An Adaptable Association Between Vertical and Horizontal Vergence

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Vertical phoria (vergence error under monocular viewing conditions) can be trained to vary with conjugate eye position. The adaptive response controls the vertical alignment of the two eyes in the absence of binocular disparity and is used to compensate for binocular changes of the oculomotor system induced by developmental and environmental factors. Vertical phoria was associated with horizontal disparity vergence by adapting vertical vergence to two vertically disparate targets separated along the depth axis. This association was primarily dependent on the horizontal vergence as opposed to monocular eye position or binocular conjugate eye position. Following this adapted association with horizontal disparity vergence, vertical phoria aftereffects were also evoked by accommodative vergence. Previous reports have demonstrated an adapted association between vertical phoria and conjugate eye position. The current report examines the difference in the vertical phoria resulting from adaptation to vertically disparate targets separated along either the vertical axis or depth axis. The amplitude of the vertical vergence aftereffect was approximately 4 times greater for targets separated along the depth axis than in the vertical meridian. The association between vertical phoria with conjugate eye position and horizontal vergence is proposed to result from a cross-coupling of vertical vergence with supranuclear regions that control conjugate and horizontal vergence eye movements. A selective interaction would enable the oculomotor system to correct disturbances in specific supranuclear regions as they interface with vertical vergence.

Vertical vergence   Horizontal vergence conjugate   Cross-coupling   Adaptation

INTRODUCTION

Binocular eye alignment is accurate to within several min arc while fixating targets over a wide range of directions and distances of gaze. Generally, this accuracy is attributed to a feedback system that uses binocular retinal image disparity as an error signal to drive disparity vergence (Rashbass & Westheimer, 1961). However, vertical binocular alignment is nearly as accurate when binocular disparity information is not present, such as in monocular occlusion (Ogle & Prangen, 1951; Schor, Maxwell & Stevenson, 1994; Zee & Ygge, 1993; Collewijn, 1994). The precision of vertical binocular eye alignment under monocular viewing conditions could result from an innate oculomotor coordinate system such as described by Helmholtz or Harms, or it could result from a binocular adaptation by the oculomotor system (Schor et al., 1994). Accuracy of vertical vergence under monocular viewing conditions is remarkable in light of the many developmental changes of the extraocular muscles and eye separation that occur during infancy (Schor, 1993), and potential environmental and age related factors such as trauma and disease that can disrupt

the oculomotor system during adulthood. These factors can produce binocular misalignments that vary with distance and direction of gaze. Fortunately the oculomotor system is able to correct many of these alignment errors with a calibration process that associates different classes of eye movements. In examples of non-comitance produced by trauma or anisometropic spectacle lenses, the compensatory adaptation response varies with eye position (Schor, Gleason, Maxwell & Lunn, 1993; Oohira, Zee & Guyton, 1991; Oohira & Zee, 1992).

Previously we observed a conditioned association between vertical vergence with either horizontal or vertical conjugate eye position (Schor et al., 1993; Maxwell & Schor, 1994). Vertical vergence was conditioned binocularly to change under monocular viewing conditions with variations of conjugate eye position. The characteristics of vertical vergence adaptation were investigated by observing the spread of aftereffects resulting from adaptation to two different vertical disparities in separate target locations (Schor et al., 1993; Maxwell & Schor, 1994). Responses to this paradigm are characterized by four general observations. First, it is possible to train the vertical phoria to change with eye position. For example, it is possible to train both a right hyperphoria to occur in right gaze and a left

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hyperphoria to occur in left gaze (Schor *et al.*, 1993; Maxwell & Schor, 1994). We refer to this as a local (noncomitant) adaptation response as opposed to the global (concomitant) adaptation response to a single vertical disparity that spreads uniformly throughout the orbital field (Schor *et al.*, 1993; McCandless, Schor & Maxwell, 1995). Second, the vertical phoria spreads to unadapted eye positions. Vertical phoria aftereffects are interpolated between the adapting positions and extrapolated beyond them. Third, the response magnitude is proportional to the amplitude of vertical disparities that stimulate disparity vergence during adaptation. Finally, the response magnitude decreases with reduced separation between the two target locations. If the target separation is <2 deg, a crowding effect completely attenuates the response that would have been manifest as a phoria aftereffect with a larger target separation.

An important question is what information is used to guide these spatially dependent changes in the adapted phoria in different directions of gaze. One possible model describes a cross-coupling between two motor systems (McCandless *et al.*, 1995), wherein a correlate of conjugate eye position provides an input to the vertical vergence system and causes the phoria to vary systematically with versional eye position. A variety of inputs in addition to conjugate eye position might be cross-coupled with vertical vergence. Given the accuracy of binocular eye movements to monocularly viewed targets in depth (Schor *et al.*, 1994) another likely cross-coupled input to vertical vergence is horizontal vergence. In this report we demonstrate that vertical vergence can be associated with both horizontal disparity vergence and accommodative vergence, independent of monocular eye position and binocular conjugate position. We also demonstrate differences in the magnitude of vertical vergence aftereffects associated with vertical conjugate and horizontal vergence eye movements.

