

Short-Term Adaptive Modification of Dynamic Ocular Accommodation

Shrikant R. Bharadwaj,¹ Indu Vedamurthy,² and Clifton M. Schor²

PURPOSE. Indirect observations suggest that the neural control of accommodation may undergo adaptive recalibration in response to age-related biomechanical changes in the accommodative system. However, there has been no direct demonstration of such an adaptive capability. This investigation was conducted to demonstrate short-term adaptation of accommodative step response dynamics to optically induced changes in neuromuscular demands.

METHODS. Repetitive changes in accommodative effort were induced in 15 subjects (18–34 years) with a double-step adaptation paradigm wherein an initial 2-D step change in blur was followed 350 ms later by either a 2-D step increase in blur (increasing-step paradigm) or a 1.75-D step decrease in blur (decreasing-step paradigm). Peak velocity, peak acceleration, and latency of 2-D single-step test responses were assessed before and after 1.5 hours of training with these paradigms.

RESULTS. Peak velocity and peak acceleration of 2-D step responses increased after adaptation to the increasing-step paradigm (9/12 subjects), and they decreased after adaptation to the decreasing-step paradigm (4/9 subjects). Adaptive changes in peak velocity and peak acceleration generalized to responses that were smaller (1 D) and larger (3 D) than the 2-D adaptation stimulus. The magnitude of adaptation correlated poorly with the subject's age, but it was significantly negatively correlated with the preadaptation dynamics. Response latency decreased after adaptation, irrespective of the direction of adaptation.

CONCLUSIONS. Short-term adaptive changes in accommodative step response dynamics could be induced, at least in some of our subjects between 18 and 34 years, with a directional bias toward increasing rather than decreasing the dynamics. (*Invest Ophthalmol Vis Sci.* 2009;50:3520–3528) DOI:10.1167/iovs.08-2577

Recalibration of neural signals allows a biological control system to restore and maintain optimal motor performance in the event of any age-, pathology-, or environment-related changes in the biomechanical plant. Ocular accommodation of humans and nonhuman primates is a good example of a biological control system whose biomechanical plant (comprising the crystalline lens, ciliary muscle, choroid, and zonules) becomes increasingly noncompliant with age, ultimately leading to a complete loss of focusing ability (absolute presbyopia).¹

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The loss of focusing ability can be primarily attributed to a decrease in lenticular compliance (compliance = 1/elasticity),^{2–4} increase in lenticular viscoelasticity,⁴ mechanical restriction in ciliary muscle movement,^{5,6} and morphologic changes in the accommodative plant.^{7–9} During the incipient stages of presbyopia, the increasingly noncompliant accommodative plant increases the neuromuscular demands required to generate the desired amount of accommodation.¹⁰

Several indirect observations suggest that the neural control of accommodation may undergo adaptive recalibration to suit the biomechanical changes in the accommodative plant. For instance, neural recalibration to age-related loss of plant compliance is suggested by an increase in the myodioter (the neuromuscular effort required to generate a diopter of accommodation¹¹) during incipient presbyopia.^{10,12} An increase in the myodioter is indicated by an age-related increase in the response AC/A ratio (the amount of vergence generated by a diopter of accommodation) and an age-related decline in the response CA/C ratio (the amount of accommodation generated by a meter angle of vergence), within the linear range of the accommodative stimulus-response function.^{10,13,14} Neural recalibration to an age-related increase in lenticular viscoelasticity is suggested by the lack of a dramatic reduction in the peak velocity of small accommodative step responses (1–3 D).^{15–17} On a more general level, neural recalibration of disaccommodation (near-to-far accommodation) is suggested by the serendipitous observation of Bharadwaj and Schor¹⁸ that repeated pilot experiments over 1 year reduced the speed and acceleration of small disaccommodative step responses of the first author, minimizing the instabilities that are usually associated with such responses. Neural recalibration may have occurred to optimize stability by slowing down the responses.¹⁸ Finally, adaptable dynamics are also suggested by the success of orthoptic training exercises (e.g., accommodative flippers and pencil push-ups) that decrease the time constant, speed up abnormally sluggish accommodative responses, and increase the rate at which accommodation responds to repetitive positive and negative focusing errors (accommodative flipper rates).^{19,20}

Apart from these indirect observations, to our knowledge, there has been no direct demonstration of the adaptation capability of accommodative step response dynamics. The main purpose of this study was to provide direct evidence for such an adaptive capacity by employing a double-step adaptation paradigm that optically stimulates increases (increasing-step paradigm) or decreases (decreasing-step paradigm) in neuromuscular efforts. Our results illustrate that the dynamics of accommodative step responses can be modified on a short-term basis, at least in some subjects ranging in age from 18 to 34 years, with increases in neuromuscular effort adapting more readily than decreases in neuromuscular effort.

METHODS

Fifteen naïve observers (except subject SRB) between 18 and 34 years (11 emmetropic subjects and 4 fully corrected myopic subjects) participated after signing an informed consent form approved by the Committee for Protection of Human Subjects, University of California

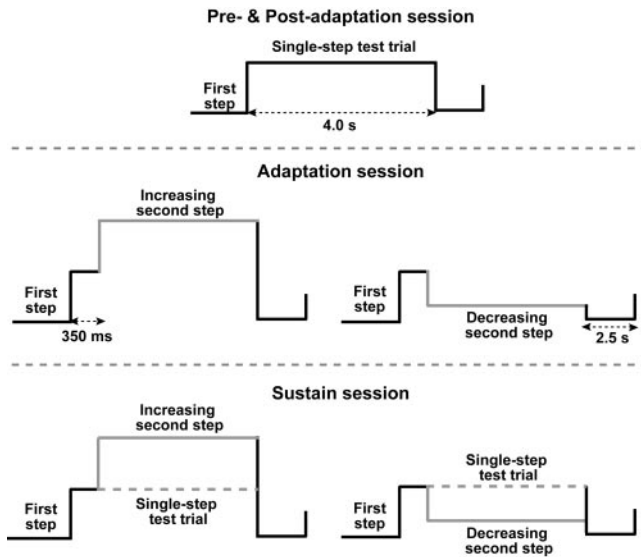


FIGURE 1. Experimental design for the increasing- and decreasing-step adaptation paradigms.

at Berkeley. The study also adhered to the tenets of the Declaration of Helsinki. Fourteen and 12 subjects participated in the increasing-step and decreasing-step paradigms, respectively. Eight subjects participated in both paradigms.

