

Adaptive Changes in Dynamic Properties of Human Disparity-Induced Vergence

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PURPOSE. Vergence eye movements undergo adaptive recalibration in response to a training stimulus in which the initial disparity is changed just after vergence begins (the double-step paradigm). In the present study the changes in the dynamic properties of convergence, speed and acceleration, were examined by using this double-step paradigm, before and after adaptation.

METHODS. Four normal subjects participated. Three-dimensional visual stimuli were provided by a head-mounted display with two liquid crystal diode (LCD) panels. To induce adaptation, a double step of disparity was used: an initial step from distances of 2 to 1 m was followed by a second step to distances of 0.7 m ("increasing paradigm") or 1.4 m ("decreasing paradigm") after a constant period of 0.2 seconds. The dynamic properties of vergence were compared before and after 30 minutes of training with these paradigms.

RESULTS. Peak velocity of convergence became significantly greater (increasing paradigm) or smaller (decreasing paradigm) after 30 minutes' training. Changes in the dynamic properties of convergence were also obvious in phase-plane (velocity versus position) and main sequence (peak velocity versus amplitude) plots. Further analysis revealed that adaptive increases in vergence velocity were accomplished by an increase in the duration of the acceleration period, whereas adaptive decreases were induced by a decrease in the maximum value of acceleration.

CONCLUSIONS. The pattern of change in the dynamic characteristics of vergence after adaptation was similar to that of saccades and the initiation of pursuit eye movements, suggesting common neural mechanisms for adaptive changes in the open-loop control of eye movements. (*Invest Ophthalmol Vis Sci.* 2001;42:1479-1486)

The response of the vergence system to a disparity stimulus has been characterized as a closed-loop feedback control system in which motor performance is modified on-line on the

basis of visual information.¹ Recently, however, it has been suggested that the initial portion of the vergence response is controlled by a different mechanism, because it is open-loop—that is, not subject to immediate feedback control because of the inherent delay imposed by the time to process new visual information. Jones² suggested that the vergence response was under control of two different processes that mediate transient and sustained components. Semmlow et al.³ proposed a dual-mode theory, in which the dynamic properties of vergence eye movements are described by a two-component control system. The initial component is not controlled by immediate, continuous visual feedback. Rather, it is preprogrammed after being activated in response to an abrupt change in disparity produced by a rapidly moving target. The slow component is mediated by a visual feedback control system. It tracks slowly moving targets and corrects for errors that follow the initial vergence response. If the initial component cannot be under continuous visual control, then adaptive modification of the underlying premotor control processes, driven by some form of error information, might be expected.

This is just the case for the other ocular motor subsystems, such as saccades⁴ and the initial portion of smooth pursuit,⁵ in which visual feedback, because of obligatory, inherent delays in visual processing, is too slow to provide immediate corrective error information to modify the initial motor command. Consequently, there is a need for adaptive modification of saccades and the initial component of pursuit. Adaptation of saccade and pursuit accuracy takes place as a form of motor learning and depends on the dorsal cerebellar vermis (e.g., Takagi et al.^{6,7}) Adaptation of vergence, too, has been demonstrated.⁸⁻¹¹ Herein, we report further studies of vergence adaptation using a double-step stimulus, similar to that used to elicit saccade and pursuit adaptation. Preliminary aspects of this work have been previously reported in a single experimental subject.¹²

METHODS

Subjects

Four normal subjects (30-38 years old) participated. They had normal corrected vision, eye motility, and stereoacuity. Subjects 1, 2, 3, and 4 had interpupillary distances of 64, 59, 65, and 64 mm and phorias at a viewing distance of 5 m of -6, -4, +1, and -4 prism diopters, respectively (exodeviations are negative). The head was immobilized with a dental bite bar. Viewing was always binocular, and refractive error was corrected with lenses. Subjects were told to maintain a gaze on the visual target. Each subject gave informed consent before the experiments. The research followed the tenets of the Declaration of Helsinki (1964) and was approved by the human experimentation committee of the Niigata University School of Medicine.

Visual Stimulation

Disparity stimuli were presented on a head-mounted display with two liquid crystal display (LCD) panels (viewing angle 30° × 22°; Sony, Tokyo, Japan).¹³ The image to stimulate each eye was drawn in either an even or odd field of the image board (CT-9800B; Cybertec, Osaka,

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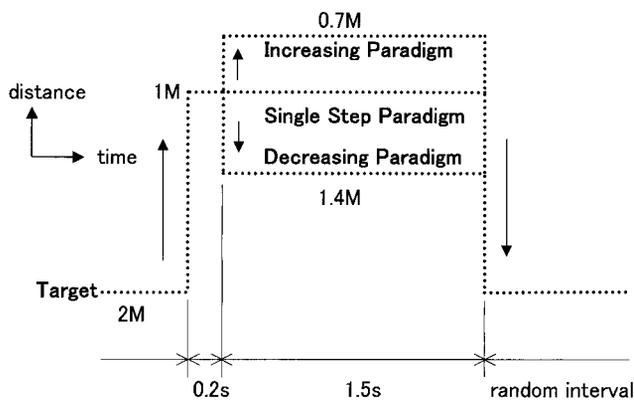


FIGURE 1. Schematic illustration of the paradigm using a double step of disparity. *Dashed line:* target movement in depth. First the target jumped from distances of 2 to 1 m, but after 0.2 seconds, to a distance of 0.7 m (in the increasing paradigm) or to 1.4 m distance (in the decreasing paradigm). In both cases the target stayed at its final position for 1.5 seconds. The intertrial interval was randomized.