These results support a model in which vertical vergence can be selectively cross-coupled with supranuclear regions that control conjugate and horizontal vergence eye movements. During adaptation, correlated activities of various oculomotor responses could become associated with vertical vergence, and following adaptation, vertical vergence would vary as gaze was shifted by the type of movement exercised during adaptation. This would allow the vertical vergence system to selectively compensate for anomalous inputs from specific supranuclear regions. Selective compensation would not be possible if it occurred in the final common pathway for vertical vergence or vertical eye position where changes would influence all vertical oculomotor responses, including those that were not in need of repair.

METHODS

During adaptive training, subjects alternated binocular fixation between two targets presented in separate locations. The targets were separated either vertically or in depth. Each target subtended a vertical binocular disparity that subjects fused using vertical disparity vergence. Vertical disparity was classified as right-*hyper* if the target was higher before the right than left eye and as right-*hypo* if the target was lower before the right than left eye. In a given pair of targets one subtended a right-hyper disparity and the other a right-hypo disparity. At the conclusion of adaptation, the vertical phoria was measured in the two adapting positions as well as other positions. The presence of a vertical phoria aftereffect indicated that the subjects had adapted vertical eye alignment to the disparities.

Equipment

Vertical eye position was measured with an SRI dual-Purkinje eye-tracker. Eye position resolution of the tracker was on the order of 1 min arc. The optical system was a Wheatstone haploscope composed of two 50% beam splitters placed at 45 and 135 deg before the right and left eye respectively. Through the beam splitters, the subjects binocularly viewed a bright Maltese cross subtending a 2 deg retinal angle. The Maltese cross was generated on a video board and displayed on a monochrome monitor located 57 cm from the entrance pupils. The beam splitters superimposed a dichoptic view of two vertical lines on the Maltese cross. The vertical lines served as a stimulus to control horizontal vergence while the Maltese cross was viewed either binocularly during adaptation or monocularly during testing. The location and disparities subtended by the Maltese cross were controlled with General Scanning mirror galvanometers that independently adjusted vertical and horizontal target position and binocular disparity. Three IBM 80286-based computers were used for mirror and target control and data acquisition. Voltage analogs representing independent right and left eye positions were saved onto hard disk and analyzed off-line.

Subjects

Five subjects (CS, MC, MP, SG, and SY) took part in this study. Experiment 1 was performed once by CS and twice by MC and SY. Experiment 2 was performed twice by MC and three times by CS and SG. All subsets of Expt 3 were performed twice by CS. MC performed the first part of Expt 3 three times and the remaining parts twice.

Pre-adaptation procedures

Prior to each experimental trial, the horizontal and vertical mirror offsets were adjusted to negate any perceived diplopia due to each subjects habitual phoria bias. Next, left and right eye positions were independently calibrated at each of the adaptation and test positions described in the following sections. During calibration, eye tracker output voltage was sampled for 1.66 sec at 60 Hz. The digitized voltages and stimulus positions were used to transform recorded voltages to eye position values for on-line displays and off-line analysis.

Horizontal positions of the two dichoptic vertical lines were adjusted so that they were fused into a single line

near the center of the Maltese cross. Since the bars extended vertically through the entire 20 deg optical field, they did not induce a vertical disparity.

Adaptation procedures

The adaptation procedures were designed to produce a non-comitant vertical phoria during changes in either vertical conjugate or horizontal vergence eye position. During adaptation subjects attempted to fuse the vertically disparate Maltese cross that was viewed binocularly (i.e. both horizontal and vertical stimuli to fusion were present). Binocular fixation was shifted between the two Maltese crosses separated in depth in the midsagittal plane or vertically in the fronto-parallel plane. The two crosses subtended vertical disparities of opposite sign. The right-hyper disparity is classified as positive and right-hypo disparity is classified as negative. Vertical target separations in the fronto-parallel plane were used since these result in larger vertical phoria aftereffects than horizontal target separations (Schor *et al.*, 1993). The adaptation targets were presented alternately in 5–10 sec intervals over a 40 min adaptation period. To avoid developing long-term biases of the phoria aftereffect in a particular direction (e.g. right-hyper in upper field and right-hypo in the lower field) the signs of the disparity stimuli were reversed for some trials. The signs of the corresponding phoria aftereffects were then reversed so that they could be averaged with the results of the other trials.

Post-adaptation procedures

Vertical vergence adaptation is characterized by a monocular vergence response (phoria) that exists in the absence of binocular vertical disparity. At the conclusion of 40 min of adaptation, the vertical phoria was measured in the two adapted directions or distances of gaze as well as in other intermediate unadapted locations along the axis containing the two adaptation targets. During the vertical phoria testing phase, the horizontal vergence was controlled with vertical fusion bars. Vertical disparity cues were eliminated by occluding one eye's view of the Maltese cross. Vertical eye positions for each condition were measured three or four times. The vertical phoria was calculated as right-eye position minus left-eye position. The resultant vertical phoria was determined by taking the difference between the post-adaptation and the pre-adaptation vertical phoria measurements.