Subjects, positioned on a bite bar and forehead rest, focused on a high-contrast, black-and-white Maltese cross. Their left eye's accommodative responses were measured (the right eye was occluded) with an infrared recording optometer (200 Hz sampling frequency; Generation V SRI International, Menlo Park, CA).²¹ The left pupil of each subject remained fully dilated throughout the experiment with phenylephrine hydrochloride. The concentration (2.5%) was much weaker than that shown to influence accommodative dynamics (10%).²² Step changes in optical blur were stimulated using a Badal stimulus optometer (SRI International).²¹ Accommodative responses were calibrated thrice on each subject by stimulating 0 to 4 D of accommodation and disaccommodation in 1-D steps and the averaged output voltages were linearly regressed against the accommodative stimuli to convert the optometer voltages into dioptric units.^{18,23} For older subjects, only 1- to 3-D stimuli were used for calibration. Because of the typically observed lag of accommodation,²⁴ the calibration slope is artificially steepened when the voltage signals are regressed against the accommodative stimuli. Steepening of the calibration slope, however, would concurrently amplify both the accommodative magnitude and dynamics for a given stimuli, without altering the relative relation between amplitude and dynamics. Furthermore, since the calibration slope of a given subject did not typically change during the experiment, accommodative response characteristics measured before and after training remained unaffected relative to each other.

Changes in accommodative step response dynamics (peak velocity and peak acceleration) were induced with a double-step adaptation paradigm, similar to those used to induce vergence^{25,26} and saccade^{27,28} adaptation (Fig. 1). Each experimental session, lasting approximately 1.5 to 2 hours, consisted of four sessions (preadaptation session, adaptation session, sustained session, and postadaptation session). Each trial in a session lasted for 4 seconds, and the inter-trial interval was 2.5 seconds (Fig. 1). Limited periods of rest were given to subjects, during which time they were asked to keep their eyes closed to avoid normal visual stimulation.

In the preadaptation session (first phase of the experiment) and the postadaptation session (last phase in the experiment), consisting of 100 and 50 trials, respectively, single-step stimuli ranging from 1 to 4 D (test stimuli) were presented in steps of 0.5 D in pseudorandomized order (Fig. 1). In the two oldest subjects (31 and 34 years of age), the

stimuli ranged from 1 to 3 D in 0.5-D steps. These stimulus amplitudes typically fell within 75% of the maximum age-matched objective and subjective amplitude of accommodation described for humans.^{1,29,30} To minimize the ability of subjects to anticipate the start of the trial, the stimulus onset was randomized by a time delay (range, 0–1000 ms) after the subject initiated the trial with a button press.

Two different adaptation sessions (second phase of the experiment), each consisting of 150 trials, were run on separate days. In the adaptation trials of the increasing-step paradigm, an initial 2-D step change in blur was followed 350 ms later by a 2-D step increase in blur (100% increment; Fig. 1). In the adaptation trials of the decreasing-step paradigm, an initial 2-D step change in blur was followed 350 ms later by a 1.75-D step decrease in blur (87.5% decrement; Fig. 1). The second-step decrement in blur was less than 100%, to ensure that the stimulus was not perceived as a transient change in blur. In four subjects, adaptation to a larger amplitude stimulus decrement was also investigated, wherein an initial 4-D step change in blur was followed 350 ms later by a 2-D step decrement in blur (not shown in Fig. 1). The results for the large-step decrement were similar to those of the small-step decrement, and hence they are not presented separately. The sustained session of the experiment (third phase of the experiment), consisting of 150 trials, was similar to the adaptation session, but 2-D single-step test trials were interleaved with the double-step trials with a ratio of five double-step trials to one single-step trial to assess the changes in response characteristics induced during adaptation by the double-step trials (Fig. 1). Each trial in the adaptation and sustain sessions of the experiment was initiated 2.5 seconds after the end of the previous trial (Fig. 1). To minimize the ability of subjects to anticipate the start of the trial, the stimulus onset was randomized by a time delay (ranging between 0–1000 ms) after the 2.5 seconds elapsed.

The second step change in the double-step stimulus was always presented at a constant delay of 350 ms, which corresponded approximately to the end of the latency period of first accommodative step response. The second-step change is likely to induce an unanticipated focus error at the end of the latency period of the first accommodative step response. This defocus error is corrected by a change in the accommodative neuromuscular effort that is guided by blur feedback. An increased neuromuscular effort is required by a double step that increases the blur during the initial accommodative response (increasing-step paradigm) and a decreased neuromuscular effort is required by a double step that decreases the blur during the initial accommodative response (decreasing-step paradigm). Repeated presentation of the double-step condition is intended to stimulate a recalibration of the relationship between the initial amount of defocus and the initial neuromuscular effort needed to correct the focus error. This recalibration may be reflected as changes in the velocity and acceleration of single-step responses as observed for double-step adaptation of disparity vergence^{25,26} and saccades.^{27,28} Ideally, the timing of the second-step stimulus would be controlled to vary in each trial with the online estimates of response latency. However, it was not possible to obtain reliable online estimates of response latency because of the relatively large fluctuations in the steady state accommodation.³¹ The second step was therefore always presented 350 ms after the first step (Fig. 1).

The increasing- and decreasing-step paradigms were conducted within 2 weeks of each other in eight subjects who took part in both training paradigms. Since response dynamics that are collected within a few weeks of each other were found not to change significantly (Bharadwaj SR, unpublished observations, 2003–2005), only one baseline (preadapted) session was conducted in these subjects, typically on the day that the increasing-step paradigm was conducted. This strategy was used to minimize fatigue and the total time required of the subject to complete the experiment. Separate adaptation, sustaining, and postadaptation sessions were conducted (in that order) for the increasing- and decreasing-step paradigms on different days, and the postadaptation data from each paradigm was compared to the preadaptation data collected a few days earlier.

