Vergence Eye Movements Under Natural Viewing Conditions

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Purpose. To determine whether there are any fundamental differences in vergence dynamics under different viewing conditions, both in instrument space and free space.

Methods. Symmetric vergence responses were measured for a variety of conditions under the traditional instrument space as well as the more natural free space viewing environment. Vergence eye movements were recorded objectively in three subjects using the infrared reflection technique. Within each environment, four conditions were tested: aperiodic self-initiated voluntary gaze shifts between two simultaneously viewed targets; periodic (0.33 Hz) voluntary gaze shifts between the same two targets; gaze shifts in total darkness to the near target following initial far target fixation in the light; and gaze shifts in total darkness to the two remembered target positions. In addition, an experiment was performed in instrument space using randomized step changes of target disparity, in which the responses served as the standard for comparison. For all conditions, target disparities ranged from 0.5° to 10°. The peak velocity of each vergence response was calculated and plotted versus its amplitude.

Results. It was found that the data for all conditions tested fell within the standard “main sequence” cluster, indicating similarity in dynamics and thus similarity in the motorneuronal controller signal. Also, the data from investigators who claimed differences in dynamics were also typically found to fall within the normal cluster.

Conclusions. This indicates that the vergence motorneuronal controller signal produced the same dynamics for a particular response amplitude, independent of both viewing environment and test condition. Invest Ophthalmol Vis Sci. 1994; 35:3486–3492.
example, there could be grossly inadequate temporal response sampling of an eye movement response to asymmetrically positioned targets (e.g., 33-msec video frame interval compared with 2-msec sampling, which is adequate for measuring saccade dynamics). Inadequate sampling would miss most of the high velocity asymmetric saccades that occur between sampling points and thus would attribute inappropriately the resultant eye position displacement entirely to a vergence movement. This would yield an abnormally high apparent peak vergence velocity for a given amplitude "vergence" (actually vergence plus an embedded saccade) movement. And, third, these other investigators' responses may indeed be different, and their apparently faster velocities have been attributed to the enriched stimulus cues present under the free space (versus instrument space) viewing environment.

These findings present a dilemma with regard to vergence eye movement dynamics and their interpretation reported during the past two decades. Therefore, we have sought to investigate symmetric vergence eye movements in normal subjects in both free and instrument space environments under different test conditions. Vergence dynamics (i.e., the amplitude versus peak velocity relationship, or main sequence) were compared to determine the degree of dynamic and neurologic commonality of the variously derived vergence responses.

MATERIALS AND METHODS

Apparatus

Two test environments were used for stimulus presentation. The free space stimulus environment consisted of two targets mounted on a 1-m optical bench (Fig. 1). The targets were carefully aligned along the subject's midline. They were each composed of a black X on a white square background, having a contrast of approximately 80%. The sizes of the targets were selected so that the entire extent of each X was visible to the subject during bifixation. Each target subtended a visual angle of 1°. An additional target, also subtending 1° and placed 6 m from the subject, was only used during calibration. An ophthalmic trial frame with appropriate lenses was positioned in the subject's spectacle plane to correct any refractive error. In contrast, the instrument space stimulus environment consisted of an optical system called the dynamic binocular stimulator (DBS) (Fig. 2). The details of this optical arrangement have been provided elsewhere. Basically, vertical luminous line targets (1° high and .25° wide) were presented on an oscilloscope screen (phosphor type P31) positioned 114 cm from point P in the DBS. Point P was optically conjugate to the entrance pupils of the subject's eyes. A variable aperture was located at P so that reducing its diameter to 0.5 mm provided blur-free viewing. For a single target, the image was optically divided in the DBS and seen by both eyes, thus providing the percept of a single vertical line in depth. Any change in lateral position of the target on the oscilloscope screen resulted in a change in its disparity and a slight change in resultant apparent depth. When two vertical lines were presented simultaneously on the screen, the percept was that of vertical lines (one fused and one seen diplopically) located along the midline at two different depth planes. The separation of the two lines on the screen was proportional to the disparity and related to perceived depth of the targets.

A previous experiment has shown that vergence dynamics using the DBS either with or without the blur component were equivalent. Thus, disparity-only stimulation was used in the instrument space en-
FIGURE 2. Instrument space target arrangement for dynamic binocular stimulator (DBS). The major components are: T = binocular disparity target; L = alignment laser light source; P = iris diaphragm; B1–B2 = beam splitters; L1–L4 = double convex achromatic lenses; M1–M2 = front surface mirrors; PC = photocells for infrared eye movement recording device; LE and RE = the left and right eyes of the subject, respectively. Drawing is not to scale.

vironment because this was simpler to provide in the DBS than combined blur and disparity stimulation.

