Adaptation of torsional eye alignment in relation to head roll

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Abstract

The coordination of head tilt, ocular counterroll and vertical vergence is maintained by adaptive mechanisms; the desired outcome being clear single vision. A disruption or imbalance in otolith-ocular pathways may result in diplopia which stimulates these adaptive processes. In the present experiment, dove prisms were used to create cyclodisparities that varied with head tilt about a naso-occipital axis (roll). A stimulus for incyclovergence was presented with the head rolled 45° to one side and a stimulus for an excyclovergence was presented with the head rolled 45° to the other side. At the end of 1 h of training, all subjects demonstrated a change in open-loop cyclovergence that would help to correct for the cyclodisparities experienced during the closed-loop training period. The change appeared to be a simple gain change in the ocular counterroll of one or both eyes. © 1999 Elsevier Science Ltd. All rights reserved.

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1. Introduction

One of the functions of the oculomotor system is to keep the two eyes properly rotated so that corresponding points of the two images fall within Panum's fusional area. Good binocular alignment is the result of neural hard wiring, orbital mechanics, binocular visual feedback, and adaptive mechanisms that help to keep the eyes well aligned even if binocular feedback is temporarily interrupted (Schor, Maxwell & Stevenson, 1994). Prior experiments have examined the capacity of the system to modify eye alignment in response to disparities introduced by optical or other means (Henson & Dharamshi, 1982; Oohira, Zee & Guyton, 1991; Oohira & Zee, 1992). In experiments that examined adaptive processes in vertical eye alignment, subjects were able to change their vertical phorias (vertical eye alignment in the absence of cues for vertical fusion) significantly after a training period of 40–60 min to disparities that changed as a function of horizontal and vertical version (Maxwell & Schor, 1994) or as a function of horizontal vergence angle (Schor & McCandless, 1995). We speculated that the normal function of

eye-position-dependent adaptive mechanisms is to maintain the coordination of extraocular muscle forces at all eye positions and to compensate for muscle weaknesses or deficits in premotor pathways where such deficits would result in eye-position-dependent disparities due to orbital mechanics.

Another situation that calls for precise coordination of the extraocular muscles is head tilt. Rotation of the head about a naso-occipital axis (roll) produces counter-rotation of the eyes about the line of sight (torsion). Because of orbital mechanics and the secondary action of the obliques (depression for the superior oblique and elevation for the inferior oblique) ocular counterroll (OCR) would be accompanied by vertical skew deviations of the eyes if left uncompensated by the oculomotor system. Additionally, superior and inferior oblique palsies cause head-position-dependent vertical phorias as do certain deficits in otolith-ocular pathways (Westheimer & Blair, 1975). In order to keep the eyes properly aligned vertically in the face of these potential problems, it seemed reasonable to assume that the oculomotor system would be able to alter vertical eye alignment in relation to head roll. Consequently, it was shown that subjects are able to adapt to vertical disparities that change as a function of head position (Maxwell & Schor, 1996) or combinations of head and

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eye position (Maxwell & Schor, 1997). The observation that adaptation occurred when head roll was about an earth-horizontal axis but not an earth-vertical axis indicated that the changes in vertical eye alignment were probably associated with a head position signal originating in the otolith organs. It seems reasonable to assume that the purpose of this adaptive mechanism is to compensate for asymmetries in otolith-ocular pathways and to coordinate head roll with ocular counterroll and vertical skew. Might there also be a mechanism to adapt OCR? The gain of OCR is quite low: ocular torsion is approximately 10% of head roll (Diamond & Markham, 1983). Consequently, it is not clear that the oculomotor system would see a change in conjugate OCR as an error in need of correction. A problem would clearly exist, however, if OCR were sufficiently unequal in the two eyes. This would lead to cyclodisparities which, if large enough, could result in diplopia. This may be why cyclovergence is more tightly controlled than cycloversion (van Rijn, van der Steen & Collewijn, 1994). The present experiments examine the capacity of normal subjects to modify the torsional alignment of the two eyes by introducing cyclodisparities that vary as a function of static head position so as to induce changes in the relationship between head position and cyclovergence.

