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Phoria adaptation as a mechanism for maintaining good binocular coordination in normal subjects

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Abstract

Papers written about phoria adaptation often discuss the modification of eye alignment as evidence for mechanisms that compensate for changes in the oculomotor system due to development, disease and injury. While clinicians often encounter patients with diplopia or other signs of ocular misalignment, most people, in fact, have nearly perfect eye alignment even when viewing far targets with one eye occluded. Evidence that good eye alignment is the result of adaptive mechanisms can be seen with the binocular misalignment that results from the monocular patching of one eye in normal subjects for extended periods of time. We have tested extensively the ability of subjects to adapt the alignment of their eyes in various viewing conditions that present binocular disparities in the context of different version, vergence and head postures. Our conclusion from these studies is that one of the primary functions of phoria adaptive mechanisms is to manage the parsing of extraocular muscle forces during everyday viewing situations. The concept of Hering's law of equal innervation is an oversimplification of a very complex process in which the relative participation of the twelve extraocular muscles needs to vary with the distance and eccentricity of the object of interest as well as the pitch and roll angles of the head. We note also that the problem of maintaining good coordination of the eyes is exacerbated with dynamic eye and head movements. I will review our work on the adaptation of vertical phoria and cyclophoria in relation to orbital eye position and head posture.

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1. Introduction

Phoria adaptation is usually thought of as a mechanism that compensates for errors in binocular alignment due to disease or injury. The present brief review addresses the issue of phoria adaptation from a non-clinical perspective and suggests that the plasticity of the oculomotor system has developed, not so much to deal with disease or injury, but to manage the complex adjustment of muscle forces required in everyday viewing situations. Our experience with phoria adaptation studies over the past twenty or so years indicates that plasticity exists to cope with the demands placed on the oculomotor system by common viewing situations even in the absence of disease and injury. For example, the relative participation of the 12 extraocular muscles changes not just with eye position relative to the orbit, but with changes in head tilt, and with horizontal vergence position. Orthoptists may utilize this natural plasticity to improve binocular coordination if the deficit is not too large.

The demand for good binocular coordination and clear single vision is met at several levels: By neuroanatomical connections in accordance with Hering's law, by orbital mechanics, by binocular fusion, and by adaptive mechanisms, the primary subject of this review. We have conducted experiments that placed demands on the adaptive system that mimic the challenges faced by the oculomotor system. Our experiments have focused on the adaptation of vertical and torsional eye alignment because vertical and torsional alignment are automatic whereas horizontal vergence may be either automatic or voluntary and may be elicited by both direct cues for distance (horizontal disparity for instance), by accommodation and by perceptual cues

(proximal vergence, perspective, loom, etc.) and is, therefore, a much more complicated subject. Our conclusion is that the oculomotor system needs to be very plastic in order to meet natural demands set by spatial geometry and maintain good eye alignment before, during and after eye and head movements. Obviously, this works very well because most people have excellent eye alignment and do not require the services of orthoptists.

Good binocular coordination is partly the result of neural connectivity. Hering's law of equal innervation suggests that binocular coordination is the result of common signals sent to the two eyes and that all eye movements can be obtained by the addition of vergence and conjugate eye movement signals. A classic example is the abducens nucleus which contains both motor neurons that innervate the ipsilateral lateral rectus muscle and internuclear neurons that cross the midline to innervate the medial rectus division of the oculomotor nucleus. If a common signal is sent to both sets of neurons (this has not been definitively shown) then both eyes are driven in the ipsilateral direction. It should be noted that the concept of Hering's law has been challenged recently and there may be greater independent innervation to agonist extraocular muscles than was once thought. In the vertical system, a series of papers by Moschovakis, Scudder and Highstein (1991) have provided evidence for Hering's law. These authors first characterized a single neuron's behavior by recording its discharge in relation to eye movements. They then filled the neuron with horseradish peroxidase which allowed them to trace the projection of that cell's axon. Some of these neurons projected in such a way as to drive both eyes in the same direction. For example, some individual up medium lead burst neurons in the rostral interstitial nucleus of

the medial longitudinal fasciculus projected to both superior oblique and inferior rectus motor neurons which means that activation of these cells would cause depression of both the ipsilateral eye (via the inferior rectus motoneurons) and the contralateral eye (via the crossed superior oblique pathway).

Binocular coordination may also be assisted by orbital mechanics. Let us consider two hypothetical situations. In the first, the axis of rotation for horizontal movements is assumed to be about a head fixed vertical axis (Figure 1A). In this instance, the elevated line of sight projected onto a tangent screen would produce a horizontal curved line. This is not a problem at far distances but at near distances the arcs described by the two eyes do not overlap so vertical disparities would ensue as the eye looks left and right at elevated eye positions.