Stimulus generation, eye movement recording, and analysis of data were controlled by a Hewlett-Packard 9000, Series 550 computer (Fort Collins, CO). Horizontal eye movements were recorded binocularly using a Skalar infrared eye movement monitor (Model 6500; Delft, The Netherlands). This eye movement system has a linear range of ±25°, a resolution of 5 minutes of arc, and a bandwidth of 200 Hz. Data were analyzed off-line and plotted on a LaserJet 4 plotter (Hewlett-Packard, Greeley, CO).

Procedure

Three subjects participated in the experiments. Their ages were 27 (RC), 33 (TH), and 45 (GH) years. One of the subjects (GH) had extensive experience in eye movement experimentation, whereas the other two subjects had minimal experience. The research followed the tenets of the Declaration of Helsinki, informed consent was obtained after the nature and possible consequences of the study were explained, and the research was approved by the Rutgers University Institutional Review Board.

Four experiments were performed in both the free and instrument space environments to compare symmetric vergence response dynamics under the eight different stimulus conditions (see Table 1). In both stimulus environments, the disparity stimulus amplitude ranged from 0.5° to 10°. Room illumination was either very subdued or totally extinguished, depending on the test condition. In the first experiment, the targets were always visible. The subject followed randomly timed computer-generated tones to execute self-initiated voluntary gaze shifts between the two targets. The second experiment was similar to the first, except that the computer-controlled tones now signaled the onset of periodic (0.33 Hz) voluntary gaze shifts between the same two targets. The third experiment involved the use of a disappearing target protocol. As before, the targets were initially presented simultaneously, and the subject was instructed to practice verging between them several times. Then the subject bifixed the far target. After a computer-generated tone, both targets were extinguished, and the subject was instructed to converge in darkness from the remembered far to the remembered near target position. The targets were then reilluminated, and the procedure was repeated. The fourth experiment was similar to the third, except that there were now multiple voluntary vergence movements executed in total darkness. After practicing vergence shifts in the light, target illumination was extinguished. The subject then immediately attempted to make repeated vergence movements to the remembered far and near target positions. In all four experiments, only convergence movements were recorded. An additional experiment was performed in the instrument environment, which consisted of presenting random step changes of a sin-

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<tr>
<th>Experiment Number</th>
<th>Procedure</th>
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<tbody>
<tr>
<td>1</td>
<td>Voluntary vergence shifts; self-initiated</td>
<td>△ ★</td>
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<tr>
<td>2</td>
<td>Voluntary vergence shifts made after tone; period 0.33 Hz</td>
<td>◆ ☆</td>
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<tr>
<td>3</td>
<td>Practice vergence shifts in light; then fixate far target, lights extinguished, verge to remembered near target</td>
<td>□ ■</td>
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<tr>
<td>4</td>
<td>Practice vergence shifts in light; then vergence shifts in total darkness to remembered near and far target positions</td>
<td>○ ●</td>
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FIGURE 3. Example of phase–plane plot showing peak velocity versus amplitude for a single vergence movement (the final steady state portion is not shown). The phase plane is useful for determining where changes in dynamics occur. Extrapolated (dotted line) fast component amplitude was used in the data analysis. $A = Amplitude; V_p = peak velocity$. Subject GH.

Analysis of Data

In the off-line data analysis procedure, the calibrated movements of each eye were subtracted to yield the overall vergence response. Records containing artifacts such as blinks or saccades during the initial portion of the dynamic responses were deleted. Only those responses that remained within the linear calibration range ($0°$ to $10°$) were used.

Vergence responses contain two components: an initial large and fast open-loop component that is directly related to the underlying motorneuronal controller signal, followed by a smaller and slower closed-loop component that reduces the residual disparity to within neurosensory tolerances (i.e., Panum’s fusional area). To ascertain the actual amplitude of the fast component, which could be masked by the subsequent slow component, the vergence movement was displayed as a computer-generated phase plane (velocity versus position). An example of a typical vergence movement along with its phase plane is shown in Figure 3. The curve associated with the initial portion of the trajectory was extended (see dashed line) to the abscissa using manual curve fitting. The magnitude at the intersection was considered to represent the amplitude of the initial fast component for that response. In no case did the difference in vergence amplitude between that found for the fast phase versus the fast-plus-slow phase exceed $1°$, and it was typically less than $.5°$. The peak velocity was also obtained from the same phase–plane plot. The amplitude and peak velocity values were obtained for each vergence movement and then graphed on a main sequence plot.

RESULTS

The paired peak velocity versus amplitude values for standard step responses in the control experiment in instrument space are presented for the three subjects in Figure 4. Also shown are the regression line and the 95% confidence interval. The regression line and the associated confidence interval provided the “standard” or norm for which the other vergence responses were compared. The slope of the regression line was approximately equal to 4. Clearly, vergence response peak velocity changed in proportion to vergence response amplitude, with a ratio of 4:1.

