



Adaptation of Vertical Eye Alignment in Relation to Head Tilt

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Binocular visual feedback is used to continually calibrate binocular eye alignment so that the retinal images of the two eyes remain in correspondence. Past experiments have shown that vertical eye alignment (measured as vertical phoria) can be altered by training to disparities that vary as a function of orbital eye position. The present experiments demonstrate that vertical eye alignment can also be trained to differ with head position when eye position (with respect to the orbit) is held constant. Changes in head position were about either an earth-vertical or earth-horizontal axis to distinguish otolith-ocular related adaptation from cervical-ocular related adaptation. Changes in head position were implemented by either by rotating the whole body (WB) or by rotating the head with the body stationary (HO). Following training, adaptation of eye alignment was observed in all cases of rotation about an earth-horizontal axis and for HO pitch rotations about an earth-vertical axis. The results illustrate the ability of the oculomotor system to compensate for imbalances in otolith-ocular pathways.

Vertical vergence Phoria Binocular alignment Hering's law Otoliths

INTRODUCTION

The accurate coordination of binocular eye movements is of obvious importance to animals with overlapping fields of view and stereoscopic vision. The close coordination of the movements of the two eyes is remarkable. Vertical saccades in the two eyes are very tightly yoked (Collewijn *et al.*, 1988; Bains *et al.*, 1992) and vertical eye positions during the fixation of near targets in tertiary positions agree to within <0.25 deg, even in the absence of cues for vertical binocular fusion (Schor *et al.*, 1994). It has often been suggested that the two eyes move together because they are driven by common signals, Hering's, so called, law of equal innervation. Hering's law has usually been interpreted to mean that all eye movements comprise combinations of symmetrical versional (conjugate) and symmetrical vergence (disjunctive) eye movement signals. In a behavioral sense this is perhaps trivial, saying that the eyes either move together or they do not. What is of greater interest is the degree to which Hering's law reflects oculomotor organization at a neural level, that is, the extent to which version and vergence are the result of 'hard-wired' bilateral pathways. An alternative possibility is that the two eyes are controlled independently, but this characteristic is usually overlooked because experimental stimuli typically evoke conjugate eye movements or because, more often than

not, the position of only one eye is recorded. Although there is considerable evidence that binocular yoking is fundamental to the organization of the oculomotor system, other behavioral, physiological, and anatomical evidence suggests that the two eyes are not always driven by a common signal [reviewed in Dell'Osso (1994)].

Although it may not be known how accurate coordination of the two eyes is achieved, it is clear that the oculomotor system needs to be able to compensate for changes in binocular alignment brought on by development, disease or injury. Extensive experimentation has shown that binocular alignment can be altered through the use of prisms (Schor, 1979; Henson & North, 1980; Oohira & Zee, 1992), lenses (Henson & Dharamshi, 1982; Lemij & Collewijn, 1992) and other optical means (Schor *et al.*, 1990; Maxwell & Schor, 1994). The visual stimulus leading to eye position-specific adaptation (retinal image disparity) in these experiments mimics the concomitant or noncomitant disparities that might result from a paresis of one or more extraocular muscles or a deficit in the underlying motor pathways.

Vertical deviations of the lines of sight in other instances might be elicited by an imbalance in one of the bilateral sensory afferent systems such as the semicircular canals or otolith organs. It is unlikely, for example, that the two saccules and utricles are perfectly matched at birth and remain so throughout life. A mechanism for maintaining balanced right and left otolith-ocular pathways would seem additionally important since unilateral stimulation of the maculae results in disjunctive vertical eye movements (Maxwell, 1920/21; Suzuki *et al.*, 1969;

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Fluur & Mellstrom, 1970; Curthoys, 1987). Utriculo-ocular pathways, presumably through the interstitial nucleus of Cajal, may be responsible for the ocular tilt reaction which consists of a coordinated head tilt, deviation of vertical eye alignment and cyclovergence (Westheimer & Blair, 1975; Lueck *et al.*, 1991). Insults to macular afferent pathways that are beyond the ability of the adaptive system to compensate may result in skew deviations (Corbett *et al.*, 1981).

In the present experiments vertical eye alignment (i.e., vertical vergence) was trained to vary with head position while conjugate eye position remained constant. During training, vertical vergence was altered by placing either a base up or base down prism before one eye in each of two head positions. For example, if the stimulus for a right hyperdeviation of the eyes (target for the right eye appears higher than the left) was presented with the head pitched up, then the stimulus for a left hyperdeviation was presented when the head was pitched down. Head position alternated between these two positions (and their associated disparities) for 60 min. Subjects adapted to different positions of either pitch (rotation within the subject's sagittal plane), roll (rotation within the subject's frontal plane) or yaw (rotation within the subject's horizontal plane). Pitch rotations were about either an earth-vertical or earth-horizontal axis to distinguish otolith-ocular from cervical-ocular adaptation, since with earth-vertical rotations the position of the maculae relative to gravity does not change. In some trials, only the head changed position (HO) and in other trials the whole body (WB) was rotated in order to examine the contribution of neck proprioceptive signals to adaptation. Following training, subjects showed a change in vertical eye alignment appropriate for disparities associated with all changes in head position about an earth-horizontal axis. Adaptation was also coupled to changes in HO pitch position about an earth-vertical axis, indicating that in some cases a neck proprioceptive signal can be used when a changing otolith signal is not present. Adaptation with WB roll rotations, on the other hand, demonstrate that a changing otolith signal is sufficient. The results imply that changes in vertical eye alignment can be associated with otolith-ocular and, in some cases, cervical-ocular pathways.