Initially, subjects were able to fuse only one of the two adaptation targets (Maxwell & Schor, 1994). This resulted in an overall (d.c.) change in the vertical phoria that reduced the disparity of the fused target and increased the disparity of the non-fused target. Eventually subjects were able to respond differentially to the two targets. Occasionally during post-adaptation phoria testing, some residual d.c. offset persisted. This d.c. offset varied in magnitude and direction across subjects. To normalize the data across all subjects, the d.c. offset for each subject in a given experiment was subtracted from the vertical phoria measures, leaving only the differential responses

(i.e. the change in vertical phoria that was normalized with respect to the phoria at the midpoint of the adapted target locations). Mean differential responses of all subjects were then plotted and statistically analyzed.

Experimental conditions

Experiment 1: adaptation to symmetric horizontal vergence. A clear demonstration of an association between horizontal vergence and vertical phoria requires ruling out other sources of information that are present during vergence movements of the eyes. These sources include monocular eye position and binocular conjugate eye position. This experiment examined whether the changes in the vertical phoria resulting from adaptation to disparities presented along the depth axis depended on horizontal vergence position or monocular eye position. During adaptation for Expt 1, the vertical disparity vergence response was associated with symmetric horizontal vergence along the midsagittal plane with no conjugate component. The adapting stimuli were presented in two locations. Each target subtended 1 deg vertical disparity (right-hypo at 0 deg horizontal vergence and right-hyper at 8 deg horizontal vergence) in symmetric horizontal vergence [Fig. 1(a)]. Subjects alternated fixation between these targets every 5 sec over a 40 min period.

After adaptation, the locations of the vertical phoria test targets were arranged to stimulate specific eye positions at two horizontal vergence angles (0 and 8 deg). The Maltese cross was presented under monocular conditions at three conjugate horizontal eye positions (4 deg left; central; 4 deg right) for each of the two vergence angles. Points A, C, D, and F in Fig. 1(a) correspond to test points that stimulate eye positions and horizontal vergence angles associated with conflicting adaptation disparities. For example, the horizontal vergence position at point A was the same as the horizontal vergence position used to adapt the far right-*hypo* disparity at point B. However, the monocular eye position of the right eye at point A was the same as the right eye position that was associated with the near right-*hyper* disparity at point E. If the vertical phoria response depended primarily on horizontal vergence position (regardless of monocular eye position), the vertical phoria at position A would be right-hypo. However, if the response depended on the monocular eye position, it would be right-hyper at point A. The same type of conflict arises for near points D and F with the far point at B. When the target was positioned to the right or left of point E at the *near* distance (in which horizontal vergence corresponded to the near right-hyper disparity at point E), one eye was in a position corresponding to the *far* adapting stimulus (right-hypo disparity) at point B.

Experiment 2: adaptation to asymmetric horizontal vergence. Experiment 1 examined whether the vertical phoria response, after adapting to symmetric convergence along the depth axis, was associated with horizontal vergence or monocular eye position. An additional input

