



Adaptation of torsional eye alignment in relation to smooth pursuit and saccades

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Abstract

The long-term fusion of vertical or horizontal disparities by vergence eye movements is known to evoke persistent changes in vertical and horizontal eye alignment. Adaptive changes in response to torsional disparities have not been well studied. Torsional eye position was measured binocularly with a video system before and after 90 min training periods in which subjects attempted to fuse cyclodisparities. Subjects trained with either a single cyclodisparity presented at a single vertical eye position or with cyclodisparities that varied smoothly from an incyclodisparity to an excyclodisparity as a function of either vertical or horizontal eye position. All five subjects showed persistent changes in binocular torsional eye alignment following both types of training. Incyclodisparities were more easily fused during training and the training aftereffect was greater in that direction. The training aftereffect was observed in relation to both saccades and smooth pursuit under both open-loop and closed-loop viewing conditions. During saccades, the dynamics of the cyclovergence training aftereffect more closely resembled the dynamics of cyclofusional movements than the dynamics of the saccades with which they were associated. © 2001 Published by Elsevier Science Ltd.

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1. Introduction

Extensive experimentation has shown that the oculomotor system has a remarkable capacity for recalibration in the face of changes resulting from development, disease and injury. Adaptation occurs in order to maintain the correct gain for tracking by smooth pursuit and the vestibulo-ocular reflex and for maintaining the accuracy of saccades. An important function of oculomotor adaptive mechanisms is to keep the lines of sight of the two eyes appropriately converged on visual targets of interest even in the absence of binocular feedback. There would be an obvious problem if the eyes drifted apart every time the view of one eye was temporarily occluded. Instead, the eyes are nearly always aligned correctly. For example, the system is able to keep the eyes aligned vertically to within a quarter of a degree when subjects fixate near targets in tertiary eye posi-

tions; a situation in which vertical misalignment might be expected to occur (Schor, Maxwell, & Stevenson, 1994). Adaptive processes can act very quickly to modify vertical misalignment of the eyes. Concomitant vertical disparities, i.e., vertical disparities that are approximately the same magnitude at all eye positions, can be significantly reduced within minutes (Maxwell & Schor, 1994; Graf, Maxwell, & Schor, submitted-a). Nonconcomitant vertical disparities, i.e., those that vary with eye position as would arise from a vertical rectus or vertical oblique muscle palsy, for example, can be reduced by half within an hour in normal subjects if the disparities are not too large (Maxwell & Schor, 1994). The resulting change in vertical alignment following 1 h of training with nonconcomitant disparities is relatively long lasting and decays with a time constant of 2 h on average if one eye is occluded following training to prevent normal binocular viewing (Graf et al., submitted-a).

There has been much less investigation concerning the plasticity of cyclovergence and torsional eye move-

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ments. Maxwell and Schor (1999) demonstrated that the torsion associated with head tilt about a nasal-occipital axis (ocular counterroll) can be adapted, at least in terms of cyclovergence. The plasticity in those experiments appeared to involve gain changes within otolith-ocular pathways. While the largest torsional movements made by humans are associated with ocular counterroll, torsion also varies systematically with horizontal and vertical eye position. In general, a specific torsional position is associated with each versional eye position regardless of how that position was reached (Donders' law). More specifically, the torsional position for a given versional eye position will be as though the eye reached that position by rotating about a single axis from primary position (Listing's law) and all eye rotation axes will lie in a single plane (Listing's plane; For a historical review see Henn, 1997). There are exceptions and provisions for each of these laws and the precise torsional position associated with a particular eye position (and the tilt and translation of Listing's plane) is affected by head pitch and roll (Haslwanter, Straumann, Hess, & Henn, 1992; Suzuki, Kase, Kato, & Fukushima, 1997; Bockisch & Haslwanter, 2001), vertical vergence (Mikhael, Nicolle, & Vilis, 1995; Straumann, & Müller, 1994) and by horizontal vergence (Mok, Ro, Cadera, Crawford, & Vilis, 1992; van Rijn & van den Berg, 1993).

The reason for Listing's Law is not known but most explanations cite either economy of movement or else stress the perceptual consequences (see Tweed, 1997 for a review). The two are not mutually exclusive and one might suppose that Listing's law reflects an efficient motor solution to different sensory challenges. One critical problem for the oculomotor system is maintaining the torsional alignment of the two eyes so that cyclodisparities do not become so large as to result in diplopia. One might expect, assuming that cyclovergence is similar to horizontal and vertical vergence in this regard, that the repetitive fusion of cyclodisparities would result in persistent changes in cyclovergence. In accordance with this expectation, Taylor, Roberts, and Zee (2000) found that when cyclovergence was sustained for 30 s, the return of cyclovergence to zero took longer or was less complete if the subjects were placed in darkness than if they were given a target with zero disparity to view.

The challenge to the oculomotor system is more complex than this and potential errors in torsional alignment may be created by changes in head tilt, horizontal vergence, and versional eye position due to orbital mechanics. It has been shown in previous experiments that the relationship between head tilt and cyclovergence may be modified by experience (Maxwell & Schor, 1999) as can the relationship between cyclovergence and horizontal vergence (Schor, Maxwell, & Graf, 2001). The present experiments examined the

capacity of the oculomotor system to modify cyclovergence in relation to horizontal and vertical eye position. Cyclovergence was measured in relation to smooth pursuit and to saccades and adaptation was evident for all subjects as an increase in the fusional range of cyclovergence movements when the disparity stimulus was present as well as in open-loop tests when there was no stimulus for cyclovergence.

2. Methods

2.1. Recording system

Eye movements were recorded with a video based system that measures eye movements in three dimensions (SensoMotoric Instruments, Germany). Horizontal and vertical positions are tracked by finding the center of the pupil in each video frame and torsional movements are tracked by comparing the position of features in the iris relative to a reference image. The SMI system is a real-time device based on the method described by Scherer, Teiwes, and Clarke (1991). The cameras, infrared-reflecting mirrors, and LEDs of the SMI system were remounted in a custom-made aluminum frame that allowed reproducible positioning of subjects relative to the camera system by use of a mouth-bite and head restraint apparatus. The system includes infrared reflecting mirrors which are located in front of each eye and the cameras are located temporally. The mirrors were adjusted precisely prior to the experiment, so that no change in torsion occurred for a Fick-gimballed, artificial eye when it was rotated into secondary and tertiary positions as should be the case since the SMI system represents eye position in Fick coordinates. Further details and examples of Listing's planes using the SMI system may be found in Schor, Maxwell, and Graf (2001).

The subjects' heads were pitched down slightly so that their interaural meatus, eyes, and the central fixation target were in the same earth-horizontal plane. Subjects fixated targets that were presented on a tangent screen (the center of which was 119 cm away) at five horizontal and five vertical positions over a range of $\pm 10^\circ$ in order to calibrate the vertical and horizontal eye position measurements. An image of each iris was taken as the subject binocularly fixated a distant target. A sample of gray levels was taken in an arc through a section of each of these images and one of these reference segments was saved for each of the two eyes. The SMI program performs a cross correlation between each incoming frame (60 Hz/eye) and the reference segment, and the shift between the two is taken as the measure of torsional rotation. Because torsion varies over time (van Rijn, van der Steen, & Collewijn, 1994) and because torsion cannot be set to

zero volitionally, we defined zero torsion as the mean torsional eye position taken while the subject binocularly fixated the center target for 5 s and all records for that session were adjusted appropriately.

No effort was made to record torsional eye movements at tertiary positions or to construct Listing's planes for the subjects in these experiments. For this reason, true primary position for each subject (the direction orthogonal to Listing's plane) was unknown and all eye measurements are presented relative to the definition of straight ahead and zero torsion given above. As a result, straight ahead as defined by the camera system and straight ahead as defined by each subject's true primary position may not coincide resulting in significant values of pre-training torsion at secondary eye positions (see Bruno & van den Berg, 1997a).