METHODS

Eye position measurement

Vertical phoria (vertical deviation of the lines of sight tested in the absence of binocular cues for vertical fusion) was measured using a variation of the Lancaster test. Subjects wore a red filter in front of their dominant eye (the right eye for all subjects) and a green filter in front of the other. Target displays were projected through a green filter onto a white tangent screen in a darkened room and subjects pointed to selected target spots with a red laser. A red line was created by placing a Maddox rod in front of a second laser. The red laser line and laser pointer could be seen only by the right eye and the green targets

could only be seen by the left eye. The subjects were instructed to visually superimpose the red line on a vertical column of green dots. This served to provide a visual cue for maintaining a fixed angle of horizontal vergence while leaving vertical vergence free to vary. The center of the target display (zero elevation) was placed at the same distance from the floor as the subject's eyes. The distance to the tangent screen was 150 cm for most experiments. A bite plate, head band, or chin cup was used to control head position depending on the experiment. Vertical phoria was measured by having the subjects place the bottom edge of the red laser dot on the top edge of a specific green spot. The red and green spots were sufficiently different in size that they were not readily fused. The experimenter marked the locations of the laser spot and target spot with a pencil line. Vertical phoria was taken as right eye position (laser spot) minus left eye position (target spot). Sets of data were always taken before and after adaptation and all figures represent the change in phoria (post-adaptation minus pre-adaptation) unless otherwise noted. Subjects AO and MW were emmetropic. CS and MC were 2D myopes with approx. 1 deg of astigmatism. These two subjects wore their corrections during the experiments. Subjects AO, MC, MW, and CS were 18, 22, 26, and 52 years of age, respectively.

Training procedures

Vertical eye alignment was trained by associating two different visual disparities with two different head positions. Changes in head position were about either the pitch, roll or yaw axis (Fig. 1). The two disparities were produced by base up or base down prisms fixed in space so that the subject looked through one of the prisms at one head position and through the other prism at the other head position. Changes in head position were either by rotation of the head only (HO), in which case the head rotated while the torso remained stationary, or the whole body (WB) wherein the head and torso rotated in unison. Pitch rotations were either about an earth-vertical or an earth-horizontal axis. All roll rotations were about an earth-horizontal axis and all yaw rotations were about an earth-vertical axis. The subjects alternated their gaze between the two head positions at their discretion, the instruction being to fuse the disparity as well as possible before switching to the other target (about every 3–10 sec). In previous experiments, it was found that effective adaptation was achieved if the training disparities were large enough to initially produce diplopia for several seconds but not so large that they could not eventually be fused. In the present experiments, prism values ranged from 1 to 2 diopters. Subjects closed one eye when shifting head position so that a binocular view of the target was seen only when the head was in the desired position and stationary. Head and eye position were established utilizing a pointer that moved with the subject's head [Fig. 1(C)]. The pointer was at the end of a plexiglass stalk that projected from a head band and was 25 cm from the front of the subject's eyes in the

midsagittal plane. During training and testing, the subject fixed his head position by aligning the pointer with the distant target as seen with the open eye. In this way, the eyes always were fixed in approximately the same conjugate position with respect to the orbit (primary position) when viewing the two training targets and the multiple test targets. Subjects were trained and tested on only one of the paradigms per day.

HO upright pitch (earth-horizontal axis)

In the *upright pitch* paradigm, two different vertical disparities were associated with two different head positions in the sagittal plane with the subject seated upright. Head position was controlled with a head band and pointer as described above. The head band was attached to a rigid support by axles that were aligned with the subject's interaural axis and in the horizontal plane. Subjects were able to change head position with little body movement. The two disparities were produced by placing a base up prism in front of the left eye when viewing one target and a base down prism in front of the left eye when viewing the other. Each of the training targets consisted of a circle superimposed on a cross. The two targets were separated by an angle of 36 deg along the primary vertical meridian and the midpoint of the two targets was 150 cm from the center of the subject's eyes. Each subject performed this experiment twice, once with the base up prism at the upper position and the base down prism at the lower position and once with the opposite prism configuration. Vertical phoria measurements were taken at pitch angles of 24 deg up to 24 deg down in 12 deg increments, before and after training.

In the majority of test trials, vertical phoria was measured for different pitch positions while orbital eye position was held constant. In additional trials, vertical phoria was also tested at a number of different orbital eye positions while head position was held constant. For example, with the head held in the 12 deg pitch up position vertical phoria was tested as before except that gaze angle was changed by eye movements rather than by head movements. This process was repeated with the head fixed in the 12 deg pitch down position. Each target was tested three times at each target position before and after training.

HO and WB on-side pitch (earth-vertical axis)

Conditions for *on-side pitch* were identical to those above except that subjects and displays were rotated 90 deg to the right (so that subjects were lying with their right ear down). Changes in pitch position of the head, therefore, were about an earth-vertical axis, producing no change in orientation of the otolithic maculae with respect to gravity. With head only (HO) rotations, subjects lay on their sides and the axis of rotation was the same as in upright pitch, namely, coincident with the interaural axis. With whole body (WB) rotation, subjects lay prone on a padded board with their heads turned to the left to face the tangent screen. The board swiveled about an axis coincident with the centers of rotation of the

subjects' two eyes (an earth-vertical axis) and had wheels on the other end to support the subjects' weight. This allowed the subjects to propel themselves from one pitch position to another without changing head position relative to the body.

HO and WB roll

Two different vertical disparities were associated with two different roll positions (45 deg to the right or to the left of earth-vertical). The training target was the same circle and cross pattern used for upright pitch except that it was rotated 45 deg to match the roll position of the subject. Roll position was established by having the subject align a head-referenced horizontal indicator (mounted on the head pointer) with one of the (head-referenced) horizontal arms of the target cross. When the indicator was aligned with one arm of the cross the head was rolled 45 deg to the left of upright and when aligned with the orthogonal arm it was rolled 45 deg to the right of upright. A chin rest helped maintain the proper head position. During training, one prism was placed in front of the left eye with the subject rolled to the left and in front of the right eye with the subject rolled to the right. The power of each prism was aligned with the subject's sagittal plane to create a head-referenced vertical disparity. Both prisms were either base up or base down so that opposite disparities were produced in the two head positions. Four oblique green lines were superimposed (with a second projector) onto the green test grid used to test upright pitch. This created a display that could specify five different roll positions ranging from -90 deg (left ear down) to +90 deg (right ear down) in 45 deg increments. It is important to note in the HO trials that the 0 and 45 deg positions were attained with head-on-neck tilts alone but the 90 deg roll positions by necessity were attained using a combination of head-on-neck and whole body rotations.