2. Methods

2.1. Video recording

Torsion was measured in both eyes using a video system. Two CCD cameras were mounted in a rigid frame that also contained two infrared-reflecting mirrors, two infrared light sources (LEDs) for each eye, and a mouth bite and head rest apparatus for head stabilization (Fig. 1A). The mirrors were mounted at a 45° angle to the line of sight with the eyes looking straight ahead and the cameras were pointed down at the mirrors (90° to the line of sight). One of the LEDs was positioned to the temporal side of the eye and the other was placed below and a few cm in front of the eye. The pitch position of the head was adjusted so that the centers of the eyes, the interaural axis, the centers of the mirrors, and the center of the tangent screen were approximately in the same earth-horizontal plane. The complete camera system was mounted on a bearing-mounted ring that could be rotated about a naso-occipital axis to place the subject in different roll positions. The axis of rotation of the apparatus was centered between the subject's two eyes.

Images from the two cameras were captured with a frame grabber (Matrox Meteor Board) and processed with custom software (Eisenman & Bascom, unpublished). A reference image was taken of each of the two irises at the beginning of each experimental session and all subsequent torsion measurements were made relative to these images. The computer program located the center and edges of the pupil of each reference image and fit an ellipse to the pupil margin. The luminance profile of a ring of pixels was taken every 1° at a prescribed radius from the center of the pupil. These 360 samples were high pass filtered (FIR digital filter) and saved as a reference string of gray levels. Subsequent images were processed in the same fashion and cross correlated with the reference string. The peak of the cross correlation — interpolated by a second order polynomial — was taken as the torsional position of the eye. Binocular torsion measurements were made in real time at 7.5 Hz per eye, displayed on a computer monitor, and also stored on a hard disk for subsequent analysis.
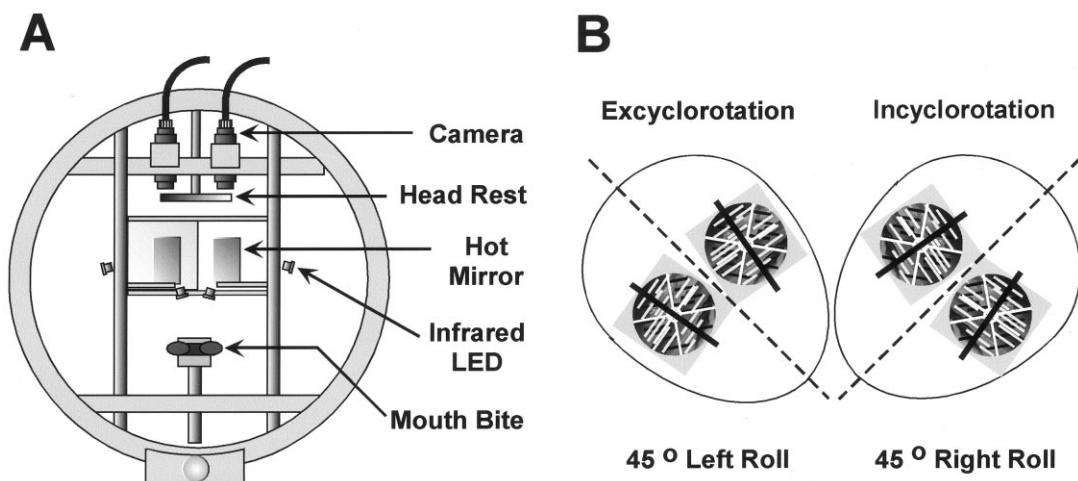

Fig. 1. (A) Video system for binocular recording of torsional eye movements. (B) Schematic illustrating one of the two training paradigms (XN). A pair of dove prisms were used to rotate the images seen by the two eyes with the tops toward each other (incyclorotation) when the head was tilted 45° to the right and away from each other (excyclorotation) when the head was tilted 45° to the left.

