



Context-specific Adaptation of Vertical Vergence to Correlates of Eye Position

CLIFTON M. SCHOR,*† JEFFREY W. McCANDLESS*

Received 14 June 1996; in revised form 23 September 1996; in final form 12 December 1996

Vertical phoria (vertical vergence in the absence of binocular feedback) can be trained to vary with non-visual cues such as vertical conjugate eye position, horizontal conjugate eye position and horizontal vergence. These prior studies demonstrated a low-level association or coupling between vertical vergence and several oculomotor cues. As a test of the potential independence of multiple eye-position cues for vertical vergence, context-specific adaptation experiments were conducted in three orthogonal adapting planes (midsagittal, frontoparallel, and transverse). Four vertical disparities in each of these planes were associated with various combinations of two specific components of eye position. Vertical disparities in the midsagittal plane were associated with horizontal vergence and vertical conjugate eye position; vertical disparities in the frontoparallel plane were associated with horizontal and vertical conjugate eye position; and vertical disparities in the transverse plane were associated with horizontal vergence and horizontal conjugate eye position. The results demonstrate that vertical vergence can be adapted to respond to specific combinations of two different sources of eye-position information. The results are modeled with an association matrix whose inputs are two classes of eye position and whose weighted output is vertical vergence. © 1997 Elsevier Science Ltd.

Adaptation Palsy Strabismus Vertical phoria Vergence

INTRODUCTION

The oculomotor system is able to maintain binocular horizontal and vertical eye alignment in spite of perturbations caused by internal factors (such as changes in ocular dimensions and orbital mechanics caused by development or injury) or external factors (such as optical distortions caused by lenses) (Schor, 1993). Vertical eye alignment responses to binocular disparity are relatively slow (Kertesz, 1983) and are aided by an adaptation process that aligns the eyes in the absence of visual feedback (McCandless *et al.*, 1996). Vertical binocular eye alignment is quantified by vertical vergence (i.e., the difference in the vertical positions of the two eyes as quantified in a Helmholtz coordinate system) (Schor *et al.*, 1994). In this coordinate system, zero vertical vergence is defined as the vertical alignment of the eyes in the plane of fixation. Experimentally, the adaptability of vertical vergence and eye alignment has been investigated by placing vertical prisms in front of one eye (Helmholtz, 1910; Henson & North, 1980). The presence of an open-loop response indicates that adapta-

tion has occurred (Welch, 1978). In the current study, the term open-loop refers to a vertical vergence response in the absence of binocular visual feedback for vertical disparity. Vertical vergence measured under open-loop conditions can be trained to vary with non-visual cues such as vertical conjugate eye position (Schor *et al.*, 1993; Schor & McCandless, 1995a), horizontal conjugate eye position (Maxwell & Schor, 1994; Schor & McCandless, 1995a), and horizontal vergence (Schor & McCandless, 1995a). In each of these conditions, several vertical disparity stimuli were presented along a single meridian (e.g., depth axis, vertical axis, or horizontal axis) during the adaptation training session. After adaptation, modified vertical vergence persisted in open-loop conditions, and the vertical vergence varied as the eyes shifted position along the adaptation axis (non-conjugate phoria) and it spread uniformly along the orthogonal axis (Maxwell & Schor, 1994). These results demonstrate that a change in open-loop vertical vergence can be associated with a change in eye position along a specific meridian.

Two important questions are whether vertical vergence can be adapted to vary simultaneously with more than one axis of eye position, and whether mechanisms responsible for adaptation to multiple axes of eye position are independent of one another. This paper

*Vision Science Group, School of Optometry, 360 Minor Hall, University of California, Berkeley, CA 94720, U.S.A.

†To whom all correspondence should be addressed [Tel (510) 642-1130; Fax (510) 643-5109; Email schor@garnet.berkeley.edu].

examines the interactions between two sources of eye position during adaptation of vertical phoria in which information from controlling pathways for horizontal conjugate eye position, vertical conjugate eye position, and convergence, was necessary to modify the open-loop vertical vergence response. In this report, the term context-specific adaptation describes a vertical vergence response that is dependent on its association with two classes of eye position (e.g., vertical and horizontal).

During context-specific adaptation, four vertical disparity stimuli were located in either the midsagittal, frontoparallel, or transverse plane. The four vertical disparities were located at the corners of a rectangular field in each plane, with opposite-sign disparities along common vertical or horizontal axes and same-sign disparities along the diagonals. The vertical disparities in each of these planes were associated with two components of eye position. Vertical disparities in the midsagittal plane were associated with horizontal vergence and vertical conjugate eye position; vertical disparities in the frontoparallel plane were associated with horizontal and vertical conjugate eye position; and vertical disparities in the transverse plane were associated with horizontal vergence and horizontal conjugate eye position. If the adaptable associations of vertical vergence with each component of eye position were independent, then the aftereffects to the four combined stimuli would cancel one another as a result of their orthogonal spread. However, if adaptation responded to unique combinations of the two sources of eye position, then all four disparity stimuli would produce aftereffects. The results showed that vertical eye alignment, measured under open-loop conditions, could be adapted to the combination of all four vertical disparities within a plane such that the signs of the vertical vergence aftereffects equalled the signs of their vertical disparity stimuli. Consequently, two sources of eye position can be used simultaneously to produce a context-dependent vertical vergence response.