Japan) with the aid of a personal computer. The visual target was a black cross ($0.63^\circ \times 1.2^\circ$), surrounded by a bright rectangle ($0.84^\circ \times 1.6^\circ$) and presented against a dark background.

Experimental Paradigm

A protocol was designed to provide repeated exposure to the training stimulus. An experimental run comprised three sessions: a preadaptation session, an adaptation session, and a postadaptation session. The preadaptation session (single-step paradigm) consisted of 21 sequential responses to a single step of disparity, in which the target jumped from 2 to 1 m, eliciting convergence. The adaptation session consisted of a double-step stimulus: an initial convergence step from distances of 2 to 1 m, followed by a second step to a distance of 0.7 m ("increasing paradigm") or 1.4 m ("decreasing paradigm"), after a constant period of 0.2 seconds (Fig. 1). This stimulus was designed to induce a large error in the initial open-loop vergence response by stepping the target backward or forward. For an interpupillary separation of 64 mm, a target distance of 2.0, 1.4, 1.0, and 0.7 m called for 1.8° , 2.6° , 3.7° , and 5.2° of vergence angle, respectively.

Throughout the training period, the time interval between trials was randomized between 1.5 and 3.5 seconds to eliminate predictive

responses, although the target always stayed in the first position for 0.2 seconds, and the second position for 1.5 seconds. Twelve subessions were presented, each consisting of 21 trials, with a brief interval of approximately 1 minute between each subession. The total testing period was approximately 30 minutes. The postadaptation session consisted of the same 21 single-step stimuli as were presented in the preadaptation session. The two types of training paradigms, increasing gain and decreasing gain, were tested on separate days.

Eye Movement Recording and Data Analysis

An infrared limbus tracker (Handaya, Osaka, Japan), which provides a resolution of approximately 0.1° , was used to monitor the horizontal position of both eyes. The sensors of the device were attached to a glass frame, which was fitted to the head-mounted device.¹⁴ Eye position was sampled at 500 Hz and stored on a computer for later off-line analysis. A calibration procedure was performed before and after the experiment, in which the subject was required to fix on targets at left 5° , center, and right 5° , to confirm that the calibration did not change during the experiment. Trials in which the subject blinked during the initiation of the vergence response were eliminated from further analysis ($<5\%$). The vergence angle was obtained by subtracting the position of the left eye from that of the right. The vergence angle was then filtered with a single-pole analog filter with a cutoff frequency of 15 Hz and then differentiated with a two-point difference algorithm to get vergence velocity. To calculate vergence latencies, a velocity criterion of 1.5 deg/sec was used. The correctness of the choice of the computer algorithm was verified for each individual trial by the experimenter.

RESULTS

Representative traces from the pre- and postadaptation sessions are shown in Figure 2. The vergence responses were markedly stereotyped during a subession, which enabled us to compare vergence dynamics using average traces. The latencies of vergence responses were consistent from trial to trial (~ 150 msec), which means that the second step of disparity, after the constant period of 0.2 seconds, occurred within the open-loop period of the vergence response. There was not a statistically significant change in latency either after adaptation or in the final vergence angle of the response (measured at 1 second). However, after the subject was trained with the increasing paradigm, the slope of the initial convergence re-

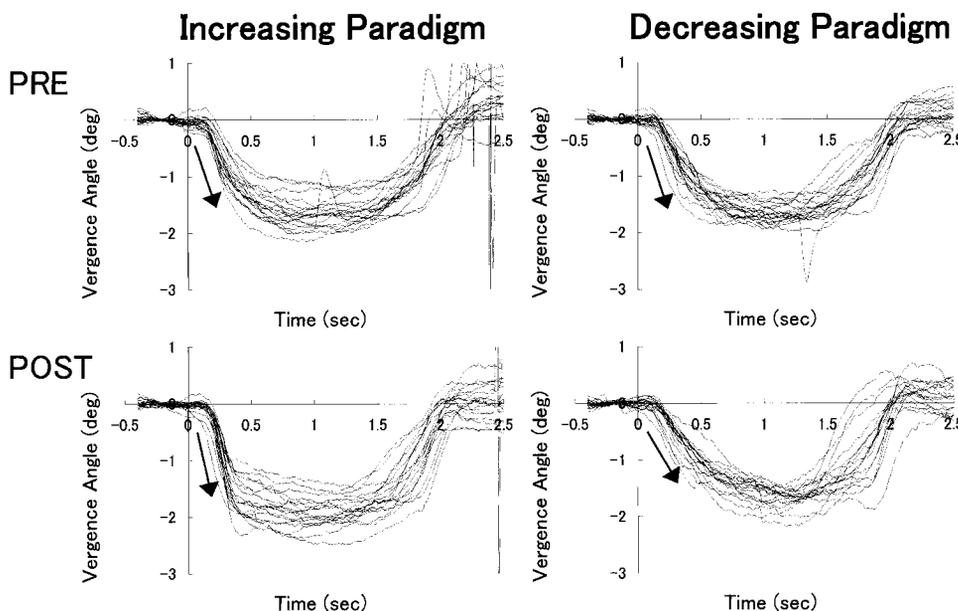


FIGURE 2. Representative traces from subject 2 to show the effect of training with the double-step paradigm. Pre, preadaptation session; post, postadaptation session. Twenty-one traces are aligned with reference to the onset of the step of disparity (time 0 indicates target onset). The y-axis indicates the vergence angle (downward deflection indicates convergence). The same disparity step (from 2 to 1 m) was presented to the subject. The slope of a line approximating the initial vergence response changed before and after training. In the increasing paradigm, the line was steeper and in the decreasing paradigm, the line was shallower (arrows). Reprinted in modified form, with permission from Elsevier Science, from Takagi M, Trillenberg P, Zee DS. Adaptive control of eye movements in humans: control of smooth pursuit, vergence and eye torsion. *Vision Res.* In press.

sponse, which reflects vergence velocity, became steeper. Similarly, after the subject was trained with the decreasing paradigm, the slope became shallower. Thus, the velocity during the initiation of vergence changed as dictated by the adaptive stimulus.