Torsional position was measured for 30 s at each static head position. Following a change in head position, torsional eye position was monitored in real time and the recording was initiated once the torsional response had leveled off (after approximately 20 s). All recordings were made with the left eye occluded except for one 30 s recording which was used to establish the subject's baseline cyclophoria. Since all measurements of torsion were made relative to the two reference images, it was necessary to determine how the reference images related to some standard position. For this purpose, the average torsional position of each eye with the head upright and both eyes viewing a distant target was assumed to be zero torsion and all data were transformed with respect to this standard.

All measurements of torsion were made with the subject looking straight ahead so that the eyes were approximately in the same horizontal and vertical position during all trials. A positive training result in these experiments was defined as a difference between pre-training and post-training measurements made at the same eye and head positions. False torsion arising from coordinate system transformations or potential misalignment of the camera axis with respect to primary position, therefore, was not an issue. Subjects viewed a fixation target that was rear projected onto a screen 1.5 m away. The left eye was occluded with a piece of white translucent paper and a small fluorescent light was placed in front of this to constrict the subject's pupils. A small pupil helped to keep the ring of sampled pixels away from the eyelids, eyelash reflections and hot spots from the LED illumination.

The accuracy of the system was tested in two ways: First, an artificial eye (gimbaled so as to rotate in accordance with Listing's law) was rotated and set by hand to index marks. Since alignment with the marks was by eye, this method provided only a rough measure of the systems accuracy. The system was also tested against a commercially available torsion monitor (SensoMotoric Instruments, Germany), a device with well documented characteristics (Scherer, Teiwes & Clarke, 1991). The output of one of the CCD cameras was passed to the two video systems simultaneously. A subject rolled his head through approximately $\pm 45°$ in a 30 s period. The two records were compared and found to precisely coincide. A linear regression performed on the two data sets had a slope of 0.94 with an R^2 value of 0.95. The first 20 s of the record were nearly noise free on both systems and produced a slope of 0.99 with an R^2 value of 0.99. To evaluate the repeatability of the measurements, torsion was measured with the artificial eye for 30 s intervals six times and the data were averaged for each 30 s time interval. The average standard deviation for the six trials was 3.2 min of arc. Additional variation in torsion could potentially have been introduced by the subject not returning

to the mouth-bite apparatus with precisely the same head tilt as when the reference images were taken but this did not turn out to be an issue. One subject exited and re-entered the mouth-bite five times and 30 s recordings were made each time using the same reference images for all recordings. The standard deviation of the means of the cyclovergence measurements for the five trials was 14 min of arc.

2.2. Training

Subjects viewed a visually rich scene that was rear projected with an LCD projector onto a tangent screen. The image was a seascape that had superimposed onto it horizontal, vertical and diagonal lines of various lengths and widths (Fig. 1B). A dove prism (25 mm square cross section) was placed before each eye in each of two head positions: 45° right ear down and 45° left ear down. Chin cups were used in place of mouth-bites during training for the subjects' comfort and continued cooperation. The roll angle was therefore only approximately 45° during training. The field of view within each prism was approximately 28°. When the head was rolled 45° to one side, the associated pair of dove prisms were rotated in opposite directions relative to each other to produce excyclo-disparities (the tops of the images rotated away from each other). When the head was rolled 45° to the other side, a second pair of dove prisms were rotated to produce incyclo-disparities (the tops of the images rotated toward each other). The centers of the two prisms were carefully aligned so as to avoid horizontal and vertical disparities that might induce torsion (Mikhael, Nicolle & Vilis, 1995). At the beginning of the training sessions, the subjects controlled the amplitude of the rotation of the prisms to produce cyclodisparities that they felt would be fusible with some effort. The subjects alternated between the two roll positions at approximately 30–60 s intervals for 1 h. After the first 30 min of training, each prism was fixed at an angle of 5° (which produced a rotation of the visual field of 10° since 1° of dove prism rotation yields 2° of image rotation). The stimulus, therefore, was a 10° excyclodeviation at one head position and a 10° incyclodeviation at the other.

Each of the five subject was trained and tested during two sessions with the two sessions separated by at least 2 days of normal binocular vision to avoid the possibility of residual aftereffect from the first session. In one session the subjects trained with excyclodisparites presented with head roll to the right and incyclodisparities with head roll to the left (to be referred to as the NX condition) and in the other session the incyclodisparites were presented on the right and the excyclodisparities on the left (the XN condition). The subjects gave their written consent to participate in these experiments.