METHODS

Equipment

Before and after adaptation, eye position was measured with a Lancaster technique (Lancaster, 1939). Subjects wore anaglyphic (red-green) glasses in front of the eyes while viewing a tangent wall located 152 cm away. The visual stimuli during vertical eye position measurements included a green cross seen by the left eye and a red laser spot and long (80 deg) vertical red line seen by the right eye. The red line was created by placing a Maddox rod in front of a second laser. These anaglyphic targets were projected on the tangent wall in a darkened room. The subjects were instructed to converge their eyes until the red vertical line was visually superimposed on the vertical limb of the green fixation cross. This served as a visual cue for maintaining a fixed angle of horizontal vergence while leaving vertical vergence free to vary. During eye alignment measures, the subjects manually

positioned the red laser spot (viewed by the right eye through the red filter) on the center of the green cross (viewed by the left eye through the green filter). Because the laser spot and green cross were non-fusible, the Lancaster technique was open-loop. The laser spot could be adjusted to appear superimposed with an accuracy of 2 arc min. The cross was positioned in each of the four adaptation directions where vertical disparities had been presented during training. The vertical phoria was measured in each of these directions as right eye position (laser spot) minus left eye position (target cross). The extent of adaptation was quantified in terms of the vertical phoria, defined as the vertical vergence measured under the open-loop viewing conditions of the Lancaster test.

During the adaptation portion of the experiment, which lasted 1 hr, subjects attempted to fuse the diplopic images produced by vertical disparities subtended by the four targets on a large blank white screen (80 × 80 deg). The four fixation targets were small black Maltese-cross patterns that subtended vertical disparities. Vertical disparities of approximately 1 deg were produced with monocular optical displacements by either prisms or afocal magnifiers placed before the subjects' eyes. Equivalent vertical disparities were produced by magnifiers and prisms when isolated points or small targets were viewed. In some experiments, a single magnifier was used in place of two prisms to simplify the optical design needed to vary disparity with gaze.

Subjects

Four subjects (CS, JM, MC, and NQ) participated in all three experiments. Each of the subjects performed each of the experiments once. All subjects had normal ocular alignment and were experienced in oculomotor adaptation experiments. Two subjects (CS and JM) were the authors. The other two subjects, who were undergraduates, had served as subjects in prior vergence adaptation experiments. They signed letters of intent and were monetarily compensated for taking part in the study. Two of the subjects (CS and MC, who were 2D myopes) wore their spectacle corrections during the study. The other two subjects (JM and NQ, who had refractive errors of less than 2D) did not wear spectacle corrections.

Experiments

During adaptation, the subjects were instructed to fuse the diplopic images of each of the four vertical disparities by alternating fixation from one disparity to another approximately every 30 sec. At the beginning of each trial, all subjects reported vertical diplopia in the four adapting positions. Gradually during adaptation, the diplopia was reduced or nulled due to the subjects' efforts to execute vertical vergence movements. At the conclusion of each adaptation session, the vertical prism or afocal magnifiers were removed and vertical vergence was measured under open-loop conditions with the Lancaster technique. The target locations and vertical disparities in the following three experiments were

TABLE 1. Summary of adapting conditions. In each of the three experiments, four vertical disparities were presented along two meridians

| Experiment 1: midsagittal plane | | |
|---------------------------------|---------------------|--------------------|
| Horizontal vergence | Conjugate elevation | Vertical disparity |
| far (2 deg) | upper (+14 deg) | +1.2 deg |
| far (2 deg) | lower (-14 deg) | -1.2 deg |
| near (19 deg) | upper (+14 deg) | -1.1 deg |
| near (19 deg) | lower (-14 deg) | +1.1 deg |

| Experiment 2: frontoparallel plane | | |
|------------------------------------|---------------------|--------------------|
| Conjugate hor. gaze | Conjugate elevation | Vertical disparity |
| left (-14 deg) | upper (+14 deg) | -0.8 deg |
| left (-14 deg) | lower (-14 deg) | +0.8 deg |
| right (+14 deg) | upper (+14 deg) | +0.9 deg |
| right (+14 deg) | lower (-14 deg) | -0.9 deg |

| Experiment 3: transverse plane | | |
|--------------------------------|-------------------------|--------------------|
| Horizontal vergence | Conjugate hor. vergence | Vertical disparity |
| far (2 deg) | left (-14 deg) | +1.1 deg |
| far (2 deg) | right (+14 deg) | -1.1 deg |
| near (13 deg) | left (-14 deg) | -1.1 deg |
| near (13 deg) | right (+14 deg) | +1.1 deg |

selected to produce different magnitudes of the two components of eye position in association with different vertical vergence stimuli. A summary of the experimental conditions is listed in Table 1.

Experiment 1 (adaptation in the midsagittal plane). Two Maltese-cross targets separated vertically by 76 cm were placed on a tangent wall 152 cm from the subject. The upper target was located 14 deg above primary gaze, and the lower target was located 14 deg below primary gaze. Each target subtended a 2.5 deg visual angle. In the far position, the horizontal vergence angle was 2 deg. Each subject alternately fixated the upper and lower targets through a 8.5% overall afocal magnifier placed in the spectacle plane before the right eye. This magnifier resulted in a 1.2 deg right-hyperdisparity (+1.2 deg) in far-upper gaze and a 1.2 deg right-hypodisparity (-1.2 deg) in far-lower gaze. No other targets were fixated during adaptation.

In the near position, the symmetric horizontal vergence angle of 19 deg was elicited with a 15Δ base-out prism before each eye. Each subject alternately fixated the upper and lower targets through an 8% overall afocal magnifier before the left eye. This magnifier resulted in a 1.1 deg right-hypodisparity (-1.1 deg) in near-upper gaze and a 1.1 deg right-hyperdisparity (+1.1 deg) in near-lower gaze. The far and near conditions were alternated approximately every 2 min. Before and after the adaptation training session, the vertical phoria was measured at various gaze elevations (-14, -7, 0, +7, and +14 deg) along the vertical conjugate axis at the far horizontal vergence position (2 deg) and near horizontal vergence position (19 deg). During the phoria measurements, base-out prisms were used to induce the same two horizontal vergence states as used during adaptation.