2.2. Training procedures

The training targets were composed of identical grid patterns for the right and left eyes except that one was red and the other was green (Fig. 1). Cyclodisparities were created by rotating the two patterns about their centers. Excyclodisparities were created by rotating the tops of the patterns away from each other and incyclodisparities were created by rotating the tops of the pattern toward each other. Because the images were projected onto a tangent screen and rotated about axes orthogonal to the screen and not the subject's line of sight, there was a slight asymmetry in the amplitude of

the cyclodisparities which was not readily perceptible and did not hinder fusion. The pattern consisted of a $40 \times 40^\circ$ grid with three concentric circles placed at the center so as to control horizontal and vertical vergence. In nonconcomitant training, the magnitude of the cyclodisparity varied linearly with vertical smooth pursuit in one set of experiments and in conjunction with horizontal pursuit in another set. Pursuit amplitude was $\pm 10^\circ$ and the cyclodisparities varied between peaks of $\pm 7^\circ$. The grids moved vertically or horizontally in a sinusoidal fashion except that at the peaks of the sinusoids the display paused for 5 s to allow the subjects to attempt to improve their cyclofusion.

Each subject completed the following four sessions of nonconcomitant (pursuit-related) adaptation: excyclodisparities in up gaze and incyclodisparities in down gaze (ExU-InD), excyclodisparities in down gaze and incyclodisparities in up gaze (ExD-InU), excyclodisparities to the right and incyclodisparities to the left (ExR-InL), excyclodisparities to the left and incyclodisparities to the right (ExL-InL). The ExU-InD condition is illustrated in Fig. 1. Subjects were instructed to maintain their gaze in the center of the grid pattern during training. Subjects pursued the center of the grid pattern as it moved up and down or left and right and tried to maintain fusion of the targets.

In preliminary experiments, subjects reported that incyclodisparities were more easily fused than excyclodisparities. In addition, experiments in vertical phoria adaptation have shown that training with a single disparity given at a single eye position results in a spread of the training aftereffect to untrained eye positions. To test whether incyclodisparities elicit greater cyclovergence movements than excyclodisparities and to test whether the adaptation aftereffect spreads to untrained eye positions, each subject completed four concomitant training sessions where a single cyclodisparity, either a 7° excyclodisparity or a 7° incyclodisparity, was presented at either up 10° or down 10° . The subjects attempted to fuse the single cyclodisparity at the single vertical eye position for 90 min.

Our primary interest in recording torsion during saccades was to examine the dynamics of the cyclovergence responses before and after adaptation in order to determine whether the adapted responses had saccade-like dynamics or dynamics that might indicate the presence of a separate cyclovergence mechanism. However, since the training was in relation to smooth pursuit and not saccades it was possible that the smoothly changing nature of the training stimulus helped to determine the dynamics of the open-loop cyclovergence responses during saccadic eye movements. For this reason, we compared the time courses of the saccade-related cyclovergence movements in this study with data collected during a different study in which subjects

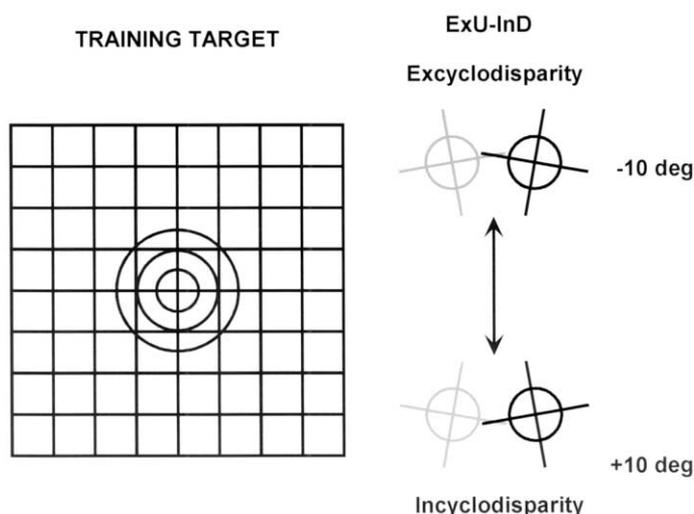


Fig. 1. Left: Training targets were $40 \times 40^\circ$ grids composed of red lines for the right eye and green lines for the left. Right: Schematic of the ExU-InD pursuit-related-training paradigm. The cyclodisparities varied smoothly from a 7° excyclodisparity at up 10° to a 7° incyclodisparity at down 10° . The right eye's target (dark target) and left eye's target (light target) were separated by 6 cm so that horizontal vergence was not stimulated. Figure not drawn to scale and ExU-InD training targets are simplified for clarity.

adapted their cyclovergence responses in relation to vertical saccades instead of pursuit movements (Schor et al., 2001). The purpose of that study was to examine the possible effect of environmental factors on the development of horizontal vergence related tilts of Listing's plane. Toward that end, subjects trained with 5° step changes in cyclodisparity that were in the opposite direction at two different distances. For example, at a simulated far distance (zero horizontal disparity) the subjects trained to an ExU-InD stimulus while concurrently training to an ExD-InU at a simulated near distance requiring a horizontal vergence of 10°. The saccades recorded at the far distance were reanalyzed using the same methods as were used in the present study so as to facilitate a direct comparison.

2.3. Testing procedures

Three-dimensional eye position was recorded before and after the 90 min training period while subjects pursued a slowly moving target (1°/s) or a target that jumped between two locations separated by 20°. The targets for the right and left eyes were identical 3.0° circles with center spots except that the target for the right eye was red and the one for the left eye was green. The circles were separated horizontally by 6 cm (the average interpupillary distance) so that there was no appreciable horizontal vergence requirement. A red filter was placed in front of the right eye and a green one before the left so that each eye saw only one target. The room was dark except for the two circles. Only the red target was visible to the right eye but the rectangular area of the projected background was faintly discernible in the left eye and might conceivably have inhibited torsional movements in that eye if a relative change between the training pattern and the border were evident. To avoid this, a round aperture was placed in front of the left eye so as to occlude the edges of the projected area. The circular targets could be fused in the horizontal and vertical dimensions but there was no disparity stimulus for torsional fusion (cyclofusion). Cyclovergence was, therefore, open loop during these measurements while horizontal and vertical eye position were closed loop. Subjects were also tested in closed-loop cyclovergence trials in which eye movements were recorded while the subjects binocularly viewed the training stimulus pattern.

Three tests were performed before and after each nonconcomitant training session, namely, smooth pursuit with the open-loop-cyclovergence targets, saccades with the open-loop targets, and smooth pursuit with the closed-loop targets. The saccade targets and the smooth pursuit end points were separated by 20° along the primary vertical or horizontal meridians. Two subjects were also tested following 3 h of training in the ExUp-InD condition and were tested while fixating the center

of the training stimulus as it stepped between two vertical positions (saccades with closed-loop cyclovergence).

Before and after concomitant training sessions, subjects were tested with smooth pursuit using the open-loop target and in closed-loop cyclovergence where they binocularly viewed the training target at the single eye position at which they trained.

2.4. Time-course measurements

After the initial data analysis was completed we observed that the change in cyclovergence following training was usually greater for closed-loop than for open-loop measurements, that is, the closed-loop post-training response was greater than the linear addition of the closed-loop pre-training response and the training aftereffect as measured with the open-loop target. This increased cyclofusional response might have indicated the presence of an additional adaptive mechanism specific to the closed-loop viewing condition. However, the open-loop measurement was always made several minutes later than the closed-loop measurement so it is possible that the training aftereffect had simply decayed over that period of time. In addition, the position profiles of the open-loop and closed-loop target movements were different in that the open-loop target described a triangle wave whereas the closed-loop target paused for 5 s at each extreme position. In order to address these concerns, the two subjects who were still available (CS and JM) were retrained on the ExU-InD and ExD-InU paradigms and tested during the training period at 20 min intervals. The open and closed-loop targets were matched for speed and both paused for 5 s at $\pm 10^\circ$. The open-loop measurements were made within 30 s of the closed-loop measurements. The open-loop response was also measured every 5 min for 20 min following training in order to measure the decay of the aftereffect. The subject kept one eye occluded between measurements. These time-course trials would establish if the acquisition phase resembled what is expected for parametric adjustments, namely, a slow increase in the aftereffect over time. Moreover, the open-loop measurements following training would give an indication of the persistence of the training aftereffect.