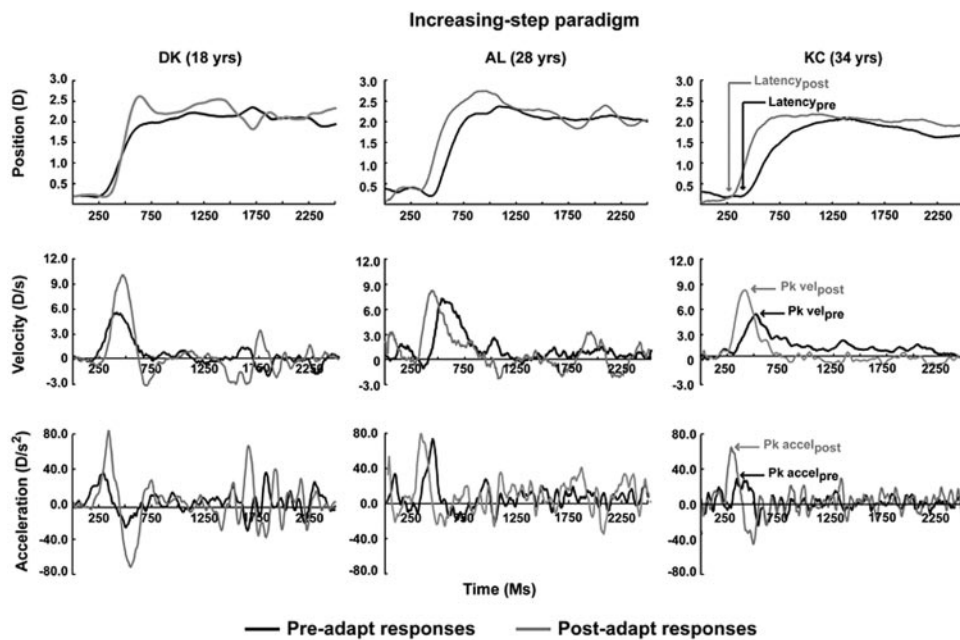


FIGURE 2. Raw traces of accommodative position (*top*), velocity (*middle*), and acceleration (*bottom*) for a 2-D step stimulus from three representative individuals in the increasing-step paradigm. The position traces are averages of five temporally aligned individual responses. No averages were calculated during actual data analyses, and the responses were analyzed individually.

Data were analyzed using three commercial statistical packages (Excel; Microsoft, Redmond, WA, MatLab; The MathWorks, Natick, MA, and SPSS, SPSS, Chicago, IL). Accommodative position traces were differentiated and smoothed with a 100-ms running-average window to obtain velocity and acceleration profiles.²³ The start and end of the accommodative response was identified with a velocity-criterion algorithm described in detail elsewhere.^{23,32} In the increasing-step paradigm, the postadaptation responses of some subjects showed instabilities and in such cases, the end of the response was confirmed through visual inspection. Response amplitude was calculated as the dioptric difference between the averaged (100 ms) accommodative states before the start of the response and after the end of the response. Single-step accommodative responses with very short latencies (<100 ms) and responses that changed nonmonotonically (~10% to 15% of the responses in each subject) were discarded from the analyses because reliable estimates of response parameters could not be obtained from these traces.

Adaptive changes in response dynamics were quantified by comparing the peak velocity, peak acceleration, and response latency before and after double-step training (Fig. 2). In the pre- and postadaptation sessions, the peak velocity and peak acceleration were grouped for each subject into 1-D bins, and all the responses within the bin were averaged. Since the response latency did not show any significant variation across response amplitude, all the single-step response latencies within an experimental session were averaged, irrespective of the amplitude of the response. The peak velocity, peak acceleration and latency of individual responses within the preadaptation and postadaptation sessions did not show any systematic trial dependent variations and therefore it is unlikely that the averaging obscured any obvious trends in the data. The pre- and postadaptation dynamics of each subject were statistically compared on an individual basis by using a two-factor repeated-measures ANOVA test. Statistical significance (defined here as $P < 0.01$) of factor 1 (adaptation magnitude) would indicate that, when the data across all response amplitudes are considered together, the preadaptation and postadaptation peak velocity and peak acceleration were significantly different from each other. Statistical significance of factor 2 (response amplitude) indicates that, when all the preadaptation and postadaptation data were considered together, the peak velocity and peak acceleration changed significantly across response amplitude. Statistically significant interaction between factors 1 and 2 indicates that the change in peak velocity and peak acceleration after adaptation was not uniform

across all response amplitudes. For data sets that violated the assumption of sphericity (i.e., the difference scores between various levels of the repeated-measures factor had unequal variances; 2 of the 12 subjects in the increasing-step paradigm and 3 of the 9 subjects in the decreasing-step paradigm), appropriate corrections to the F -value (Greenhouse-Geisser correction) was applied before computing statistical significance. The pre- and postadaptation response latencies were compared by using a Student's t -test.

RESULTS

Increasing-Step Paradigm

Usable data were collected from 12 subjects. Data from the two remaining subjects were discarded because most of their responses had extremely short latencies (<100 ms). Figure 2 shows representative raw traces from three subjects who gave usable data in the increasing-step paradigm. The static and dynamic (peak velocity and peak acceleration) characteristics of preadaptation single-step responses were comparable to those described in previous experiments^{23,33} (Fig. 2). The increase in dynamics after adaptation (9/12 subjects) were associated with response instabilities in three subjects (e.g., subject DK in Fig. 2) but not in the others (e.g., subject KC in Fig. 2). In most subjects, the latency of the single-step responses decreased after double-step stimulation, irrespective of whether the peak velocity and peak acceleration showed adaptive changes (Fig. 2, Table 1).

The preadaptation peak velocity increased significantly with response amplitude in six subjects (ANOVA factor 2, $P < 0.001$; Figs. 3b, 3c, 3e, 3h-j), saturated at larger response amplitudes in three subjects (ANOVA factor 2, $P < 0.01$; Figs. 3a, 3d, 3f) and did not change with response amplitude in the remaining three subjects (ANOVA factor 2, $P > 0.01$; Figs. 3g, 3k, 3l). Unlike the preadaptation peak velocity, the preadaptation peak acceleration did not change significantly with response amplitude in the majority of the subjects (ANOVA factor 2, $P = 0.03$ -0.94 across subjects; Fig. 4). Similar to earlier studies,^{23,34} the standard deviations of preadaptation peak acceleration were larger than those of preadaptation peak velocity (Figs. 3, 4). However, when the standard deviations of

TABLE 1. Response Latency of Accommodation before and after Training in the Two Paradigms