For WB trials, the subject wore a foam cervical collar that restricted head-on-neck movements. It was not possible for the subject to adopt a 90 deg roll position while wearing the collar so data are limited to the upright and two 45 deg roll positions. The roll position to be tested was specified by projecting a red laser line onto one of the green lines or columns of green spots. The laser line also served to control horizontal vergence angle (as when pitch was tested) by the subject visually fusing the red laser line with the appropriate green line or column of spots (both in the subject's midsagittal plane). All phoria measurements were made at the single green spot in the center of the display. Each measurement was repeated three times for each of the five head positions before and after the training period.

HO and WB yaw

Two different vertical disparities were associated with two different yaw positions. Head rotations were about an earth-vertical axis. In WB trials, head position was controlled by a mouth-bite apparatus. The axis of rotation was approx. 5 cm in front of the eyes where the mouth-

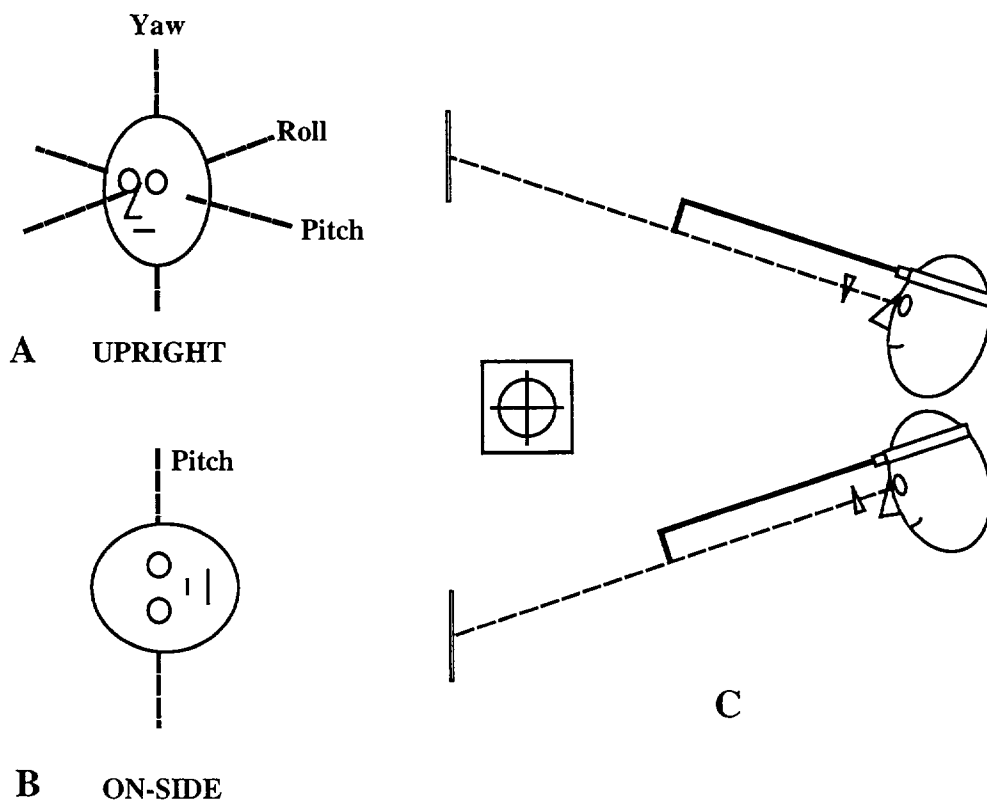


FIGURE 1. (A) Rotational axes. Positive rotations are for nose up pitch, yaw to the right and right ear down roll. (B) On-side pitch. Rotation about an earth-vertical axis with the subject rolled 90 deg to the right. (C) Upright pitch training paradigm. Head position was established by aligning a head mounted pointer with a distant target. Two different vertical disparities were created at each of two head positions by viewing one target through a base up prism and the other target through a base down prism. Each target consisted of a cross superimposed on a circle (inset).

bite apparatus was attached to a vertical support. In HO trials, the axis of rotation was approximately through the center of the head. Subjects alternated gaze (head position) between two targets that were separated by 36 deg along the primary horizontal meridian. Two prisms were arranged so that the subject looked through one prism with the right eye when turned toward the right target and the left prism with the left eye when turned toward the left target. The prisms were either both base up or base down so that the resulting disparities were opposite in sign for the two head positions (e.g. a right hyperdisparity on the right and a left hyperdisparity on the left). Testing was essentially the same as for adaptation to pitch position except that the target points were along the primary horizontal meridian rather than the primary vertical meridian.

Data analysis

Phorias were calculated as right eye position minus left eye position so positive values represent right hyperphorias. Linear regressions were performed on each subject's data set for each experimental condition. Table 1 presents the mean response slope (deg of phoria adaptation/deg head tilt) for n subjects for each test condition. Stimulus slopes are defined as positive for trials in which right hyperdisparities were presented for

up pitch, right yaw and right roll and left hyperdisparities were presented for down pitch, left yaw and left roll. 95% confidence intervals were calculated for the response slopes such that $CI = \bar{b} \pm t_{0.025} * SE(\bar{b})$, where \bar{b} is the mean of the regression coefficients and SE is the standard error of the mean. Confidence intervals that do not include zero indicate nonzero slopes and a positive training effect.