2.5. Subjects

Two of the five subjects needed corrective lenses in order to see the targets clearly. Large (7.5 cm diameter) minus lenses were placed immediately in front of the red and green filters approximately 4 cm in front of the subjects' eyes. The target displays were slightly increased in size in order to compensate for the minification caused by the lenses. The three authors and two

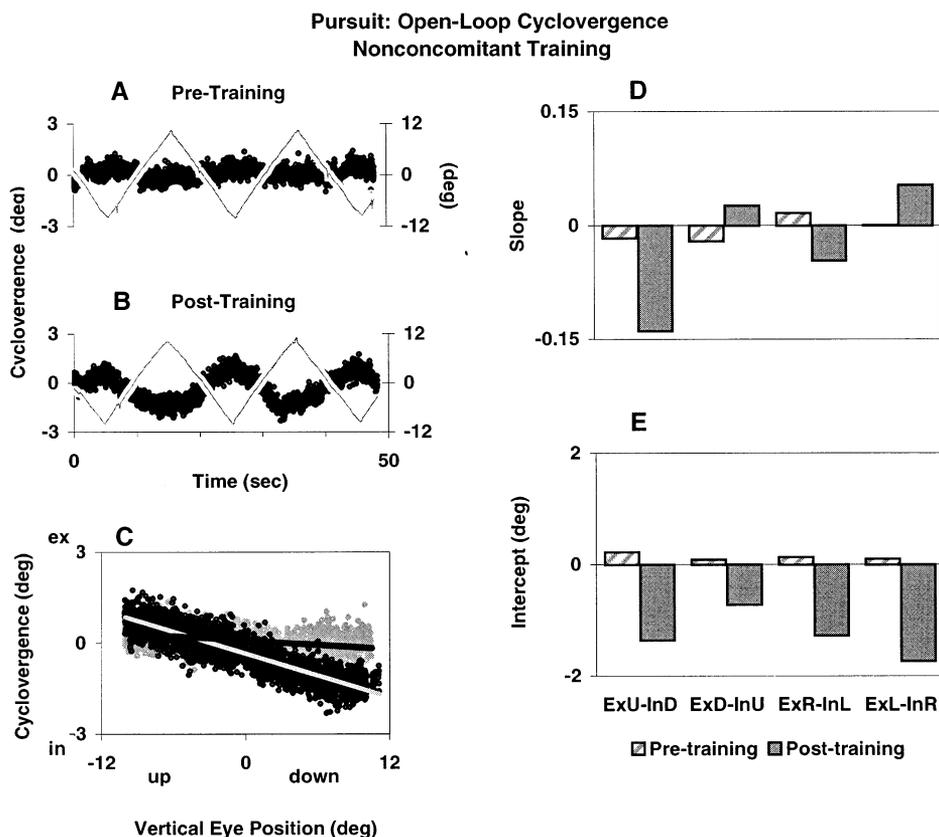


Fig. 2. Open-loop cyclovergence in relation to smooth pursuit as a function of time before (A) and after (B) nonconcomitant training (ExU-InD, subject EG). C: Cyclovergence as a function of vertical eye position for data shown in A & B. Solid lines were fit by linear regression for pre-training (light symbols and dark lines) and post-training (dark symbols with light lines). The slopes and intercepts of linear regressions for all subjects were averaged together and are presented in D (slopes) and E (intercepts). Down, left, and excyclovergence are signed positive.

naïve subjects served as subjects and all signed written consent forms.

2.6. Data analysis

Horizontal, vertical, and torsional eye positions were monitored in real time to verify the quality of the recording and then saved to hard disk for later analysis. Cyclovergence was obtained by subtracting left eye torsion from right eye torsion. While the SMI system measures each eye position at 60 Hz, the images of the right and left eyes are taken essentially simultaneously. Measurements are presented in Fick coordinates using the right-hand rule where down and left are positive in sign as are intorsion for the left eye, extorsion for the right eye, and excyclovergence. The SMI program calculates a quality index based on a ratio between the autocorrelation of the reference image and the cross-correlation of the reference image with each new image segment. The quality index is associated with each frame and saved in the data file. Frames with low quality index values indicate that eye position was not tracked reliably and were excluded from analysis.

3. Results

3.1. Nonconcomitant adaptation

3.1.1. Smooth pursuit with open-loop cyclovergence

All subjects showed evidence of adaptation in most of the nonconcomitant paradigms and the effects of training were seen in both open-loop and closed-loop responses. The open-loop cyclovergence responses were tested using red and green circles as described in Section 2 so that there was a stimulus for horizontal and vertical fusion but not for cyclofusion. An example of the effect of training on open-loop cyclovergence (RE-LE) during smooth pursuit is shown in Fig. 2A–C for one of the subjects (EG). Pre-training and post-training open-loop cyclovergence measurements are plotted as a function of time in 2A and 2B and as a function of vertical eye position in 2C. A linear regression was performed on cyclovergence as a function of vertical eye position and the slopes and intercepts of these fits were used to quantify adaptation for each subject in each condition. For subject EG in the ExU-InD condition illustrated in Fig. 2, there was little vertical eye position related cyclovergence before training (slope =

–0.024, intercept = 0.08) but following training the cyclovergence changed with vertical eye position in a way that was consistent with the training stimulus (slope = –0.12, intercept = –0.35). The difference in the post-training and pre-training slopes is –0.096 which reflects the position-related cyclovergence required by the stimulus. The difference in the intercepts of the regression lines is –0.43 meaning that there was an overall shift toward an incyclodeviation of the eyes. The gain of the training response, i.e. the slope of the aftereffect divided by the slope required by the stimulus is 0.14, or, 14% of the stimulus demand.

A similar regression analysis was performed for each of the five subjects in each of the four stimulus conditions (ExU-InD, ExD-InU, ExR-InL, ExL-InR). The average changes in the slopes and intercepts for the five subjects taken as a group are illustrated in Fig. 2D and E for each condition. As Fig. 2E illustrates, there was an overall incyclodeviation of the eyes following training regardless of the training paradigm. The mean change in intercept (post–pre) ranged from –0.81 to –1.83° for the four conditions. The sole exception to this generalization was subject CS who had an intercept change of 0.5° in the excyclovergence direction in the ExD-InU condition. These objective measurements co-

incide with the subjective observation of each of the subjects (including CS) that it was much more difficult to fuse excyclodisparities than incyclodisparities regardless of where in the field the excyclodisparities were presented. Overall, subjects had the largest training aftereffect, as evidenced by the magnitude of the slope, with excyclodisparities in the upper field and incyclodisparities in the lower. This was true for all subjects except for GH who had the largest slope in the ExL-InR condition. The average slope for the ExU-InD condition was –0.12° cyclovergence/deg vertical eye position meaning that the slope of the aftereffect was 17% of the required slope. The slopes of the other three paradigms were somewhat less and averaged 7% (ExD-InU), 9% (ExR-InL), and 8% (ExL-InR) of the slope required by the stimulus.