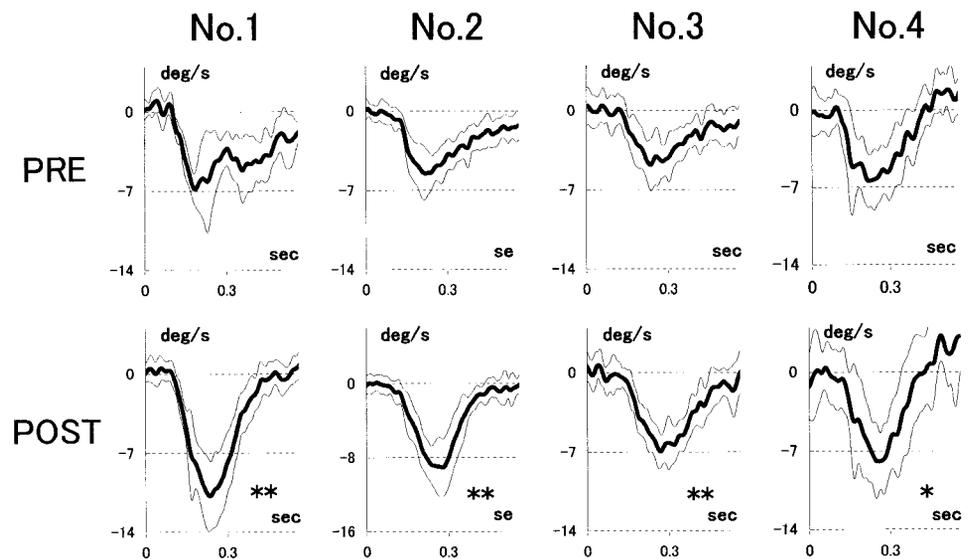
Figure 3 shows a comparison of the average of 21 velocity traces in the pre- and the postadaptation sessions. With the increasing paradigm (Fig. 3A), peak average values increased by 57%, 65%, 40%, and 20% in subjects 1, 2, 3, and 4, respectively. These changes were significant in all subjects, when the difference between peak velocities was tested with the Mann-Whitney rank sum test. With the decreasing paradigm (Fig. 3B), the peak average values decreased to 68%, 76%, 93%, and 58% in subjects 1, 2, 3, and 4, respectively. These changes were significant in subjects 1, 2, and 4.

In a further analysis of the dynamic properties of the response, we used phase-plane plots (eye position versus eye velocity). An example of an average trace from subject 2 is shown in the upper panel of Figure 4. Solid vertical arrows

indicate 150 msec after the onset of the vergence response and thus identify the open-loop portion. Curved dotted arrows indicate the direction of eye motion relative to time. Several observations were notable: First, the very initial portion of the response was unchanged; the pre- and postadaptation responses overlapped in the initial approximately 0.2° of movement. Secondly, in the increasing paradigm, peak velocity of convergence was increased and shifted to a later portion of the convergence response. Thirdly, also in the increasing paradigm, the peak velocity relative to the vergence amplitude reached at the end of the open-loop period (150 msec after the onset of eye movement) was much larger after adaptation.

To evaluate these last two points quantitatively, two further analyses were performed. First, pre- and postadaptation values for peak velocity and those for vergence amplitude at peak velocity were compared, by using the Mann-Whitney rank sum test (Fig. 4, middle and lower panels). In the increasing paradigm, peak velocity increased significantly in all cases, and the point at which peak velocity was reached was shifted to a later