The main sequence data in both the free and instrument space environments for the eight stimulus conditions are plotted for representative subject GH (Fig. 5). Also shown are the standard step values. Overlap of data points suggests that the general initial dynamics and, therefore, motorneuronal controller signals are similar for all stimulus conditions.

For comparison, the velocity versus (total) amplitude data from other studies are plotted in Figure 6 along with our standard step disparity values (see Fig. 4). It can be seen that the data from the different studies all fall reasonably well (with one exception) within our cluster of standard step data points. This suggests that the main sequence vergence dynamics are dependent on the response amplitude only; they

FIGURE 4. Main sequence, or peak velocity versus amplitude, for standard vergence step responses for all three subjects showing data for different stimulus amplitudes. Also shown is the regression line (solid) and 95% confidence interval (dashed).
FIGURE 5. Main sequence for the eight experimental conditions (see Table 1) for subject GH. Symbols: Voluntary = triangles; predictable = diamonds; disappearing target = squares; and complete darkness = circles; free space = open symbols; instrument space = filled symbols. Also shown are the standard steps (x) from Figure 4.

are independent of both stimulus condition and viewing environment.

As an additional comparison, our standard step values in humans were compared with those found in the cat22 and monkey23 (Fig. 7). Again, a linear relationship was found across species, although the slopes differed considerably. This suggests that neural coding for velocity is similar across species, differing only in the associated gain for velocity generation.

DISCUSSION

The assessment of dynamics using the peak velocity–amplitude relationship, or main sequence, clearly demonstrates that vergence eye movements are remarkably similar under a variety of stimulus conditions. This suggests that the basic motoneuronal controller signals are essentially the same, thereby producing movements with similar overall general dynamics. Several more recent studies, including the present one, have indicated that the peak velocity for a vergence response, with either disparity-only or with the addition of blur and proximity, is proportional to the response amplitude (approximately 4:1 ratio9,11,13,14,20,24). This proportionality is close to that reported by Bahill et al5–8 nearly two decades ago for disparity-only stimulation.

One may then justifiably ask why there has been confusion and even doubt cast upon the Bahill et al5–8 results. There are at least three primary reasons.

First, there was a failure to be aware of or to recognize and/or accept data already in the literature. In addition to the results of Bahill and colleagues,5–8 which were actually derived from two other studies,7,8 similar results were reported more than two decades ago by Tenjin for disparity-only stimulation in both normal individuals and in patients with head trauma,10 and more than three decades ago by Rashbass and Westheimer in normal subjects.8 In fact, some of those who criticized the Bahill et al results actually presented data of their own in the same paper showing this predicted 4:1 relationship.11,13,14,24

Second, in a study of asymmetric vergence,11 the velocities reported were far in excess of those predicted by the main sequence. However, the sampling interval used was extremely long (one video frame, with most analyses performed over either three or five frame periods), which likely resulted in a combined vergence plus asymmetric saccade being identified as the overall “vergence” motor response. The velocity attributed to a vergence movement was calculated simply as the slope between eye position at the beginning of the movement to that either three or five video frames later. There are two ways in which embedded saccades could affect the difference in amplitude between the two eyes during the sampling interval. (1)
Saccade-related dysjunctive transients, consisting of a brief divergence followed by convergence (which occurs during all saccades) could occur at the instant of sampling and be inadvertently added to the vergence movement. (2) When vergence and saccadic movements occur together, there is an apparent enhanced higher-velocity vergence response. Zee et al have attributed this to the influence of pause neurons on the saccadic and vergence control circuitry during combined movements. Thus, in both cases, the increased amplitude difference between the two eyes was due to interactions between saccade and vergence rather than to the vergence movement alone. The use of a long sampling interval simply served to obscure the dynamic features of any saccade that may occur and, in effect, to remove from analysis the saccade–vergence interactions that could account for the observed enhancement in vergence velocity.

And (3), some authors found what they believed to be very fast vergence responses for large amplitude movements under free space conditions. This led them to speculate that in free space, the additional monocular and binocular depth cues “enhanced” the motor response. However, their amplitude–peak velocity data were in fact similar to and fit on the main sequence data of Bahill and colleagues, as well as our present data. Thus, these presumed velocity-enhanced responses were actually normal and followed the basic amplitude-dependent, neural velocity coding common to all the vergence response types tested.

In conclusion, the present results using main sequence analysis clearly show a commonality in basic vergence dynamics under a variety of situations, suggesting that the neural controller program is dependent only on the response amplitude. These findings also shed light on and resolve a long-standing controversy in the oculomotor literature regarding apparent differences in basic vergence dynamics by demonstra-
ting their equivalence in the main sequence relationship. Lastly, comparison of our human results with those of lower species provides evidence for a common neural metric underlying vergence control.

Key Words
vergence, instrument space, free space, main sequence, motoneuronal control

References