This is a graphical way of showing that when the eyes are converged, a single point in space located in tertiary gaze will be projected onto the retina with vertical disparities. Therefore, if the rotation axes were actually gimbaled this way, the oculomotor system would need to compensate for these vertical disparities with vertical vergence movements (Schor, Maxwell & Stevenson, 1994; Maxwell & Schor, 2006). Alternatively, if the axes of rotation for horizontal movements rotated with the eye, i.e., if they were eye-fixed (Figure 1B), the line of sight of the two eyes would describe straight horizontal lines on a tangent screen meaning that the eyes would automatically be aligned vertically at all eye positions and vergence angles. Do orbital mechanisms constrain the eyes to rotate in a way consistent with either head-fixed or eye-fixed axes? Possibly. Experiments over the past twenty years,

Fig 1 A. If the eyes are elevated and the axes for horizontal rotations are fixed relative to the head then the lines of sight will not intersect vertically when the eyes rotate left and right. B. If the axes of rotation for horizontal are fixed relative to the eye then the lines of sight will always intersect. C. Without pulleys, horizontal rotations are similar to head-fixed axes. D. With the horizontal rectus pulley near midline, horizontal rotations are similar to eye-fixed rotations. E. The actual pulley location is half-way between eye-fixed and head fixed.

primarily by Joel Miller and Joe Demer (Miller, 2007; Miller et al., 2003) have suggested the existence of what they refer to as muscle pulleys. The muscle pulleys are fibroelastic sheaths through which the extraocular muscles are free to slide. The presence of pulleys changes the effective origin of the muscle from the back of the orbit to the location of the pulley. If the pulleys for the horizontal rectus muscles were on the coronal equators of the eye (Figure 1D “hypothetical pulley”), then activation of the horizontal recti with the eye elevated would produce movements consistent with an eye-fixed vertical axis wherein the axis for horizontal rotation is tilted back by the same amount that the eye is elevated. If there were no pulleys, the eye would rotate more like there were head-fixed axes (Figure 1C “no pulley”). Experimental evidence suggests that the pulleys cause rotations that are approximately half way between eye-fixed and head fixed (Figure 1E “actual pulley”).

It is unlikely that equal innervation and orbital mechanics alone would produce perfect coordination of the two eyes. Of course, if there is binocular vision then fusional mechanisms are employed to achieve good binocular alignment, but there are instances such as occlusion by the nose in lateral gaze, when the view of one eye is temporarily obscured. In such cases, it is advantageous to have the eyes maintain good alignment despite the lack of fusion. There are several pieces of evidence to suggest the importance of adaptive mechanisms in maintaining good alignment. First, long-term monocular occlusion studies reveal heterophorias in most subjects. We assume this is because adaptation is lost over time. Second, patients with cerebellar lesions exhibit a loss of binocular coordination and the cerebellum is implicated in the adaptation of several types of eye movements. Third, eye

alignment can be improved with training (orthoptics). Lastly, we can produce adaptive changes rather easily in the laboratory (Maxwell & Schor, 2006) and that is the subject of the remainder of this review.

2. The effect of monocular occlusion on cyclophoria

Monocular occlusion studies have been used to show the non-adapted state of ocular alignment. The effect of long-term occlusion on vertical alignment has been documented for humans and monkeys (Liesch & Simonsz, 1993; Viirre, et al., 1987). We have shown recently the effect of eight hours of monocular occlusion on the torsional alignment of the eyes during open-loop testing (cyclophoria) (Graf, Maxwell & Schor, 2002). Our subjects viewed a 10 by 10 degree grid of 25 fixation targets while the horizontal, vertical and torsional positions of each eye were recorded by video-oculography. Four of the five subjects had significant changes in the torsional alignment of the eyes due to the patching and all four of these subjects developed excyclophorias wherein the upper poles of both eyes rotated temporally. This result suggests that the non-adapted torsional state of the eyes is excyclophoria. In general, occlusion studies in normal subjects show that adaptive mechanisms are required to keep the eyes well aligned in the absence of binocular visual feedback. Adaptation, is short lived and misalignment of the eyes ensues within hours if binocular vision is prevented.