RESULTS

HO upright pitch

Following 1 hr of training, vertical phoria changed significantly with pitch position in a direction appropriate for the preceding training (Table 1). The change in vertical alignment (post-adaptation phoria minus pre-adaptation phoria) as measured with the Lancaster test is plotted as a function of pitch position for all trials and all subjects (Fig. 2). Eye position with respect to the orbit was controlled by the head-fixed pointer so conjugate eye position was nearly identical (centered in the orbit) for all head positions. Figure 2(A) illustrates the adaptation that resulted when the prisms were arranged so that a left hyperdisparity existed with the head pitched up 24 deg and a right hyperdisparity was perceived when the head was pitched down 24 deg. Figure 2(B) shows the results

TABLE 1. Magnitude of adaptation

	Stim	n	Slope	Upper CI	Lower CI	b = 0
Upright pitch	-	4	-0.010	-0.008	-0.013	*
	+	4	0.012	0.017	0.006	*
On-side HO pitch	-	3	-0.006	-0.001	-0.010	*
	+	3	0.004	0.016	-0.007	
On-side WB pitch	-	3	-0.002	0.008	-0.013	
	+	3	0.000	0.003	-0.002	
HO Roll	-	4	-0.005	0.013	-0.022	
	+	4	0.011	0.021	0.001	*
WB Roll	-	3	-0.011	-0.002	-0.021	*
	+	3	0.011	0.017	0.005	*
HO Yaw	-	3	-0.001	0.012	-0.014	
	+	3	0.003	0.012	-0.006	
WB Yaw	-	4	0.001	0.006	-0.004	
	+	4	0.000	0.003	-0.002	

Stim, direction of stimulus slope; n, number of subjects; slope, mean regression coefficient (deg phoria/deg head tilt) for n subjects; upper CI, lower CI, upper and lower bounds of 95% confidence interval.

*Slope is unequal to zero.

for the opposite prism configuration. In every instance the adaptation was in the direction appropriate to eliminate the disparity presented during training. Note that even though training occurred only at pitch angles of ± 18 deg, adaptation was evident at all eye positions tested.

HO and WB on-side pitch

If the changes in eye alignment were dependent only on an otolith-derived head position signal, then no adaptation should be associated with changes in pitch about an earth-vertical axis since in this instance the orientation of the otoliths does not change with respect to gravity. Significant adaptation did occur, however, in HO

on-side pitch as can be seen in Fig. 3 which shows the results for three subjects with two different prism arrangements. While of considerably lower gain and somewhat more variable [subject MW's phoria does not increase monotonically with head position in Fig. 3(B)] than for upright pitch, on average, the vertical alignment of the eyes changed in a direction consistent with the preceding training. This result indicates that for on-side pitch, adaptation relied on a source other than the otoliths for head position information. A possible alternative source might be a head position signal from neck proprioceptors.

To test this possibility, we excluded the neck position signal by having subjects adapt in on-side pitch using whole body rotation. With WB rotation, head position changes were the same as with HO on-side pitch except that there was no movement of the head with respect to the body and, therefore, no change in neck proprioception. The change in eye alignment following training varied from subject to subject [Fig. 3(C) and (D), dashed lines) but in no case did the adaptation appropriately reflect the previous training. The absence of adaptation supports the hypothesis that neck proprioception may be used for head position-specific adaptation in the absence of a changing otolith signal, at least in pitch. This negative result also suggests that higher level cues, such as head position with respect to the environment, are not associated with adaptable phoria pathways.

HO and WB roll

Subjects viewed the training target binocularly with a prism placed before the right eye when the head was rolled 45 deg to the right and before the left eye when the head was rolled to the left. The prisms were either both base up or base down so that opposite disparities were

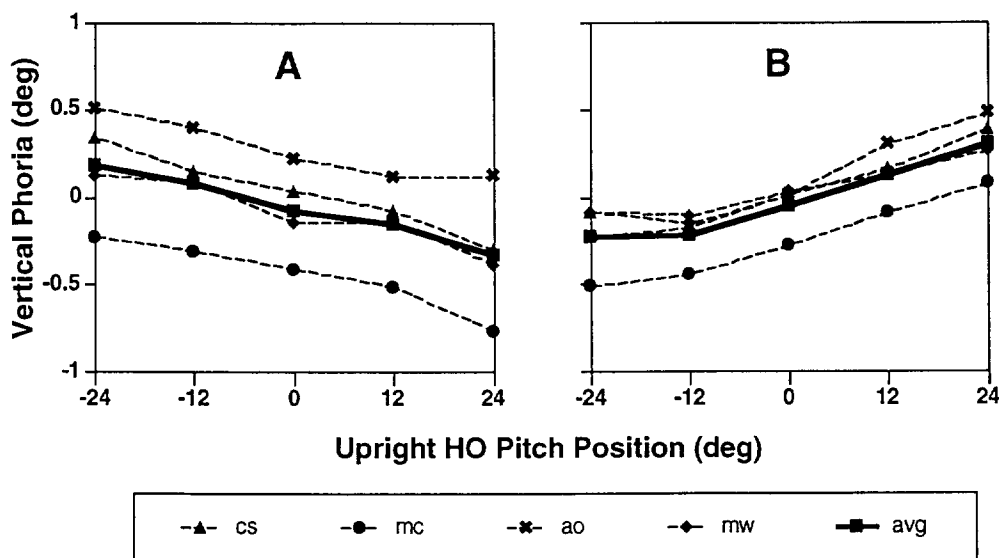


FIGURE 2. Change in vertical phoria (right eye - left eye) after 1 hr of training to two different binocular disparities. (A) Prisms were arranged to produce a left hyperdisparity when the head was pitched up and a right hyperdisparity when the head was pitched down. (B) The opposite prism configuration. Dashed lines represent individual adaptive responses and heavy solid lines are the means of the four responses. The symbols representing individual subjects are maintained in subsequent figures.

