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# Comparison of the time courses of concomitant and nonconcomitant vertical phoria adaptation

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#### Abstract

Vertical phoria adaptation was measured before, during, and after 1 h of training with either a prism or magnifying lens. With the prism (concomitant adaptation) a single vertical disparity was presented at primary position. With the magnifier (nonconcomitant adaptation) two vertical disparities of opposite sign were presented along the vertical meridian. Following adaptation, binocular vision was prevented with an eye patch, and vertical phorias were measured periodically along the primary vertical meridian over the course of 8 h. Despite individual variation, adaptation followed approximately exponential time courses. The average time constants for the decay of concomitant and nonconcomitant adaptation were 31 and 83 min, respectively. There was no consistent relationship between the rates of acquisition and decay nor was there a strong relationship between the gains of the adaptive responses and the rates of decay although there was a general trend for the gains of the nonconcomitant responses to be higher and the rate of decay slower than the concomitant responses. The results support the notion that concomitant and nonconcomitant phoria adaptation involve different mechanisms but not the contention that adaptation to prisms is easier or more robust than adaptation to lenses. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Vergence; Prism adaptation

#### 1. Introduction

Phoria is defined as a relative deviation of the visual axes from alignment with a fixation target in the absence of binocular feedback (e.g., when one eye is occluded). Under such conditions, the covered eye assumes a resting position determined by the open-loop components of vergence, subject to individual variation. Open-loop components that operate without retinal disparity feedback include proximal, tonic and cross-linked inputs (Maddox, 1893). Phoria adaptation refers to the ability of the oculomotor system to adjust the tonic component of the phoria over time to correct oculomotor alignment errors induced by developmental changes, disease or injury (see Leigh & Zee, 1999, for a review).

Binocular alignment errors may be simulated optically with ophthalmic lenses or prisms. A prism placed in front of one eye produces a constant disparity across

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the field (concomitant disparity). An afocal magnifying lens placed before one eye, on the other hand, produces a disparity that increases with eccentric eye position. Phoria changes, or adapts, over time in response to either of these conditions to reduce the optically induced disparity (Carter, 1965; Henson & Dharamshi, 1982; Ogle & Prangen, 1953; Schor, Gleason, Maxwell, & Lunn, 1993).

The adapted phoria returns to baseline levels (decays) after a prism is removed. If appropriate feedback from retinal-image disparity is present when the prism is removed, then decay occurs quickly (Henson & North, 1980; Ogle & Prangen, 1953). If however, binocular vision is prevented when the adapting disparity stimulus is removed, decay is much slower (Ellerbrock, 1950; Ogle & Prangen, 1953). As the duration of training is increased, the rate of decay decreases (Ellerbrock, 1950; Ludvigh, McKinnon, & Zartzeff, 1964).

The decay rate of adaptation to nonconcomitant disparity has not been quantified but may differ from rates measured for concomitant adaptation if it is true, as Maxwell and Schor (1994) have speculated, that there

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are separate mechanisms underlying concomitant and nonconcomitant adaptation. Using a linear regression analysis of phoria changes during adaptation to a nonconcomitant stimulus, these authors decomposed the adaptive response into two components, an overall (concomitant) shift in vertical phoria and an eye-position-dependent (nonconcomitant) change. Since this result coincided with subjective reports that one of the two opposite-disparity targets was fused nearly immediately (at the expense of making the disparity at the other position more difficult to fuse), they postulated two mechanisms: a fast concomitant shift that allowed for single vision at one target location and a sloweracting nonconcomitant component that could produce eye-position-dependent changes in phoria that conformed to local stimulus demands. It is important to note that these authors did not directly test the rate of adaptation to concomitant disparities (to a prism, for example) but speculated that the initial overall shift in phoria resulted from a concomitant mechanism.

The rate of decay of concomitant vertical disparity (prism) adaptation has been reported previously (Ellerbrock, 1950; Ogle & Prangen, 1953) but the decay rate for nonconcomitant vertical disparity adaptation has not. The current study provides an estimate of the time of decay of nonconcomitant vertical phoria adaptation and directly compares it to the rate of decay of concomitant adaptation measured under similar experimental conditions. The rates at which the adaptive responses to prisms and lenses were acquired are also examined and compared to the rates of decay.

## 2. Methods

#### 2.1. Subjects

Four adult subjects were used in this study and these subjects gave prior written consent. The subjects were either emmetropic or allowed to wear their refractive correction during the experiment. All four had normal binocular alignment.