3. Eye-position-dependent vertical phoria adaptation

The simplest type of vertical phoria adaptation is concomitant (or comitant) adaptation where the resulting change in vertical eye alignment is the same magnitude at

Fig 2 A. Concomitant adaptation: Subjects attempted to fuse a single disparity presented at the straight-ahead position for 30 minutes. B. Vertical phoria is the difference between pre-training and post-training measurements. Stimulus position and vertical phoria are plotted in degrees. C. Acquisition and decay of concomitant adaptation for one subject. Vertical line at 0 indicates the time at which training ended. D. Nonconcomitant stimulus. E. Change in vertical phoria. F. Acquisition and decay for one subject.

all eye positions. This type of adaptation results from adaptation to prisms but in our experiments we wanted to observe the spread of adaptation from one eye position to another (Maxwell & Schor, 2004). To do this, we limited the subject's training experience to a single eye position (usually straight ahead; Figure 2A) and measured the training aftereffect at 45 different eye positions over a 16 by 18 degree grid. The subject's vertical phoria (open-loop vertical eye alignment) was tested before and after 30 minutes of training to a vertical disparity presented at the straight-ahead position. The testing targets were presented monocularly and were, therefore, open loop for

vertical eye position. It was important to maintain the correct horizontal vergence angle and to do this we presented vertical lines that spanned the aperture for each eye. The vertical lines were seen by both eyes so horizontal eye position was closed loop. Following the 30 minute training period, all of our subjects adapted in the appropriate direction for the stimulus when tested open loop. Figure 2B shows the change in vertical phoria between pre-training and post-training. Even though the subjects only trained at the straight ahead position, the training aftereffect spread fairly evenly to positions where the subjects did not train.

Next, we added a second vertical disparity at a second vertical eye position to create a nonconcomitant stimulus that would require vertical vergence to change with vertical eye position (Figure 2D) much as placing a magnifying lens in front of one eye requires a nonconcomitant (incomitant) change in eye alignment. Again, our goal was to observe the spread of the training aftereffect so the subjects received experience only at the two target positions as shown in Figure 2D. Following 40 minutes of training, the open-loop testing showed that the subjects adapted in the direction appropriate for the stimulus, that is, they developed right hyperphorias in the upper field and left hyperphorias in the lower (Figure 2E). There was a gradient spread of vertical phorias in between the two training positions and an even spread of phorias to the left and right. This pattern was consistent with a gain change in the vertical ocular muscles. We modeled these results using Orbit™ (Miller, Pavlovski, & Shamaeva, 1999), a model of orbital mechanics (Eidactics, San Francisco) developed by Joel Miller employing the current knowledge of orbital mechanics including muscle pulleys, muscle strengths, muscle geometry and so forth. The model assumes that one eye is viewing and the other eye is occluded and follows Hering's law. The pattern of vertical phorias resulting from a simple change in the efficacy of the superior oblique muscle of one eye results is very similar to the pattern of vertical phorias obtained by adapting to our nonconcomitant training stimulus. The complex pattern of nonconcomitant adaptation may look more complex than adaptation to a concomitant disparity but it is simplified by orbital mechanics. It appears to result from a simple gain change in one or more muscle pathways but subsequent experiments indicate that the adaptation might not occur at the level of the final common pathway (motor neurons and

muscles).

There are reports in the literature and anecdotal reports from our subjects that concomitant (prism) adaptation is faster than adaptation to nonconcomitant stimuli such as anisometropic lenses but no direct comparison had been made. We had also speculated that nonconcomitant adaptation would last longer than concomitant adaptation (Maxwell & Schor, 1994). To test this, we compared the acquisition and decay of concomitant and nonconcomitant adaptation following one hour of training in conditions that were as closely matched as possible (Graf, Maxwell & Schor, 2003). Vertical phorias were tested every 10 minutes during the training (acquisition) period for one hour. The decay of the training aftereffect was then measured periodically for 8 hours (Figures 2C, F). Surprisingly, the time constants for acquisition were nearly identical for concomitant and nonconcomitant training. In hindsight, we believe that adaptation to prisms is not faster but simply seems faster because it is easier to binocularly fuse the concomitant stimulus than the nonconcomitant one. When a subject fuses the disparity at the location of the upper target during nonconcomitant training, the disparity of the lower target becomes twice as large. When the subject then fuses the lower target the upper disparity becomes larger and these two disparities will compete against each other throughout training until eye-position-specific adaptation actually occurs. Obviously, this is not an issue during concomitant training and so adaptation seems more rapid. Even though the rates of acquisition of adaptation were similar, the rates for the decay of the aftereffect were significantly different. For concomitant adaptation, the average decay time constant was 31 minutes meaning that the response had completely decayed in about 1.5 hours. For nonconcomitant adaptation, the average decay

time constant was 83 minutes meaning that it had completely decayed in about 4.5 hours. The rates of decay are specific for one hour of training and there is certainly the possibility that longer periods of training would increase the time of decay.

