



Head-position-dependent Adaptation of Nonconcomitant Vertical Skew

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Vertical phoria can be trained to vary with either head position or orbital eye position. The present experiments show that subjects can simultaneously adapt their eye-position-specific (nonconcomitant) vertical phorias in different directions at different head positions. Eye-position-dependent and head-position-dependent adaptive pathways, therefore, are not independent. Rather, the adaptation of vertical skew takes into account both eye and head position. In additional experiments, the magnitude of the nonconcomitant adaptive response was shown to be related to otolith output, increasing with head tilt ipsilateral to the tilt position at which training was received and decreasing in the contralateral direction. Copyright © 1997 Elsevier Science Ltd

Bielschowsky head-tilt phenomenon Ocular tilt reaction Space sickness Vertical phoria

INTRODUCTION

Eye-position-dependent (EPD) vertical phoria (defined for simplicity as the relative vertical positions of the two eyes in the absence of cues for vertical fusion) can be adapted in human subjects by having them train with vertical disparities that vary as a function of orbital eye position (Schor *et al.*, 1993; Maxwell & Schor, 1994). Such an adaptive mechanism might normally be used to compensate for extraocular muscle palsies or for deficits in underlying premotor pathways wherein the magnitude of the deficit varies with eye position due to orbital mechanics. Vertical phoria can also be adapted with respect to head position (Maxwell & Schor, 1996). Presumably, head-position-dependent (HPD) adaptation exists to compensate for bilateral imbalances in otolith-ocular pathways and to maintain good coordination between head tilt, torsion and vertical skew deviation (i.e., vertical binocular eye alignment).

The question arises as to how independent or interdependent the EPD and HPD adaptive pathways might be. One might argue that if EPD adaptation exists to correct muscle palsies and HPD adaptation exists to correct otolith imbalances, then the two mechanisms could be entirely independent. The site of EPD vertical phoria adaptation in that case might be close to the final common pathway, since the compensation required by a muscle palsy would be similar at all head positions. The site of HPD phoria adaptation, on the other hand, cannot

be too close to the final common pathway since it has been shown that different vertical phorias can exist for the same conjugate eye position following HPD adaptation (Maxwell & Schor, 1996). If the two adaptive mechanisms are independent then EPD adaptation is not contingent on head position and it should not be possible to adapt to different sets of eye-position-specific disparities at different head positions.

Such a scheme is almost certainly overly simplistic. Extraocular muscle forces and head position are intimately related. For example, the set of innervations to the vertical recti required to hold the eye in primary position with the head tilted about a naso-occipital axis (roll) is not the same as with the head held upright because of ocular counterroll and the secondary actions of the obliques which would produce vertical skew if left uncompensated by the vertical recti. The relative participation of the vertical recti and obliques also depends on horizontal version and vergence. Such a complex parsing of muscle forces might favor an adaptive system that would allow for the adaptation of vertical skew for many different combinations of head and eye positions. If this were true then EPD adaptation could be specific to the head position at which training was received and it might be possible to adapt concurrently to different sets of eye-position-specific disparities at different head positions.

The present experiments examined the interdependence of EPD and HPD adaptation. Subjects trained with eye-position-dependent vertical disparities that were increasingly right-over-left at one head position and increasingly left-over-right at another. Following a 1 hr training period, all subjects demonstrated oppositely directed nonconcomitant vertical phorias at the two head

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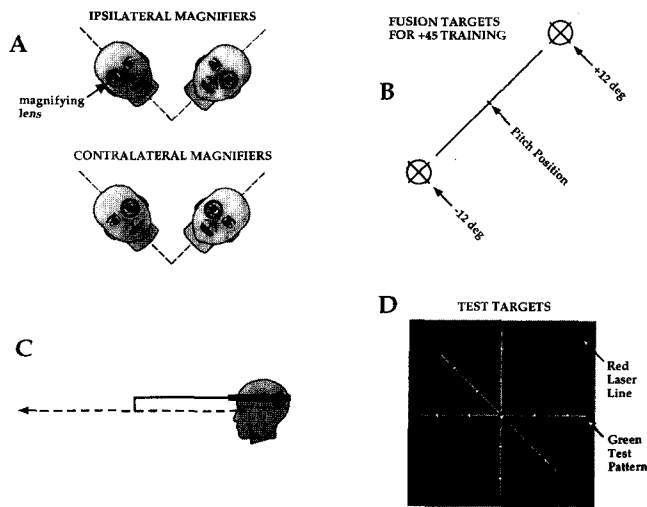