#### 2.2. Phoria measurement

Vertical eye position was measured subjectively using a red-green anaglyph technique. The subject viewed red-green targets through red-green filters in an otherwise darkened room. The subjects were presented with targets at five different elevations: +9, +4.5, 0, -4.5, -9deg. Positive values denote upward gaze and negative values denote downward gaze. The targets (Fig. 1, test stimulus) consisted of a set of two short green horizontal lines (seen only by the green-filtered eye) placed on either side of a circular red target with a central fixation spot (seen only by the red-filtered eye). The red circle

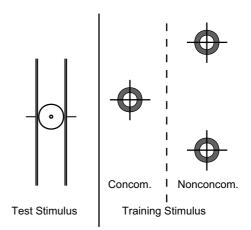


Fig. 1. *Methods.* The test stimulus consisted of a central red circle and fixation spot (black lines) and two short horizontal green lines (gray lines), seen by the red-filtered right eye and green-filtered left eye, respectively. Two vertical red lines and two vertical green lines were fused by the subject in order to control horizontal vergence. The concomitant training stimulus consisted of one set of circles and crosses presented at center position. The nonconcomitant training stimulus consisted by 18 deg along the vertical meridian (not drawn to scale).

subtended a visual angle of 2 deg of arc. The subject was instructed to use a game-pad controller to align vertically the red fixation spot with the green horizontal lines. The final position chosen by the subject was recorded on a PC computer. Because horizontal vergence could affect vertical phoria, horizontal eye alignment was held constant (2 deg convergence) by having the subject fuse two red and two green vertical lines that spanned the height of the screen. Vertical phoria (right eye position–left eye position) was tested at each vertical target position three times, and the order in which the target positions were presented was randomized. Head position was fixed with a bite-bar and was the same for all sessions.

Stimuli were generated on a PC computer and rearprojected onto a tangent screen by an Epson EP-5000 LCD projector. The viewing distance to the screen was 150 cm, with the screen subtending 30 deg by 30 deg.

#### 2.3. Concomitant adaptation

Initial baseline phoria measurements were made at five elevations: +9, +4.5, 0, -4.5, -9 deg. A single adaptation stimulus was presented to the subject at the center position. Center position is defined as a point on the screen at the same height as the subject's eyes. The stimulus used for adaptation consisted of a black cross, superimposed upon a circle (Fig. 1, training stimulus),  $\approx 3$  deg in diameter, on a white background. The subject viewed the target with a base-up prism in one session or base-down prism in another session, placed in front of the left eye. The base-up prism produced a vertical disparity that required a right hypervergence in order to be fused and the base-down prism produced a vertical disparity that required a left hypervergence. The initial vertical disparity was 4 prism diopter, and was increased incrementally (step size = 1 prism diopter) when the subject reported that the target was double but could be fused with effort in a reasonable amount of time ( $\sim$ 1 min). Three subjects were able to fuse 6 prism diopter by the end of training, and the fourth (CAB) was able to fuse 4 prism diopter. Vertical phoria was measured at 10-min intervals throughout the training period according to the procedure described above. The training period lasted for 60 min, not including the time taken to measure the phorias. At the conclusion of the training period, the subjects immediately patched their left eye to prevent fusion. Subsequent phoria measurements were taken at 10, 20, 40 and 60 min after patching and then hourly for a total of 8 h. Each condition (base-up and base-down) was performed three times for each subject. A period of at least 48 h separated experimental sessions to prevent possible contamination by residual effects from the previous session.

#### 2.4. Nonconcomitant adaptation

In the nonconcomitant paradigm, the targets consisted of two vertical-disparity stimuli, one presented at up 9 deg and the other at down 9 deg along the primary vertical meridian (see Fig. 1). Disparity was produced by an afocal magnifier (8%) centered in front of the right eye in one session and in front of the left eye in another session in order to create opposite-signed disparity patterns for the two nonconcomitant conditions. When the magnifier was placed in front of the left eye, it produced a left hyperdisparity of 0.72 deg (9 deg \*0.08) when the subject fixated the upper target and a left hypodisparity of 0.72 deg when the subject fixated the lower target. These disparities produced diplopia which stimulated vertical vergence movements. When the afocal magnifier was in front of the right eye, the disparities were reversed. The testing procedure was the same as in the concomitant condition. Each of the two conditions, right eye magnified (REM) and left eye magnified (LEM), was performed three times for each subject.