	Increasing-step Paradigm			Decreasing-step Paradigm		
	Preadaptation (ms)	Postadaptation (ms)	Change (%)	Preadaptation (ms)	Postadaptation (ms)	Change (%)
DK	338.6 ± 149.9	351.3 ± 128.9	3.7 NS	338.6 ± 149.9	305.9 ± 159.2	-9.6*
EH	414.1 ± 148.6	191.1 ± 83.1	-53.8***			
JE	444.1 ± 121.3	366.6 ± 82.5	-17.5***	344.1 ± 91.3	280.5 ± 182.1	-18.5***
JT	378.9 ± 77.3	223.1 ± 118.8	-47.3***			
GSA	430.4 ± 89.7	355.2 ± 106.2	-17.5***			
JW	361.4 ± 159.1	245.5 ± 110.3	-32.1***	361.4 ± 159.1	367.4 ± 130.4.3	1.7 NS
JW II				361.4 ± 159.1	249.9 ± 134.0	-30.8***
ER				327.1 ± 104.9	236.9 ± 161.9	-27.6***
SRB	343.4 ± 78.9	295.7 ± 114.6	-13.9**	343.4 ± 78.9	406.8 ± 89.4	18.5**
AL	353.6 ± 58.5	201.3 ± 87.5	-43.1***	353.6 ± 58.5	213.7 ± 113.5	-39.6***
JOS	409.8 ± 131.8	223.3 ± 148.4	-45.5***	409.8 ± 131.8	309.1 ± 152.6	-24.6***
KS	344.7 ± 136.9	238.6 ± 84.5	-30.8***			
PRM	313.5 ± 95.5	400.2 ± 213.9	27.6 NS	363.5 ± 115.4	164.9 ± 82.2	-54.7***
PRM II	313.5 ± 95.5	410.1 ± 196.3	30.8 NS			
KC	351.2 ± 90.8	156.1 ± 120.1	-55.5***	351.2 ± 90.8	231.1 ± 106.2	-34.2***

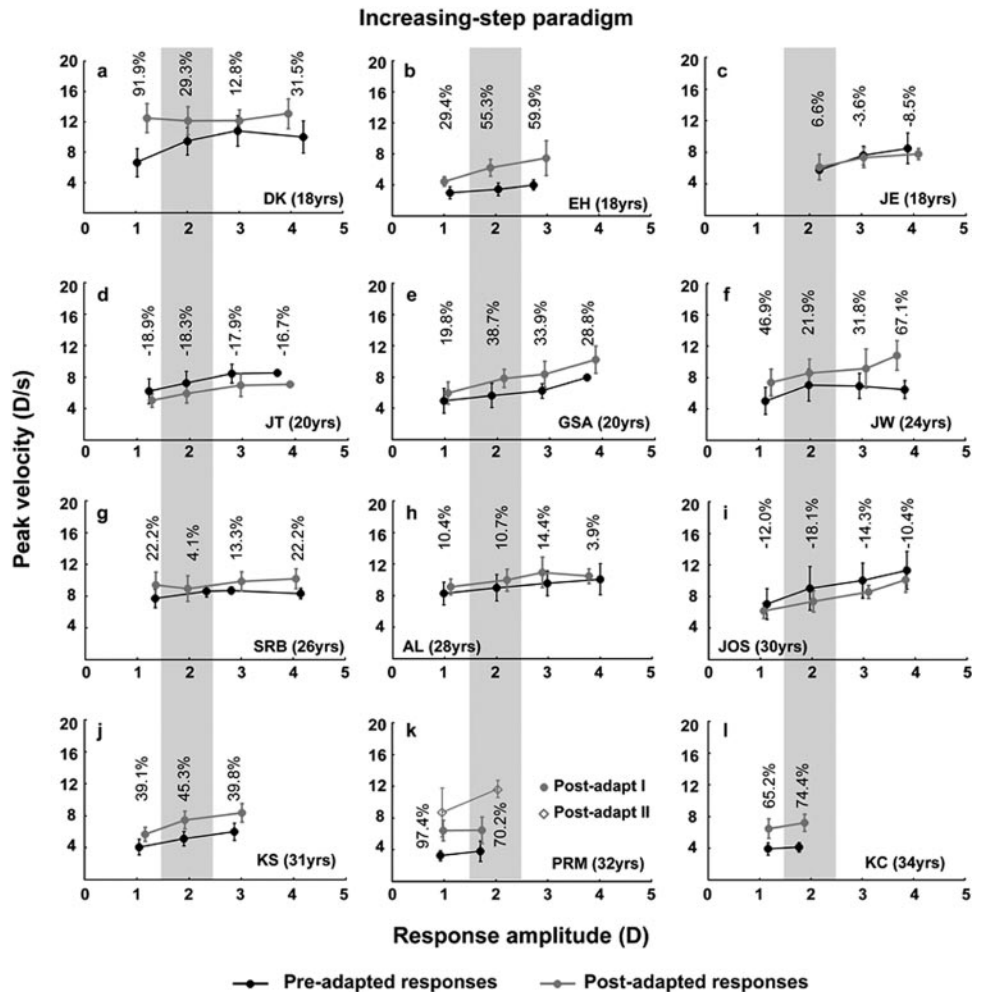
Data show the mean response latency ± SD and the percentage change in latency after training [(postadaptation latency/preadaptation latency) × 100%] in the increasing-step and the decreasing-step paradigms. Positive and negative numbers in the percentage change column indicate an increase and decrease in latency following the training, respectively.

* P < 0.05; ** P < 0.01; *** P < 0.001.

peak velocity and peak acceleration were normalized to their respective means (coefficient of variation), the statistical variability was similar for both parameters.

The postadaptation peak velocity was significantly larger than the preadaptation peak velocity across different response amplitudes in nine subjects, irrespective of whether

FIGURE 3. (a-l) Mean (±SD) peak velocity of accommodation as a function of response amplitude for the preadaptation and postadaptation sessions for each subject in the increasing-step paradigm. (k) Repeatability data from subject PRM. The numbers above each pair of black and gray circles indicate the percentage change in peak velocity with adaptation. Shaded areas: single-step test stimulus amplitude. In the preadaptation session, the ±1 SD of response amplitude (not shown, for clarity) ranged from 0.08 to 0.31 D for the 1-D stimulus, to 0.14 to 0.36 D for the 2-D stimulus, to 0.21 to 0.33 D for the 3-D stimulus across subjects. In the postadaptation session, the ±1-SD of response amplitude ranged from 0.11 to 0.32 D for the 1-D stimulus, to 0.1 to 0.39 D for the 2-D stimulus, to 0.21 to 0.35 D for the 3-D stimulus across subjects.