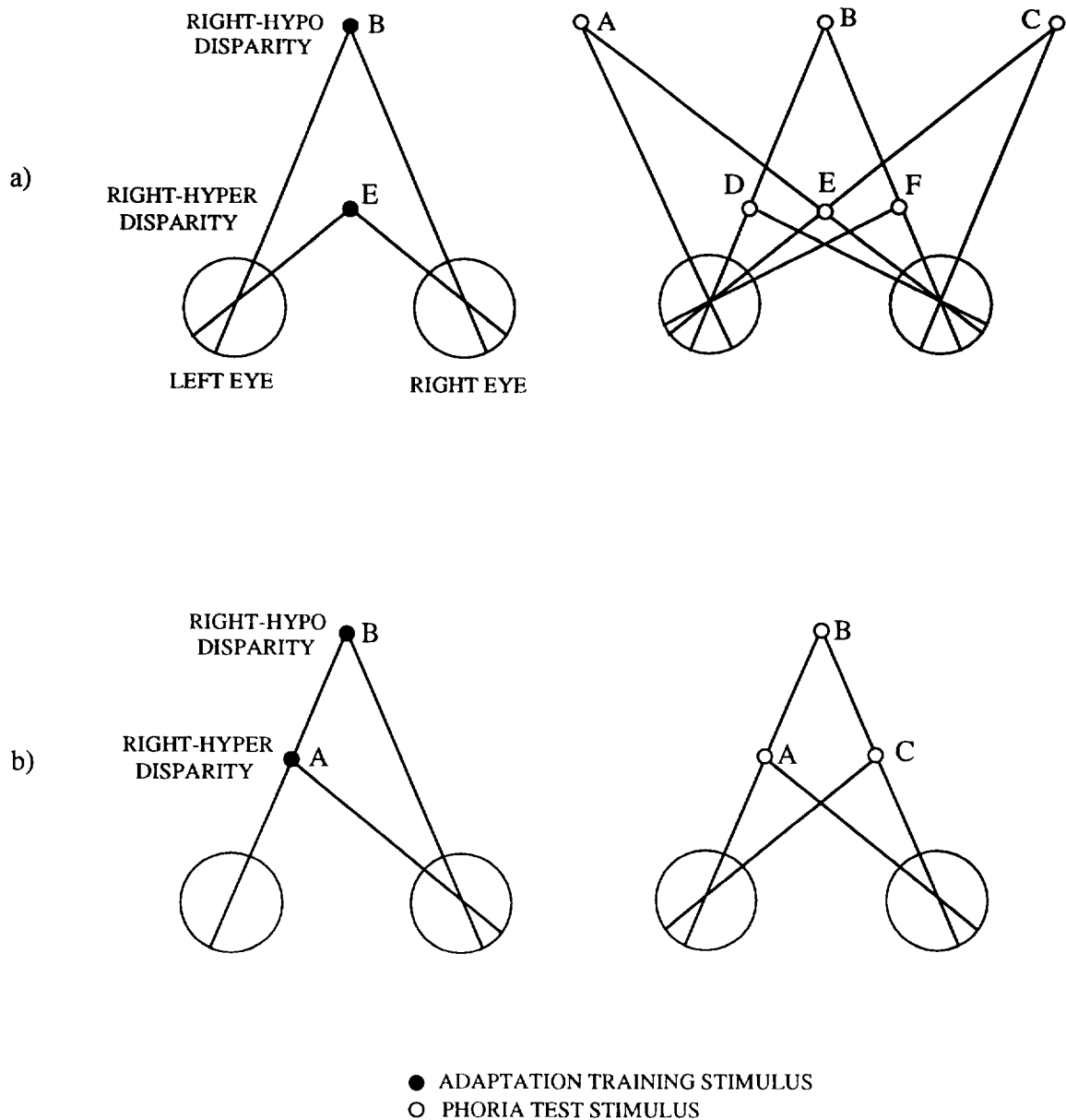● ADAPTATION TRAINING STIMULUS
O PHORIA TEST STIMULUS

FIGURE 1. Adaptation and test stimuli for (a) Expt 1 (symmetric horizontal vergence during adaptation) and (b) Expt 2 (asymmetric horizontal vergence during adaptation).

to the vertical vergence response could be conjugate eye position. Experiment 2 tested this possibility using an asymmetric vergence adapting stimulus that contained both horizontal conjugate and vergence components, as shown in the left panel of Fig. 1(b). The targets were located at 4 deg symmetric vergence (point B) and 12 deg asymmetric vergence with a 4 deg leftward conjugate component (point A). Each target subtended a 1 deg vertical disparity (right-hypo at 4 deg and right-hyper at 12 deg). During adaptation the left eye remained horizontally fixed 2 deg to the right, and the right eye shifted horizontal gaze position from 2 deg to the left at the far point (B) to 10 deg to the left at the near point (A).

The vertical phoria aftereffect was tested in the two adapted positions (A and B) as well as in a rightward asymmetric position not stimulated during adaptation (C). The conjugate component of asymmetric vergence responses to points A and C are opposite in sign. Point

A requires a leftward conjugate component whereas point C requires a rightward conjugate component. Both points require the same horizontal vergence component. During adaptation a right-hyper disparity was associated with a 12 deg convergence component and a 4 deg leftward conjugate component. If the vertical phoria aftereffect depends on only the horizontal vergence eye position, the phoria at C will equal that at A, even though the conjugate components of these two positions are different. If the response depends primarily on the conjugate component, the vertical phoria aftereffect would have opposite signs (right-hyper vs right-hypo) at points A and C respectively.