FIGURE 1. Methods: (A) Vertical disparities were created by placing afocal magnifiers before one eye with the head tilted 45 deg to the right or to the left. (B) Training targets for roll to the right. Identical targets (from the subject's point of view) were also present for roll to the left. (C) Subjects maintained pitch and roll head position by aligning a head-mounted pointer with a distant target. (D) Test pattern with the red laser line positioned for testing the subject at +45 deg.

positions. The specificity of the EPD adaptation to the head position at which training was received was also tested. It was found that, on average, the EPD adaptive response fell to half its value with the head rolled 60 deg contralateral to the position at which training was received. The EPD adaptive response increased in magnitude for head tilts ipsilateral to the position at which training was received.

METHODS

Training procedures

The purpose of the first paradigm was to try to train EPD vertical phoria to be increasingly right-over-left as a function of eye elevation at one head position and increasingly left-over-right with eye elevation at a second head position. Two afocal magnifying lenses were mounted on an instrument platform in front of the subject so that when the subject's head was rolled to the right (right ear toward the right shoulder) one of the magnifiers was in front of one eye and when the subject rolled to the left the other magnifier was in front of the other eye. The lenses were in front of either the eye ipsilateral to the direction of head roll or in front of the contralateral eye [Fig. 1(A)]. During training, subjects alternately viewed two vertically separated targets at each of two head positions. The two training targets were 24 deg apart in the subject's midsagittal plane [Fig. 1(B)]. An example of the training procedure is as follows: with the head rolled 45 deg to the right and ipsilateral magnification, the upper target (at 12 deg elevation) appeared higher in the right eye than the left (a right hyper-disparity) and the lower target (at -12 deg elevation) appeared higher in

the left eye than the right (a left hyperdisparity). In order to fuse the targets visually, therefore, the subject needed to produce a right hyper-deviation of the visual axis when looking at the upper target and a left hyper-deviation when looking at the lower target. The reverse deviations were required when the head was tilted 45 deg to the left. The subjects alternated their gaze between the four fusion targets (two eye elevations at each of two head positions) at their discretion. The instruction was to attempt to fuse each disparity as well as possible before changing gaze to the next target. The power of the lenses was selected so that the subjects experienced diplopia initially but were able to fuse the targets within approximately 10–20 sec at the onset of training. Stronger lenses were substituted as adaptation progressed and the subjects were able to fuse the targets within 2 or 3 sec (after approximately 20 min of training). The consistent use of lenses between subjects was not a concern, since the objective was to compare the gains of EPD adaptation for different head positions within a single experimental session (and not between subjects or sessions). Most subjects started a session with 4–6% magnification and ended with 6–8% magnification. The training period lasted for 1 hr.

A head-mounted plexiglass rod protruded 25 cm in front of the subjects' eyes in the midsagittal plane [Fig. 1(C)]. A vertical bar attached to the end of the rod allowed the subjects to establish and maintain the correct head position during training and testing. Proper pitch position (head tilt about an interaural axis) was attained by aligning the end of the bar with a mark midway between the two training targets or the center point of the test pattern. The correct roll position was established by aligning one vertical edge of the bar with a line connecting the two fusion targets or with the appropriate green line on the test pattern.

The second experiment was designed to test the spread of EPD adaptation to head positions not specifically adapted. The training paradigm was the same as in the prior experiment except that the subjects maintained a single head position (45 deg left, 45 deg right, or upright) throughout the 1 hr training period. Vertical disparities were created by an 8% afocal magnifier placed before the right eye. After training, the subjects were tested at five vertical eye positions in each of 3–5 different roll positions.