Pre-training

Post - Pre (XN)
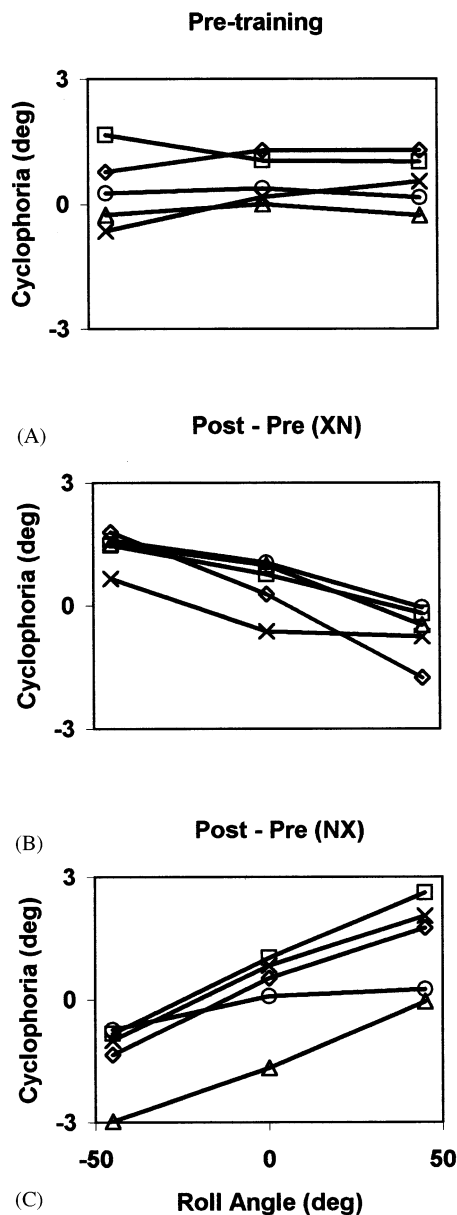
Post - Pre (NX)

(A)

(B)

(C)

Fig. 2. Cyclophoria plotted as a function of head roll for five subjects. XN trials are trials in which incyclodisparities were associated with roll to the right and excyclodisparities were associated with roll to the left and NX trials had the opposite configuration. Confidence intervals are smaller in size than the data point symbols.

2.3. Data analysis

The data acquisition program automatically indicated which video frames were not tracked successfully (because the pupil center or edge was not found, for example) and these frames were not included in subsequent analysis. The mean number of frames rejected on this basis was nine out of the 225 recorded during the 30 s trial. Cycloversion was calculated as the average of right eye torsion and left eye torsion, $(T_R + T_L)/2$, and cyclophoria (the difference in the torsional positions of the two eyes with one eye occluded) was calculated as

right eye torsion minus left eye torsion, $T_R - T_L$. Positive values represent clockwise cycloversion (from the subject's point of view) and excyclophoria, and negative values represent counterclockwise cycloversion and incyclophoria. Subjects were tested before and after the 1 h training period and the change in torsion for each eye was calculated (post-training minus pre-training), as was the change in cyclophoria. The pre-training values used in subsequent calculations were the averages of values obtained prior to the two training sessions and two other sessions in which the subjects were not adapted. Means and 95% confidence intervals were calculated for the data collected at each head position. The intent of the training was to induce a change in cyclophoria that varied with head roll, for example, a greater excyclophoria with roll to the right and a greater incyclophoria with roll to the left. Therefore, a positive training effect was indicated if the confidence intervals calculated for the subject's change in cyclophoria with the head tilted 45° to the right did not overlap with the confidence intervals calculated for the change in cyclophoria measured with the head tilted to the left, and the difference between the two was in a direction appropriate for the stimulus.

