

Quantitative assessment of divergence eye movements

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Purpose: This study sought to quantify divergence eye movements and differences between divergence and convergence to smoothly moving ramp, step, and disappearing step stimuli. **Methods:** Eight visually normal, adult subjects participated in three experiments investigating the dynamics of responses using an infrared limbal eye tracker. **Results:** There were four primary findings: (1) a smooth tracking behavior was observed for slow ramps while the fast ramps elicited smooth tracking combined with a high-velocity, step-like behavior; (2) the high-velocity components observed in the faster ramps had a similar main sequence as divergence steps; (3) divergence dynamics to disappearing steps starting at the subject's near dissociated phoria level were similar to corresponding step responses; and (4) the high-velocity components from divergence ramps were dependent on initial vergence position, whereas the high-velocity components from convergence ramps were not. **Conclusion:** The results suggest a preprogrammed component is present in divergence similar to convergence; however, unlike convergence, the high-velocity components from divergence ramp responses are dependent on initial vergence position.

Keywords: vergence eye movement, convergence, divergence, vergence dynamics

Citation: Yun Lee, Y., Chen, T., & Alvarez, T. L. (2008). Quantitative assessment of divergence eye movements. *Journal of Vision*, 8(12):5, 1–13, <http://journalofvision.org/8/12/5/>, doi:10.1167/8.12.5.

Introduction

Vergence eye movements enable depth perception utilizing the medial and lateral recti muscles to rotate the eyes inward (convergence) or outward (divergence). The rotation projects the object of interest to the fovea that contains the largest density of photoreceptors, hence giving the brain the greatest resolution of the desired object.

Studies on convergence have a long history (Westheimer & Mitchell, 1956). The disparity vergence system was first described as a single feedback control system (Rashbass & Westheimer, 1961). However, studies have shown that a dichotomy in the neural control strategy is necessary to describe the dynamics of a convergence eye movement under a variety of environmental stimuli. Vergence, similar to many systems controlled by the central nervous system, is responsible for accurately attaining the intended target and achieving this final position relatively quickly. Control engineering principles dictate that these behaviors are best attained using very different strategies. Feedback control is accurate because it continuously compares the current position of the eye with the location of the intended target; however, it cannot drive a fast movement

in the presence of processing delays. Vergence latencies are typically 180 to 220 msec for step responses (Alvarez, Semmlow, Yuan, & Munoz, 2002; Ciuffreda, & Tannen, 1995). Latencies have also been reported as low as 80 msec (Busettini, Fitzgibbon, & Miles, 2001; Busettini, Masson, & Miles, 1997). Preprogramming or feedforward control is fast even when delays are present, but not necessarily accurate.

Significant behavioral evidence exists to support a preprogrammed element within convergence control. Jones showed that by stepping a non-fusible target (a vertical line paired with a horizontal line), a transient vergence response was generated. Under these conditions, the vergence system cannot use an external visual feedback system since an error signal is not generated. Jones then developed a theory that convergence was composed of a “fusion initiating” and a “fusion sustaining” component (Jones, 1980; Jones & Stephens, 1989). Similarly, Semmlow, Hung, Horng, and Ciuffreda (1993) reported that by presenting a step stimulus that would disappear in a mere 50 or 100 msec, a transient convergence response was generated. Furthermore, when using a crossed stimulus for 200 msec within patterns, transient convergent responses were observed but for similar uncrossed stimuli,

divergence was observed for only small step changes (Busettini, Miles, & Krauzlis, 1996).

A main sequence analysis showed that the transient component of the disappearing steps had similar dynamics compared to step responses which is evidence of a preprogrammed response (Semmlow et al., 1993). Furthermore, by varying ramp speeds, two distinct convergent behaviors have been described where ramps faster than 2.7°/s generated step-like responses to smooth inward stimuli (Semmlow, Hung, & Ciuffreda, 1986). Alvarez, Semmlow, and Yuan (1998) showed that if the initial transient response of convergence steps did not attain approximately 80% of the intended vergence amplitude, then a secondary high-velocity component would be generated which cannot be described using solely feedback theory. The behaviors described above give support for a preprogrammed element within convergence. These findings led to the development of the dual-mode theory specifying that convergence is composed of a preprogrammed element with feedback control (Hung, Semmlow, & Ciuffreda, 1986).

The dual-mode model can accurately simulate convergence responses (Horng, Semmlow, Hung, & Ciuffreda, 1998a, 1998b; Hung, 1998; Hung et al., 1986). Radisavljevic-Gajic (2006) has also modeled vergence movements using dynamic equations that decouple the slow and fast components. Principle component analysis has shown that for convergence, the majority of variance can be explained by two main components (Semmlow & Yuan, 2002).

The dualistic nature of vergence control also is supported by neurophysiological evidence. Mays and colleagues have found midbrain neurons that code for velocity and other neurons that code for position (Gamlin & Mays, 1992; Mays, Porter, Gamlin, & Tello, 1986). Case studies have reported disruption in “slow vergence” accompanied with normal “fast vergence” in two patients with unilateral mediolateral pontine infarctions and have concluded that vergence signals are distributed in the pontine nuclei (Rambold, Sander, Neumann, & Helmchen, 2005).