Experiment 2 (adaptation in the frontoparallel plane). Four Maltese-cross targets separated horizontally and vertically by 76 cm were placed on the tangent wall 152 cm from the subjects. Each target was located in one of four quadrants with a 14 deg horizontal and 14 deg vertical eccentricity. Each target subtended a 2.5 deg visual angle. In the leftward positions (horizontal version angle of -14 deg), each subject alternately fixated the upper and lower targets through a 6% overall afocal magnifier placed before the left eye. This magnifier induced a 0.8 deg right-hypodisparity (-0.8 deg) in left-upper gaze and a 0.8 deg right-hyperdisparity (+0.8 deg) in left-lower gaze.

In the rightward positions (horizontal version angle of +14 deg), each subject alternately fixated the upper and lower targets through a 6.5% overall afocal magnifier placed before the right eye. This magnifier induced a 0.9 deg right-hyperdisparity (+0.9 deg) in right-upper gaze and a 0.9 deg right-hypodisparity (-0.9 deg) in right-lower gaze. The left and right conditions were alternated approximately every 2 min. Vertical phoria was measured before and after the adaptation training session along the vertical conjugate axis at horizontal version angles of -14, -7, 0, +7 and +14 deg. At each horizontal version angle, the vertical phoria was measured at elevations of -14, -7, 0, +7 and +14 deg.

Experiment 3 (adaptation in the transverse plane). Two Maltese-cross targets separated horizontally by 76 cm were placed on a tangent wall 152 cm from the subject. The targets were located 14 deg to the left and right of primary gaze. Each target subtended a 2.5 deg visual angle. In the far positions, the asymmetric horizontal vergence angle was 2 deg. Each subject viewed the left far target (horizontal version = -14 deg) through a 2Δ base-up prism placed before the left eye. This prism induced a 1.1 deg right-hypervertical disparity in left far gaze. Each subject viewed the right far target (horizontal version = +14 deg) through a 2Δ base-up prism before the right eye. This prism induced a 1.1 deg right-hypodisparity in right far gaze. Prisms were positioned to stimulate right-hyper- and left-hypervergence as the eyes alternately fixated the left and right targets, respectively.

In the near positions, the asymmetric horizontal vergence angle of 13 deg was stimulated with a base-out prism before either the left or right eye when fixating the leftward or rightward target, respectively. Each subject viewed the left-near target (horizontal version = -14 deg) through a 15Δ base-out prism and 2Δ base-down prism placed before the left eye. The 2Δ prism induced a 1.1 deg right-hypovertical disparity in left-near gaze. Each subject viewed the right-near target (horizontal version = +14 deg) through a 15Δ base-out prism and 2Δ base-down prism placed before the right eye. The 2Δ prism induced a 1.1 deg right-hypervertical disparity in right-near gaze. The near and far conditions were alternated approximately every 2 min.

Before and after the adaptation training session, the phoria was measured along the horizontal conjugate axis

at the far-horizontal vergence position (2 deg) and near-horizontal vergence position (13 deg). At each horizontal vergence position, the vertical phoria was measured at horizontal eccentricities of -14 , -7 , 0 , $+7$ and $+14$ deg. However, in the near position, the vertical phoria was not measured at 0 deg because the edge of each base-out prism occluded this part of the view. During the phoria measurements, base-out prisms were used to induce the same two states of horizontal vergence as used during adaptation.

Analysis procedure

Vertical vergence adaptation was quantified by the change in vertical phoria from the pre-adapted state to the post-adapted state. In each of the three experiments (midsagittal plane adaptation, frontoparallel plane adaptation, and transverse plane adaptation), the vertical phoria was measured with gaze directed at the four adapting positions as well as intermediate positions (-7 , 0 , $+7$ deg along the horizontal and/or vertical axis). The results were analyzed by computing the vertical phoria response gradient (the change in vertical phoria along an axis), which has no units. For example, if the vertical phorias at eye elevations -14 , -7 , 0 , $+7$ and $+14$ deg were -1.0 , -0.5 , 0.0 , $+0.5$ and $+1.0$ deg, respectively, the vertical phoria response gradient would be $2 \text{ deg}/28 \text{ deg}$, or 0.07 . The response gradients were computed through linear regression along the horizontal and vertical conjugate axes which contained several phoria measurements. The response gradients along the depth axes, which contained only two phoria measurements, were computed by dividing the mean change in vertical phoria (deg) along the depth axes by the target separation (deg) along the depth axes. Within an adapting plane, four response gradients were computed. Two response gradients were computed along each of the two adapting meridians within a plane. Response gradients of opposite sign along parallel meridians of adaptation provided evidence that the subjects had adapted to all four disparities. If the subjects had adapted to only two targets of opposite disparity, the response gradients would have been similar in both sign and amplitude in parallel meridians as a result of the orthogonal spatial spread of vergence aftereffects from the adapted meridian (Maxwell & Schor, 1994).

As a method of summarizing the response gradients, the mean response gradient magnitude was computed along each of the two adapting meridians within an adapting plane. The mean response gradient magnitude is the mean of the absolute values of the response gradients of an adapted meridian. For example, in the midsagittal plane, if the mean response gradient along the depth axis was -0.04 in the upper position and $+0.02$ in the lower position, the mean of the response gradient magnitudes in the depth axis would be 0.03 . The mean response gradient magnitude provides a concise method of summarizing the phoria response.