3.2. Smooth pursuit with closed-loop cyclovergence

Subjects were tested before and after the 90 min training period while viewing the training stimulus as it smoothly moved up and down (ExU-InD, ExD-InU) or left and right (ExR-InL, ExL-InR). Fig. 3A–C show an example of a closed-loop pursuit trial for the same subject and adaptation session shown in Fig. 2. A linear

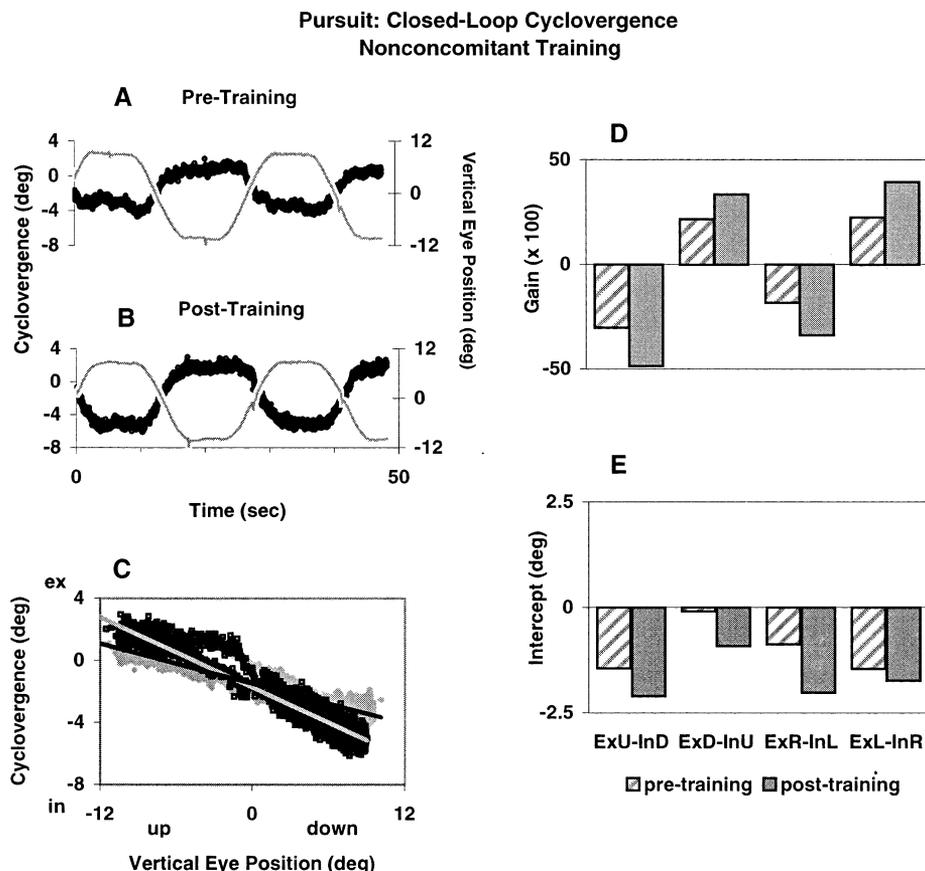


Fig. 3. Closed-loop cyclovergence in relation to smooth pursuit as a function of time before (A) and after (B) nonconcomitant training (ExU-InD, subject EG). C: Cyclovergence as a function of vertical eye position. Solid lines were fit by linear regression as in Fig. 2. The average slopes and intercepts are presented in D and E. Gains equal the slope of the regression lines (as in 3C) divided by the stimulus slope (0.7).

regression of cyclovergence on vertical eye position gives a slope of -0.21 for this subject's data before training and a slope of -0.38 after training meaning that the subject's closed-loop cyclovergence changed with vertical eye position by 30% of the stimulus demand before training and by 54% of the demand after training. This is similar to the mean cyclovergence responses of the five subjects taken as a group for this training paradigm: 32% before training and 48% after training. Fig. 3D and E show the mean eye-position-related gains and intercepts for the five subjects taken as a group for the four nonconcomitant training conditions. As with the open-loop response, the greatest response after training was observed when excyclo disparities were in the upper field and incyclo disparities were in the lower (ExU-InD). The mean gains in Fig. 3D are given as a percentage of the stimulus requirement (measured change in slope/ slope required by stimulus) and given the same sign as the slope to illustrate the direction of change.

Pre-training, subjects had larger incyclovergence movements than excyclovergence movements as can be seen in the negative intercept values in Fig. 3E. The only individual exceptions were GH and MH in the ExD-InU condition and GH in the ExR-InL condition. Post-training, the magnitude of the incyclovergence bias was even greater in 18 of the 20 training sessions. These changes in slopes and intercepts of closed-loop cyclovergence indicate that one effect of training was to increase the range of cyclofusion for each subject especially in the incyclovergence direction.

3.3. Saccades with open-loop cyclovergence

Torsion was measured binocularly following the pursuit-related training as the subjects fixated the center of the open-loop target as it jumped 20° vertically or horizontally depending on the training condition. The linear regression analysis used for the smooth pursuit data was not appropriate for analyzing cyclovergence in relation to saccades since the dynamics of the cyclovergence response did not follow vertical eye position very closely for some subjects, that is, the response was not linear. The primary interest in recording torsion during saccades was to examine the dynamics of the adapted cyclovergence responses. Toward that end, and to illustrate the range of dynamics, the record from the session for which each subject had the largest training aftereffect as determined from the smooth pursuit analysis is presented in Fig. 4. This was the ExU-InD condition for all subjects but GH who showed the largest effect in the ExL-InR condition. The traces in Fig. 4 were obtained by averaging together four complete cycles of saccades (e.g. up-down-up). The data were averaged by aligning the first half of the trial with the beginning of the downward (or rightward) saccade and the second

half of the trial with the beginning of the upward (or leftward) saccade. The two segments were then combined into one record and 12 s of those records are shown in the left column of Fig. 4.

The presence of a small eye-position-related, open-loop cyclovergence for subjects EG and JM before training indicates that the true primary positions for these subjects (the position orthogonal to Listing's plane) were not aligned with the optical axis of the camera system. It also means that the peak to peak sizes of the retinal cyclodisparities used for training were slightly less than the 14° specified by the projected image. The largest pre-training cyclovergence was observed for subject JM (approximately a 2° difference between 10° up and 10° down). The pre-training and post-training cyclovergence movements for these two subjects had relatively fast components that coincided with the saccades. The other three subjects had essentially no eye position related differences in their open-loop cyclovergence before training and a quantitative analysis is not required to see that the cyclovergence movements did not follow the time courses of the vertical saccades: The post-training cyclovergence responses did not attain a maximum amplitude until 1 s (GH), 2 s (CS), or 5 s (MH) after the beginning of the vertical eye movement.

It was possible that the smoothly changing nature of the training stimulus helped to determine the dynamics of the open-loop cyclovergence response even for saccadic eye movements. For this reason, we compared the time courses of the saccade-related cyclovergence movements in this study to those obtained in a separate study in which subjects adapted their cyclovergence responses in relation to vertical saccades instead of pursuit movements (Section 2). The right column in Fig. 4 shows the average open-loop cyclovergence responses for the four subjects who participated in that study as they made saccades between the two far target positions; the same distance used in the present experiment. There is no obvious difference in the dynamics for most of the subjects and the time courses are remarkably similar for most of the subjects in the two conditions.