#### 2.5. Occlusion-only

Previous studies have shown that a vertical phoria develops after long-term monocular occlusion (Charnwood, 1951; Graf, Maxwell, & Schor, 2002; Marlow, 1924; Sethi, 1986). For example, Charnwood (1951) found 2 prism diopter of hyperphoria after 10 consecutive days of patching. Because the occlusion-related vertical phoria may have affected our adaptation-related aftereffect, as a control condition we had subjects wear an eye patch over their left eye in three separate sessions and measured vertical phoria over the course of 8 h, following the same paradigm described above.

## 2.6. Data analysis

Three separate measurements of vertical phoria were taken for each of the five vertical eye positions during each test period. These three values were averaged together and the average values were plotted as a function of vertical eye position and fit by linear regression. Representative averaged data for one subject (EWG) and the subsequent linear fits are depicted in Fig. 2, where it can be seen that concomitant training resulted in a fairly uniform change in vertical phoria across the five tested vertical positions. The nonconcomitant training, on the other hand, resulted in marked changes in vertical phoria in relation to eye elevation. Based on these and previous results (Maxwell & Schor, 1994), adaptation was quantified by the *y*-intercept from the

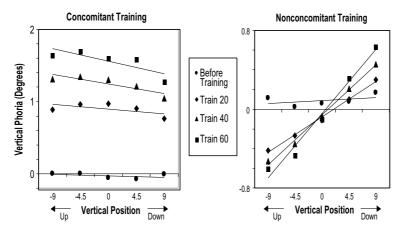


Fig. 2. Linear regressions fit to concomitant (left panel) and nonconcomitant data (right panel) for data collected before and during a 1 h training period. Offset values (*y*-intercepts) were used to quantify the effects of the concomitant condition and slope values were used to quantify the results of the nonconcomitant condition.

linear regression in the concomitant training condition, and by the slope of the regression in the nonconcomitant training condition. This analysis ignores the small changes in slope that may have occurred with concomitant training and the changes in intercept that may have occurred with nonconcomitant training.

The average *y*-intercept or slope data from each session was averaged over the three sessions for each subject and plotted as a function of time for each of the four test conditions (two concomitant and two nonconcomitant) and these averages were fit with exponential functions of the form  $Ke^{-ax} + C$  where *K* represents the amount of vertical phoria decay; the time constant, *t*, is equal to 1/a and represents the amount of time for 63% of *K* to decay to a steady baseline and *C* is an estimate of the value to which the phoria decays. The amplitude of the adapted phoria for each subject at the initial time of occlusion equals the sum of *K* and *C* and the gain of the response is the sum of *K* and *C* divided by the stimulus amplitude.

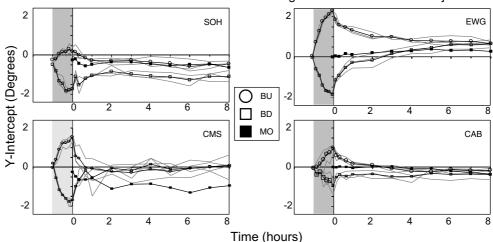
## 3. Results

Results for the four conditions (two concomitant and two nonconcomitant) as well as the data from the occlusion-only control condition are presented for each subject in Fig. 3 (concomitant condition) and Fig. 4 (nonconcomitant condition). The data in the gray shaded region (to the left of zero) represents the build up of the adaptive response over a 1-h period, and the section to the right of zero represents the decay of the aftereffect over an 8-h period. The three individual training sessions for each condition are shown with gray lines and are relatively consistent for individual subjects. The open symbols represent the average *y*-intercept of the regression analysis for the concomitant condition (Fig. 3) and the average slope of the regression for the non-concomitant condition (Fig. 4). The solid symbols correspond to the *y*-intercepts (Fig. 3) or slopes (Fig. 4) of the regression plots for the occlusion-only condition. Qualitatively, it can be seen that the general trend was a change in phoria consistent with the stimulus demands during the training period, followed by a gradual decrease of the aftereffect toward a level at or close to the pre-adapted state during the occlusion period.

A more quantitative analysis of the decay is provided in Figs. 5 and 6, and in Table 1. Fig. 5 illustrates the analysis technique on the data of one subject (EWG) for each of the four stimulus conditions. The symbols represent the average of the three trials that were performed for each paradigm. Superimposed on the averaged data are exponential fits (solid lines) for the acquisition and decay portions of the data. The same analysis was performed on all four subject's data, and Fig. 6 shows the exponential fits for individual subjects (gray lines) as well as for the average of the four subjects (black lines). The averages for the concomitant and nonconcomitant trails are also shown together in the inset of Fig. 6 to facilitate a visual comparison (thin lines: concomitant, thick lines: nonconcomitant).