Experiment 3(a): accommodative vergence. If horizontal disparity vergence can be coupled with vertical phoria, an interesting question is whether the phoria aftereffect can be driven by other components of horizontal vergence (such as accommodative or voluntary vergence) or only the horizontal vergence component stimulated during
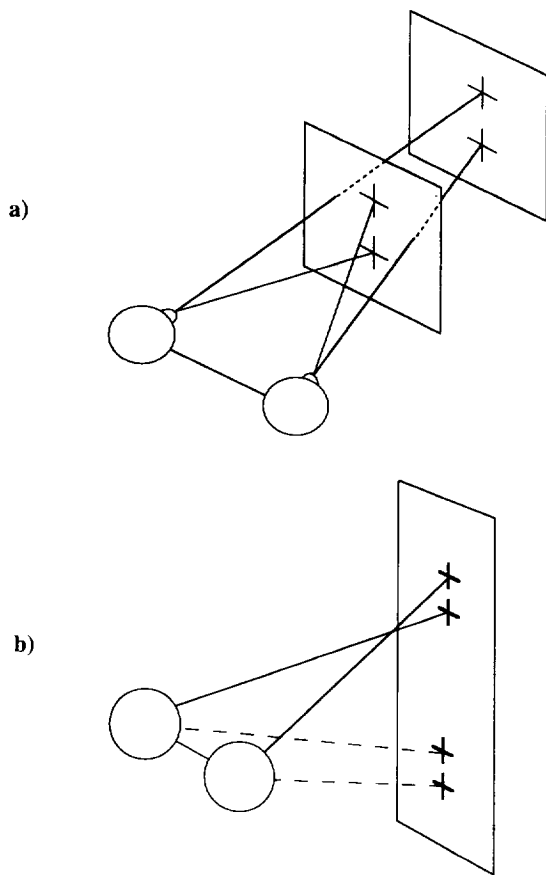
FIGURE 2. Stimulus positions used in Expt 3 for adaptation along (a) the depth axis in the midsagittal plane and (b) the vertical meridian in the frontoparallel plane.

adaptation (in this case disparity vergence). This issue was examined by first adapting the subjects along the depth axis to associate horizontal disparity vergence with the vertical vergence [as in Fig. 2(a)]. Then, the vertical phoria was tested in association with vergence stimulated either monocularly with lens induced accommodation (accommodative vergence) or binocularly with horizontal disparity (disparity vergence). If vertical phoria aftereffects were not specific to the horizontal vergence component used during the training period, then a change of vertical phoria should be elicited by monocularly stimulating accommodative vergence. During adaptation, a 1 deg right-hypo disparity was viewed at 2 deg symmetric horizontal vergence, and a 1 deg right-hyper disparity was viewed at 12 deg symmetric horizontal vergence. The vertical phoria response was tested at horizontal vergence positions of 2, 8.5, and 12 deg. Disparity vergence positions were induced with vertical

fusion bars, and accommodative vergence positions were induced with lenses before the right eye while the left eye was occluded.

Accommodative vergence was increased and monitored on an oscilloscope until the accommodative vergence equaled 2, 8.5, or 12 deg. The specificity of the vertical phoria aftereffect was also tested in an absolute presbyope (subject CS) by evoking voluntary vergence responses which have been shown previously to be an expression of accommodative vergence (McLin & Schor, 1988; Gnadt, 1992). The subject was asked to converge in the absence of a horizontal fusion cue while the horizontal vergence was monitored on an oscilloscope. The vertical phoria was sampled when the voluntary vergence reached a pre-specified amplitude (2, 8.5, or 12 deg).

Experiment 3(b): spatial crowding for vergence and conjugate eye position. Effects of small target separations upon amplitude of vertical vergence adaptation were compared for vertically disparate targets separated either along the depth axis in the midsagittal plane [Fig. 2(a)] or along the vertical axis in the fronto-parallel plane [Fig. 2(b)]. The separation between the adapting targets was either narrow (2.5 deg) or wide (10 or 18 deg). Adaptation was along the vertical meridian in which vertical phoria aftereffects are greater than along the horizontal meridian (Schor et al., 1993: Maxwell & Schor, 1994). The vertical disparity ranged from 10% to 20% of the target separation. Previously, this range was found to produce large amounts of vertical phoria adaptation (Schor et al., 1993). During adaptation a 0.5 deg change of vertical disparity was presented with the 2.5 deg separation, and a 2.0 and 1.8 deg change of vertical disparity was presented with the 10 deg depth and 18 deg vertical separations respectively. The 10 deg horizontal vergence change was from 2 to 12 deg convergence positions. Along the depth axis, the 12 deg vergence stimulus was the largest that the subjects could comfortably fuse over the 40 min adaptation period. Along the vertical meridian, the 18 deg separation was the widest target spacing that yielded accurate measures of eye position. The adaptation axis, target separation, target positions, and vertical disparities for the four adaptation conditions of Expt 3(b) are listed in Table 1.

Following 40 min of adaptation to either the narrow or wide separations in depth, the vertical phoria was tested at four horizontal vergence angles of 2, 6, 8.5, and 12 deg. Similarly, following 40 min of adaptation to either the narrow or wide separations along the vertical meridian, the vertical phoria was tested at six gaze elevations and depressions of ±1.25, ±6, and ±9 deg.

TABLE 1. Adaptation conditions [Expt 3(b)]

Adapting axis	Target separation (deg)	Target positions (deg)	Vertical disparity (deg)
Depth	Narrow (2.5)	6, 8.5	±0.25
Vertical	Narrow (2.5)	−1.25, +1.25	±0.25
Depth	Wide (10)	2, 12	±1.0
Vertical	Wide (18)	−9, 9	±0.9

RESULTS

Experiment 1: symmetric vergence. The mean changes in vertical phoria for all subjects in Expt 1 are shown as a function of horizontal conjugate eye position in the bar graph of Fig. 3(a). Vertical phoria was right-hypo at the far distance in all three horizontal directions of gaze, and right-hyper at the near distance in all three directions. Standard deviation bars overlap for conjugate eye positions at a given viewing distance, indicating that the direction of the aftereffect depended on horizontal vergence angle and not orbital eye position.