To quantify the time courses for the open-loop data presented in Fig. 4, the average pre-training trace was subtracted from the average post-training trace to obtain a difference trace that represented the effect of training. In most cases, the difference trace was well fit by an exponential function. Exponentials were fit to the difference trace for each subject (using IGOR PRO, WAVEMETRICS) for each condition and an example of this procedure is shown in Fig. 5 for subject EG where the top panel shows the average pre-training and post-training data and the center panel shows the difference trace. The time constants for individual subjects and conditions are given in Table 1. The difference traces

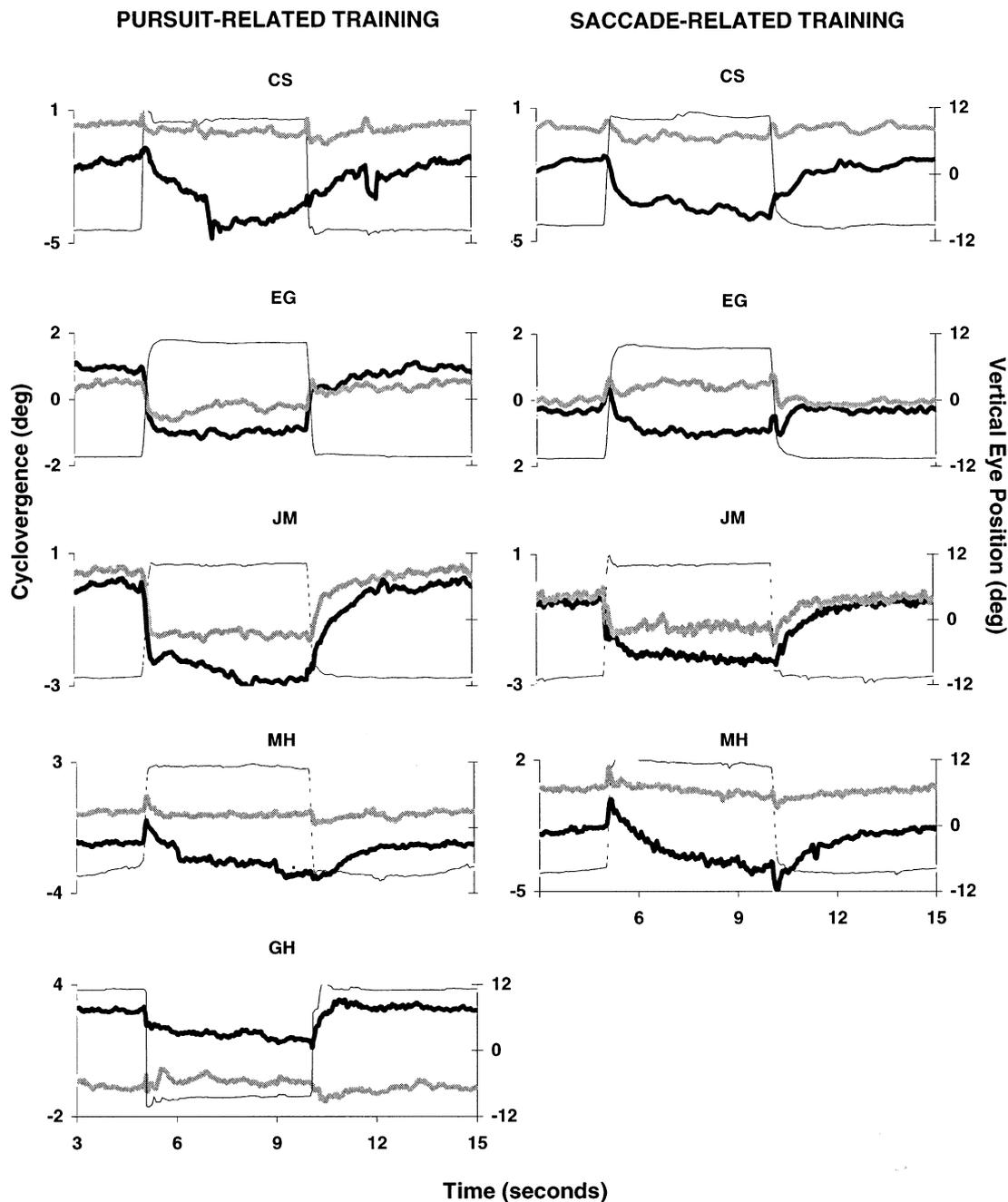


Fig. 4. Open-loop cyclovergence for individual subjects in relation to 20° vertical saccades (thin lines) following pursuit-related (left column) and saccade-related (right column) training. Each trace is the average of four cycles. See text for averaging technique. Light traces: Pre-training. Dark-traces: Post-training.

for the four subjects who participated in both studies were averaged together and fit with exponential functions (bottom panel Fig. 5). The time constants for these averages appear in Table 1 and at the bottom-right of Fig. 5 alongside the corresponding exponential. The mean time constants for the four subjects were quite similar for training in relation to pursuit movements (gray lines) and training to saccades (black lines). The average time constants for cyclovergence movements from incyclovergence toward excyclovergence are 0.8 s and 0.7 s for the pursuit-related and saccade-re-

lated training paradigms, respectively, and 1.8 s and 0.8 s for the respective excyclovergence to incyclovergence movements. The average training-related change in cyclovergence, therefore, had a time constant of 1.0 s, that is, 63% of the change in cyclovergence occurred within 1 s of the beginning of the saccade. While this comparison does not rigorously prove that the dynamics are the same for pursuit-related and saccade-related adaptation it suggests that the dynamics seen in the present experiment were not due to the smoothly changing nature of the training stimulus. The dynamics

of the cyclovergence movements in both cases were slower than the saccades that elicited them.

3.4. Saccades with closed-loop cyclovergence

The five subjects were not routinely tested with a closed-loop stimulus during saccades but two subjects were tested with closed-loop cyclovergence in additional sessions in which ExU-InD training lasted for 3 h. Following training, both subjects were able to almost completely fuse the 7.0° disparities when viewing the training target binocularly. Fig. 6 shows the average response of each subject to 20° vertical saccades. Before training, EG's cyclovergence varied a total of 3.8° from the upper target position to the lower which is about 27% of the total cyclodisparity requirement of 14°. After training, the cyclovergence change increased to 6.4° or 46% of the stimulus demand. Subject JM had a total change in cyclovergence before training of 5.4° (38% of the stimulus) and after training it was 7.2° (51%). The pre-training and post-training traces (upper panels of Fig. 6) represent the dynamics of closed-loop cyclofusion and were fit with exponential functions. The time constants of these fits are shown on Fig. 6 (pre and post). A difference trace (pre-training and post-training) was calculated for the closed-loop data in the same manner as that for the open-loop data described earlier. Exponential functions were fit to the difference traces and the time constants are displayed on the graphs in the lower half of Fig. 6 as the closed-loop difference trace time constant (CLD). Time constants were also obtained from exponential fits to open-loop cyclovergence difference traces (not shown) made during saccades following the 3 h training period and those time constants are presented in Fig. 6 as the open-loop-difference-trace time constant (OLD). The time constants for the difference traces were similar to those obtained for pre-training and post-training traces in the closed-loop condition and these were similar to the time constants obtained for the difference traces in the open-loop condition. In all cases the time constants were much longer than would be expected if the dynamics of the cyclovergence movements were directly linked to the dynamics of the saccades. All of the cyclovergence movements measured, therefore, had approximately the same dynamics regardless of viewing condition (open or closed loop) and the time courses of these cyclovergence movements were not saccade-like. The only exceptions were the pre-training open-loop cyclovergence measurements observed in subjects EG and JM whose saccades were made in tertiary positions relative to their true primary positions.