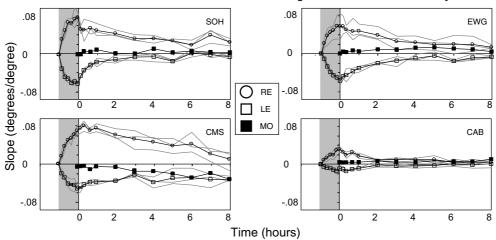
# *3.1. Time constants for the decay of nonconcomitant and concomitant adaptation*

The data in Table 1 indicate a difference in the decay time constants for the concomitant and nonconcomitant



Concomitant Condition: Raw and Averaged Data for Individual Subjects

Fig. 3. Acquisition and decay of concomitant adaptation. Changes in phoria for individual sessions (gray lines) and the averages of three sessions (black lines). The ordinate represents concomitant vertical phoria change, quantified as the *y*-intercept of the linear regression, as illustrated in Fig. 2. Data to the left of time zero represents data taken during training; data to the right represent measurements made after training. Open circles represent data taken in the base-up condition; open squares represent data from the base-down condition. Filled squares represent data from the monocular occlusion (MO) control condition.



Nonconcomitant Condition: Raw and Averaged Data for Individual Subjects

Fig. 4. Acquisition and decay of nonconcomitant adaptation. Changes in vertical phoria for individual sessions (gray lines) and the averages of three sessions (black lines). The ordinate represents nonconcomitant adaptation as the slopes of the linear regressions (degrees of vertical phoria per degree of vertical eye elevation) as illustrated in Fig. 2. Data to the left of time zero represents data taken during training, data to the right represent measurements made after training. Open circles represent data taken in REM condition; open squares represent data from the LEM condition. Filled squares represent data from the occlusion-only control condition.

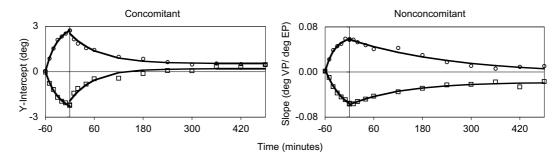


Fig. 5. Exponential functions were fit to the averaged data for each subject for all four conditions. The data and exponential fits for the acquisition phases (left of the dotted line) and decay phases (right of the dotted line) of adaptation are shown for one representative subject (EWG).

adaptive responses. The average decay time constant for the concomitant base-up prism condition averaged 33 min and the decay time constant for the concomitant base-down condition averaged 29 min. These values are smaller than the decay time constants obtained in the nonconcomitant conditions which were 58 min for the LEM condition and 125 min for the REM condition. The time constant for subject CMS was not included in the average for the REM condition because this data was approximately linear ( $R^2 = 0.95$ ) and not fit well by an exponential. Extrapolation of the linear fit indicates a decay to baseline after 630 min for this subject. The average time constant for all subjects and both concomitant conditions was 31 min. The average time constant for all subjects (but CMS in the REM condition) and both nonconcomitant conditions was 83 min, indicating that adaptation decayed more slowly in this condition. The responses would be expected to totally dissipate in about three time constants, or, 1.5 h for concomitant and 4 h for nonconcomitant adaptation.

For each individual, the time constants for concomitant training were shorter than for the nonconcomitant except for subject SOH who had one concomitant time constant that was longer than one of the nonconcomitant time constants.

#### 3.2. Adaptation response gain and amplitude

The parameters K and C from the exponential fits were used to quantify the gain of the adaptation. Gain represents the proportion of the stimulus to which the subject responded and it is equal to the sum of K and Cdivided by the magnitude of the training stimulus. The gains for the four subjects and four conditions are given in Table 1. The average response for each condition is also given and was determined by first averaging together all of the data for a given condition and then fitting those averages with an exponential. For that reason, they may differ somewhat from the mean. Overall, subjects adapted more completely to the nonconcomitant than to the

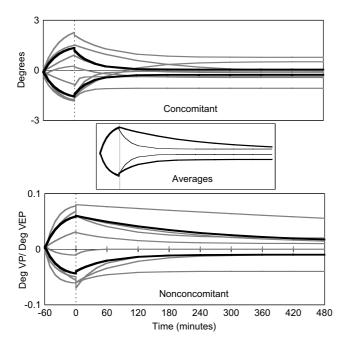


Fig. 6. Data for all four subjects were averaged together for each condition, then fit with exponential functions. Individual subject data (gray lines) and averaged data (black lines). The insert shows the exponentials for the averaged concomitant data (thin lines) and non-concomitant data (thick lines) normalized and plotted on the same graph.

concomitant disparities. In the concomitant condition, the training stimulus was a vertical disparity of 3.4 deg (6 diopter) for three of the four subjects, and 2.3 deg (4 diopter) for the fourth (CAB). The average gain across subjects for the two concomitant conditions was 0.38 and 0.46 for base-up and base-down prisms, respectively. The average gains for the LEM and REM nonconcomitant conditions were 0.59 and 0.70, respectively.