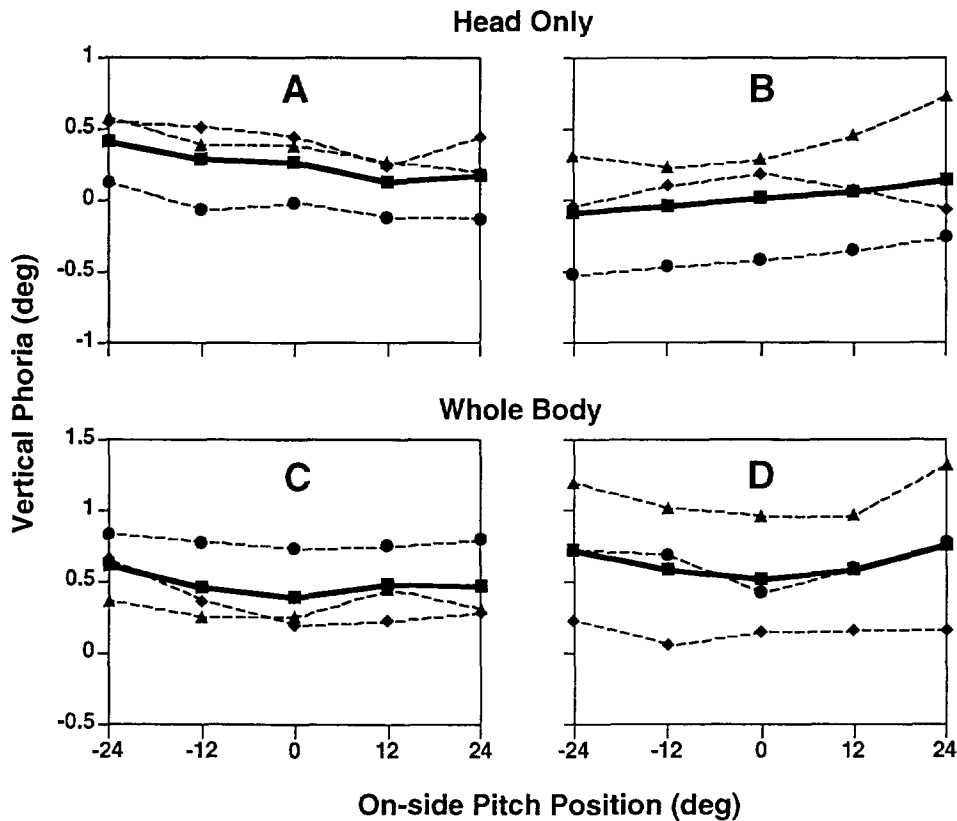


FIGURE 3. On-side pitch. Pitch rotations of the head were about an earth-vertical axis for both training and testing of vertical eye alignment. (A) and (B) Head only head rotations. (C) and (D) Whole body head rotations. (A) and (C) Left hyperdisparity trained at the upper pitch position and a right hyperdisparity at the lower. (B) and (D) Right hyperdisparity at the upper position and left hyperdisparity at the lower.

produced on the two sides. Eye alignment following training was such that it would tend to eliminate the disparities that were present during training. Figure 4 shows the results for each of two prism configurations for four subjects. (A) and (B) are similar to previous figures and show the individual (dashed lines) and mean (solid lines) changes in vertical phoria. Although in the correct direction for the training stimulus overall, the individual responses shown in Fig. 4(A) (right hyperdisparity with rolls to the left and left hyperdisparities with rolls to the right) are quite variable, particularly for subject AO. The responses shown in Figure 4(B), for the opposite prism configuration, are much more similar to each other and conform more closely to the demands of the stimulus. For both prism configurations, the adaptive response levels off at the two extreme head positions. It must be remembered, however, that the subjects could not tilt their heads 90 deg solely by head-on-neck movements. The 90 deg roll positions, therefore, were attained by a combination of WB and HO movements and each subject may have used a different combination of the two. This may account for the reduced aftereffect in the 90 deg roll positions. While it may be worthwhile repeating these experiments with greater control over HO rotations in extreme roll positions, the end points suggest the importance of a cervical source of head position information, since the output of the utricles would be maximal at the 90 roll position regardless of how the head

attained that position. An alternative interpretation would be that the response was maximal at the two head positions where training was received (± 45 deg) and dropped off at more extreme angles of roll. The present experiments cannot distinguish between these two possibilities.

Examination of the mean pre-training [Fig. 4(C) and (D), dashed lines] and post-training (solid lines) vertical phoria measurements may explain the dissimilarity of responses to the two prism configurations illustrated in Fig. 4(A) and (B). The pre-adaptation data show that all of the subjects had a right hyperphoria for rolls to the left and a left hyperphoria for rolls to the right. Since the pretraining vertical deviation of the eyes was already appropriately directed for the prism arrangement illustrated in Fig. 4(A), there was less need for an adaptive response. This argument is supported by a comparison of the post-adaptation responses for the two prism configurations (solid lines) which are quite similar in shape (though opposite in sign). The pre-adaptation data were consistent with the secondary actions of the oblique eye muscles in relation to the ocular counterroll that would have occurred in these head positions. However, since these experiments show that roll-specific adaptation of eye alignment is possible, it is unclear why all subjects had distinct pre-training phorias (that is, why they were not orthophoric).