A Increasing Adaptation



B Decreasing Adaptation

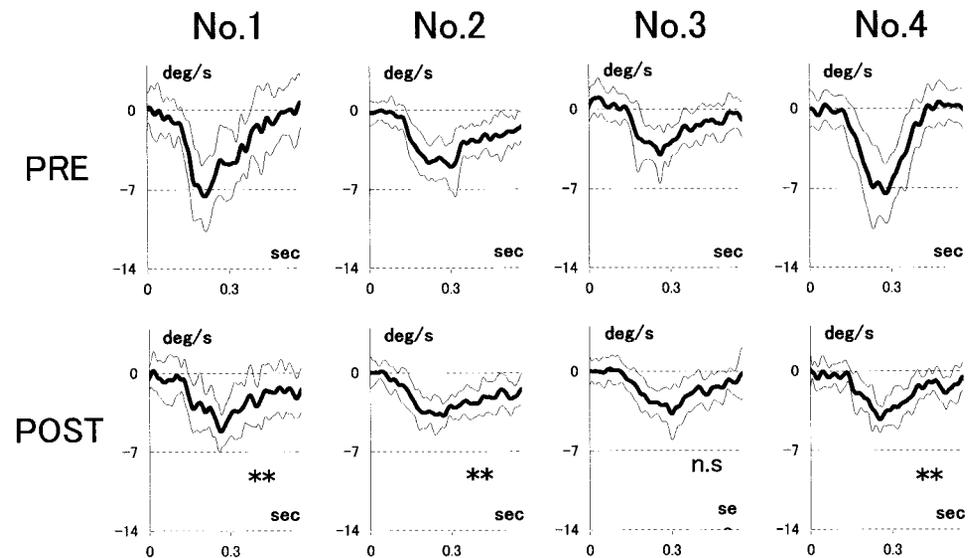


FIGURE 3. Comparison of velocity profiles between pre- and postadaptation responses for all four subjects: (A) increasing adaptation, (B) decreasing adaptation. *Thick line:* average velocity of 21 traces; *thin lines:* one SD. The x-axis indicates the time after the first target jump; the y-axis indicates the vergence velocity (downward deflection indicates convergence). After training, peak velocity increased (A) or decreased (B). The significance of differences of peak velocities between pre- and postadaptation were tested using the Mann-Whitney rank sum test. n.s.: $P > 0.05$; $*0.05 > P > 0.01$; $**P < 0.01$.

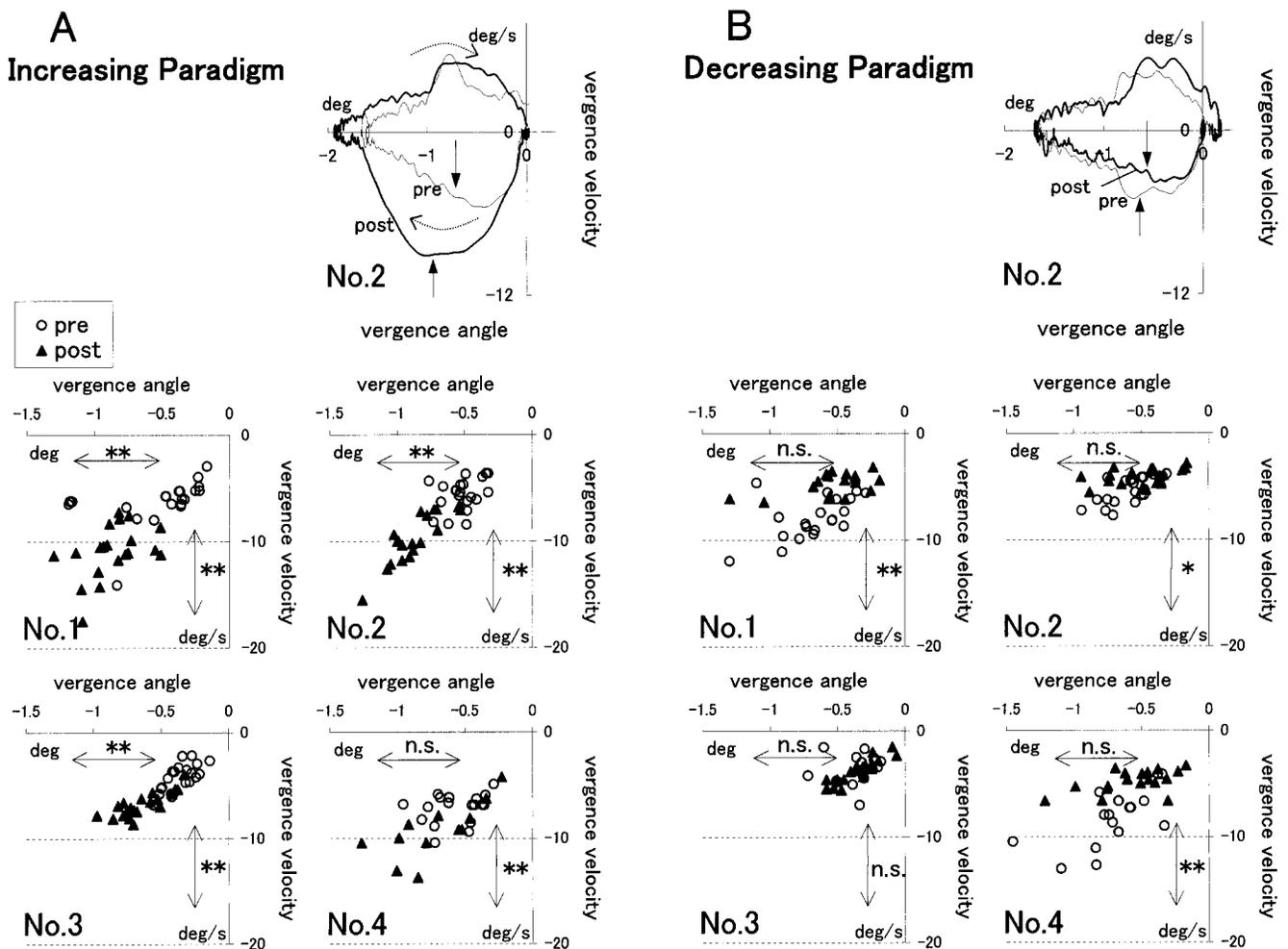


FIGURE 4. *Top:* Example of phase-plane trajectories (average traces) of pre- and postadaptive vergence responses for subject 2. (A) Increasing paradigm; (B) decreasing paradigm. The x-axis indicates the average vergence angle (negative deflection indicates convergence) and the y-axis the average vergence velocity. *Top, straight arrows:* end of the 150-msec open-loop period; *top left, curved arrows:* direction of eye motion relative to time, with the onset of the eye movements at the right axis. *Middle and bottom:* peak velocity for each trace plotted for all subjects, with peak velocity on the y-axis and vergence amplitude at peak velocity on the x-axis. (○) Preadaptation responses; (▲) postadaptation responses. The significance of differences for peak velocity and vergence amplitude was tested with the Mann-Whitney rank sum test and is indicated along the vertical and horizontal arrows, respectively. n.s.: $P > 0.05$; $0.05 > P > 0.01$, $**P < 0.01$.

portion of the convergence response in three of four subjects. With the decreasing paradigm, peak velocity decreased significantly in three subjects, but there was little change in the point in the trial when peak velocity was reached.