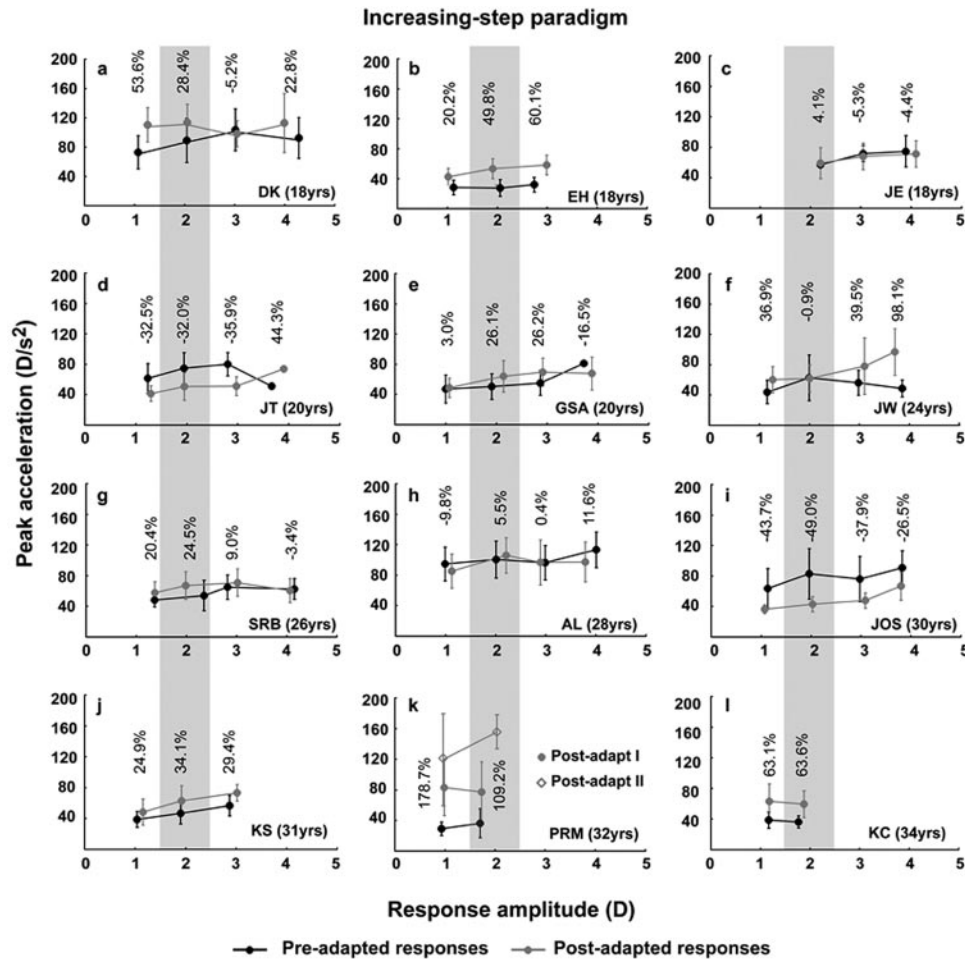


FIGURE 4. (a–l) Mean (± 1 SD) peak acceleration of accommodation as a function of response amplitude for the preadaptation and postadaptation sessions for each subject in the increasing-step paradigm. (k) Repeatability data from subject PRM. All other features shown in this figure are similar to those shown in Figure 3.

the preadaptation peak velocity increased or saturated as a function of response amplitude (ANOVA factor 1, $P < 0.001$; Fig. 3). The pre- and postadaptation peak velocities were similar to each other in two subjects (ANOVA factor 1, $P = 0.71$; Figs. 3c, 3i) and the postadaptation peak velocity was significantly lower than the preadaptation peak velocity in the remaining one subject (ANOVA factor 1, $P < 0.001$; Fig. 3d). Six of 12 subjects showed a statistically significant increase in peak acceleration with adaptation (ANOVA factor 1, $P < 0.01$; Fig. 4), whereas the remaining showed either no change (ANOVA factor 1, $P > 0.01$; Figs. 4c, 4e, 4g, 4h) or a decrease (ANOVA factor 1, $P < 0.01$; Figs. 4d, 4i) in peak acceleration with adaptation. For peak velocity and peak acceleration, the interaction between adaptation magnitude and response amplitude was not statistically significant in most subjects, confirming that the change in peak velocity and peak acceleration with adaptation was similar across different response amplitudes (Figs. 3, 4).

In those subjects who showed statistically significant changes with adaptation, both peak velocity and peak acceleration typically changed simultaneously with adaptation (e.g., compare data from subjects DK and EH in Figs. 3, 4), with the average magnitude of change being similar for both parameters (Figs. 3, 4). Although the change in peak velocity and peak acceleration appeared to spread across the three different response amplitudes, the magnitude of adaptation was definitely variable across these response amplitudes and across different subjects.

Decreasing-Step Paradigm

Usable data were collected from nine subjects. Data from the three remaining subjects were discarded because most of their responses had extremely short response latencies (< 100 ms). In general, responses in the adaptation and postadaptation sessions of the decreasing-step paradigm were more variable than those in the increasing-step paradigm. The changes in peak velocity and peak acceleration in the postadaptation session were less prevalent in the decreasing-step paradigm when compared with the increasing-step paradigm. The peak velocity decreased after decreasing-step adaptation in four of the nine subjects (ANOVA factor 1, $P < 0.001$; raw trace from subject JW in Figs. 5, 6b, 6c, 6e, 6g). Similarly, the peak acceleration decreased significantly after adaptation in three of the nine subjects (ANOVA factor 1, $P < 0.01$; Figs. 7b, 7c, 7g). In the remaining subjects, the postadaptation peak velocity and peak acceleration either remained the same (ANOVA factor 1, $P > 0.01$) or increased (ANOVA factor 1, $P < 0.01$) after adaptation (raw traces from subjects DK and KC in Figs. 5, 6, 7a, 7d, 7i). The interaction between adaptation magnitude and response amplitude was not statistically significant for both peak velocity and peak acceleration in most subjects indicating that the change in dynamics after adaptation was generalizable across response amplitudes ($P = 0.20$ – 0.96 across subjects; Figs. 6, 7). The response latency reduced with adaptation irrespective of whether the other dynamic parameters also changed (Fig. 5, Table 1).