Vertical phoria measurements

Vertical phoria was measured with a Lancaster test in which the visual images seen by the right and left eyes were isolated with red and green filters (Lancaster, 1939). A pattern of green test targets [Fig. 1(D)] was projected onto a tangent screen 150 cm away from the subject and could be seen only by the green-filtered eye. The subject controlled the position of a red laser pointer and the laser spot could be seen only by the red-filtered eye. The difference between the tangent screen positions of the red laser spot and the green target was taken as the phoria measurement. The red filter was worn before the subject's dominant (sighting) eye and phoria was always

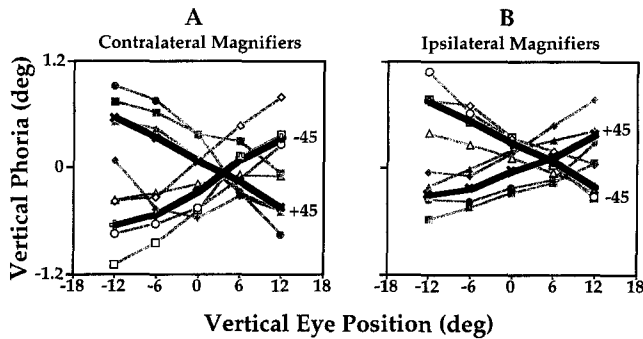


FIGURE 2. Change in vertical phoria following training with magnifiers on the eye contralateral (A) or ipsilateral (B) to the side of head tilt during training. Phoria was tested with the head rolled to the left 45 deg (open symbols) or right (solid symbols). Symbols remain constant for individual subjects (light lines) in all subsequent figures. Heavy lines: responses averaged across subjects.

calculated as right eye position minus left eye position. The laser dot and target location (the intersection of the long green vertical line and horizontal tick mark) did not make good fusion stimuli and should not have affected eye alignment during testing. A red vertical (with respect to the subject) laser line was projected onto one of the green lines of the test pattern—the one at the roll angle to be tested—and the subjects were instructed to keep the red and green lines (both in their sagittal planes) visually superimposed in order to control horizontal vergence, while leaving vertical eye deviation free to vary. Horizontal vergence would produce artifactual vertical phorias if the phoria measurements were not made precisely in the subject's sagittal plane. Controlling both head position and horizontal vergence angle ensured that such artifacts did not occur. Phoria measurements were made before and after the training period and subsequent figures and analysis represent the change in vertical phoria that resulted from training. Each measurement was made three times and the order of the post-training measurements was systematically varied in order to average out any decay that might have occurred in the training aftereffect over the time required by data collection.

Four subjects were used in these experiments, each of whom had normal eye alignment when viewing binocularly. Two of the subjects had refractive errors of approximately 2D and wore their corrective lenses during the experiments. Each subject gave his or her written informed consent.

RESULTS

Training at two roll positions

All subjects were able to adapt simultaneously their nonconcomitant vertical phorias in opposite directions for the two head positions at which training was given. Subjectively, the subjects did not consider training at two head positions with two sets of disparities any more

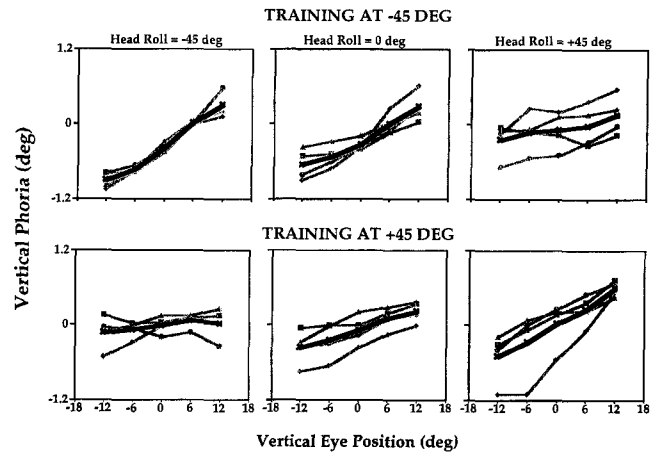


FIGURE 3. EPD vertical phoria at three different roll positions following training to a magnifying lens on the right eye and the head tilted 45 deg to the left (top row) or to the right (bottom row).