Many studies have compared convergence and divergence behaviors reporting differences between the systems. Divergence is in the opposite direction of convergence; yet, it is not merely negative convergence. Dynamic analyses have generally reported that convergence is faster than divergence in humans (Hung, Zhu, & Ciuffreda, 1997; Zee, Fitzgibbon, & Optican, 1992) and macaque monkeys (Maxwell & King, 1992). Unlike convergence, divergence dynamics are dependent on the initial position of the stimulus; hence, dynamic comparisons need to account for differences in initial position (Alvarez, Semmlow, & Pedrono, 2005). Using a gap paradigm, researchers report that divergence can demonstrate shorter latencies than nongap responses; however, convergence did not show temporal differences (Coubard, Daunys, & Kapoula, 2004). When investigating the adaptive affects of sustained near convergence, nonlinear differences in an

adaptive mechanism are noted between convergence and divergence (Patel, Jiang, White, & Ogmen, 1999). Furthermore, it has been shown that convergence and divergence have different influences on saccadic movements during saccade–vergence interaction studies (Busettini & Mays, 2003). Vertical saccade–vergence interaction shows that convergence velocities do not typically vary but divergence is dependent on the upward or downward vertical saccadic movement (Kumar, Han, Dell’osso, Durand, & Leigh, 2005). Convergence and divergence also exhibit distinct dysfunctions (Schor, 1988). Neurophysiologists have shown different cells encode convergence and divergence (Gamlin, Yoon, & Zhang, 1996; Mays, 1984; Mays & Porter, 1984; Mays, Porter, & Tello, 1986; Nitta, Akao, Kurkin, & Fukushima, 2008; Zhang & Gamlin, 1998; Zhang, Gamlin, & Mays, 1991). Hence, differences between the behaviors of the two systems should be anticipated.

This study has two goals: (1) to search for evidence of a preprogrammed behavior in divergence responses and (2) to quantify dynamic differences between convergence and divergence responses to smoothly moving ramp stimuli.

Methodology

Subjects

Eight subjects, 18 to 63 years of age, who could all easily perform the paradigms described below, participated in this study. There were four males and four females. Previous research has shown that vergence dynamics decrease with age (Rambold, Neumann, Sander, & Helmchen, 2006); however, our eldest subject had similar vergence dynamics to the other seven younger subjects. Hence, his data were included in this analysis. All subjects had normal binocular vision assessed by the Randot Stereopsis Test and used correction if needed for the experiment. All subjects signed informed consent before the experiments, which was approved by the New Jersey Institute of Technology (NJIT) Institutional Review Board (IRB). Two of the subjects (Subjects 4 and 5) knew the objective of this study prior to the experiment, while the other six subjects were naive.

Materials and apparatus

Visual stimuli were displayed via a dynamic haploscope. Two computer screens were used to generate a symmetrical disparity vergence stimulus consisting of a pair of vertical lines. Accommodative vergence was held constant; hence, any changes in dynamics were believed to be caused by the disparity vergence system. The stimulus displays were placed 56 cm away from the subject. Each

Ramp velocity	Initial position (°)	Final position (deg)	Stimulus duration (s)
Stimuli for Subject 1 where the closest vergence angle position was 18°			
2°/s	18	12	3
4°/s	18	6	3
6°/s	18	2	2.7
10°/s	18	2	1.6
Stimuli for Subjects 2 through 4 where the closest vergence angle position was 20°			
2°/s	20	12	4
4°/s	20	4	4
6°/s	20	2	3
10°/s	20	2	1.8

Table 1. Initial position, final position, and stimulus duration for the various divergence ramp stimuli.

target was a vertical line 3 cm in height by 2 mm in width and remained constant throughout the experiment when a visual stimulus was present. Two partially reflecting mirrors were positioned in the midline of the subject's vision to project the two vertical lines from the computer screens into the eyesight of the subject. Before the experiment, the targets projecting from the computer screen were adjusted with the mirrors to calibrate the visual stimulus with real targets located at measured distances from the subject's midline. During the experiment, only the visual stimulus displayed by the computer screens was seen by the subject. The subject's head was restrained using a custom chin rest to eliminate head

movements thus avoiding any vestibular influences in the experiment.

Vergence eye movements were recorded using an infrared limbal tracking system ($\lambda = 950$ nm) manufactured by Skalar Iris (model 6500). All of the eye movements were within the linear range of the system ($\pm 25^\circ$). The left-eye and right-eye responses were calibrated, recorded, and saved separately for offline analysis. Digitization of the eye movements was performed with a 12-bit digital acquisition (DAQ) hardware card using a range of ± 5 volts (National Instruments 6024 E series, Austin, TX). The entire system was controlled by a custom LabVIEW™ program which generated the visual stimulus and digitized the individual eye movements sampling at a rate of 200 Hz, which was well above the Nyquist frequency for vergence eye movements. A custom Matlab™ 7.0 (Waltham, MA) program was used for offline data analysis.