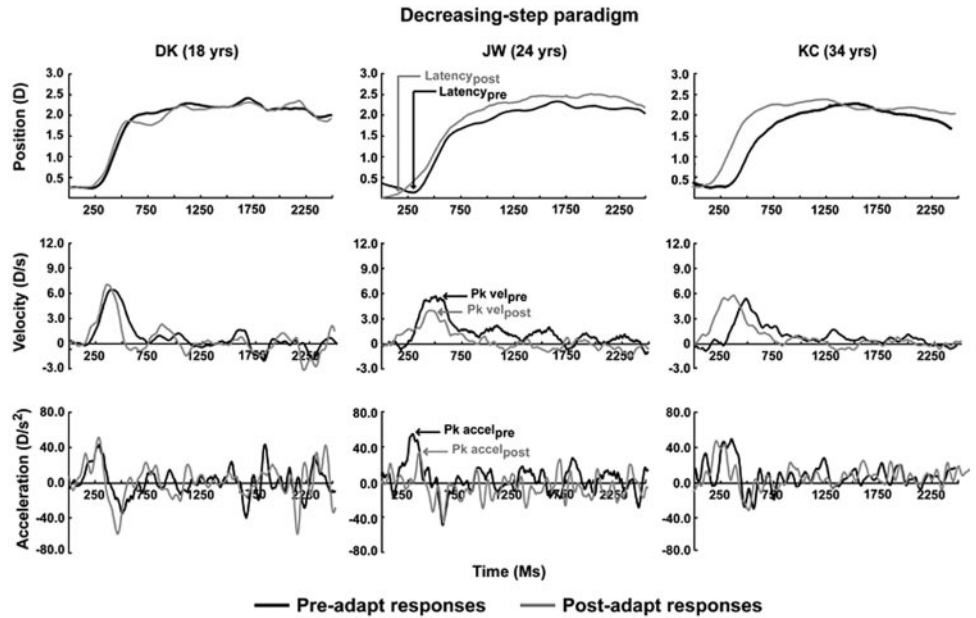


FIGURE 5. Raw traces of accommodative position (*top*), velocity (*middle*), and acceleration (*bottom*) for a 2-D step stimulus from three representative individuals in the decreasing-step paradigm. The position traces are averages of five temporally aligned individual responses. No averages were calculated during the actual data analyses and the responses were analyzed individually.

The increasing- and decreasing-step paradigms were repeated in subject PRM (Figs. 3k, 4k) and subject JW (Figs. 6c, 7c), respectively, by repeating the adaptation-, sustaining-, and postadaptation phases of the experiment. Repeatability was tested after 15 and 8 days after the first session was conducted in subjects PRM and JW, respectively. In subject PRM, the peak velocity and peak acceleration in the increasing-step paradigm increased significantly after adaptation in both sessions (Figs. 3k, 4k). The increase in peak velocity and peak acceleration in the two sessions were not significantly different from each other (peak velocity: $P = 0.51$; peak acceleration: $P = 0.89$). In this subject, the response latency also increased after adaptation in both sessions (Table 1). The peak velocity and peak

acceleration in the decreasing-step paradigm of subject JW decreased significantly in the first session (Figs. 6, 7), but they failed to decrease significantly in the second session (Figs. 6, 7). The response latency increased after adaptation in the first session, whereas it decreased after adaptation in the second session (Table 1). Overall, the changes in response dynamics for subject JW in the decreasing-step paradigm was less repeatable than the change in dynamics for subject PRM in the increasing-step paradigm (Figs. 3, 4).

To assess the presence of any age-related trends in the data, we computed a correlation coefficient between the magnitude of change in peak velocity and peak acceleration of 2-D step responses with the subject's age (18–34 years). Subjects

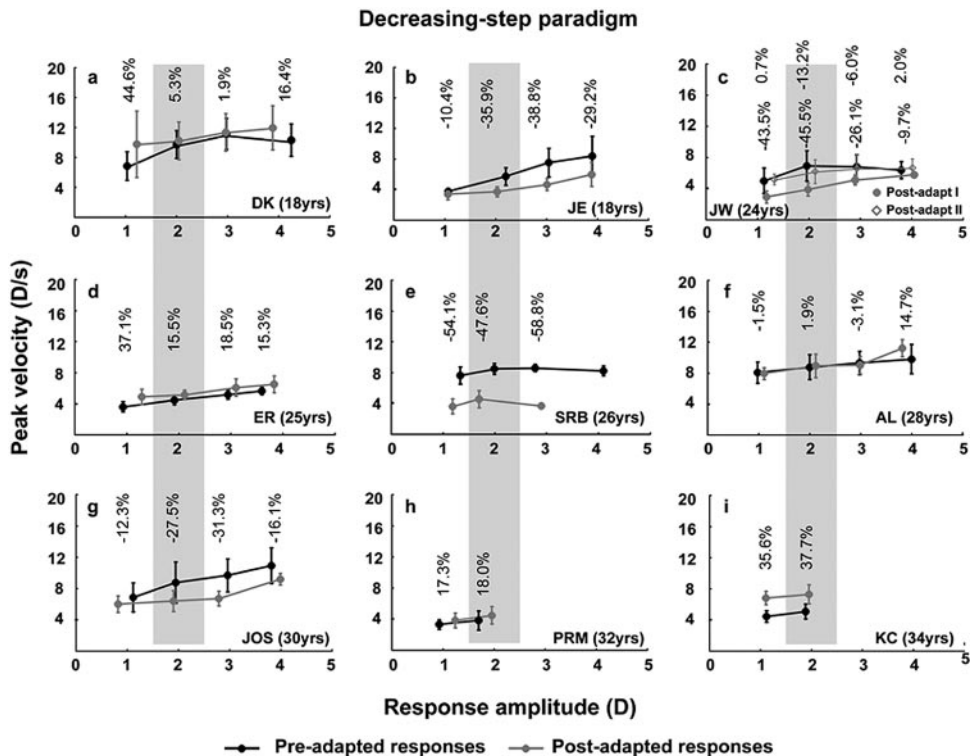


FIGURE 6. (a–i) Mean (± 1 SD) peak velocity of accommodation as a function of response amplitude for the preadaptation and postadaptation sessions for each subject in the decreasing-step paradigm. The numbers above each pair of *black* and *gray* circles indicate the percentage change in peak velocity with adaptation. (c) The repeatability data from subject JW, with the *bottom* set of numbers showing percentage adaptation from the first trial and the *top* set showing data from the second trial. *Shaded area*: the single-step test stimulus amplitude used in this experiment. In the postadaptation session, the ± 1 -SD of response amplitude (not shown, for clarity) ranged from 0.06 to 0.28 D for the 1-D stimulus, to 0.12 to 0.37 D for the 2-D stimulus, to 0.27 to 0.43 D for the 3-D stimulus across subjects.