difficult than adapting at one head position with one set of disparities. Figure 2(A) shows the change in vertical phoria (post-training minus pre-training) resulting from training with a magnifying lens in front of the left eye when the head was tilted to the right and in front of the right eye when the head was tilted to the left (contralateral magnification). Vertical phoria was measured at five different eye elevations at each head position. Figure 2(B) shows the change in phoria resulting from training with the opposite lens configuration (ipsilateral magnification). The change in EPD vertical phoria in each subject was appropriately directed to reduce the diplopia experienced at the two eye elevations at which training was received. The slopes of linear regressions performed on the averaged data (heavy symbols in Fig. 2) for contralateral magnification are 0.043 deg vertical phoria per deg of eye elevation for left roll and -0.042 for right roll (about one-half of the change in phoria required by an 8% magnifier). For ipsilateral magnification, the coefficients are -0.040 for left roll and 0.029 for right roll.

Training at one roll position

Subjects trained for 1 hr with a magnifying lens in front of their right eyes with their heads rolled either 45 deg to the right, or, in a different set of trials, 45 deg to the left. The magnifying lens was always on the right eye during training, regardless of the direction of head tilt. Figure 3 shows the changes in vertical phoria for four subjects following a 1 hr training period with the head tilted to the left [Fig. 3 (top)] or to the right [Fig. 3 (bottom)]. Vertical phoria was tested at five vertical eye positions with the subjects' heads upright, tilted 45 deg to the left and 45 deg to the right. For all subjects, the training aftereffect was greatest at the head position at which training was received and decreased with head tilt to the contralateral side.

The effect of head position on the magnitude of the

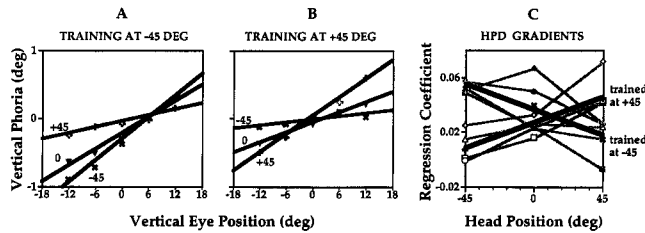


FIGURE 4. The mean data from Fig. 3 with lines fit by linear regression for each roll position tested (+45, 0, and -45 deg) following training with the head tilted to the left (A) or to the right (B). (C) Heavy line: slopes of the regression lines shown in (A) and (B) plotted as a function of the head position at which the EPD measurements were made. Light lines: slopes of regression lines fit to EPD data (not shown) for individual subjects.

training aftereffect was made more obvious by plotting the average changes in vertical phoria measured at each of the three head positions on the same graph [Fig. 4(A) and (B)]. The lines in Fig. 4 were fit by linear regression. The head-position-related fall-off in the magnitude of the training aftereffect was quantified by plotting the regression coefficients [i.e., the slopes of each of the lines shown in Fig. 4(A) and (B)] as a function of the head position at which the measurements were made [Fig. 4(C)]. The average change in EPD slope from one head position to the next was 4.2×10^{-4} for both the right and left training positions, demonstrating that EPD training was equally effective for training with the head tilted to the left and right, that is, there was no predisposition for vertical phoria to change in a particular direction independent of training. Based on these regression coefficients, no training aftereffect would be expected (i.e., the EPD slope would be zero) at a head position 120 deg contralateral to the head position at which training was obtained.

Testing at 90 deg roll

The results shown thus far could be interpreted in two ways: the decrease in training effect with head positions contralateral to the head position at which training was received might mean that the adaptation was directly proportional to otolith output, since utricular discharge varies with head position. Alternatively, it may reflect a tuning effect wherein the adaptive response was specific to the head position at which training was received. If the former were true then the training aftereffect should increase with further ipsilateral roll since the discharge of ipsilaterally activated hair cells would increase with 90 deg roll. If, on the other hand, the adaptive response were tuned to the head position at which training was received then vertical phoria should decrease with further ipsilateral roll. To test this, three of the four subjects trained once again with a magnifying lens on the right eye and the head rolled 45 deg to the right but were tested with the head upright, tilted 45 deg to the right, and tilted 90 deg to the right. The fourth subject was unable to perform these experiments because he was unable to