It is possible to make an additional comparison of the two adaptation conditions by analyzing the phoria response *amplitude* at the same test eye elevation for the concomitant and nonconcomitant adaptation conditions. Recall that the y-intercept and slope measures used in the analysis took into account all of the eye positions tested to find a single value that characterized the phoria along the vertical meridian. If instead, the data for each eye position is plotted for the four adaptation conditions it is possible to get an indication of the decay of the amplitude of the phoria at each eye position (see Fig. 7). In Fig. 7 it can be seen that the initial amplitude of the response is higher in the concomitant conditions than in the nonconcomitant conditions for all elevations tested. Fitting exponential functions (the star symbols and solid lines of Fig. 7) to the averaged subject data for each of the five points tested in the four conditions gave higher time constant values for nonconcomitant conditions relative to the concomitant conditions at all nonzero eye positions. For example, in the left-hand column, which shows the data for phoria measured at 9 deg down, the initial concomitant phoria values were 1.3 and -1.4 deg for the base-up and basedown conditions. The time constants of decay for these vertical positions were 29.7 and 26.3 min, respectively. Conversely, the nonconcomitant conditions had initial values of 0.42 deg and -0.73 deg for the LEM and REM conditions, and time constants of decay of 513.1 and 399.47 min. Thus, although the nonconcomitant condition had a higher response gain than the concomitant condition, the actual response amplitude was higher in the concomitant condition. Despite this, the calculated time constant of the exponential fit to the nonconcomitant data was consistently greater than the concomitant time constants at the same eye elevation.

Table 1

The gains (G) of the adaptive responses were derived from exponential functions fit to the decay data where G = (K + C)/stimulus magnitude

Subject	Concomitant condition						Nonconcomitant condition					
	Base up			Base down			LEM			REM		
	G	ta	td	G	ta	td	G	ta	td	G	ta	td
CAB	0.38	*	59	0.41	91	6	0.12	21	167	0.37	77	91
CMS	0.44	27	14	0.48	19	21	0.75	24	50	1.00	37	*
EWG	0.62	29	62	0.45	29	71	0.75	45	83	0.75	24	200
SOH	0.06	27	59	0.48	26	18	0.87	15	44	0.75	19	91
Average	0.38	28	33	0.46	27	29	0.59	23	58	0.70	27	125
Average both condi- tions	G	ta	td				Average both condi- tions	G	ta	td		
	0.42	28	31					0.63	26	83		

See Section 2 for details. ta: time constants for the build up of the response over 1 h; td: the time constants for the decay of the response measured over 8 h. Asterisks mark cases where exponentials were not an appropriate fit. LEM: left eye magnified. REM: right eye magnified.

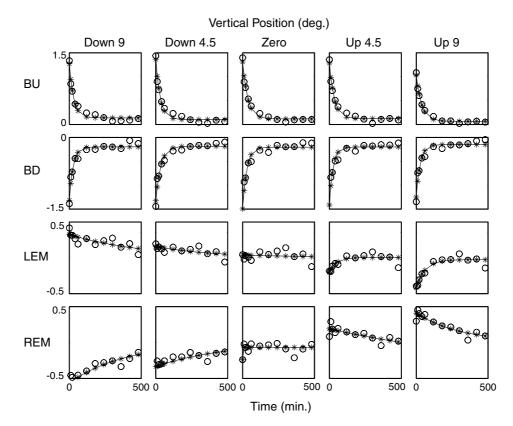


Fig. 7. Temporal decay of vertical phoria amplitude at each tested eye elevation for both the concomitant and nonconcomitant adaptation conditions. Changes of vertical phoria from the pre-adapted state are averaged for four subjects and plotted as a function of time after the adaptation task was completed. Rows represent data from the two concomitant conditions (BU and BD) and nonconcomitant conditions (LEM and REM). Columns show data from the five eye elevations where phoria was measured. Open circles are the averaged data, star symbols and the thin line represent the exponential fit to the data.