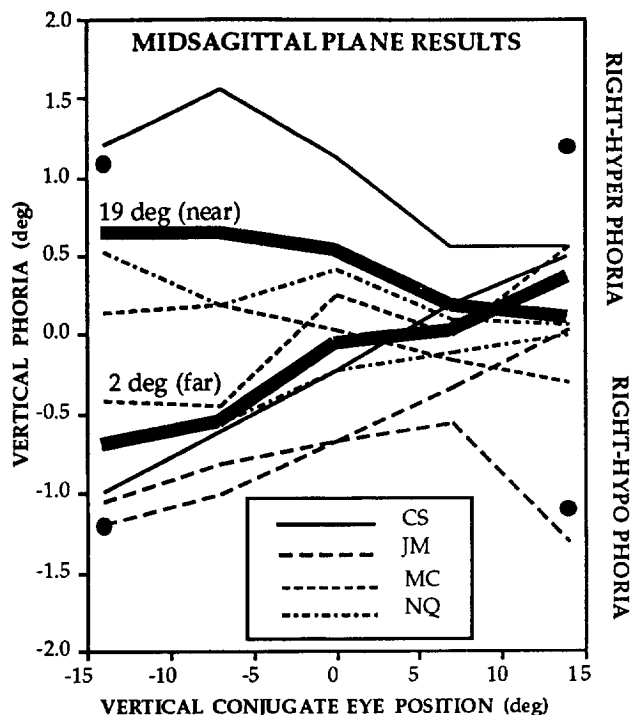


FIGURE 1. Change in vertical phoria following training to vertical disparities in the midsagittal plane. The two dark curves represent the mean vertical phorias measured at five eye elevations along the vertical adaptation axis in the far horizontal vergence position (2 deg) and the near horizontal vergence position (19 deg) for all four subjects. The eight light curves represent the individual responses of the four subjects at the two horizontal vergence positions. The filled circles represent the disparity stimulus locations. (For the disparity stimulus specifications, the vertical axis corresponds to disparity [deg] instead of vertical phoria.)

RESULTS

Adaptation in the midsagittal plane

The vertical phorias produced by adaptation in the midsagittal plane were measured along vertical meridians at horizontal vergence positions of 2 and 19 deg. As shown by the heavy lines in Fig. 1, the mean phoria varied with both horizontal vergence and vertical conjugate eye position. The eight light curves represent the individual responses of the four subjects at the two horizontal vergence positions (2 and 19 deg). The filled circles represent the disparity stimulus positions. Along the vertical conjugate meridian (abscissa), the mean response gradient was -0.021 ($t = 4.41$, $P < 0.05$, 95% confidence interval = -0.037 to -0.006) in the near position and $+0.038$ ($t = 9.01$, $P < 0.01$, 95% confidence interval = 0.025 to 0.051) in the far position. The difference in mean response gradients along the vertical conjugate meridian was 0.059 . Along the depth meridian, the mean response gradient was -0.014 in the upper position ($+14$ deg) and $+0.078$ in the lower position (-14 deg). The difference in mean response gradients along the depth meridian was 0.092 . The mean response gradient magnitude along the vertical conjugate adapting axes was 0.030 (the mean of 0.021 and 0.038). The mean