Secondly, a main sequence analysis was used, in which peak vergence velocity during the first 150 msec of the vergence movement (the open-loop period) was compared with the vergence amplitude 150 msec after the onset of vergence. This is shown for pre- and postadaptation values in Figure 5. A linear regression line, passing through the origin, was fitted to the data points using a least-squares technique, and in all cases the significance of the correlation was at $P < 0.0001$. A main sequence ratio¹⁵ was calculated as the peak velocity within 150 msec divided by the vergence amplitude at 150 msec, and then the difference between pre- and postadaptation values was tested with the Mann-Whitney rank sum test. Significant changes in the main sequence relationships were seen in three of four subjects for increasing adaptation (subjects 1, 2, and 3), but only in one subject (number 1) for decreasing adaptation. Thus, with the increasing paradigm in particular, the results suggest that vergence adaptation induced not only a change in the amplitude of response in the open-loop period to a given

disparity but also in the relationship of peak vergence velocity to a given vergence amplitude.

We also noted the slope of the initial vergence velocity response to assess changes in vergence acceleration. For the increasing paradigm (Fig. 3A), the initial slope of the velocity trace, which reflects the amplitude of acceleration, did not change, but the duration of the acceleration period, as reflected in the length of the slope, was longer after adaptation. In contrast, in the decreasing paradigm (Fig. 3B), the slope of the velocity trace decreased with training, indicating that the amplitude of acceleration decreased. Figure 6 shows the average acceleration traces from subject 2. Although the traces are noisy, the increase in the duration of acceleration with the increasing paradigm and the decrease in the amplitude of acceleration with the decreasing paradigm are seen clearly.

Figure 7A shows the progressive change in the velocity profile in subject 2 during a training session. At the beginning of the training period with the increasing paradigm, individual peaks were seen both at the first (1 m) and the second (0.7 m) target steps. The first peak increased to approximately 13 deg/sec by the third subsession and subsequently changed little, indicating that a large part of the adaptive change in peak