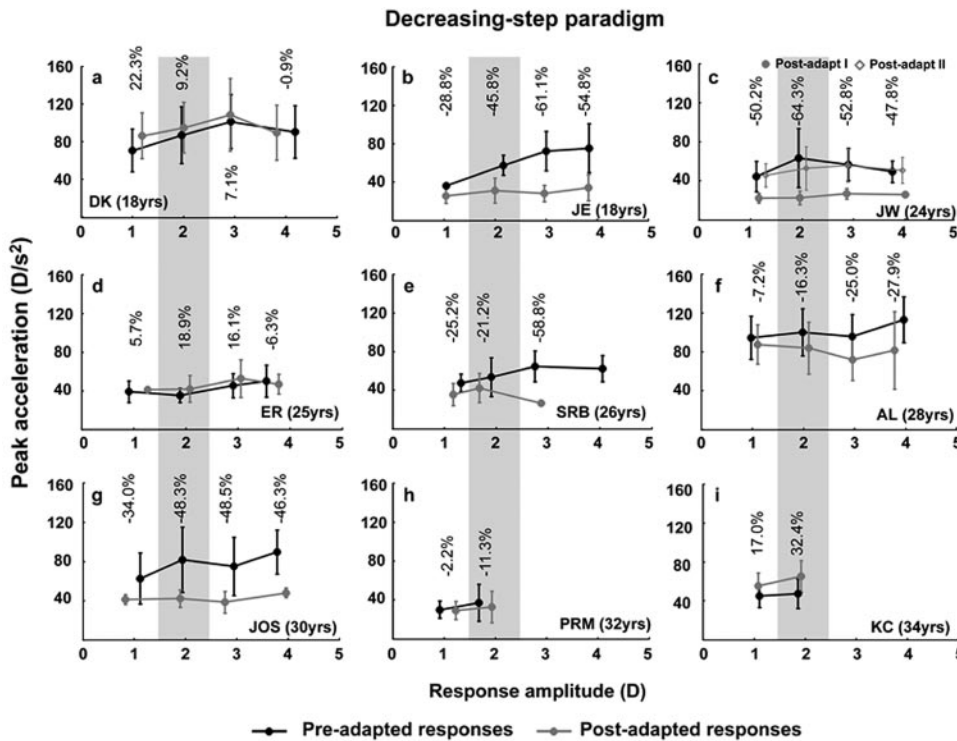


FIGURE 7. (a–i) Mean (± 1 SD) peak acceleration of accommodation as a function of response amplitude for the preadaptation and postadaptation sessions for each subject in the decreasing-step paradigm. (c) The repeatability data from subject JW. All other features are similar to those in Figure 6.

whose dynamics did not change significantly with adaptation and whose adaptive changes were in the direction opposite than expected (e.g., reduction of peak velocity in the increasing-step paradigm) were not included in the correlation calculation. Since the data of three of the nine subjects in the decreasing-step paradigm were excluded for these reasons, no correlation coefficients were computed for this paradigm. There was only a modest, statistically insignificant correlation between the age of the subject and the magnitude of adaptation of peak velocity ($r = 0.48$; $P = 0.09$) and peak acceleration ($r = 0.39$; $P = 0.21$) in the increasing-step paradigm. No such age-related trend was apparent in the magnitude of adaptation of peak velocity and peak acceleration in the decreasing-step paradigm.

To assess whether the preadapted dynamics of the individual determined the magnitude of change in dynamics that occurred after training, a correlation coefficient was computed between the preadapted peak velocity and peak acceleration and the magnitude of change in these parameters after adaptation (Fig. 8). The dynamics of only the 2-D step responses were included in this analysis and the exclusion criteria imposed in the age correlation (see earlier paragraph) were applied to this analysis too. There was a statistically significant negative correlation between preadaptation peak velocity (Fig. 8a) and peak acceleration (Fig. 8b) with the respective magnitudes of adaptation in the increasing step paradigm. No such trends were apparent in the decreasing-step paradigm.

DISCUSSION

Until now, only indirect observations have suggested that the accommodative control system may recalibrate in response to changes in neuromuscular demand.^{10,13,18,19} By employing a double-step adaptation paradigm, we have directly demonstrated that the peak velocity and peak acceleration of single-step accommodative responses can change on a short-term basis, at least in some subjects ranging from 18 to 34 years, in response to optically stimulated changes in neuromuscular

demand (Figs. 3, 4, 6, 7). Unlike response latency (Table 1), adaptive changes in peak velocity and peak acceleration were dependent on the direction of training (Figs. 3, 6), suggesting that stimulus anticipation cannot explain the results completely. In many subjects who showed adaptive changes in the anticipated direction, both peak velocity and peak acceleration changed after training, suggesting that adaptive changes in peak velocity were brought about by integrated changes in the peak acceleration (Figs. 3, 4, 6, 7).¹⁷ Of note, the peak velocity increased after increasing-step adaptation even in those subjects where the preadaptation peak velocity saturated at larger response amplitudes (Figs. 3a, 3d, 3f). This suggests that the saturation of peak velocity observed here and in previous experiments^{17,33,35} does not reflect an upper limit of velocity that the accommodative system is capable of generating for a given response amplitude.³⁶ There was no obvious correlation between the magnitude of adaptation and the subject's age