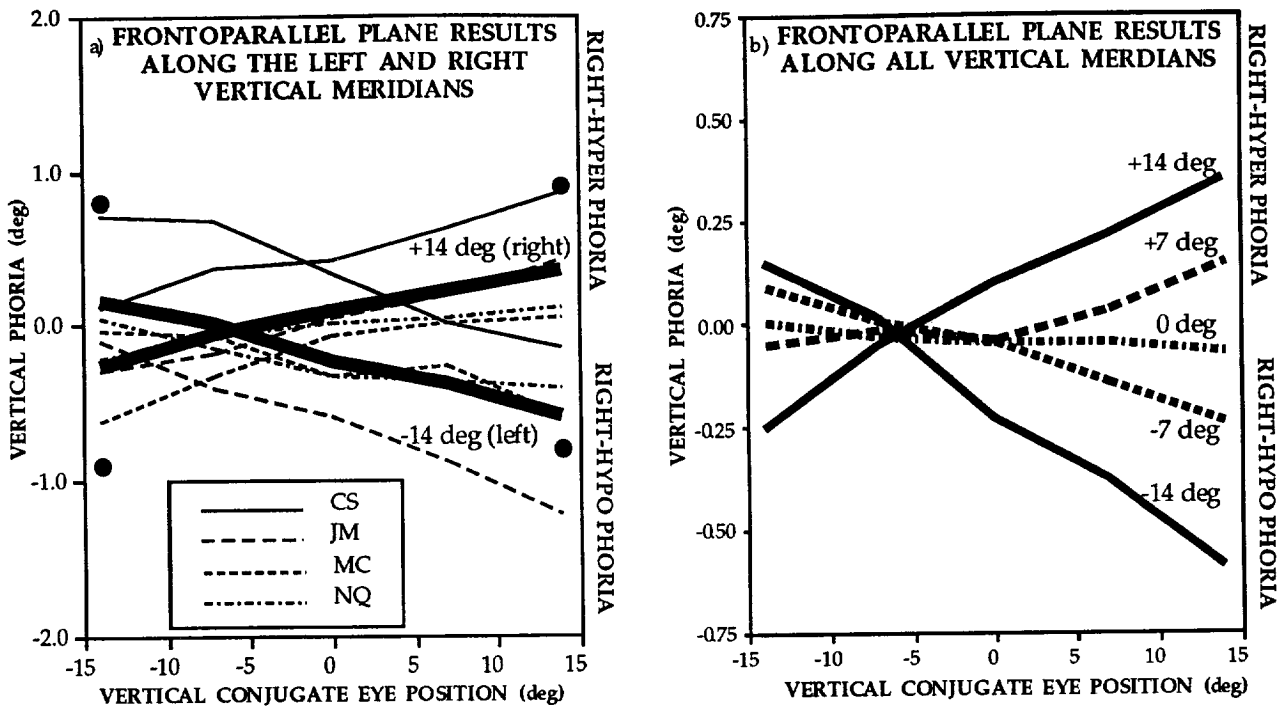


FIGURE 2. Change in vertical phoria following training to vertical disparities in the frontoparallel plane. The filled circles represent the disparity stimuli positions. (For the disparity stimuli specifications, the vertical axis corresponds to disparity [deg] instead of vertical phoria.) (a) The two dark curves represent the mean vertical phorias measured at five eye elevations along the vertical adaptation axis at the left horizontal version position (-14 deg) and the right horizontal version position (+14 deg). The eight light curves represent the individual responses of the four subjects at the two horizontal version positions. Four different light line types correspond to the four subjects. Generally, half of the light curves have positive slopes (corresponding to the +14 horizontal version position) and half have negative slopes (corresponding to -14 horizontal version position). (b) The five dark curves represent the mean vertical phoria responses along vertical meridians at all five horizontal eccentricities (-14, -7, 0, +7 and +14 deg). Note that the range along the y-axis is different in Fig. 2(b) compared with Fig. 2(a).

response gradient magnitude along the depth axes was 0.046 (the mean of 0.014 and 0.078). The opposite sign of the mean response gradients along parallel axes suggests that the subjects adapted vergence in response to all four of the vertical disparity stimuli.

Adaptation in the frontoparallel plane

The vertical phorias produced by adaptation in the frontoparallel plane were measured along vertical meridians at five horizontal conjugate version positions ranging from -14 to +14 deg. As shown in Fig. 2, the mean phoria varied with both horizontal and vertical conjugate eye position. Figure 2(a) illustrates the individual subject responses and the mean responses along the vertical meridians at the two most extreme horizontal version positions (-14 and +14 deg). The filled circles represent the disparity stimulus positions. Figure 2(b) illustrates the mean vertical phoria along the vertical meridians at all horizontal conjugate version positions (-14, -7, 0, +7 and +14 deg). Note that the range along the y-axis is different in Fig. 2(b) compared with Fig. 2(a). The slopes are greatest at ±14 deg, with interpolation of slopes at horizontal eccentricities between ±14 deg.

Table 2 lists the vertical response gradients along vertical meridians along five horizontal eccentricities for frontoparallel plane adaptation. Along the vertical

conjugate meridian, the mean response gradient was -0.027 ($t = 22.3, P < 0.001, 95\%$ confidence interval = -0.031 to -0.023) in the left position and +0.021 ($t = 16.5, P < 0.001, 95\%$ confidence interval = 0.017 to 0.025) in the right position. The difference in mean response gradients along the vertical conjugate meridian was 0.048. Along the horizontal conjugate meridian, the mean response gradient was -0.014 ($t = 5.74, P < 0.01, 95\%$ confidence interval = -0.021 to -0.006) in the lower position and +0.033 ($t = 13.5, P < 0.001, 95\%$ confidence interval = 0.025-0.040) in the upper position. The difference in mean response gradients along the horizontal conjugate meridian was 0.047. The change in response gradient is summarized by the mean response

TABLE 2. Statistical analysis of adaptation results in the frontoparallel plane

| Horizontal version (deg) | Slope | 95% Confid. interval | T-statistic | P-value |
|--------------------------|--------|----------------------|-------------|---------|
| -14 | -0.027 | -0.031 to -0.023 | 22.3 | <0.001 |
| -7 | -0.012 | -0.014 to -0.009 | 16.9 | <0.001 |
| 0 | -0.002 | -0.004 to -0.001 | 4.1 | <0.05 |
| 7 | +0.007 | 0.000 to 0.013 | 3.0 | <0.05 |
| 14 | +0.021 | 0.017 to 0.025 | 16.5 | <0.001 |

The slope represents the vertical response gradient along a vertical axis at five different horizontal eccentricities.

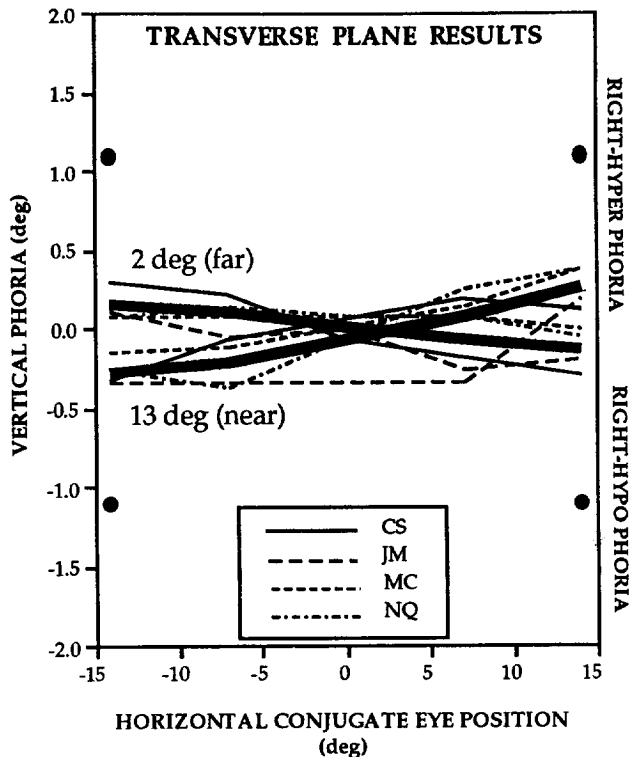


FIGURE 3. Change in vertical phoria following training to vertical disparities in the transverse plane. The two dark curves represent the vertical phoria measured at five eccentricities along the horizontal axis in the far horizontal vergence position (2 deg) and the near horizontal vergence position (13 deg). The eight light curves represent the individual responses of the four subjects at the two horizontal vergence positions. The filled circles represent the disparity stimuli positions. (For the disparity stimuli specifications, the vertical axis corresponds to disparity [deg] instead of vertical phoria.)

gradient magnitude. Along the vertical conjugate adapting axes it was 0.024 (the mean of 0.027 and 0.021) and along the horizontal conjugate adapting axes it was 0.024 (the mean of 0.014 and 0.033). The opposite sign of the mean response gradients along parallel axes suggests that the subjects adapted vergence to all four of the disparity stimuli.