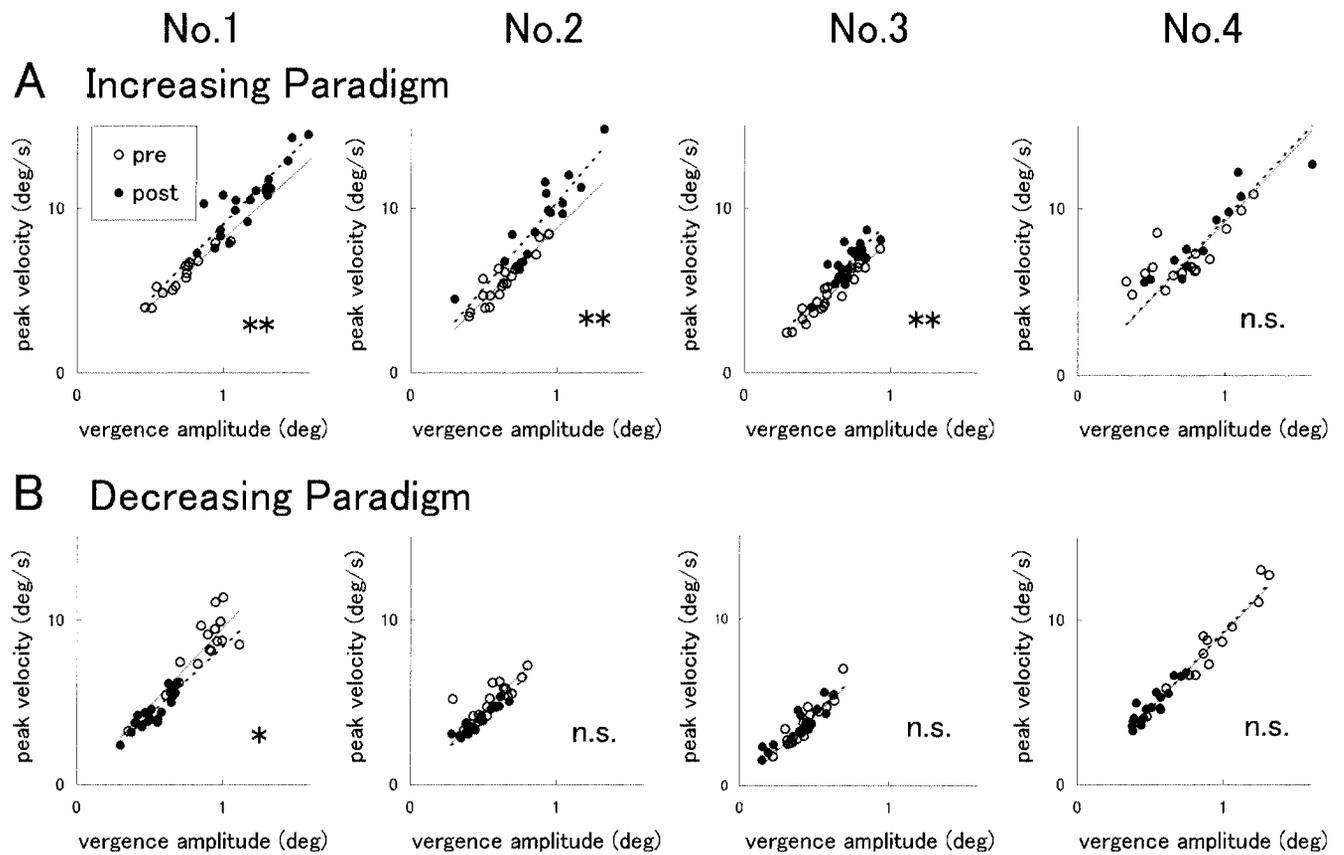


FIGURE 5. Main sequence analysis of pre- and postadaptive vergence response in the four subjects. (A) Increasing paradigm; (B) decreasing paradigm. The x-axis indicates the vergence amplitude 150 msec after vergence onset and the y-axis the maximum vergence velocity during the first 150 msec after vergence onset. (○) Preadaptation responses; (●) postadaptation responses. Linear regression lines, which pass through the origin, are also shown in each panel. *Solid line*: preadaptation response; *dashed line*: postadaptation response. A main sequence ratio was calculated as peak velocity within the first 150 msec of vergence response divided by the vergence amplitude, at 150 msec. Statistical differences were tested using the Mann-Whitney rank sum test. Statistical differences are given in each panel. n.s.: $P > 0.05$, * $0.05 > P > 0.01$, ** $P < 0.01$.

velocity was completed in the first 10 minutes of training. The second peak showed little change, but the two peaks gradually fused into one. Figure 7B shows the change in the velocity profile during decreasing training from the same subject. At the beginning, a double-peaked response, first convergence and then divergence, was seen. During training, the second divergence peak disappeared and the first convergence peak became smaller.

We can also see in these traces differences in the initial acceleration between the increasing and decreasing paradigms. With the increasing adaptation paradigm the initial slope of the vergence velocity trace did not change but the duration of acceleration (as reflected in the duration of the slope) increased after training. With the decreasing adaptation paradigm, the slope of the initial response became smaller.

We further analyzed the changes in initial acceleration by obtaining the value of vergence velocity at every 10 msec from the average trace of each subsession and calculating a correlation coefficient between the value of the vergence velocity in each epoch and the progress of adaptation training (1st to 12th subsessions). In Figure 8, the correlation coefficients are plotted for each time epoch of the convergence response. In general, during the open-loop period, the correlation coefficients with the decreasing paradigm were larger approximately 30 to 40 msec earlier than those with the increasing paradigm. In other words, for adaptation in the decreasing paradigm, the very early part of the vergence response showed a positive correlation, whereas for adaptation in the increasing paradigm, adaptation was better correlated with a later portion

of the response but still within the open-loop period. (Because subject 4 did not show a robust adaptation in the increasing paradigm, there was not a significant negative correlation in lower right panel.)

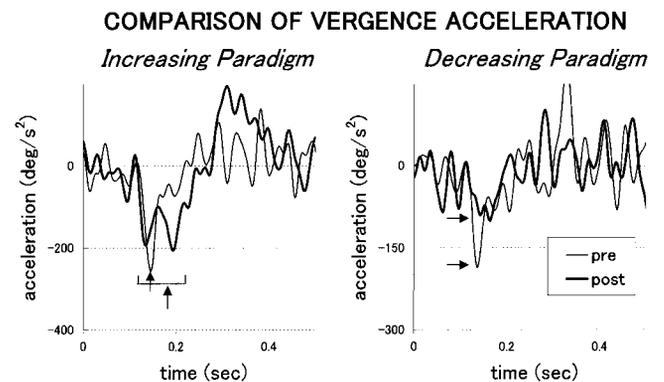


FIGURE 6. Change in average vergence acceleration traces with the increasing paradigm (left) and the decreasing paradigm (right) in subject 2. *Thin line*: preadaptation; *thick line*: postadaptation. Downward deflection indicates convergence. With the increasing paradigm, the duration of acceleration was extended as indicated by the vertical arrows; with the decreasing paradigm, the amplitude of acceleration was diminished as indicated by the horizontal arrows. Reprinted in modified form, with permission from Elsevier Science, from Takagi M, Trillenberg P, Zee DS. Adaptive control of eye movements in humans: control of smooth pursuit, vergence and eye torsion. *Vision Res.* In press.