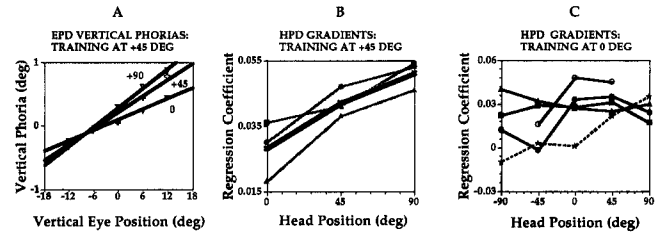


FIGURE 5. (A) Change in EPD phoria following training to a magnifying lens on the right eye and the head tilted 45 deg to the right and with phoria tested with the subject rolled 0, 45 and 90 deg to the right. (B) Heavy line: slopes of the regression lines shown in (A) plotted as a function of the head position at which the measurements were made. Light lines: slopes of the regression lines fit to EPD data (not shown) for individual subjects. (C) Solid lines: slopes of regression lines fit to EPD phoria responses for individual subjects (not shown) following training with the head erect. Dashed line: vertical phoria prior to training for one subject (see text for details).

adequately maintain fusion of the red and green sagittal lines with his head rolled 90 deg. The magnitude of the EPD response increased for all three subjects for ipsilateral 90 deg roll [Fig. 5(A, B)], suggesting that the training effect was not tuned specifically to the training position but was contingent on otolith output.

Training with the head erect

Given that the magnitude of the adaptive response was proportional to otolith output when training was received with the head tilted, it is not clear how the adaptive response would spread following training with the head upright where the utricles are not stimulated. With the head erect, vertical skew training would not be associated uniquely with either left or right tilt-sensitive hair cells. To test this, three subjects were trained with their heads upright and were tested at five head positions, from 90 deg right roll to 90 deg left roll in 45 deg increments. Following training, two of the three subjects had approximately the same EPD adaptive response at all five head positions tested [Fig. 5(C), triangle and squares]. The adaptive response of the third subject [Fig. 5(C), circles] was similar at the upright training position and with 45 and 90 deg roll to the right, but fell off precipitously with roll to the left. This subject was retrained and retested on a different day at three head positions (upright, +45 and -45) and the pattern of adaptation was nearly identical [Fig. 5(C), open circles]. It may be worth noting that, unlike the other two subjects, this subject had a prominent pre-training nonconcomitant hyperphoria that increased with roll to the right [Fig. 5(C), dashed line] which might indicate an otolith asymmetry or a muscle palsy that is normally compensated for with the head erect.

DISCUSSION

All subjects were able to adapt their EPD vertical phorias in opposite directions at two different head positions simultaneously. This means that the EPD and

HPD adaptive mechanisms are not independent but that adaptation involves an association of eye and head position pathways. Perhaps it is more accurate to say that there is one adaptive mechanism that takes both eye and head position into account. The fact that different EPD vertical phorias may exist for the same eye position suggests that adaptation is not at the level of the final common pathway. This makes sense since the change in innervation required to adapt a vertical skew with the head tilted to the left would not have the same effect with the head tilted to the right because of ocular counterroll and the change in relative participation of the vertical rectus muscles and the obliques. The results of training EPD vertical phoria at a single roll position indicated that adaptation was associated with an otolith signal when the head was tilted during training. Broadly speaking, there are two populations of utricular hair cells relevant to these experiments; those with activity that increases with right roll and those with activity that increases with left roll. The subjects' ability to adapt to oppositely directed nonconcomitant disparities at two head positions might be the result of associating each of the two adaptive responses with one of the two populations of hair cells (or with both in a push-pull fashion). The lack of head position specificity following training with the head erect might have occurred because neither population of hair cells was uniquely active in that situation.