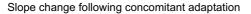
#### 3.3. Response asymmetries

Figs. 3 and 4 and Table 1 indicate that vertical phoria for many subjects did not return to baseline after 8 h of occlusion or that they had returned to baseline in one condition (REM, for example) but not the other (LEM). The parameter C of the linear regression is an estimate of the vertical phoria remaining after the exponential had reached an asymptote and ranged from -0.44 to 0.77 in the base-up condition (average = 0.04) and 1.08 to 0.51 in the base-down condition (average = -0.28). For nonconcomitant training C ranged from -0.04 to 0.00 in the LEM (average = -0.01) and 0.01 to 0.02 in REM condition (average = 0.01). A nonzero value of C means either that a portion of the aftereffect is expected to persist indefinitely, or, that the aftereffect has decayed to a nonzero asymptote as though the baseline had changed. The latter case is best illustrated by subjects SOH and EWG in Fig. 3 where the traces seem to decay to a common value away from the original baseline. The asymmetries in the C values and time constants may indicate an inherent difference in the ability of individual subjects to adapt to either right hyperdiparities or left hyperdisparities. It is also possible that some of the apparent shifts in baseline and asymmetries in decay is due to the effect of long-term occlusion.

# 3.4. Effect of monocular occlusion on the decay of phoria adaptation aftereffects

It was possible that the asymmetries observed between the two stimulus conditions (e.g. base-up versus basedown) could have been caused by an occlusion effect that added to the adaptation response. A control condition measuring phoria change as a result of long-term monocular occlusion was used to test the potential effect of occlusion on the decay of phoria adaptation to vertical disparity. The changes in vertical phoria (intercept and slope) resulting from 8 h of monocular occlusion without prior adaptation are illustrated for individual subjects by the solid symbols in Fig. 3 (y-intercepts) and Fig. 4 (slopes). After 8 h of monocular occlusion of the left eye, subjects CMS, CAB, and SOH developed left hyperphorias (shifts in the *y*-intercept) of 1.0, 0.3 and 0.6 deg respectively whereas EWG developed a right hyperphoria of 0.3 deg.

After 8 h of occlusion, CMS developed a sizable nonconcomitant vertical phoria of -0.03 deg phoria/deg



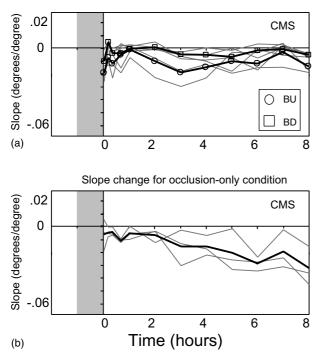


Fig. 8. Differences between slope changes after concomitant adaptation (a) and slope changes obtained in the occlusion-only control condition (b) for subject CMS.

version relative to the pre-occlusion phoria state. Smaller shifts were observed in subjects (SOH and EWG), who showed a change of  $\approx 0.01$  deg phoria/deg version of vertical phoria by the end of the 8-h occlusion period and the remaining subject showed little or no nonconcomitant change.

If the effect of prolonged occlusion on vertical phoria were the same in both the occlusion-only and adaptation conditions, then the influence of occlusion on the decay rate could be subtracted from the post-adaptation responses. Fig. 8 shows an example where this does not appear to be true. Fig. 8a shows that there was little change in slope for subject CMS following concomitant adaptation. Fig. 8b shows, however, a significant change in slope for the same subject during the occlusion-only condition. The fact that there was essentially no change in slope following adaptation indicates that the two responses did not add linearly in this instance and that subtraction of the occlusion-only response was not justified. The same argument could be made for the y-intercept component of the concomitant data of CMS shown in Fig. 3 where a sizable change in vertical phoria developed over time in the occlusion-only experiment (filled squares) but following base-up and base-down concomitant adaptation, phoria decayed symmetrically to zero which does not suggest the presence of an occlusion-related component. In other cases, notably, for EWG in the concomitant condition and SOH in the nonconcomitant condition, subtraction of the occlusiononly data would make the decay functions more symmetrical but since the results were equivocal, we decided that subtracting the occlusion-only effect from the data was not clearly warranted. Accordingly, all data were plotted and all time constants were calculated without the subtraction.