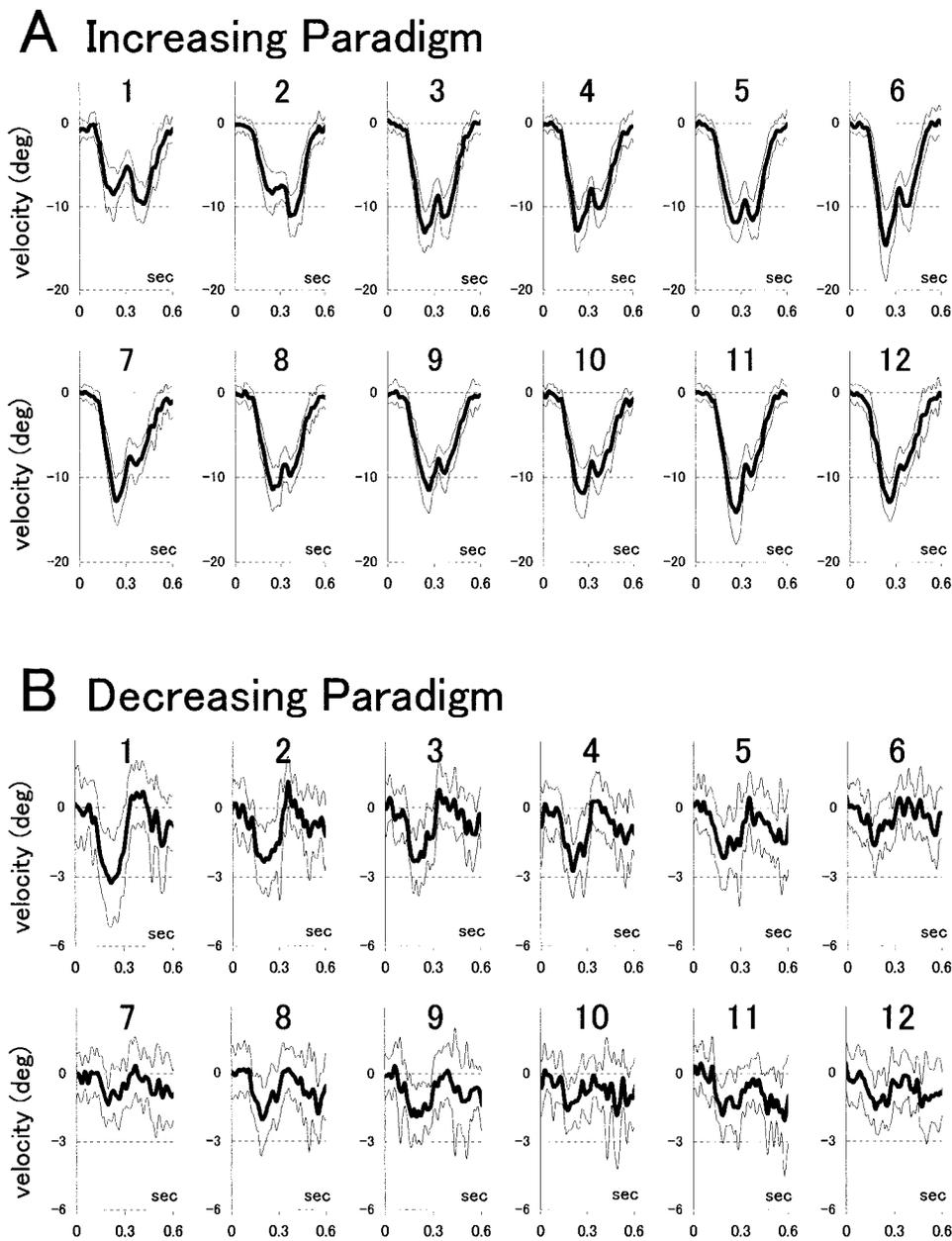


FIGURE 7. Change in the velocity profile during the adaptation session from subject 2: (A) increasing paradigm; (B) decreasing paradigm. Each panel shows average (*thick line*) and one SD (*thin line*) of 21 trials in each subsession. The x-axis indicates time after target jump; y-axis indicates vergence velocity (downward deflection indicates convergence). The *number* at the top of each panel indicates the subsession during the adaptation session. The double-peaked response gradually fused to one greater or smaller peak as adaptation progressed during the increasing or decreasing training paradigm, respectively.

This result is consistent with the idea that for increasing adaptation, the duration of acceleration becomes longer, but for decreasing adaptation the peak amplitude of acceleration becomes smaller. To exclude the possibility that these correlations were due to a change in vergence latency, we examined the relationship between latency and progression of training in a similar way and found no significant correlation.

DISCUSSION

The capability of the vergence system to undergo an adaptive modification of its initial response to a given change in disparity has been demonstrated previously by changing the disparity just after the eye has begun moving in response to the initial disparity⁸ or by using a step-ramp stimulus, in which case the disparity continues to increase after the initial step change in disparity.¹¹ We have replicated this capability for vergence adaptation in this study, also using the double-step stimulus. In our study, as previously reported in other studies of vergence

adaptation,^{8,10,11,14} adaptation was exceedingly rapid, with the major change requiring only approximately 100 trials, which took just 10 minutes of training. As also reported previously, the adaptive changes in the vergence response were relatively large compared with saccade and pursuit adaptation in similar types of training paradigms.^{4,16} Our study, however, added new qualitative and quantitative information about the adaptive response, which also allowed us to compare the mechanisms of vergence, saccade, and pursuit adaptation. In particular, we scrutinized the adapted responses by using a phase-plane analysis,¹⁷ a main sequence analysis,¹⁸ and an interval-by-interval correlation analysis.

The main sequence analysis allowed us to look for changes in the dynamic properties of the vergence response after adaptation by comparing pre- and postadaptation values for the peak vergence velocity within the open-loop period with a given-sized vergence amplitude at the end of the open-loop period. By confining the analysis to the first 150 msec of vergence tracking we could largely exclude effects of visual