4. Vertical phoria adaptation in relation to head position

Eye-position-dependent phoria adaptation is familiar to orthoptists as it pertains to adaptation to prisms and anisometropic spectacles. Less familiar, perhaps, is head-position-specific phoria adaptation. The relative participation of the 12 extraocular muscles varies with head position and there were several reasons to predict that eye alignment should be plastic with respect to changes in head position. First, the secondary action of the obliques could potentially cause vertical skew (and vertical diplopia) during ocular counterroll (OCR). The primary agonists for OCR are the superior oblique for the eye ipsilateral to the head rotation and the inferior oblique for the contralateral eye. The secondary action of the superior oblique is depression and the secondary action of the inferior oblique is elevation meaning that a head roll could potentially result in vertical skew. Secondly, OCR changes the actions of the other extraocular muscles (Klier & Crawford, 1998; Scherberger et al., 2001). For example, the muscle forces required for a pure vertical eye movement would be different when the head is rolled than when the head is upright. Third, electrical stimulation of each utricle results in skew deviation (Suzuki, Goto, Tokumasu, & Cohen, B., 1969; Fluor & Mellstrom, , 1970), therefore, the output of the two utriculo-ocular pathways must be balanced. Fourth, skew deviation is known to accompany some cerebellar lesions (Kono, Hasebe, Ohtsuki,

Fig 3 A. Methods: A base up prism in front of the right eye created a left hyperdisparity when the head was rolled to the right (+45 degrees) and a base up prism in front of the left eye created a right hyperdisparity when the head was rotated to the left (-45 degrees). The targets were presented directly in front of the subjects at about eye level. B. Results: Measurements are the difference between pre-training and post-training.

Kashihara & Shiro, 2002; Versino, Hurko & Zee, 1996). We assume that this is due to a loss of adaptation. Lastly, the ocular tilt response is the synchronized action of head roll, conjugate OCR and vertical skew and can be elicited by unilateral electrical stimulation of the midbrain around the area of the interstitial nucleus of Cajal (Lueck, 1991; Westheimer & Blair, 1975) and lesions in this area can result in head tilt and vertical skew deviation (Gresty et al., 1992). The two sides of the brainstem must be kept balanced in order to avoid vertical skew. Most labs have reported little vertical skew with head tilt, however, and we assume this is because of adaptive mechanisms.

Our first experiment associated vertical disparities with head roll (rotation about a naso-occipital axis)(Maxwell & Schor, 1996). For example, with the head rolled 45 degrees to the right, a base up prism in front of the right eye produced a left hyperdisparity that would require a left hypervergence to resolve (Figure 3A). When the subject rolled his head 45 degrees to the left, a base up prism in front of the left eye produced a right hyperdisparity requiring a right hypervergence to resolve. The subjects were told to fuse the targets at one head position as well as possible before switching to the other position. In prior experiments we have found that giving a subject as large a disparity as they could fuse with some effort provided the most robust adaptation. In this case, subjects were given prisms of 1 to 2 diopters. The subjects alternated their head positions about every 10 seconds for 60 minutes. Their vertical phorias (open-loop alignment) were tested before and after the training period. Figure 3B shows that the subjects adapted as expected with a right hyperphoria with the head tilted to the left and a left hyperphoria with the head tilted to the right.

We were unable to tell from the last experiment if the changes in vertical phoria were associated with a head position signal from the otolith organs or with the accompanying ocular counterroll (i.e., cross-axis adaptation between the vertical recti and the obliques). In order to resolve this issue, we performed the same experiment except that the two opposite vertical disparities were associated with head pitch (rotation about the interaural axis) instead of head roll. Unlike roll, with vertical pitch there is little change in torsional eye position at the straight ahead position and little change in the tilt of Listing's plane (Bockisch & Haslwanter, 2001). Therefore,

Fig 4 A. Methods: Subjects alternately fused a left hyperdisparity when the head was pitched up 18 degrees and a right hyperdisparity when the head was pitched down 18 degrees. Conjugate eye position was identical for the two head positions. B. Results: Measurements are post-training minus pre-training. Adaptation was in relation to pitch about either an earth-horizontal axis (upright) or an earth-vertical axis (on-side) aligned with gravity (g). Arrows on abscissa: head positions at which training was received.

any change in vertical phoria would probably be associated with an otolith signal. As with the prior experiment, subjects attempted to fuse vertical disparities of opposite sign at two different positions of head pitch (up and down 18 degrees) and their vertical phorias were tested open-loop before and after one hour of training (Figure 4A). The subjects adapted appropriately for the stimulus. Figure 4B shows that the aftereffect spread evenly in between and extrapolated beyond the two positions at which the subjects trained (indicated by arrows). Adaptation in the absence of OCR strongly suggests that the adaptation was related to a head position signal.