Adaptation in the transverse plane

The vertical phorias produced by adaptation in the transverse plane were measured along horizontal meridians at 2 and 13 deg horizontal vergence positions. As shown in Fig. 3, the mean vertical phoria along the horizontal axis varied with both horizontal vergence and horizontal conjugate eye position. The eight light curves represent the individual responses of the four subjects at the two horizontal vergence positions (2 and 13 deg). The filled circles represent the disparity stimulus positions. Along the horizontal conjugate meridian, the mean response gradient was -0.010 ($t = 13.1$, $P < 0.01$, 95% confidence interval = -0.013 to -0.008) in the far position and $+0.019$ ($t = 8.11$, $P < 0.01$, 95% confidence interval = 0.009 to 0.029) in the near position. The difference in mean response gradients along the horizontal conjugate meridian was 0.029. Along the depth

TABLE 3. The mean response gradient magnitudes in all three adapting planes

| Adapting axis | Adapting plane | | |
|---------------------------|----------------|------------|------------|
| | Mid. | Fro. | Tra. |
| Vertical conjugate axis | 0.030 (17) | 0.024 (28) | |
| Depth axis | 0.046 (28) | | 0.036 (28) |
| Horizontal conjugate axis | | 0.024 (28) | 0.015 (11) |

The values in parentheses are the separations in degrees between the adapting axes. The mean response gradients were measured in the two adapting axes for each adapting plane. Mid., midsagittal; Fro., frontal; Tra, transverse.

axis, the mean response gradient was -0.025 in the left position (-14 deg) and $+0.048$ in the right position ($+14$ deg). The difference in mean response gradients along the vertical conjugate meridian was 0.073. The mean response gradient magnitude along the horizontal conjugate adapting axes was 0.015 (the mean of 0.010 and 0.019). The mean response gradient magnitude along the depth axes was 0.036 (the mean of 0.025 and 0.048). As in the prior experiments, the opposite sign of the mean response gradients along parallel axes suggests that the subjects adapted vergence to all four of the disparity stimuli.

Summary of results

The results for the three orthogonal planes of adapting stimuli indicate that vertical vergence can be simultaneously adapted in association with any two components of eye position. The two sources of adaptive eye-position information were not independent of one another because the mean response gradients along parallel meridians were of opposite sign. If the two eye-position sources were independent of one another, the orthogonal spread of the vertical vergence response associated with one eye-position source would have nulled the orthogonal spread of the vertical vergence response associated with the other eye-position source (Maxwell & Schor, 1994).

The mean response gradient magnitudes are summarized in Table 3. The table also lists (in parentheses) the separation in deg between the adapting axes. For example, the two vertical adapting axes of adaptation in the midsagittal plane were separated by 17 deg. Likewise, the two depth axes of adaptation in the midsagittal plane were separated by 28 deg. As shown in Table 3, the mean response gradient magnitudes along the adapting axes were equal in the frontoparallel plane but different in the midsagittal and transverse planes. These differences are related to the separation between adapting axes. In the frontoparallel plane, the separation between the two horizontal adapting axes (28 deg) was equal to the separation between the two vertical adapting axes (28 deg). Likewise, the response gradients along the vertical and horizontal axes in the frontoparallel plane were also equal (0.024). In the midsagittal plane, the separation between the depth adapting axes (28 deg) was 1.6 times greater than the separation between the vertical

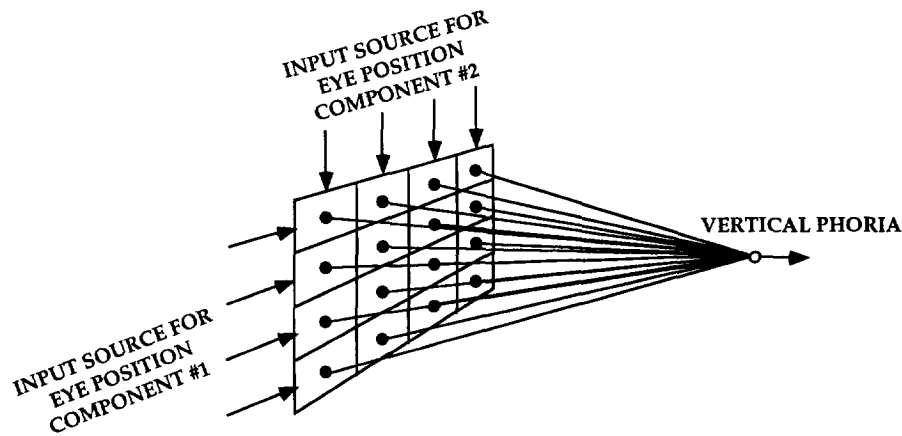


FIGURE 4. Conceptual model architecture of the association matrix that combines two sources of eye-position information to produce the context-specific vertical phoria response. The filled circles represent AND gates that are active only if both inputs are active. The lines represent weights that are proportional to the input activity. The open circle represents a summing junction that sums the weighted inputs to produce the vertical phoria response.

adapting axes (17 deg). Similarly in the midsagittal plane, the mean response gradient magnitude along the depth adapting axis (0.046) was 1.5 times greater than the mean response gradient magnitude along the vertical adapting axis (0.030). In the transverse plane, the separation between the depth adapting axes (28 deg) was 2.5 times greater than the separation between the horizontal adapting axes (11 deg). Similarly in the transverse plane, the mean response gradient magnitude along the depth adapting axis (0.036) was 2.4 times greater than the mean response gradient magnitude along the horizontal adapting axis (0.015). The close relationship between response gradient and axes separation suggests that the variations of response gradients across orthogonal meridians could be related to crowding effects (reduced adaptation responses associated with narrow target separations) (Schor *et al.*, 1993). Presumably, the separation could be increased to a distance at which the two adapting meridians would no longer interfere with one another.