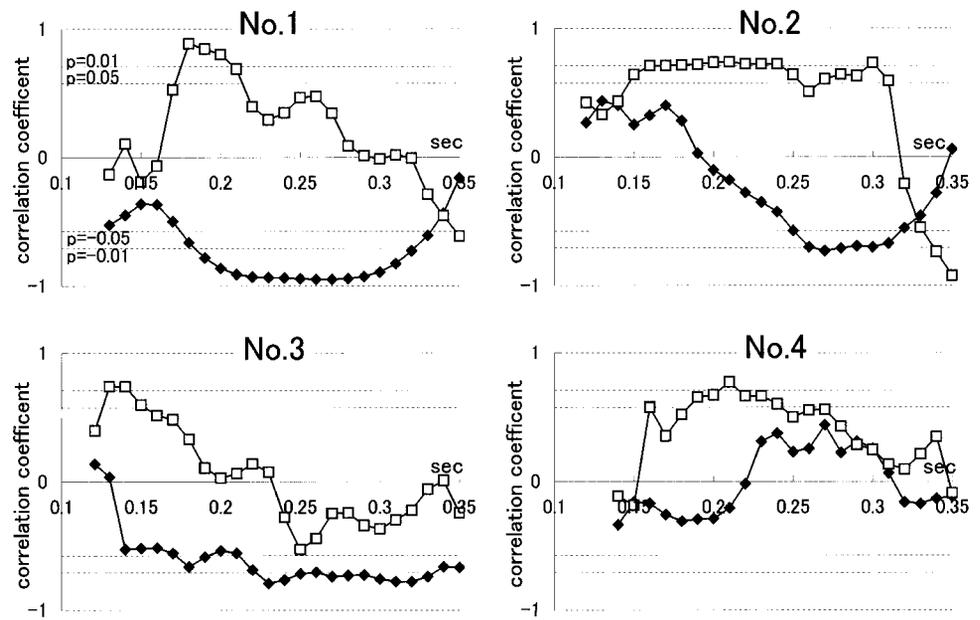


FIGURE 8. Correlation coefficients between average vergence velocity in every 0.01-second epoch and progression of training for all four subjects. The x-axis is the time segment after the first target jump, and the y-axis is the value of the correlation coefficient. (◆) Increasing paradigm; (□) decreasing paradigm. A positive correlation coefficient indicates a decrease in vergence velocity and a negative correlation coefficient an increase. *Dashed horizontal lines* (from top to bottom): $r = 1$, $r = 0.71$ ($P = 0.01$), $r = 0.58$ ($P = 0.05$), $r = -0.58$ ($P = -0.05$), $r = -0.71$ ($P = -0.01$), and $r = -1$.

feedback on the initial response. In the increasing paradigm we found significant changes in the main sequence for vergence eye movements in three of four cases, supporting the idea that adaptation to an increasing stimulus is accompanied by a change in the dynamic properties of the vergence response and not just a change in the mapping of the amplitude of the preprogrammed movement to the amplitude of a given disparity. On the contrary, with the decreasing paradigm, we found significant changes in the main sequence in only one of four subjects.

The phase-plane and correlation analyses confirmed several features of the adaptive response that could also be appreciated in the time plots. First, for the responses with the increasing paradigm, the point when peak velocity was reached occurred later in the trial. This finding is compatible with the idea that adaptation to a stimulus calling for an increased response is accomplished by an increase in the duration, not by the maximum value of eye acceleration. For the responses in the decreasing paradigm, there was little change in the point in the trial when peak velocity was reached. This finding is compatible with the idea that adaptation to a stimulus calling for a decreased response is accomplished, at least in part, by a decrease in the maximum value of eye acceleration. This interpretation was also supported by the results of the correlation analysis between the value of the vergence velocity in each epoch and the progress of adaptation training (Fig. 8). They showed that vergence eye velocity within an individual trial changed earlier in the decreasing than in the increasing paradigms.

Our present findings are in many ways analogous to those reported for adaptation of saccades and the open-loop portion of pursuit. For pursuit, adaptation in paradigms calling for an increased response is accomplished by an increase in the duration of the acceleration period, whereas adaptation in paradigms calling for a decreased response is largely accomplished by a decrease in the maximum value of eye acceleration in the open-loop period.⁷ Saccade peak velocity approaches a saturation for large-amplitude saccades, and, when adaptation to muscle weakness is required, increases in the size of larger saccades are probably accomplished by an increase in the duration, rather than by an increase in the maximum value of the saccade velocity command.^{19,20} In vergence (and presumably saccades and pursuit), the maximum value of eye acceleration during the open-loop period may be relatively

limited, necessitating an increase in the duration of the period during which peak eye acceleration is maintained when vergence innervation must be increased further.

The site of vergence adaptation in the central nervous system is not known. One mechanism may be a higher level cognitive adjustment in vergence innervation, because the visual stimulus was repetitive and called for the same change in amplitude. However, even when single- or double-step stimuli were presented so that the net vergence response should have been the same, motor modifications still appeared after double-step training, excluding a pure cognitive effect.⁸ Similarly, in our paradigm the time of occurrence of the initial target step was randomized, eliminating prediction in the initial vergence response. Changes in attention level or fatigue²¹ also could be factors. However, the same pattern of trial and rest periods in the different training paradigms caused significantly different modifications in the dynamic pattern of responses. Alternatively, adaptation may reflect changes in the lower-level motor machinery that generates premotor vergence commands and may be related to the function of the cerebellum.

Many data suggest that in the cases of saccades and the open-loop portion of pursuit, the posterior vermis of the cerebellum and the underlying fastigial oculomotor region are involved in mediating adaptive changes in similar double-step paradigms.^{6,7,20,22,23} In the posterior vermis there are cells sensitive to disparity,²⁴ and vergence-related activity is also found in the portions of the pons that relay information to the dorsal cerebellar vermis.²⁵ These findings suggest that the posterior vermis could also be involved in the adaptive control of the open-loop portion of vergence eye movements. Neurophysiological investigation is needed to help settle this question.

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