctuations of accommodation. *Ophthalmic Physiol Opt.* 1993;13:258-265.
43. Beers APA, Van Der Heijde GL. Age-related changes in the accommodation mechanism. *Optom Vis Sci.* 1996;73:235-242.
44. Yamada T, Ukai K. Amount of defocus is not used as an error signal in the control system of accommodation dynamics. *Ophthalmic Physiol Opt.* 1997;17:55-60.
45. Mordt JA, Ciuffreda KJ. Static aspects of accommodation: age and presbyopia. *Vision Res.* 1998;38:1643-1653.
46. Choi M, Weiss S, Schaeffel F, et al. Laboratory, clinical, and kindergarten test of a new eccentric infrared photorefractor (PowerRefractor). *Optom Vis Sci.* 2000;77:537-548.
47. Mallen EA, Wolffsohn JS, Gilmartin B, Tsujimura S. Clinical evaluation of the Shin-Nippon SRW-5000 autorefractor in adults. *Ophthalmic Physiol Opt.* 2001;21:101-107.
48. Wang L, Wang N, Koch DD. Evaluation of refractive error measurements of the WaveScan Wavefront system and the Tracey Wavefront aberrometer. *J Cataract Refract Surg.* 2003;29:970-979.
49. Gekeler F, Schaeffel F, Howland HC, Wattam-Bell J. Measurement of astigmatism by automated infrared photoretinoscopy. *Optom Vis Sci.* 1997;74:472-482.
50. Vilupuru AS, Kasthurirangan S, Glasser A. Dynamics of accommodative fatigue in rhesus monkeys and humans. *Vision Res.* 2005;45:181-191.
51. Liu JS, Lee M, Jang J, et al. Objective assessment of accommodation orthoptics. I. Dynamic insufficiency. *Am J Optom Physiol Opt.* 1979;56:285-294.
52. Bobier WR, Sivak JG. Orthoptic treatment of subjects showing slow accommodative responses. *Am J Optom Physiol Opt.* 1983;60:678-687.
53. Sterner B, Abrahamsson M, Sjostrom A. Accommodative facility training with a long term follow up in a sample of school aged children showing accommodative dysfunction. *Doc Ophthalmol.* 1999;99:93-101.
54. Glasser A, Kaufman PL. The mechanism of accommodation in primates. *Ophthalmology.* 1999;106:863-872.
55. von Helmholtz HH. Mechanism of accommodation. In: Southall JPC, ed. *Helmholtz's Treatise on Physiological Optics.* New York: Dover; 1909; chap. 12:143-173.
56. Glasser A, Campbell MCW. Presbyopia and the optical changes in the human crystalline lens with age. *Vision Res.* 1998;38:209-229.
57. Croft MA, Kaufman PL, Crawford KS, Neider MW, Glasser A, Bito LZ. Accommodation dynamics in aging rhesus monkeys. *Am J Physiol.* 1998;275:R1885-R1897.