Fig 5 A. Methods: Magnifying lenses produced nonconcomitant disparities when the subjects viewed targets in the upper and lower fields. The lenses were on opposite eyes for head roll to the right and left resulting in nonconcomitant disparity gradients in opposite directions. B. Results: Vertical phoria measurements are post-training minus pre-training with the head tilted to the right (+45) or left (-45).

In order to confirm this supposition, we repeated the experiment but with one major change: The subjects were rolled 90 degrees so that the pitch rotations of their heads were now about an earth-vertical axis. All other parameters were identical to the upright pitch condition. Since, the otolith organs respond to changes in their orientation relative to gravity, with an earth-vertical axis, the output of the otoliths does not vary. Therefore, if the changes in vertical phoria were related to an otolith signal, then no adaptation should be observed. As predicted, there was no head-position-related change in vertical phoria following one hour of training (Figure 4B, right). There was also no response when we attempted to adapt vertical phoria in relation to

yaw rotation (rotation about a dorsal-ventral axis) with the head upright and rotation about an earth-vertical axis (data not shown). The fact that rotations about an earth-vertical axis fail to induce adaptation indicates that adaptation represents a change in otolith-ocular responses. It also indicates that adaptation is a low-level phenomenon and cannot respond to the higher-level construct of gaze (eye and head) position in the world.

One of the principles we have found from these types of experiments is that adaptation spreads to other eye and head positions unless there is specific training to do otherwise. The conformation of the training aftereffect to a complex stimulus can be quite specific as is illustrated by the following experiment: We repeated the head-roll-related vertical phoria adaptation experiment described above except that, instead of prisms, we placed afocal magnifying lenses in front of the eyes at each of the two head positions (Figure 5A)(Maxwell & Schor, 1997). So for example, with the head rolled 45 degrees to the right, a magnifying lens was placed in front of the right eye and when the head was rolled to the left a lens was placed in front of the left eye. This means that when the head was rolled to the right and the subject looked up, the image seen by the right eye was higher than that seen by the left (i.e., a right hyperdisparity) and when the subject looked down, the right eye's image was lower than the left's (a left hyperdisparity). With the head rolled to the left the opposite occurred, i.e., a left hyperdisparity when the subject looked up and a right hyperdisparity when the subject looked down. In other words, we were asking the oculomotor system to adapt the subjects' nonconcomitant vertical phorias in opposite directions based on head position. All of the subjects performed this task easily and Figure 5B shows the results. An important

conclusion from this experiment is that nonconcomitant adaptation cannot be at the level of the final common pathway (motor neurons, extraocular muscles, etc.) since adapted muscles or motor neurons could not have two different gains simultaneously. It also shows that head-position-dependent and eye-position-dependent adaptation were not independent but both head and eye position were taken into account simultaneously and this must occur in a location where those signals intersect. We suggest the cerebellum, not just because it is known to be involved in the adaptation of other oculomotor processes such as saccades and the vestibulo-ocular reflex, but because it is a location where signals from many different modalities intersect. Importantly, it has been demonstrated that patients with cerebellar dysfunction do not adapt as well to prism as do normal subjects (Kono et al., 2002).

5. Conclusions

The oculomotor system is extremely plastic. Vertical eye alignment can be adapted in relation to orbital eye position and head position. Vertical phoria can also be adapted in opposite directions in relation to changes in vergence angle has been demonstrated in other experiments (Schor & McCandless, 1995a,b). We have shown that cyclophoria (the open-loop torsional alignment of the eyes) is also highly adaptable and can be modified to change in relation to head position (Maxwell & Schor, 1999), to vertical and horizontal eye position (Maxwell, Graf & Schor, 2001) and to vergence angle (Schor, Maxwell & Graf, 2001).

The alignment of the eyes can be modified in any situation that is normally encountered if it involves the intersection of two or more low-level cues. We have never achieved adaptation in relation to high-level cues such as distance

perception (Schor & McCandless 1995b), eye or head position in the world, and so on. The training aftereffect generalizes to all eye and head positions unless constrained to do otherwise. In order to elicit nonconcomitant vertical phoria adaptation, for example, at least two different disparities must be given. Most often, the changes in phoria look like simple gain changes.

Adaptation requires constant reinforcement using binocular disparity feedback. Monocular occlusion studies show that many normal subjects have latent phorias that may reveal the non-adapted alignment of the eyes. Fusional vergence keeps the eyes well aligned during binocular viewing and adaptive mechanisms keep the eyes well aligned during and after eye and head movements even when the view of one eye is temporarily occluded.

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