Adaptation to wide target separations in the transverse plane

The magnitude of the response gradient, unaffected by crowding between adapting meridians, can be estimated from prior two-point adaptation studies. For example, prior two-point adaptation studies examined the response gradient along a single depth axis (Schor & McCandless, 1995a). The disparity amplitudes and target separation along the depth axis in that study were approximately equal (within 10%) to those for transverse plane adaptation in the current study. The earlier two-point adaptation experiments resulted in a response gradient of approximately 0.12 along the depth axis (Schor & McCandless, 1995a). For four-point adaptation within the transverse plane, the response gradient along the depth axis was 0.036 (Table 3), which is approximately 60% smaller than the response gradient for two-point adaptation. This suggests that the 28 deg horizontal separation between the two depth axes was narrow

enough to have attenuated the adaptation response along the depth axis for transverse plane adaptation. Presumably, an increase in the horizontal separation between the two depth axes would reduce this crowding effect. As a test of this possibility, an additional set of transverse plane adaptation experiments was conducted in which the horizontal separation between depth axes was increased from 28 to 36 deg, and all other parameters were identical to the previous transverse plane experiments. The mean response gradient magnitudes of the two subjects (JM and CS) tested on this additional experiment were 97% larger than those of the previous transverse plane experiment. This increase suggests that the crowding effects of vertical vergence adaptation can be reduced by increasing the separation between parallel axes that contain different disparity stimuli. Prior studies of two-point adaptation along a vertical and horizontal axis used target separations that were not comparable to the target separation in the current study; consequently, no other meridians were reassessed.

DISCUSSION

Previously, non-conjugate (two-point) adaptation of the vertical phoria was modeled as a cross-coupling between an input source (conjugate eye position) and an output (vertical vergence) (McCandless *et al.*, 1996). In that model, cross-coupling weights that were established during adaptation were proportional to the product of neural correlates of conjugate eye position and vertical disparity vergence. Context-specific adaptation observed in this study can be modeled by modifying the input of the prior model structure with an association matrix (Fig. 4; McCandless & Schor, 1997b). For adaptation to multiple vertical disparities in the frontoparallel plane, the association matrix model uses two input sources representing horizontal and vertical eye-position-specific neurons such as those in the nucleus prepositus hypoglossi (McFarland & Fuchs, 1992) and interstitial nucleus of Cajal (King *et al.*, 1981). Each cell in the

association matrix represents an AND gate that responds to simultaneous activity of unique combinations of the two input sources. The output of this matrix is weighted during adaptation using the same rules as proposed in the cross-coupling model (McCandless *et al.*, 1996), and the outputs are combined together to form the vertical vergence response. Following training, the weights remain fixed and they continue to scale combined neural correlates of conjugate eye position into a vertical vergence signal.

Presumably, the output could represent any motor activity modified through context-specific adaptation. Like the association matrix model, the Cerebellar Model Architecture Computer (CMAC) also represents information processing in the brain (Albus, 1981). In the CMAC, a response is recalled from a look-up table for every input that occurs during practice. In our association matrix model, the response is computed. Simultaneously active inputs are combined via AND gates, and during training they are weighted with the product of combined eye-position innervation and correlated vertical disparity vergence. After training these weights remain fixed and they scale correlates of combined sources of eye position to produce a vertical vergence response. Eye position combinations not practiced during training can produce changes in vertical phoria as long as they involve combinations of neurones that were active during training. The AND gates provide a symbolic means of combining active eye-position sources and they represent the context-specific interactions during adaptation.

The context-specific adaptation results showed that the pathways conveying associated adaptation stimuli are not independent because information from both pathways must be used simultaneously to produce the correct vertical vergence response. The multiple adaptive responses are not simply a linear summation of associations between vertical vergence and two independent classes of eye position, since independent summation would have resulted in a nulling or cancellation of adaptive responses in our 4 point adaptation paradigm.

The context specificity of non-conjugate vertical vergence adaptation is not unique considering other examples of coordinated activity between vertical vergence and other components of the oculomotor system. For example, vertical binocular eye alignment under both open-loop and closed-loop conditions is accurate in different tertiary directions of gaze even though, depending on the coordinate system, vertical disparity and the stimulus for vertical eye alignment can vary with distance and direction of gaze (Schor *et al.*, 1994). It is likely that the precision of vertical eye alignment in tertiary gaze is aided by an adaptable calibration process. Another example is the adaptive association of vertical vergence with combined head tilt and conjugate vertical eye position (Maxwell & Schor, 1996, 1997). With rightward head tilt, a right-hyperdisparity was presented in upward gaze and a right-hypodisparity was presented in downward gaze (Maxwell & Schor, 1997). With leftward head tilt, the vertical

disparity directions were reversed such that a right-hypodisparity was presented in upward gaze and a right-hyperdisparity was presented in downward gaze. The ability of subjects to adapt to these types of mixed stimuli indicates that eye-position-dependent pathways are not independent of head-position-dependent pathways (Maxwell & Schor, 1997). Information from both pathways could be combined simultaneously via the association matrix to produce the correct open-loop vertical vergence response.