3. Results

Before training (Fig. 2A), most of the subjects demonstrated a small pre-existing cyclophoria. The pre-training cyclophoria represents the difference in eye alignment between binocular viewing (the reference condition which was assigned a value of zero) and monocular viewing. The mean cyclophoria values for the five subjects were 1.46, 1.30, 0.16, and 0.38° when the head was erect. Cyclophoria was relatively stable during the 30 s recording period with an average standard deviation of 22 min of arc. There was no consistent relationship between head roll and cyclophoria for the subjects as a group although, individually, three of the five subjects had small but statistically different cyclophorias when comparing 45° roll to the left to 45° roll to the right. The slopes of linear regression lines fit to the pre-training data for the five subjects (the average of four sessions per subject) are 0.006, −0.007, 0.000, −0.001, 0.013 with a mean slope of 0.002° of cyclophoria per degree of head roll. Expressed in degrees, the difference in cyclophoria between 45° of roll to the left and right, therefore, was 0.54, 0.63, 0.00, −0.09 and 0.12° with respect to the five subjects with a mean difference of 0.18°.

Each of the five subjects showed a significant change in cyclophoria following 1 h of training. The changes in cyclophoria (post-training minus pre-training) for five subjects at each of the three head positions tested (45° left roll, 45° right roll, and upright) are shown in Fig. 2

for the NX and XN training conditions. The change in cyclophoria relative to head position represents the effect of training to the two sets of cyclodisparities at the two roll positions. The offsets in the data points are idiosyncratic changes in cyclophoria that are not a function of head position and will not be further analyzed. The confidence intervals for all of these points are less than 0.11° which are too small to be represented in these figures. The mean confidence interval for the points included in these plots is 0.05°. The endpoints (at −45 and +45°) are different at the 95% significance level meaning that there was a positive training effect in all cases. For XN trials the slopes of lines fit by linear regression to the change in cyclophoria data for the five subjects are: −0.040, −0.019, −0.022, −0.018, and −0.016 with a mean slope of −0.023° of cyclophoria change per degree of head roll. This means that the average difference in cyclophoria between 45° head roll to the right and to the left was 2.07° and the aftereffect (cyclophoria change) was approximately 10% of the change demanded by the stimulus (±10°). For NX trials, the slopes of lines fit by linear regression to the change in cyclophoria data for the five subjects are: 0.034, 0.038, 0.032, 0.011, and 0.034 with a mean slope of 0.030° of cyclophoria change per degree of head roll. This means that the average difference in cyclophoria between 45° head roll to the right and to the left was 2.70° or 13% of the change demanded by the stimulus.

There was a great deal of variation between subjects and experiments as to which eye reflected the change in cyclophoria. In some cases most of the change was observed in the right eye's position, in other cases most of the change was observed in the left eye, and in others the change was split more or less evenly between the two eyes. For the five subjects as a group, for NX trials, approximately 68% of the mean change in cyclophoria was mediated by the right eye and 32% by the left. For XN trials, 44% of the change in cyclophoria was mediated by the right eye and 56% by the left. There did not appear to be a correlation between which eye manifested the change and which eye was occluded during testing (always the left eye).