#### 3.5. Vertical phoria responses during training

Vertical phoria was measured every 10 min during the 1 h training period and these data are illustrated in Figs. 3 and 4 for concomitant and nonconcomitant conditions, respectively. Exponential fits for the acquisition data are shown in Fig. 5, for subject EWG, and a fit through the averaged data are displayed in Fig. 6. The time constants for these fits are given in Table 1. Overall, there were no marked differences in time constants for the four conditions and there was no consistent pattern as to which type of adaptation had the longer time constant. The gain results reported above show that adaptation was not complete for any of the subjects for any of the conditions but on the whole nonconcomitant adaptation was more complete than concomitant adaptation (63% vs. 42%, respectively). Linear regression analysis (not shown) demonstrated that there was no consistent relationship between the time constants of acquisition and the time constants of decay nor was there a strong relationship between the gains of adaptation and the time constants of decay although there was a general trend for nonconcomitant adaptation to be more complete and have a slower rate of decay than concomitant adaptation. These results do not support the notion that concomitant adaptation is easier or more robust than nonconcomitant adaptation.

# 4. Discussion

#### 4.1. Presence of two mechanisms

The presence of two vergence adaptation mechanisms is supported by the decay data in that the two disparity conditions (concomitant and nonconcomitant) produced different decay rates when the data were fit by exponential functions. In the concomitant condition, the decay of the aftereffects occurred with an average time constant of 31 min and the averaged time constant for the concomitant condition was 83 min, nearly three times as long.

The primary purpose of these experiments was to establish a time course for the decay of nonconcomitant phoria adaptation and compare it under similar experimental conditions to the decay of concomitant adaptation. We expected dissimilar time courses of both acquisition and decay based on the results of Maxwell and Schor (1994) who surmised that there were different mechanisms for concomitant and nonconcomitant training. Their speculation was not based on a direct comparison of adaptation to concomitant and nonconcomitant disparities but to an analysis of the concomitant and nonconcomitant components (y-intercept and slope, respectively) of the adaptive response to nonconcomitant training data. A linear regression analysis data had indicated the presence of a concomitant component, which increased rapidly over the first 16 min and then declined as the nonconcomitant component (the slope) increased. Their data coincided with subjective reports that one of the two targets during training (usually the lower one) was fused almost immediately while making the other disparity larger and therefore harder to fuse. Their data also seemed to give credence to anecdotal reports that it is easier to adapt to prisms (concomitant stimulus) than to magnifying lenses (nonconcomitant stimulus). The present experiments do not support these conclusions. Little difference was seen in the time constants of exponential fits to the acquisition data and the completeness of the adaptation was generally greater in the nonconcomitant training condition than the concomitant condition. Still, it remains that subjects typically report that training seems easier with prisms than lenses. We suspect that it is simply because binocular fusion is easier to achieve when there is only a single disparity and when subjects reported that they were adapting well, what they really meant was that they were fusing well. In fact, the concomitant component of adaptation in the data of Maxwell and Schor (1994) was not sufficient in itself to account for fusion of either of the two training targets since the vertical phoria was offset by only about 40% of the stimulus amplitude. Since the targets at one position were reportedly fused, the remaining 60% must have been achieved by disparity vergence. The reason that adaptation and disparity vergence is easier for concomitant and more difficult with nonconcomitant disparities is because of the spread of adaptation from one eye position to another (Henson & Dharamshi, 1982; Maxwell & Schor, 1994). As pointed out by Henson and Dharamshi (1982) this spread aids concomitant adaptation since the same vertical vergence is needed everywhere, but inhibits the fusion of nonconcomitant disparities since the persistence of vertical vergence from one eye position may interfere with fusion of the disparities at another.

Our aim was to test concomitant and nonconcomitant adaptation under as similar conditions as possible and the testing methods, training targets, training times and other conditions were identical for the experiments. The one component that was not possible to objectively equalize were the sizes of the disparities since one disparity was given in one case and two oppositely signed disparities were given in the other. We ended up choosing the size of the disparities based on the ability of our subjects to fuse them and used disparities that were "difficult but possible" to fuse. As a result, the maximum size of the nonconcomitant disparities was smaller (a 0.72 deg right hyperdisparity in one position and a 0.72 deg left hyperdisparity at the other) than the concomitant disparities (3.4 or 2.3 deg, depending on the subject) even though the nonconcomitant disparities were judged as more difficult to fuse. We cannot rule out the possibility that the decay time constants for nonconcomitant adaptation were longer than for concomitant adaptation because the nonconcomitant disparities were smaller allowing for more complete adaptation assuming there is a positive relationship between completeness of adaptation and length of time constant. If this were true then it could be argued based on the higher gains and longer time constants, that the nonconcomitant disparities were more easily adapted than concomitant ones, just the opposite as was predicted.