Experiment 2: asymmetric vergence. Changes in vertical phoria produced in Expt 2 are shown as a function of horizontal conjugate eye position in Fig. 3(b). The aftereffect was right-hypo phoria at the far point B and a right-hyper phoria at both near points A and C. The magnitude of the aftereffects at point A and C were compared to reveal the combined association of horizontal versions and vergence with vertical vergence. If versions had no influence on the aftereffect then the vertical phoria aftereffect should be equal at both near positions. However, if versions did influence the aftereffect, the vertical phoria should be reduced at point C compared to point A by the aftereffect associated with

FIGURE 4. Amplitude of vertical phoria aftereffects for Expt 3(a). The adaptation stimuli were associated with 2 and 12 deg symmetric horizontal vergence and the vertical phoria response was tested at horizontal vergence positions of 2, 8.5, and 12 deg. Disparity vergence positions were induced with fusion bars and accommodative vergence positions were induced with lenses before the right eye while the left eye was occluded.
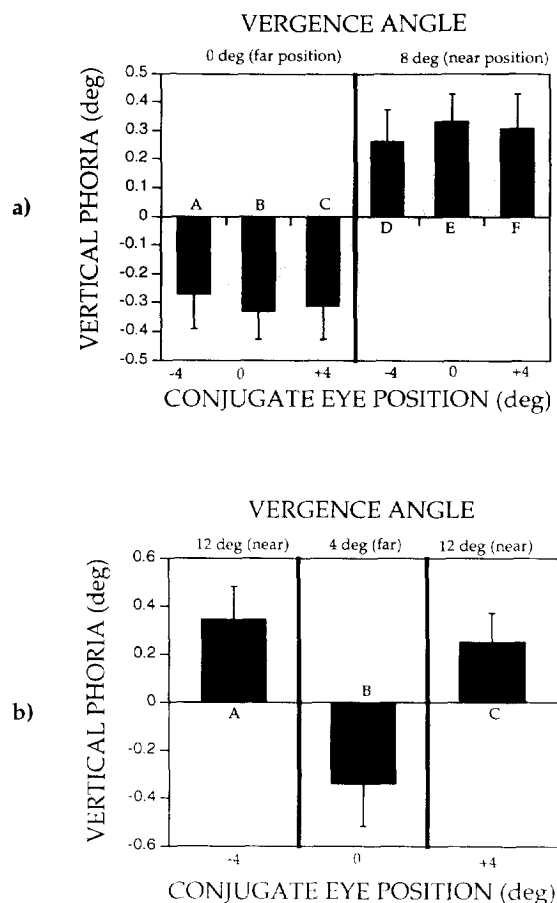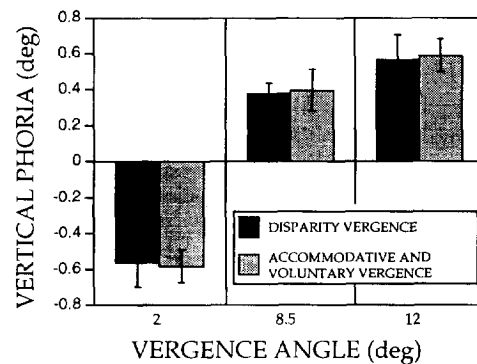
FIGURE 3. Amplitude of vertical phoria aftereffects for (a) Expt 1 and (b) Expt 2. The results are plotted as a function of conjugate horizontal eye position for far and near viewing distances. The labeled points (A–F and A–C) correspond to the eye positions shown in Fig. 1. Plus and minus values correspond to right-hyper and right-hypo phorias respectively. The vertical bars represent standard deviations.

the version component corresponding to the right-hypo disparity. Inspection of the figure reveals a small difference between the right-hyper phoria at point C and point A, however the overlapping standard deviation bars indicates the difference was not significant. The small difference might be contributed by the 4 deg version component, which based on prior studies would have been small (Schor, 1993; Maxwell & Schor, 1994). The results clearly demonstrate an influence of horizontal vergence on the vertical phoria aftereffect.

Experiment 3(a): accommodative vergence. After subjects CS and MC adapted to the associated horizontal and vertical disparity vergence, the vertical phoria was tested in association with horizontal disparity vergence and accommodative or voluntary vergence. The results in Fig. 4 show the differential components of the vertical phoria response for disparity vergence and accommodative and voluntary vergence.