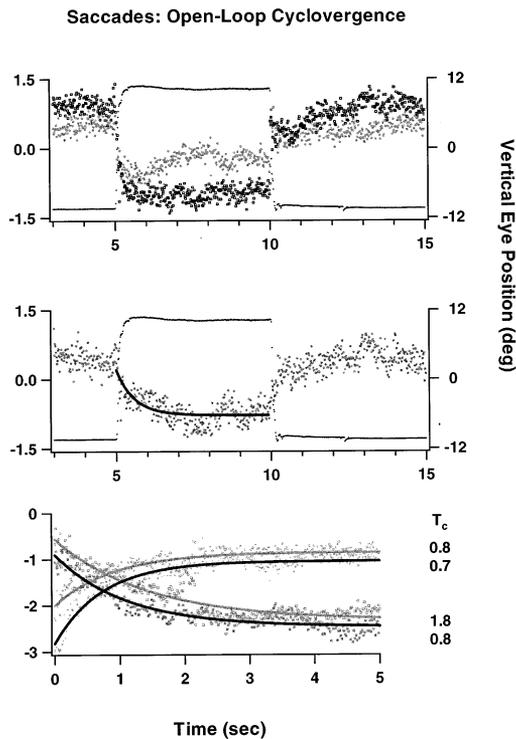


Fig. 5. Upper panel: Pre-training (light circles) and post-training (dark squares) cyclovergence as a function of time (ExU-InD paradigm, subject EG). Each trace is the average of four cycles. Broken line: Vertical eye position. Middle panel: Difference trace obtained by subtracting the pre-training from the post-training data and fit with an exponential (solid line). Bottom panel: Difference traces for four subjects averaged together and fit with exponentials. Light lines: Pursuit-related training. Dark lines: Saccade-related training. Tc: The time constants of the exponentials shown to the left.

Table 1
Time constants of exponentials fit to the difference traces (pre-training–post-training) of the saccade data shown in Fig. 4 for four subjects

Subject	Time Constants (post-training–pre-training)			
	Pursuit-related		Saccade-related	
	Ex → In	In → Ex	Ex → In	In → Ex
CS	1.1	0.4	0.5	1.1
EG	0.6	1.0	0.6	0.3
JM	2.6	0.9	0.7	1.3
MH	2.8	1.0	1.3	1.2
AVG	1.8	0.8	0.8	0.7

Ex → In: Excyclovergence to incyclovergence movements. In → Ex: Incyclovergence to excyclovergence movements. The data of all four subjects were averaged together and then fit with exponentials to obtain the average time constant (AVG) for each paradigm.

3.5. Concomitant adaptation

3.5.1. Smooth pursuit with open-loop cyclovergence

All of the subjects reported that it was easier to fuse incyclodisparities than excyclodisparities and the results of the nonconcomitant experiments seemed to bear this

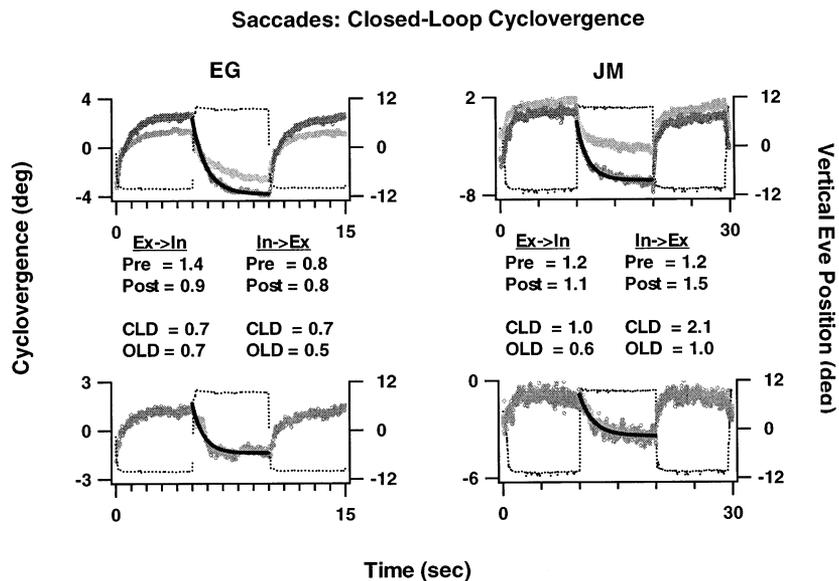


Fig. 6. Upper panel: Closed-loop cyclovergence in relation to vertical 20° saccades (dotted lines) for two subjects before (light symbols) and after (dark symbols) 3 h of training. Each trace is the average of four cycles. Lower panel: Difference trace obtained by subtracting pre-training from post-training data. Pre & Post: pre-training and post-training time constants from exponential fits (solid black lines). OLD: Time constants from open-loop difference trace derived by subtracting pre-training from post-training averages (data not shown). CLD: Time constants from closed-loop difference trace derived by subtracting pre-training from post-training averages.

out in that most subjects showed a bias in the incyclovergence direction. It is possible that there is an inherent eye position related bias in cyclovergence. In order to test this more directly, the fusional ranges and the ability to modify torsional eye alignment for each of the five subjects was examined before and after they trained with a single disparity that was presented at a single vertical position (up or down 10°) for 90 min. The results from these experiments would also demonstrate whether or not the training aftereffect was specific to the eye position at which training was received or spread to non-trained eye positions.

All subjects showed significant training aftereffects for both excyclodisparities and incyclodisparities whether the training was received at up 10° or down 10° . A typical result is shown in Fig. 7A–C wherein subject JM trained with a 7° incyclodisparity presented at a vertical eye position of down 10° . There is little difference in cyclovergence in relation to vertical eye position either before or after training and the change in the slope of the regression lines from pre-training to post-training is only -0.003° cyclovergence per degree vertical eye position. There is, however, an offset of approximately 2° in the direction appropriate for the stimulus. The mean slope values for the five subjects shown in Fig. 7D show that, in general, subjects had very little vertical eye position related changes in open-loop cyclovergence following training and the average changes in slopes for the four conditions, ExU, ExD, InU, InD were -0.017° , 0.004° , 0.033° , and -0.013° , of cyclovergence per degree of vertical eye position,

respectively. Because the amplitude of the aftereffect was similar at all vertical eye positions, it can be concluded that adaptation was not specific to the position at which training was received but spread concomitantly to untrained positions.

Four of the five subjects showed the greatest amount of adaptation when the incyclodisparity training stimulus was in the lower field and all five subjects showed greater adaptation to incyclodisparities than to excyclodisparities (7E). The average change in intercept when subjects trained with incyclodisparities was -2.06 (29% of the stimulus demand) when in the lower field and -1.93 (27%) when in the upper. For training with excyclodisparities, the corresponding values were 1.17 (17%) in the lower field and 0.80 (11%) in the upper.

3.6. Concomitant adaptation: closed-loop cyclovergence

Closed-loop cyclovergence measurements were made while the subjects attempted to fuse the training stimulus as it was presented at a single eye position (up or down 10°). Unlike the other testing paradigms, eye position was measured only at the single position at which training was received and so only the average cyclovergence value is given (instead of a slope and intercept). Fig. 8 shows that the effects of training on closed-loop responses were similar to those observed in conjunction with open-loop measurements. Pre-training, four of the five subjects had greater fusion of incyclodisparities than excyclodisparities and of those,