The preliminary results of similar experiments by McCandless & Schor (1996) indicate that EPD vertical phorias can also be adapted in association with viewing distance. In those experiments, elevation-dependent vertical phoria was trained in one direction for distant targets and in the opposite direction for near targets. Just as the set of innervations to the vertical recti and obliques required to hold the eyes at a particular elevation is not the same with the head rolled to the right or to the left because of ocular counterroll, the set of innervations required to hold the eyes at a particular elevation is not the same with targets at different viewing distances because of horizontal vergence. In line with this result is the observation that vertical eye alignment in the absence of cues for vertical vergence is very precise during fixations of near-eccentric targets, where geometrical considerations suggest a vertical misalignment might occur (Schor *et al.*, 1994). While the visual axes would not be misaligned in these circumstances if orbital mechanics forced eye rotations to exactly follow a Helmholtz coordinate system (Schor *et al.*, 1994; Collewijn, 1994), a more likely explanation is that the oculomotor system is adapted for good binocular alignment at different version and vergence positions (Schor *et al.*, 1994; Ygge & Zee, 1995).

We assume that the purpose of the head-tilt-related adaptive mechanism is to maintain the coordination of head tilt, ocular counterroll, and vertical skew. The loss of proper coordination is evident in patients with deficits in otolith-ocular pathways (Corbett *et al.*, 1981; Brandt & Dieterich, 1987; Gresty *et al.*, 1992) and in patients with superior oblique (SO) palsies who exhibit ipsilateral eye

elevation in association with head roll (the Bielschowsky head-tilt phenomenon). The manifestation of these symptoms indicates that the deficits are beyond the adaptive capacity of the system, although the magnitude of the vertical skew in a positive Bielschowsky test may itself indicate an adaptive process (Kommerell & Klein, 1986). Robinson (1985) has shown, using a model of orbital mechanics that the vertical skew associated with a SO palsy is far greater than would be expected simply from the loss of the secondary action of the SO and argues that the increased skew is due to a long-term change in innervation to the superior rectus muscle. A loss in coordination between head tilt and torsion (vertical skew has not been tested) has been implicated in space motion sickness where presumably the adaptive response required to compensate for bilateral asymmetries in the otolith organs in normal gravity produces an inappropriate response in a micro-gravity environment (von Baumgarten & Thümler, 1978; Lackner *et al.*, 1987; Diamond & Markham, 1991).

The present experiments are similar in some respects to those in which sinusoidal pitch was associated with horizontal image motion in a roll-position-specific manner in cats (Baker *et al.*, 1987). For example, when a cat lay on its left side, pitch up rotations about its interaural axis were coupled to rightward (cat-referenced) visual motion and pitch down rotations to leftward visual motions. With the cat on its right side, the coupling was reversed. These animals were able to adapt the gains of their cross-coupled vestibulo-ocular reflexes in opposite directions at the two head positions. Peterson *et al.* (1991) have speculated that different populations of Purkinje cells mediate VOR cross-coupling at the two head positions and that such context-specific plasticity might be too complex to train long-term changes in brainstem synaptic weighting. It should be noted that in the present experiments the EPD adaptive response was not maximal at the head position at which training was received but was proportional to head tilt, increasing with ipsilateral and decreasing with contralateral roll. While this finding does not exclude the possibility of a complex association matrix, it is suggestive of a gain change and not a response tuned to particular head position.

One might begin to wonder whether vertical phoria can be adapted in virtually any context-dependent manner. In fact, this is not so. We were unable to adapt vertical phoria substantially in relation to changes in head position about an earth-vertical axis (Maxwell & Schor, 1996). It also was not possible to adapt EPD vertical phoria in relation to higher-level distance cues such as loom, even though it is possible to adapt vertical phoria in relation to horizontal vergence angle (Schor & McCandless, 1995). Nor was it possible to produce adaptation to two opposing disparities that were presented at the same conjugate eye position but that followed oppositely directed saccades (Gleason *et al.*, 1993). The cases in which adaptation is possible all seem to involve fairly low level stimulus cues in experimental paradigms that mimic deficits that might naturally occur. Such adapta-

tion takes into account head position, horizontal and vertical conjugate eye position and vergence angle. In the present experiments, adaptation might also involve cross-coupling between oblique and vertical rectus pathways but, if so, there must be in addition a more explicit otolith input, since vertical phoria can be adapted in relation to changes in pitch position (Maxwell & Schor, 1996), where there is little or no change in torsion (Bucher *et al.*, 1992).

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