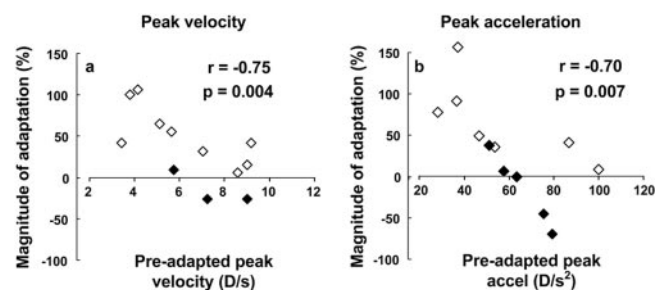


FIGURE 8. Magnitude of change (%) in peak (a) velocity and (b) acceleration in the increasing-step adaptation paradigm plotted as a function of the preadaptation dynamics. Positive and negative values in the ordinate scale indicate increase and decrease in peak velocity and acceleration with adaptation, respectively. Filled black symbols: subjects whose dynamics did not change significantly or those whose dynamics changed in the direction opposite that anticipated. These subjects were not included in the calculation of the correlation coefficient.

(18–34 years) in the small number of individuals we tested ($n = 15$). This result must be confirmed on a larger sample size.

Adaptive changes were larger in the increasing-step paradigm than in the decreasing-step paradigm in several subjects, including those for whom data were available from both training paradigms. This directional bias is unlikely to be due to accommodative fatigue from prolonged periods of stimulation,^{37–39} for fatigue would only bias the magnitude of adaptation toward lower values in both paradigms. When compared to the increasing-step paradigm, a slightly smaller adaptation stimulus was used in the decreasing-step paradigm (1.75 D vs. 2 D in the increasing-step paradigm) to ensure that the adaptation stimulus was not perceived as a transient change in blur. Although a smaller adaptation stimulus may be expected to produce a smaller change in dynamics, the difference of 0.25 D between the two paradigms appears too small to account for the observed directional bias in adaptation. Further, the results of the decreasing-step paradigm using a 2-D adaptation stimulus (first step size of 4 D) were similar to those seen with a 1.75-D adaptation stimulus in four subjects (results not shown separately). This suggests that the smaller stimulus size did not account for the reduced adaptation in the decreasing-step paradigm. A second possibility for the smaller adaptation response in the decreasing-step paradigm may be that, with the lag of accommodation, the second step decrement in blur brought the visual target into focus while the system was responding to the first stimulus, thereby negating the need for accommodation to respond to the second step. The decreasing-step paradigm may therefore not have stimulated any change in neuromuscular demand. The directional bias in adaptation may also reflect strategies used to minimize errors encountered during the normal growth and ageing processes. For instance, robust adaptation of horizontal vergence⁴⁰ and the accommodation-vergence coupling gains⁴¹ to sustained convergence stimuli (than to sustained divergence stimuli) may be a strategy to correct the physiological exophoria and minimize any undue demands on the fusional vergence system during the growth of the cranium.^{42,43} Perhaps, the bias in adapting more effectively to increases in neuromuscular effort is also an age-related strategy to compensate for the biomechanical changes in the accommodative plant (e.g., increased lenticular viscoelasticity,⁴ increased posterior restriction of ciliary muscle⁶). Accommodation could therefore be predisposed to increase the neural gain to the increasing step paradigm used in our experiment. Further experiments are warranted to explore these different possibilities.

The results of this study and the indirect observations made by earlier studies^{10,13,15–17,19,20} qualitatively support the presence of adaptive capability in accommodation. However, our results cannot be directly compared to these earlier studies because the time scale and the magnitude over which neuromuscular effort was modified were very different in these studies. For instance, adaptation to age-related changes would involve a gradual change in neuromuscular effort occurring over several years.^{10,12,13,15,16} Similarly, the change in the neural control of disaccommodation observed by Bharadwaj and Schor¹⁸ and the speeding of abnormally sluggish accommodation after orthoptic training^{19,20} occurred over a span of several weeks. In contrast, in our experiment, adaptive changes occurred in response to dramatic changes in neuromuscular effort that occurred over a very short period (e.g., 100% change in effort within a few hours in the increasing-step paradigm). It is therefore possible that the neural mechanisms underlying adaptation in our experiment could be different from the mechanisms that triggered adaptation in the earlier studies. Indeed, different neural mechanisms have been proposed for adaptive regulation of saccadic accuracy to errors after muscle paresis (long-term changes) and to errors induced

experimentally using a double-step paradigm (short-term changes).⁴⁴ Whatever the underlying adaptive mechanisms may be, our results indicate that the accommodative system possesses the capacity to change its dynamic neural control pattern for a given response amplitude and that this capacity may be used to compensate for any age- or environment-related biomechanical changes in the accommodative plant.

Similar to accommodation, the peak velocity and peak acceleration of vergence step responses also increase after double-step increase in disparity and the peak velocity decreases after double-step decrease in disparity.^{25,26} The dynamics of saccades also increase after double-step increase in target eccentricity and they reduce after double-step decrease in target eccentricity.^{27,28} Qualitative similarities in the adaptive characteristics of accommodative and vergence step responses are somewhat expected given their neural coupling⁴⁵ and the similarity in their neural control strategies.^{17,46} Adaptive changes in accommodation (Figs. 2, 4) and vergence^{25,26} are different from those of saccades in that, unlike accommodation and vergence, adaptive changes in saccade amplitude and dynamics occur in conjunction with each other.^{27,28} This difference perhaps stems from the ballistic neural control of saccades.⁴⁷ The dynamics of saccades is determined by a preprogrammed pulse innervation and its response amplitude is determined by integrating the pulse innervation to produce a step innervation.⁴⁷ Any change in the pulse innervation would therefore influence both the dynamics and the amplitude of saccades.⁴⁷ However, accommodation^{17,48} and vergence⁴⁶ step responses are only partially ballistic, with an initial open-loop pulse innervation controlling the response dynamics and an independent closed-loop step innervation that determines the response amplitude. Any change in response amplitude induced by changes in the characteristics of the pulse innervation would therefore be corrected by the adjusting the size of the step innervation in response to blur and disparity feedback.^{17,46}

CONCLUSIONS

The peak velocity and peak acceleration of accommodative step responses can be modified, at least in some subjects ranging from 18 to 34 years, in response to short-term changes in optically stimulated neuromuscular demands. There appears to be an adaptive bias toward increasing than decreasing the dynamics of accommodative step responses.

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