**Pursuit: Open-Loop Cyclovergence
Concomitant Training**

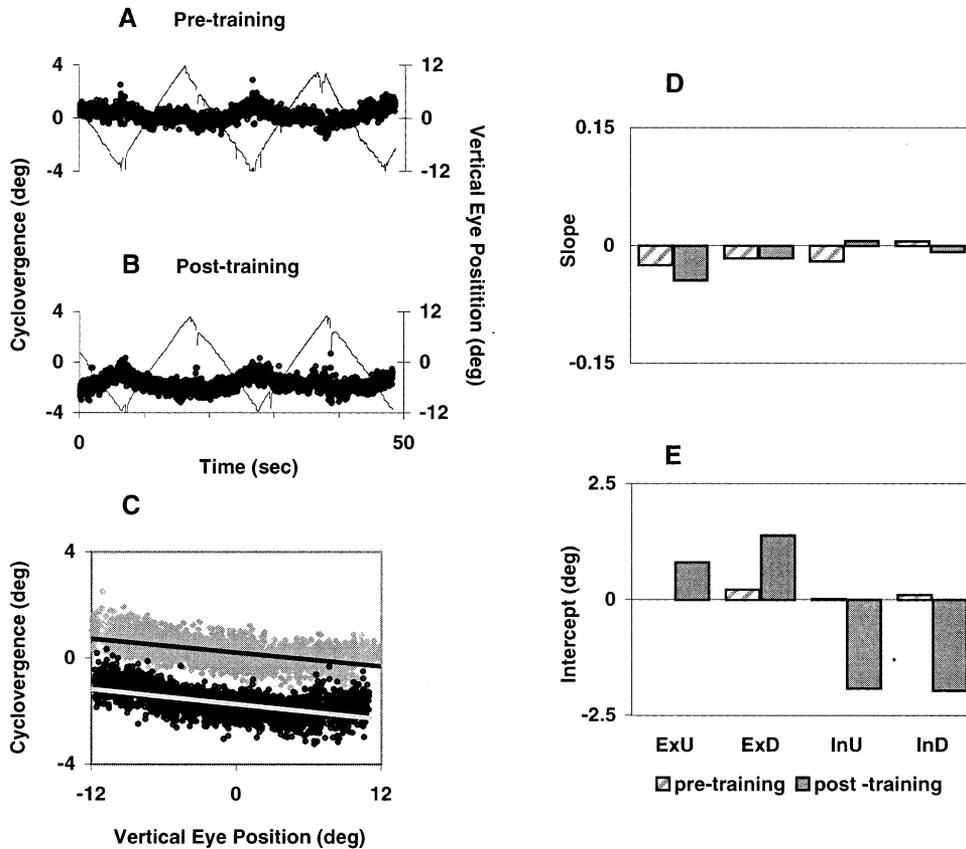


Fig. 7. Open-loop cyclovergence in relation to smooth pursuit as a function of time before (A) and after (B) concomitant training (InD, subject JM). C: Cyclovergence as a function of vertical eye position with lines fit by linear regression as in Fig. 2. The average slopes and intercepts for all four subjects are presented in D and E, respectively.

three of four had greater fusional responses when the incyclodisparities were in the lower field. Post-training, the subjects continued to have greater fusion of incyclodisparities. Pre-training, the average fusional responses for excyclodisparities were 23% and 25% of the stimulus requirement when the stimulus was in the upper and lower fields, respectively. For incyclodisparities pre-training, the fusional responses were 31% and 46% of the stimulus demand. Post-training the average fusional responses for excyclodisparities increased to 54% and 52% of the stimulus requirement in the upper and lower fields, and fusion of the incyclodisparities increased to 71% and 81% of the stimulus demand in the upper and lower fields, respectively. The open and closed-loop cyclovergence measurements following concomitant training confirm the subjective reports that incyclodisparities are more easily fused than excyclodisparities and that adaptation is more robust in that direction.

**Closed-Loop Cyclovergence
Concomitant Training**

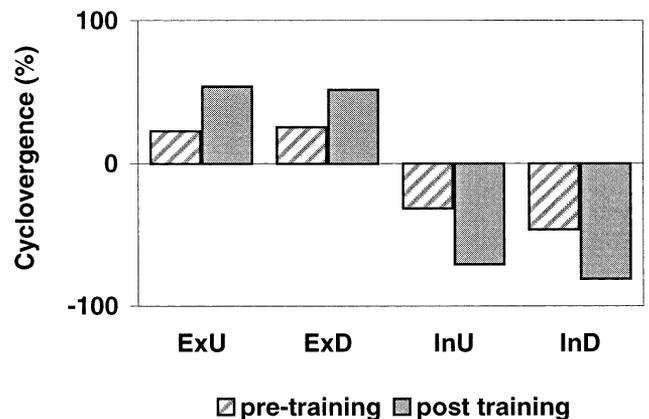


Fig. 8. Closed-loop cyclovergence before and after concomitant training measured at the eye position at which training was received (up or down 10°). Average of five subjects given as a percentage of the stimulus requirement (7°).

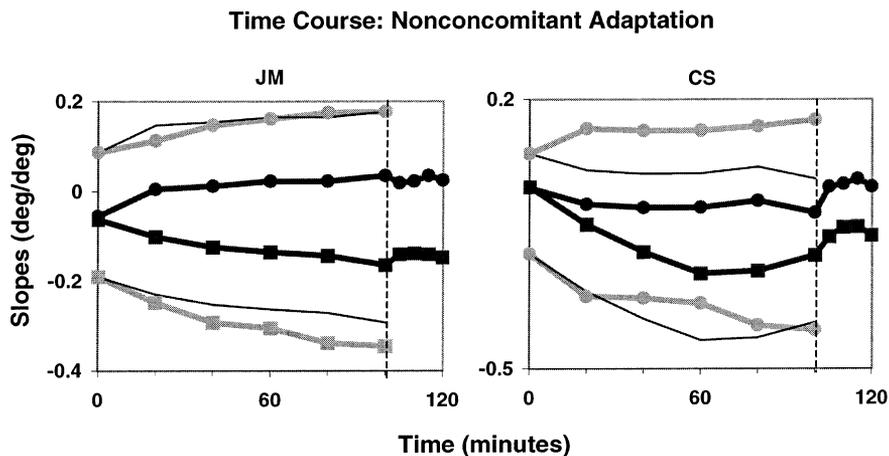


Fig. 9. Time course of nonconcomitant training. Slopes of linear regressions of cyclovergence on vertical eye position for the ExU-InD (circles) and ExD-InU (squares) paradigms. Heavy black lines: open-loop measurements. Gray lines: closed-loop measurements. Thin black lines: Open-loop measurements, offset so as to start at the same initial value as the closed-loop response. Dotted lines indicates the time at which training ceased.

3.7. Time course: nonconcomitant adaptation

The pre-training and post-training responses for the two subjects who participated in the time-course trials were similar to the responses measured for them previously in that both subjects showed a greater nonconcomitant training aftereffect for the ExU-InD than the ExD-InU paradigm (Fig. 9). Subject CS, in fact, showed little or no evidence of adaptation when measured with cyclovergence open-loop in the ExD-InU condition. For the trials in which adaptation did occur, the slopes of both open-loop (heavy black lines) and closed-loop responses (gray lines) increased gradually over the 100 min training period (Fig. 9) which is what would be expected for a parametric type adjustment. Broadly speaking, the increases in the open-loop and closed loop cyclovergence measurements followed similar patterns as is most easily seen in Fig. 9 by comparing the heavy gray (closed-loop) and thin black (open-loop values offset to start at the same initial value as the closed-loop measurements) lines. The closed-loop slopes increased at a faster rate than the open-loop slopes for subject JM in the ExU-InD condition, and for subject CS in the ExD-InU condition there was a moderate increase in the slopes of the closed-loop cyclovergence measurements but a slight decrease in the slopes of the open-loop measurements. These two cases indicate a possible dissociation between open and closed-loop adaptation and suggest that it is possible to increase the cyclofusional range without a concurrent change in the open-loop response. This supposition is only valid if the adaptation aftereffect were reasonably persistent. If, on the other hand, the adaptation aftereffect were very short lived then the smaller open-loop response that was observed may simply have been the result of the rapid decay of the aftereffect over

the 30 s required to take the data. To test this possibility, the open-loop response was measured in 5 min intervals for 20 min following training with the subject keeping one eye occluded when not being tested with the open-loop targets. As can be seen in the data to the right of the dashed line in Fig. 9, there was a slight decrease in the slopes over the 20 min post-training period for both subjects but the nonconcomitant aftereffect was fairly persistent and the amount of decay does not fully explain the difference between open and closed loop cyclovergence changes. Therefore, there remains the possibility that the increase in cyclofusional range that results from training involves an adaptive process in addition to the one that is manifest by open-loop cyclovergence measurements.