The adaptable association between vertical vergence and various combinations of eye position and horizontal vergence is ideally suited to compensate for non-concomitant variations of vertical skew resulting from injuries such as trochlear palsy. However, recovery from paralysis of the superior oblique is frequently accompanied by head turns and tilts (ocular torticollis) that are necessary to achieve binocular alignment in some but not all gaze directions (Kommerell & Klein, 1986). It is likely that these variations of vertical skew with changing direction of gaze are beyond the limits of the adaptation process. Such limits are demonstrated by the reduction of non-conjugate adaptation to two vertical disparities as their separation is reduced (Schor *et al.*, 1993). However, lesser anomalies produced by injuries or optical distortions produced by anisometric spectacles are within the range of this adaptive process.

These types of synergistic links within the central nervous system simplify control of motor responses. In the context-specific adaptation experiments, a specific vertical vergence response became a conditioned (preprogrammed) response that was specified by two components of eye position (such as horizontal and vertical conjugate eye position). Preprogrammed responses occur for other motor movements as well, such as posture control and locomotion (Brandt, 1988; Latash, 1993). Preprogrammed patterns of activity for posture control are initiated by mutually interactive pathways from several sources (visual, vestibular, and somatosensory) (Brandt, 1988; Clement, 1988). Similarly, the results of context-specific adaptation suggest that the preprogrammed (open-loop) vertical vergence can be specified by mutually dependent pathways from two eye-position sources. Our results provide an example of the adaptability of a preprogrammed oculomotor response (vertical vergence) formed by synergistic links with other oculomotor subsystems.

REFERENCES

- Albus, J. S. (1981). *Brains, robotics, and behavior* (pp. 139–179). Peterborough, NH: BYTE Books.
- Brandt, T. (1988). Sensory function and posture. In Amblard, B., Berthoz, A., & Clarac, F. (Eds), *Posture and gait: development, adaptation, and modulation* (pp. 127–136). Amsterdam: Excerpta Medica.
- Clement, G. (1988). Adaptation of postural control to long-lasting unusual constraints or repetitive stimulations. In Amblard, B., Berthoz, A., & Clarac, F. (Eds), *Posture and gait: development, adaptation, and modulation* (pp. 145–153). Amsterdam: Excerpta Medica.

- Helmholtz, H. von (1910). In Southall, J. P. C. (Ed.) *Treatise on physiological optics, Vol. III: The perceptions of vision* (pp. 58–59). New York: Dover Publications.
- Henson, D. B. & North, R. (1980). Adaptation to prism-induced heterophoria. *American Journal of Optometry*, 57, 129–137.
- Kertesz, A. E. (1983). Vertical and cyclofusional disparity vergence. In Schor, C. M. & Ciuffreda, K. (Eds), *Vergence eye movements: basic and clinical aspects* (p. 324). Woburn, MA: Butterworth.
- King, M. W., Fuchs, A. F. & Magnin, M. (1981). Vertical eye movement-related responses of neurons in midbrain near interstitial nucleus of Cajal. *Journal of Neurophysiology*, 46, 549–562.
- Kommerell, G. & Klein, U. (1986). Adaptive changes of the otolith-ocular reflex after injury to the trochlea. *Neuro-ophthalmology*, 6, 101–107.
- Lancaster, W. B. (1939). Detecting, measuring and interpreting ocular deviations. *Archives of Ophthalmology*, 22, 867–880.
- Latash, M. L. (1993). *Control of human movement* (pp. 234–244). Champaign, IL: Human Kinetics.
- Maxwell, J. S. & Schor, C. M. (1994). Mechanisms of vertical phoria adaptation revealed by time-course and two-dimensional spatiotopic maps. *Vision Research*, 34, 241–251.
- Maxwell, J. S. & Schor, C. M. (1996). Adaptation of vertical eye alignment in relation to head tilt. *Vision Research*, 36, 1195–1205.
- Maxwell, J. S. & Schor, C. M. (1997). Head-position-dependent adaptation of non-concomitant vertical skew. *Vision Research*, 37, 441–446.
- McCandless, J. W. & Schor, C. M. (1997a) A neural net model of the adaptation of binocular vertical eye alignment. *Network: Comput. Neural Systems*, 8, 55–70.
- McCandless, J. W. & Schor, C. M. (1997b) An association matrix model of context-specific vertical vergence adaptation. *Network: Comput. Neural Systems*, in press.
- McCandless, J. W., Schor, C. M. & Maxwell, J. S. (1996). A cross-coupling model of vertical vergence adaptation. *IEEE Transactions on Biomedical Engineering*, 43, 24–34.
- McFarland, J. L. & Fuchs, A. F. (1992). Discharge patterns in nucleus prepositus hypoglossi and adjacent medial vestibular nucleus during horizontal eye movement in behaving macaques. *Journal of Neurophysiology*, 68, 319–372.
- Schor, C.M. (1993). Sensorimotor adaptation and the development of the horopter. In Simons, K. (Ed.), *Early visual development, normal and abnormal* (pp. 237–249). New York: Oxford University Press.
- Schor, C. M., Gleason, G., Maxwell, J. & Lunn, R. (1993). Spatial aspects of vertical phoria adaptation. *Vision Research*, 33, 73–84.
- Schor, C. M., Maxwell, J. S. & Stevenson, S. B. (1994). Isovergence surfaces: the conjugacy of vertical eye movements in tertiary positions of gaze. *Ophthalmology and Physiology of Optics*, 14, 279–286.
- Schor, C. M. & McCandless, J. W. (1995a) An adaptable association between vertical and horizontal vergence. *Vision Research*, 35, 3519–3527.
- Welch, R. B. (1978). *Perceptual modification: adapting to altered sensory environments* (pp. 8–9). New York: Academic Press.

Acknowledgements—The authors would like to thank Scott Stevenson for proposing some of the experiments and James Maxwell for conducting a preliminary trial. This project was supported by NIH grant #EYO-3532.