While these experiments demonstrated that all five subjects were capable of changing their cyclophorias in accordance with the demands of the training stimuli, measurements were made at only three head positions: the two positions at which training was received and the upright position. In order to examine more closely the adaptive process and the relationship between changes in cyclophoria and head position, two of the subjects (S1 and S2) participated in an additional NX experiment following the same procedures as before except that their cyclophorias were measured at eleven different head positions (−75° to +75° in 15° increments). The pre-training and post-training data are shown in Fig. 3 which also includes trend lines fit by third order polynomials. In each of the two subjects
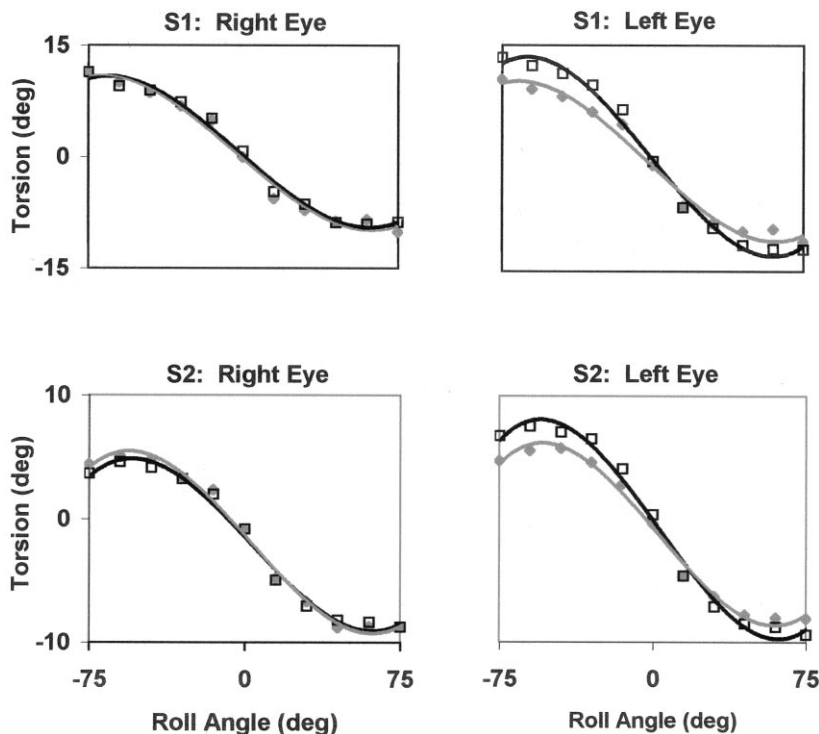

Fig. 3. Torsion measured at eleven roll positions for subjects S1 and S2 (XN training condition). Ocular counterroll of the left and right eyes pre-training (light lines and triangles) and post-training (black lines and open squares).

most of the adaptive change was seen in the left (occluded) eye and the maximum OCR for each eye, pre-training and post-training, occurred at approximately 60° head tilt. To an approximation, the post-training response is a scaled version of the pre-training response. In fact, the post-training data is quite well duplicated by multiplying the pre-training data by a gain factor and introducing a slight offset (not shown). These results suggest that the training aftereffect is not specific to the head position at which training was received ($\pm 45°$) but represents a change in the gain of OCR for one or both eyes.

4. Discussion

All five subjects had significant changes in cyclophoria following 1 h of training. The change in cyclophoria that was measured with one eye occluded was, on average, 10–13% of the requirement of the stimulus during training. The closed-loop cyclovergence during training and the training aftereffect might have been more robust had a larger field of view been used during training (Kertesz & Sullivan, 1978; Howard, Sun & Shen, 1994) but the field of view was limited to approximately 28° by the dove prisms. A greater adaptive response might also have been achieved with a longer training period. The gain of the adaptation was low when compared to eye or head-position-related changes in vertical phoria observed in previous experiments which were as high as 50% following 1 h of adaptation (Maxwell & Schor, 1994, 1996, 1997). It is possible that in viewing cyclodisparities there is a higher sensory component to fusion than with vertical fusion so that complete motor fusion is not necessary in order to eliminate diplopia. Toward the end of the training period, perceptually, our subjects reported diplopia immediately after a change in head position but single vision followed within a few seconds of fixation when attending the center of the display. If attended to, the periphery of the display was still seen diplopically, however. It should be pointed out that when producing cyclodisparities, the size of the vertical and horizontal components increase with distance from the center of rotation, so it is understandable that the center might appear fused while the periphery remains diplopic. Because disparity gradients do not always represent ocular misalignment, the visual system needs to be able to distinguish the disparities that occur as a result of slant of an object away from the vertical horopter from disparities that are created by errors in cyclovergence as would occur with a superior oblique palsy, for example. It has been suggested (Kertesz, 1983; Howard, 1993) that cyclodisparities in the center of the visual field are fused by the sensory system while cyclodisparities in the peripheral visual field are necessary to drive motor cyclofusion (cyclovergence). Furthermore, these authors have postulated that cyclodisparities in horizontal contours are related exclusively to ocular torsion whereas those in vertical contours may be related to either slant or torsional misalignment of the eyes. It is possible, and perhaps likely, that cyclovergence during training with the prisms in place was larger than that measured afterwards with monocular viewing but this could not be tested since the dove prisms could not be used in conjunction with the video system. We cannot estimate, therefore, the proportion of cyclofusion that might have been contributed by either sensory fusion or fusional cyclovergence. Several subjects also showed significant overall changes in cyclophoria at all three head positions tested which are seen as dc shifts in Fig. 2B, C. In the case of vertical phoria adaptation (Maxwell & Schor, 1994), it was common for subjects to shift their vertical phorias concomitantly within the first few minutes so that targets in the lower part of the visual field would be seen singly at the expense of producing larger disparities in the upper field. Nonconcomitant vertical phoria adaptation would then proceed more slowly. It is possible that the same strategy is used during adaptation to cyclodisparities but we have no evidence to support this conjecture.