4. Discussion

4.1. Summary

The present experiments have demonstrated that subjects can modify the binocular torsional alignment of their eyes and the adaptation can either be concomitant or nonconcomitant. Subjectively, incyclodisparities were reported to be more easily fused and objective measurements during closed-loop viewing indicated that the cyclofusional and open-loop responses were, in fact, greater for incyclovergence. The training aftereffect had approximately the same dynamics following saccade-related and pursuit-related training and so we suspect the adaptation mechanism was the same in the two cases and was related to eye position regardless of how the eye achieved that position. The time constants of the training-aftereffects measured open loop were so similar to the time constants of the closed-loop fusional

responses that we assume that the training aftereffect is due to the addition of a cyclovergence movement and not the adaptation of a three dimensional saccade controller. This is opposed to the much faster saccade-like cyclovergence movements that were seen pre-training for two subjects in association with saccades that were presumably made between tertiary positions relative to their true primary positions.

4.2. Analysis

The adaptation effects reported in this study might not seem large. Presumably, longer training times would result in more complete adaptation and adaptation might also be facilitated by using a larger visual field, a more visually rich pattern, and disparities that are scaled with actual eye position instead of target position, in other words, stimuli that more faithfully reproduce naturally occurring deficits. Still, a change in cyclovergence of two or three degrees is not insignificant and it would be unusual for the oculomotor system to have to deal with cyclodisparities as large as those presented in this study.

Incyclovergence movements were consistently larger than excyclovergence movements before and after adaptation. In vertical phoria adaptation experiments where subjects adapted to vertical disparities of one sign in the upper field and the opposite sign in the lower field, it was often observed that subjects fused whatever disparity was in the lower field almost immediately even though this made the disparities in the upper field larger and more difficult to fuse (Maxwell & Schor, 1994). The advantage of this strategy by the oculomotor system may be to produce clear single vision in at least part of the oculomotor range and it might be more useful for the best vision to be in the lower field since humans probably spend more of their time with their eyes depressed than elevated as was suggested by Henson and Dharamshi (1982), and Lemij and Collewijn (1991). In the present experiments, most subjects offset their torsional eye alignment in the incyclovergence direction. This asymmetry may serve a purpose analogous to the offset in vertical phoria and allow for clear single vision in one field at the expense of larger disparities in the other although the preference in this case was for the direction of the cyclovergence movement rather than the direction of vertical gaze. The results of the closed-loop pursuit and fixation measurements show that with enough training subjects are able to successfully fuse fairly large excyclodisparities so their inability to fuse them initially seems to be a function, not of any constraints on the system, but on a lack of experience in making or need to make excyclovergence movements of any size. Interestingly, when subjects are monocularly occluded for long periods of time, most develop an excyclophoria (Graf, Maxwell, &

Schor, submitted-b) so it is possible that the system is well used to compensating in the incyclovergence direction.

The present experiments have established that torsional eye movements, at least with respect to cyclovergence, are adaptable. The training aftereffect was measured in relation to both smooth pursuit and saccades. A detailed study of the dynamics of these eye movements was not the intent of this study and this topic should be more systematically examined using a larger number of stimulus conditions, greater averaging, and, perhaps, higher temporal resolution. Nevertheless, we are able to make some general observations. The time constants of pre-training and post-training closed-loop cyclovergence movements were not noticeably different and the time constants of the cyclovergence movements attributable to the adaptive process i.e., the difference traces, were similar to the other two. The average time constant was about 1 s and the change in cyclovergence started with the initiation of the saccade. The 20° saccades in these experiments lasted approximately 120 ms whereas the typical cyclovergence movement was only 63% complete after 1 s. The relatively slow dynamics of the training aftereffect did not appear to be due to the slowly moving nature of the training stimulus since the time constants of cyclovergence movements made after training cyclovergence in association with saccades were nearly identical. The results of the present experiments do not allow us to speculate as to whether the dynamics of the response may become more saccade-like given a longer training period but this is a possibility. The use of an exponential fit may tend to overestimate the amount of time taken for a change in cyclovergence but we are reasonably confident that the primary component of the cyclovergence training aftereffect was not saccade-like. Nevertheless, there is a hint of a faster component in a few of the records (the difference trace in Fig. 5, for example) so we would not want to completely rule out the possibility that a 3-D controller is modifiable especially with longer periods of adaptation. More extensive experimentation should resolve this issue which is important since it pertains to the adaptability of the Listing's plane relationship between horizontal, vertical, and torsional eye movements.

4.3. Listing's law and cyclovergence adaptation

Whether or not our results show that Listing's plane is adaptable would depend on what one thinks Listing's law represents. If in the case of saccades, Listing's law results from a three-dimensional saccade controller (van Opstal, Hepp, Suzuki, & Henn, 1996, for example) then our results may not pertain since most of the adaptation seemed to result from the addition of cyclovergence movements with slow dynamics post-saccadically.

This is unlike the rapid cyclovergence movements observed during saccades in the pre-training trials of EG and JM and for saccades between tertiary positions described in other studies (Straumann, Zee, Solomon, Lasker, & Roberts, 1995; Ferman, Collewijn, & van den Berg, 1987a). On the other hand, if Listing's law simply describes the relationship between horizontal, vertical and torsional eye positions regardless of how the eyes attains those positions, as it was classically defined, then clearly that relationship was altered in the present experiments, at least for the eye positions measured (we did not measure torsion at enough positions to say what the effect on the planes may have been). Rapid dynamics are not a usual criterion for constructing Listing's planes and Listing's Law is often tested with respect to static eye position (Ferman, Collewijn, & van den Berg, 1987b; Straumann, Zee, Solomon, & Kramer, 1996) and to smooth pursuit (Ferman et al., 1987a,b; Straumann et al., 1996) and a cyclovergence component, if present, would be included in such measurements. In addition, there may also be a slow cyclovergence component in relation to saccades. Binocular recordings have shown that torsion may be unequal in the two eyes during saccades between tertiary positions resulting in transient excyclovergence movements (Straumann et al., 1995; Bruno & van den Berg, 1997b). These transients are corrected by torsional drifts that can outlast the saccade by more than a second (Straumann et al., 1995; also see Ferman et al., 1987b for post-saccadic drifts measured monocularly). Whether the corrective drift movements involve the cyclovergence system and are subject to adaptation remains to be determined.

4.4. Previous attempts to modify torsional eye movements

Melis & Van Gisbergen (1995) attempted to adapt torsion by rotating the background of a target during horizontal saccades. Their subjects were presented with a grating or checkerboard pattern on which was superimposed two target spots. The pattern was rotated by 10° about an axis perpendicular to the end target as subjects shifted their gaze from one target to the other. This procedure was analogous to the classic saccade-adaptation paradigm in which a target is stepped forward or backward during saccades to simulate saccadic dysmetria and thereby stimulate a gain correction. The subjects in their study showed no evidence of adaptation and they concluded that there was no basis for supposing a purely visual basis for Listing's law. However, horizontal and vertical saccades are normally quite accurate and fixations relatively stable so that even small post-saccadic errors are perceptible and might evoke an adaptive response. Cyclovergence, on the other hand, is less well controlled (van Rijn et al., 1994)

and even the large roll tilts of the retina with respect to the environment associated with ocular counterroll are not readily noticed. Experiments in vertical phoria adaptation have suggested to us that the key to attaining significant effects in these types of experiments is for the training paradigm to mimic a naturally occurring deficit in oculomotor performance (Maxwell & Schor, 1997). It is possible that the stimuli in the experiments of Melis and van Gisbergen (1995) simply looked to the system like a pattern that tilts rather than a torsional motor error in need of correction. The advantage of using large-field cyclodisparities as stimuli is that they will appear to the system as misalignments of the eyes. This is especially true with respect to horizontal lines since vertical shear does not ordinarily occur in visual scenes and will therefore signal a torsional misalignment of the two eyes (Kertesz, 1983; Howard, 1993). One function of the oculomotor system is to keep the images obtained by the two eyes in alignment and errors, if sufficiently large, will produce diplopia which has been shown in many experiments to drive vertical and horizontal vergence adaptation. The present experiments have shown that this is also true for cyclodisparities.

Acknowledgements

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