# 4.2. Ecological reference for nonconcomitant and concomitant disparity adaptation

The long time constant for nonconcomitant vertical phoria adaptation is beneficial for compensating nonconcomitant ocular deviations produced by weakness or partial loss of function of individual ocular muscles responsible for vertical movements. These disturbances require a long-term correction. In contrast, there are probably few natural conditions that produce constant concomitant vertical deviations of the two eyes and those deviations might be more easily fused with disparity vergence and not necessitate long-term changes in vertical eye alignment. One such condition might occur during ocular counterroll to head tilt where the secondary actions of the obliques would produce a vertical skew if left uncompensated (discussed in Maxwell & Schor, 1996). In this situation the overall gain of the vertical recti would need to be adjusted to compensate for this potential error created by the secondary actions of the obliques. Additionally, temporary vertical deviations occur when the eyes have small convergence errors and the head is tilted. For example, if the eyes overconverge and the head is tilted to the right, the right visual axis will be higher than the left and will produce a concomitant right hypodisparity. Steinman and Collewijn (1980) have shown that in certain tasks, convergence errors can be quite large (many degrees), such that head tilts would cause vertical disparities. Stevenson, Lott, and Yang (1997) have shown that vertical disparity vergence responds reflexively to patterns with both horizontal and vertical disparity, but the horizontal vergence response is independent and has some volitional component. Thus it is possible that the vergence system does selectively adapt vertical vergence responses to the vertical component of oblique disparities that occur in natural viewing conditions. The rapid, short-term concomitant vertical phoria adaptation might help reduce vertical disparities without necessitating accurate horizontal convergence. Because the head tilt is temporary it would be beneficial to have a short decay time constant of the vertical phoria response to the concomitant vertical disparity field.

# References

- Carter, D. (1965). Fixation disparity and heterophoria following prolonged wearing of prisms. *American Journal of Optometry and Archives of American Academy Optometry*, 42, 141–152.
- Charnwood, L. (1951). The diagnostic and therapeutic use of monocular occlusion. *British Journal of Physiological Optics*, 8, 43–56.
- Ellerbrock, V. (1950). Tonicity induced by fusional movements. American Journal of Optometry and Archives of American Academy Optometry, 27, 8–20.
- Graf, E. W., Maxwell, J. S., & Schor, C. M. (2002). Changes in cyclotorsion and vertical eye alignment during prolonged monocular occlusion. *Vision Research*, 42(9), 185–194.
- Henson, D. B., & Dharamshi, B. G. (1982). Oculomotor adaptation to induced heterophoria and anisometropia. *Investigative Ophthal*mology and Visual Science, 22(2), 234–240.
- Henson, D. B., & North, R. E. (1980). Adaptation to prism-induced heterophoria. American Journal of Optometry and Physiological Optics, 57, 127–137.

- Leigh, R. J., & Zee, D. S. (1999). *The neurology of eye movements* (3rd ed.). New York: Oxford University Press.
- Ludvigh, E., McKinnon, P., & Zartzeff, L. (1964). Temporal course of the relaxation of binocular duction (fusion) movements. *Archives D Ophthalmologie*, 71, 389–399.
- Maddox, E. E. (1893). *The clinical use of prisms and the decentering of lenses* (2nd ed.). Bristol, England: John Wright and Company.
- Marlow, F. (1924). The relative position of rest of the eyes and the prolonged occlusion test., vol. vii. Philadelphia: F.A. Davis Co.
- Maxwell, J. S., & Schor, C. M. (1994). Mechanisms of vertical phoria adaptation evealed by time-course and two-dimensional spatiotopic maps. *Vision Research*, 34(2), 241–251.
- Maxwell, J. S., & Schor, C. M. (1996). Adaptation of vertical eye alignment in relation to head tilt. *Vision Research*, 36(8), 1195– 1205.
- Ogle, K., & Prangen, A. (1953). Observations of vertical divergences and hyperphorias. Archives D Ophthalmologie, 49, 313–334.
- Schor, C. M., Gleason, G., Maxwell, J., & Lunn, R. (1993). Spatial aspects of vertical phoria adaptation. *Vision Research*, 33(1), 73– 84.
- Sethi, B. (1986). Heterophoria: a vergence adaptive position. Ophthalmic and Physiological Optics, 6(2), 151–156.
- Steinman, R. M., & Collewijn, H. (1980). Binocular retinal image motion during active head rotation. *Vision Research*, 20(5), 415– 429.
- Stevenson, S., Lott, L., & Yang, J. (1997). The influence of subject instruction on horizontal and vertical vergence tracking. *Vision Research*, 37(20), 2891–2898.