The maximum amplitude of OCR for each of the two subjects who were tested between $\pm 75°$ was elicited with a roll position of approximately 60° which is in agreement with previous studies (Diamond & Markham, 1983; Bucher, Mast & Bischof, 1992). The post-training values for OCR for the right and left eyes looked like scaled versions of the pre-training values so it may be that the result of training was to increase the OCR gain of one eye and (or) decrease the gain of the other eye. If this were true then cyclophoria would be the result of unequal OCR and not the product of a distinct cyclovergence system. Our experiments do not indicate conclusively which of these two possibilities is correct but the feasibility of independent, eye-related neural pathways is supported by recent experiments in which the horizontal eye position sensitivities of position-vestibular-pause neurons in the vestibular nuclei were shown to be more closely related to the position of either the right or left eye individually than to the versional position of the two eyes together (Tomlinson, McConville, King, Paige & Na, 1994).

Little is known about the neural substrate underlying ocular counterroll, especially the otolith-derived component that is associated with static head tilt. Both eyes are driven by each utricle but there is no reason to expect these eye movements to be inherently conjugate. Rather, conjugacy is likely to be the

result of constant recalibration of otolith-ocular and canal-ocular pathways. A distinction is usually made between static OCR, as mediated by the otolith organs, and dynamic counterroll, as mediated by the otoliths and semicircular canals. In the present experiments, torsion measurements were initiated 20 s after head position was changed to a new position. Since the time constant of the torsional VOR is reportedly less that 6 s (Seidman & Leigh, 1989) we assume that our measurements were made during a response dominated by the otolith contribution to counterroll. Roll rotations of the head were head-on-neck and not whole body but cervical-ocular reflexes probably do not play a role in OCR in normal subjects (Nelson, 1971; Viéville & Masse, 1987; Ott, 1992; Morrow & Sharpe, 1993).

4.1. Cyclophoria adaptation

Mack and Chitayat (1970) investigated the source of perceptual adaptations to cyclodisparities created by a pair of dove prisms by measuring adaptation of the subjective vertical in conjunction with objective measurements of cyclovergence. Torsion was measured by comparing iris features in 35 mm photographs taken before and after training with oppositely-rotated dove prisms (5° in each eye). While similar to the present experiments, these authors did not find a change in cyclophoria. The subjects in that study trained with smaller disparities than our subjects, and for less time, but, given the significant aftereffects observed in our experiments, it is unlikely that the smaller disparities and shorter training duration alone were responsible for the different outcome. Unfortunately, their results are difficult to evaluate since only three photographs were taken pre-training and post-training. Given what is now known about the instability of torsion (van Rijn et al., 1994), so few samples may not have been adequate to measure small changes in cyclovergence reliably.

The adaptation of torsion is implied in clinical studies where orthoptic methods were used to alleviate torsional diplopia (reviewed in Wick & Ryan, 1982). However, with orthoptic training of torsion, it may be that only the fusional range (either sensory or motor or both) is enhanced but there is no change in cyclophoria, that is, no change in ocular alignment would be measured with the eyes disassociated.

The adaptation of otolith-ocular reflexes has been implicated in space motion sickness. von Baumgarten and Thumler (1978) have hypothesized that compensation for otolith asymmetries, which on earth is adaptive, becomes maladaptive in a microgravity environment and experimentation seems to bear this out (Lackner, Johnson, Graybiel & Money, 1987; Diamond & Markham, 1991).

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