For this experiment, horizontal disparity vergence was driven symmetrically with vertical fusion bars before both eyes, and accommodative vergence was driven asymmetrically with a lens before the right eye. Voluntary vergence was also evoked during monocular fixation. As shown by Expt 1, the vertical phoria aftereffect measured at a fixed horizontal vergence angle remained constant as horizontal conjugate eye position was varied. Therefore, in Expt 3(a), any difference between the vertical phoria associated with horizontal disparity vergence and the vertical phoria associated with accommodative vergence would not be due to differences in horizontal conjugate eye position in the two test conditions. As shown in Fig. 4, the same vertical phoria aftereffects appeared in association with disparity vergence and accommodative and voluntary vergence. This result indicates the vertical phoria aftereffect was not selective for the specific components of horizontal vergence that were associated with vertical vergence during adaptation.

Experiment 3(b): spatial crowding for vergence and conjugate eye position. Vertical phoria is plotted with ● as a function of horizontal vergence angle [Fig. 5(a, c)] or vertical conjugate position [Fig. 5(b, d)] in response to
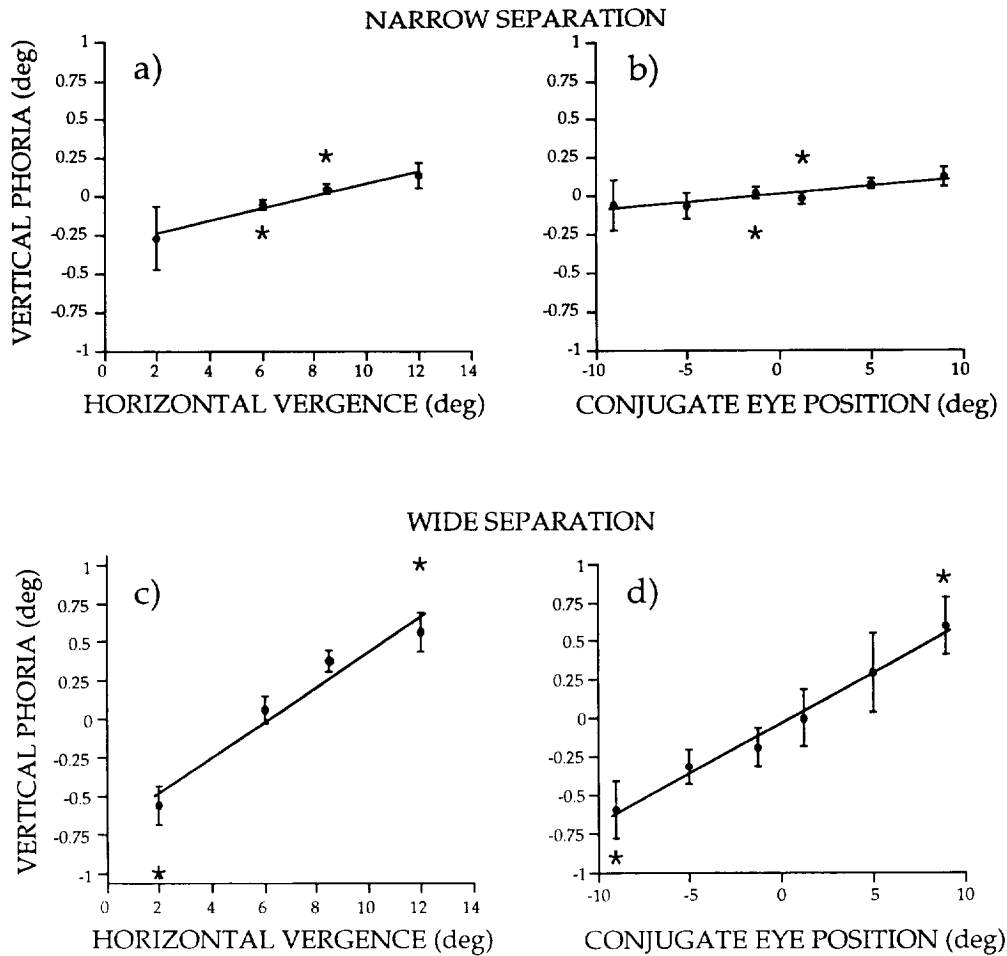
FIGURE 5. Vertical phoria aftereffects (●) for Expt 3(b). ★ indicate the positions of the adapting stimuli. (a) Adaptation was along a depth axis in the midsagittal plane with a narrow (2.5 deg) target separation. (b) Adaptation was along a vertical axis in the frontoparallel plane with a narrow (2.5 deg) target separation. (c) Adaptation was along a depth axis in the midsagittal plane with a wide (10 deg) target separation. (d) Adaptation was along the vertical axis in the frontoparallel plane with a wide (18 deg) target separation. Straight lines are linear regressions used to quantify the magnitude of vertical vergence aftereffects as a function of horizontal vergence and vertical conjugate eye position. Note that the amplitude of vertical vergence aftereffects indicated by the regression slopes of the narrow separation was approximately 4 times greater for targets separated along the depth axis than along the vertical axis, whereas the response magnitudes to wide separations was approximately 1.5 times greater for targets separated along the depth axis compared with the vertical axis.

adapting to the target separations in depth and along the vertical meridian respectively. The ★ represent the stimulus positions and their vertical disparities. The straight lines are linear regressions with slopes that relate changes of vertical phoria to either vertical conjugate eye position or horizontal vergence angle. For narrow target separations the slope of the regression function was approximately 4 times greater for targets separated along the depth axis than the vertical axis (0.041 vs 0.011); for wide target separations the slope was approximately 1.5 times greater for targets separated along the depth axis than the vertical axis (0.11 vs 0.065).