The data thus far have indicated that changes in eye

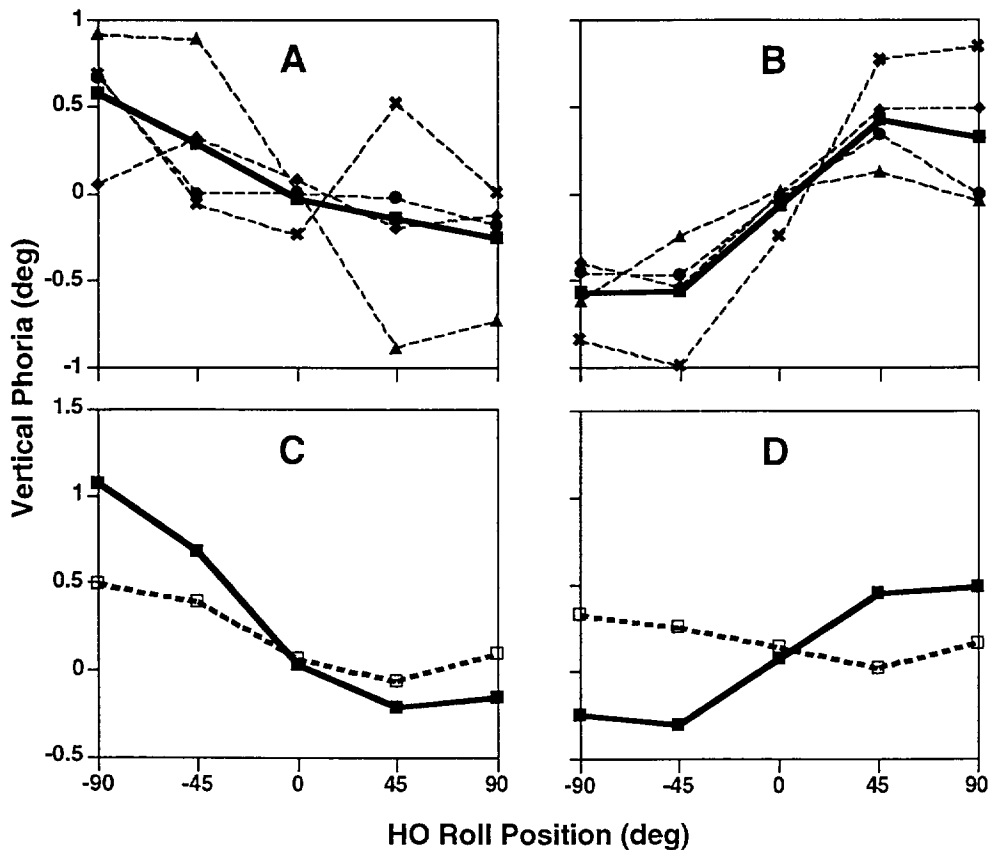


FIGURE 4. Vertical phoria following training in two different roll positions, head only rotation. (A) and (B) Change in eye alignment following same format as previous figures. (C) and (D) Mean pre-adaptation vertical phoria (dashed lines) and mean post-adaptation phoria (heavy lines) for four subjects. (A) and (C) Left hyperdisparity with head tilted to the right and a right hyperdisparity with the head tilted to the left. (B) and (D) Opposite prism configuration.

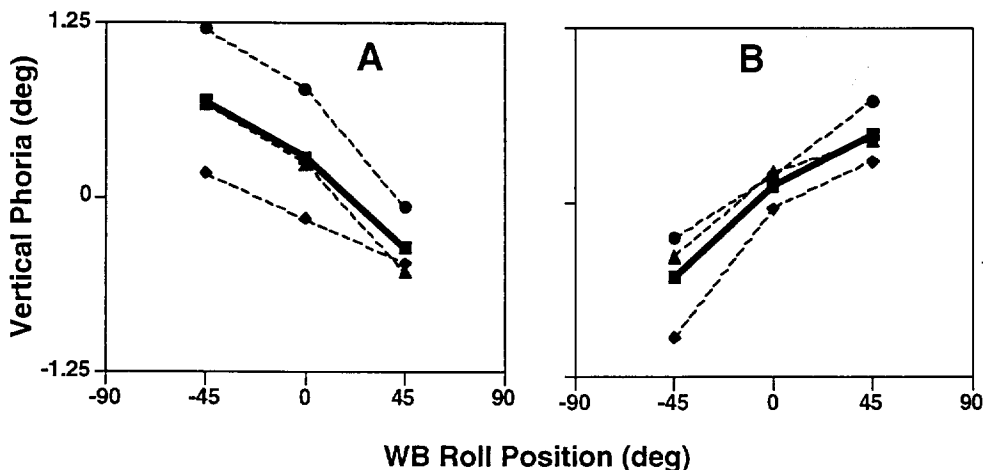


FIGURE 5. Change in vertical phoria following training in two different roll positions, whole body rotation. (A) Left hyperdisparity with head tilted to the right and a right hyperdisparity with the head tilted to the left. (B) Opposite prism configuration. Note difference in scale from previous figures.

alignment can be associated with different head-on-neck positions. The magnitude of the upright pitch response as compared to that for on-side pitch also suggests a significant otolith contribution. In order to test the plasticity of otolith-ocular pathways in the absence of changing neck proprioception, subjects were trained with roll position-specific disparities as above but with whole

body rotation. The head was fixed with respect to the neck through the use of a cervical collar which almost completely prevented head-on-neck movements. The collar would, presumably, also support the head against the forces of gravity, meaning that muscle tension in the neck need not change significantly for the two head postures. As with HO roll, the adaptive response to WB