DISCUSSION

The vertical phoria aftereffect of adaptation to vertical disparity along the depth axis was driven by horizontal vergence. As shown by Expt 1, the conjugate or individual horizontal eye positions did not affect the response. Experiment 2 confirmed that horizontal vergence was

primarily associated with the vertical phoria aftereffect and that horizontal conjugate eye position played a minimal role in affecting the response. Interestingly, in a prior experiment, two subjects showed modest vertical phoria adaptation in response to vertical disparities separated laterally at the same target distance (Schor et al., 1993; Maxwell & Schor, 1994). This provides support for training a modest association between horizontal versions and vertical vergence aftereffects. If a stronger association could have been adapted between vertical phoria and horizontal conjugate eye position, the results of Expt 2 would have revealed larger changes in vertical phoria at the near viewing distance in leftward (point A) than rightward (point C) gaze.

Experiment 3 examined the difference in vertical phoria after adapting to targets separated along the vertical axis or depth axis. As shown by Expt 3(b), crowding effects minimize adaptation of the vertical phoria to targets with small vertical separations (e.g. 2.5 deg) in the

fronto-parallel plane (see also Schor *et al.*, 1993), however there was robust adaptation to targets separated by 2.5 deg along the depth axis in the midsagittal plane. Interestingly, in Expt 3(a), the vertical phoria aftereffect that was trained in association with horizontal disparity vergence was transferred to accommodative and voluntary horizontal vergence. These observations are consistent with a cross-coupling model which links vertical vergence to a supranuclear site that represents both accommodative and horizontal disparity vergence, e.g. the supraoculomotor nucleus (Mays, 1984; Judge & Cumming, 1986; Zhang, Mays & Gamlin, 1992).

There are numerous examples of associated activity within the oculomotor system. The most well known is the near triad in which convergence, accommodation, and pupil constriction are associated such that when either accommodation or convergence are stimulated alone, all three motor systems respond (Maddox, 1893; Muller, 1826; Alpern, 1969). These interactions are under a limited degree of adaptive control (Miles, Judge & Optican, 1987; Schor & Tsuetaki, 1987). A second example is the association of cyclo-vergence with both convergence and vertical conjugate eye movements (Nakayama, 1983). The eyes incyclo-rotate in upgaze and excyclo-rotate in downgaze. In addition, the vestibulo-ocular reflex gain can be modulated by head translation and rotation coupled with convergence (Paige, 1991; Post & Leibowitz, 1982; Hine & Thorn, 1987; Schwarz, Busettini & Miles, 1989; Snyder & King, 1992), and the horizontal vestibulo-ocular response can be elicited from vertical vestibular stimulation (Schultheis & Robinson, 1981). All of these motor associations could result from an innervation of one motor system by a correlate of activity of another motor system, conveyed by synaptic connections that were made more effective during adaptation.

Recent empirical evidence has shown that vertical vergence can also be associated with a sensory input stimulated by head pitch and roll when the body is upright and the eyes remain in the primary position of gaze (Maxwell & Schor, 1995). However, we have been unable to associate vertical vergence aftereffects with the context of perceptual cues to distance (i.e. loom, overlap, relative size, and relative motion) in the absence of any other associated motor activity (Schor & McCandless, 1995), suggesting that the associations we have observed involving vertical vergence result from low-level interactions. A variety of supranuclear regions of the brainstem and possibly the pons and cerebellum might serve as inputs to the adaptive system for vertical vergence (King, Fuchs & Magnin, 1981; McFarland & Fuchs, 1992; Gamlin, 1991; May, Porter & Gamlin, 1992; Zhang & Gamlin, 1994).

Cross-links between these supranuclear regions and vertical vergence or vertical eye position cells could be established during the training or adaptation phase and formed between only those neurons that were actively associated during adaptation. Vertical vergence aftereffects can be specific to head position, conjugate eye

position, and horizontal vergence posture depending on which of these were coupled during training. This selectivity could provide the oculomotor system the means to correct anomalies in specific supranuclear regions as they interface with vertical vergence. If modifications were made more peripherally in the final common pathway for vertical vergence or vertical eye position, the changes would influence all vertical vergence responses and vertical conjugacy of all classes of eye movements, including those that were not in need of repair.

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