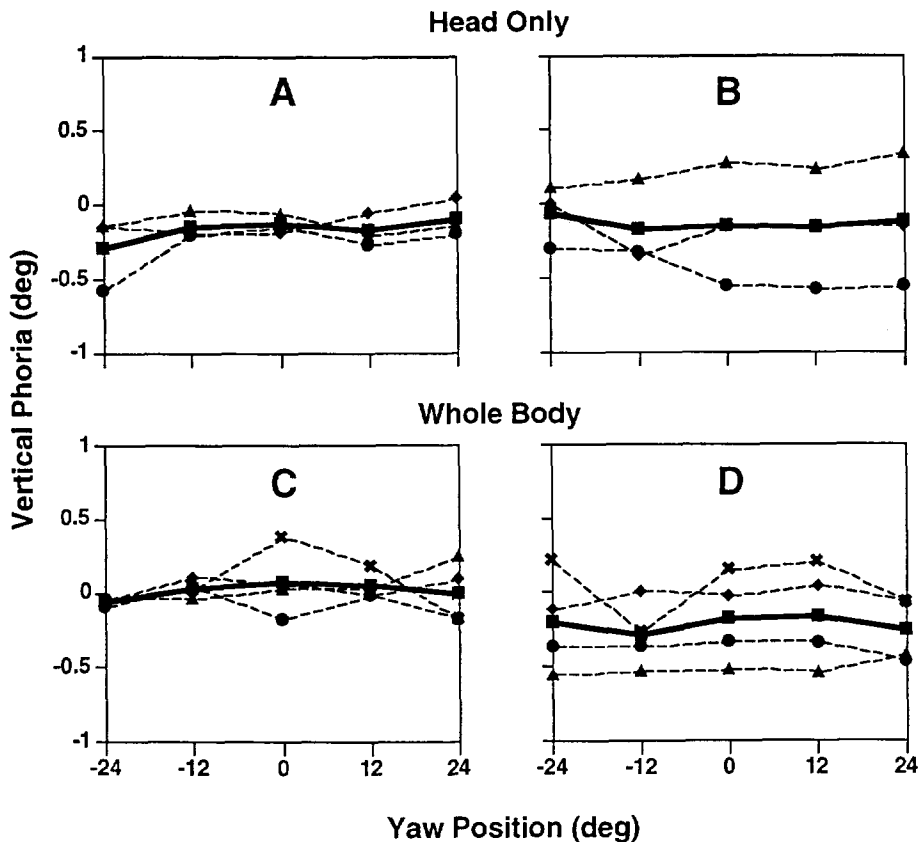


FIGURE 6. Change in vertical phoria following training in two different yaw positions. (A) and (B) Head only head rotations. (B) and (C) Whole body head rotations. (A) and (C) Left hyperdisparity with head turned to the right and a right hyperdisparity with the head turned to the left. (B) and (D) Opposite prism configuration.

roll was substantial for each of the three subjects in each of the two prism configurations (Fig. 5). Clearly, robust adaptation of eye alignment can occur in the absence of changing neck proprioception. It is reasonable to conclude that the otoliths are involved in head position-specific phoria adaptation when changes in head position are about an earth-horizontal axis.

Adaptation to HO and WB yaw

Two disparities of opposite sign were presented in relation to two different yaw positions. The axis of rotation in HO trials was approximately through the center of the subject's head. The axis of rotation in WB trials was about 5 cm in front of the subject's eyes. Figure 6 shows the change in vertical eye alignment for subjects tested in each of two prism configurations. Figure 6(A) and (C) show the change in phoria after training with both prisms base up which caused a left hyperdisparity when the head was turned to the right and a right hyperdisparity when the head was turned to the left. Figure 6(B) and (D) show the results for the opposite prism configuration (both prisms base down). No consistent training after-effect was seen for either HO (upper panels) or WB (lower panels) training. Unlike HO on-side pitch, HO yaw rotation about an earth-vertical axis does not support phoria adaptation. The reason for this is unclear but may be related to the fact that pitch rotations are normally

about an earth-horizontal axis and are, therefore, associated with changes in otolith orientation with respect to gravity, whereas yaw rotations are normally about an earth-vertical axis and are not usually associated with a varying otolith signal.

Gaze position specificity

For the data illustrated in Fig. 2 (upright pitch adaptation), conjugate eye position with respect to the orbit had been held constant during training and testing (primary position). It was possible that phoria adaptation was not dependent on head position, specifically, but on gaze position (eye position with respect to the world). If phoria adaptation is head position-dependent only, then vertical phoria should not change with eye position in the orbit. If, on the other hand, adaptation is gaze-dependent, then any combination of eye position and head position that results in the same gaze angle should produce the same vertical eye alignment. To test this possibility, vertical phoria was measured before and after pitch-specific training at a number of orbital eye positions with the head fixed at one of several pitch positions. Figure 7 shows vertical phoria as a function of vertical eye position following pitch-dependent adaptation. Figure 7(A) illustrates cases in which the prisms were arranged during training to induce a left hyperphoria with the head pitched up and a right hyperphoria with the head pitched

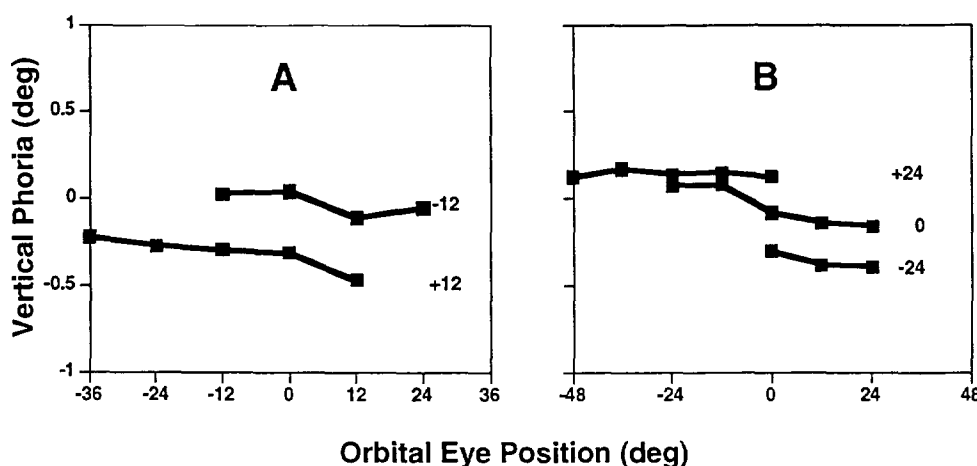


FIGURE 7. (A) Changes in vertical phoria as a function of orbit-referenced eye position measured for two different fixed pitch positions (+12 and -12 deg) following adaptation to a left hyperdisparity at a pitch position of 18 deg up and a right hyperdisparity at a pitch position of 18 deg down. Average of two subjects. (B) Changes in vertical phoria measured at three head positions (+24, 0, -24 deg) following adaptation to a right hyperdisparity at the 18 deg pitch up position and a left hyperdisparity at the 18 deg pitch down position. Average of three subjects.

down. The two line segments correspond to the two head positions at which the measurements were made; up 12 deg and down 12 deg. The lines represent the average responses for two subjects. The change in phoria was fairly constant for all orbital eye positions, that is, the adaptation was not gaze-specific but depended primarily on head position. The head position-dependent change in phoria is evident as an offset between the two lines in Fig. 7(A). Figure 7(B) shows the results with the opposite prism configuration (right hyperdisparity for up pitch and left hyperdisparity for down) and represents the average responses for three subjects at three fixed head positions (+24, 0 and -24 deg). These data also indicate that adaptation was head position-specific and not gaze-specific.

DISCUSSION

Head position-specific adaptation

Our past and present experimental results suggest that accurate vertical alignment of the two eyes is the result of adaptive processes that rely on binocular visual feedback for calibration. In the present experiments, vertical eye alignment was trained to vary with different pitch and roll head positions. Since conjugate eye position and horizontal vergence were constant during binocular training and testing, this result demonstrates that different vertical phorias can exist for the same (conjugate) eye position. Since the head was stationary during training and test measurements, it seems probable that head position-dependent changes in vertical eye alignment were associated with a static head-position signal as would arise from the otoliths or from neck proprioceptors. The presence of adaptation following WB roll rotations (about an earth-horizontal axis) suggests that eye alignment can be associated with an otolith-derived signal in the absence of changing neck proprioception.

The occurrence of measurable adaptation following HO on-side pitch training (with head rotations about an earth-vertical axis) indicates that a changing otolith signal is not always necessary for head position-dependent adaptation. It seems likely that a head position signal originating in neck proprioceptors is involved in these trials since no adaptation occurred when that afferent signal was eliminated in WB on-side pitch trials. This negative result also supports the view that phoria adaptation is a lower level process that is not normally dependent on higher level cues such as head position in space. The observation that upright pitch produced a larger adaptive response than on-side pitch may indicate that the adaptation measured in upright pitch was primarily due to changes in otolith-ocular and not cervical-ocular pathways.

The facility with which eye alignment adapted in relation to a neck proprioceptive signal (in HO on-side pitch) is somewhat surprising when the plasticity of other cervical-ocular responses is considered. The horizontal cervical-ocular reflex (HCOR) is normally quite small in cats (Baker, Goldberg, Peterson & Schor, 1982), rabbits (Barmack & Pettorossi, 1988) and humans (de Graaf, Bekkering, Erasmus & Bles, 1992) as is neck mediated ocular counterroll OCR; (de Graaf *et al.*, 1992; Ott, 1992). In rabbits, the HCOR does not appear to change even 3-5 weeks after unilateral canal plugging (Barmack & Pettorossi, 1988). A significant increase in the COR of cats has been demonstrated several days after bilateral plugging (Baker *et al.*, 1982). The COR and OCR are also substantial in patients with long standing labyrinthine disfunction (Bles & de Graaf, 1991; de Graaf *et al.*, 1992). What is remarkable about the present experiment is that the change in vertical phoria occurred after only 1 hr of training.

The correct coordination of vertical eye deviation, head tilt and ocular counterroll is necessary to avoid

abnormal ocular tilt responses (Corbett *et al.*, 1981; Gresty *et al.*, 1992). Assuming that an adaptive mechanism exists to maintain this coordination, we expected vertical eye alignment to adapt in relation to roll position. Adaptation to HO upright pitch was more surprising since the balance of muscle forces would not be expected to change substantially for static changes in head position in this plane. Ocular counterroll may reach 6 deg in roll (Diamond & Markham, 1983) but there is no systematic change in torsion during pitch (Bucher, Mast & Bischof, 1992). It is possible that pitch adaptation reflects a more "general purpose" adaptive mechanism wherein any combination of inputs to the mechanism can be adapted to each other if they normally are associated. This may also explain why HO yaw rotation did not result in adaptation. Normally, changing neck proprioception would coincide with a changing otolith signal for any tilt (pitch or roll) about an earth-horizontal axis. Since yaw rotations are usually about an earth-vertical axis, no pre-existing association between otolith and neck afferents is available for adaptation. While it was not feasible to test every combination of head-referenced and earth-referenced tilt, this argument would predict that adaptation would occur in relation to any rotation (WB or HO) about an earth-horizontal axis (e.g. WB upright pitch, on-side yaw) and for HO (but not WB) roll rotations about an earth-vertical axis.

CONCLUSION

Correct binocular alignment involves a complex parsing of signals to the twelve extraocular muscles that is contingent on conjugate eye position, horizontal vergence, and on head position. The distribution of muscle forces is not the same with the head tilted because of the primary and secondary actions of the obliques, even if the eyes remain centered in the orbit. The relative participation of the vertical recti and obliques also varies with abduction and adduction due to orbital mechanics. The challenge to the oculomotor system is to maintain the coordination of these various elements despite changes due to development, disease or injury. The capacity for the oculomotor system to do this is extraordinary. The present experiments reveal an adaptive mechanism that may exist to compensate for imbalances in otolith-ocular and cervical-ocular pathways that would otherwise result in vertical deviations of the lines of sight. Vertical phoria can also be adapted in relation to horizontal and vertical eye position (Maxwell & Schor, 1994; McCandless *et al.*, 1996) and to horizontal vergence (Schor & McCandless, 1996). The coordination of horizontal and vertical eye movements has also been demonstrated in cross-axis adaptation of the vestibulo-ocular reflex (Schultheis & Robinson, 1981; Baker *et al.*, 1987), cross-axis adaptation of post-saccadic drift (Kapoula *et al.*, 1993) and cross-axis compensation for differences in the planes of action of the semicircular canals and extraocular muscles (Robinson, 1982; Ezure & Graf, 1984a,b; Viirre *et al.*, 1987). In addition, there is evidence to suggest that saccades and the VOR can be disconjugately adapted

under certain conditions (Vilis *et al.*, 1983; Snow *et al.*, 1985; Viirre *et al.*, 1987, 1988). The need to coordinate horizontal, vertical and torsional eye movements is evident in oculomotor organization. For example, individual vertical vestibular neurons may project to motor and premotor neurons serving vertical, horizontal and torsional eye movements (McCrea *et al.*, 1987; Graf & Ezure, 1986) and there is a rich network of interconnections between cell groups that primarily control horizontal, vertical or torsional eye movements; the nucleus prepositus, vestibular y-group, and interstitial nucleus of Cajal, for instance (Belknap & McCrea, 1988). Many of these structures also project to and receive projections from the cerebellum, where complex associations between inputs might be modified (Peterson *et al.*, 1991).

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