Experimental design

This study sought two major aims: (1) to determine if behavioral evidence exists to support a preprogrammed, feedforward control mechanism in divergence and 2) to quantify any differences between the convergence and divergence system for smoothly moving stimuli. To address the first goal, two experiments were conducted which utilized three types of visual stimuli: ramp, disappearing step, and step. During ramp stimulation, four different types of ramp stimuli were used (2, 4, 6, 10°/s ramp stimulus) in each experimental session to elicit divergence responses. Divergence ramps began at an initial position of 18° or 20°, depending upon the closest position

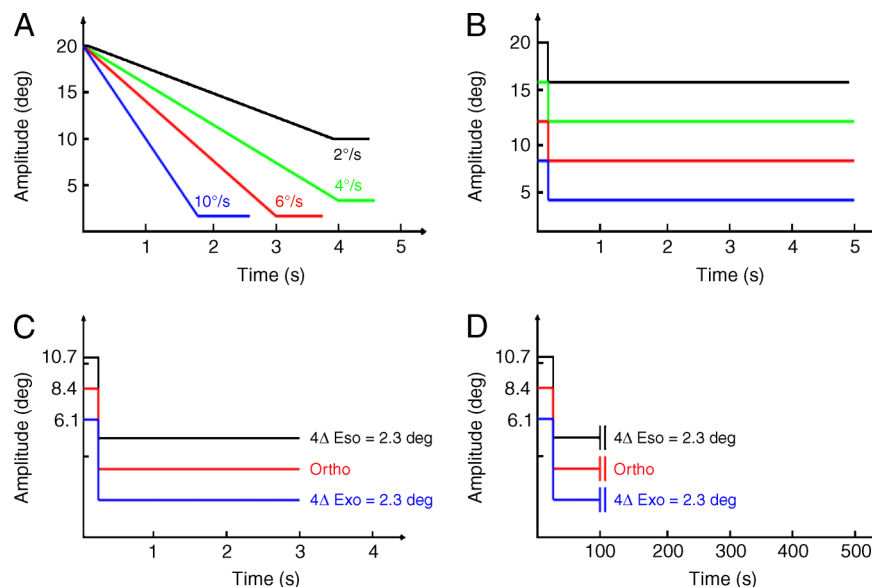


Figure 1. Divergence visual stimuli (A) ramp stimuli, (B) step stimuli used in comparison with ramps, (C) step stimuli used in comparison with disappearing steps, (D) disappearing step stimuli. Note panels C and D were designed for the designated near dissociated phoria levels studied (4Δ esophore, orthophore, or 4Δ exophore). Similarly, 2 and 6 deg steps and disappearing were also studied.

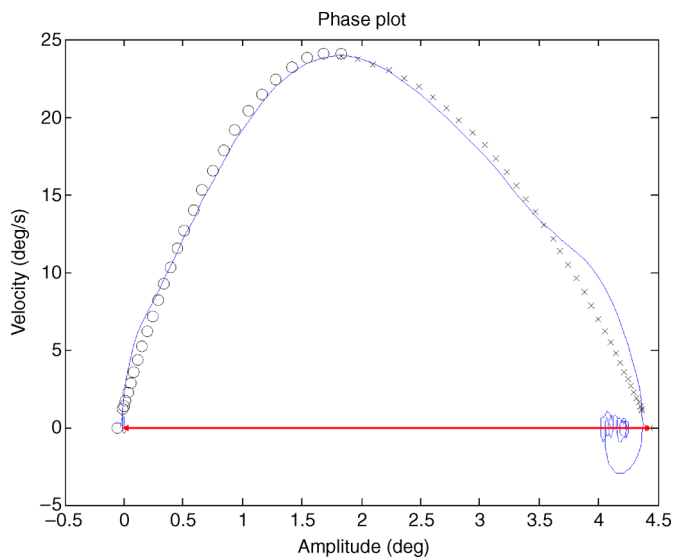


Figure 2. Example of second-order polynomial fit to a typical divergence 4° step response. The polynomial curve for the increasing portion is denoted with “o” and the polynomial for the decreasing portion is denoted with “x.” Note that the divergence response is plotted with both position and velocity as positive for clarity. The isolated “o” indicates the initial position of the responses where the isolated “x” represents the final position. The response amplitude is the difference between these two points or the red arrow. This method was applied to all high-velocity components included in the main sequence analysis.

of convergence the subject could comfortably fuse. The stimulus stopped when it reached 2° or a duration when the subject was likely to blink. Typically after 4 seconds, the subjects were more likely to blink and a 2° final vergence position was comfortable for the subjects who participated. Four subjects participated in the ramp and step experiment. For Subject 1, the near vergence angle was 18° and for Subjects 2 through 4 it was 20° . The stimuli parameters for divergence ramps are summarized in Table 1 and shown in Figure 1A. The dynamics of eye movements elicited by ramps were compared with the dynamics of 4° steps starting at different initial vergence positions (20° , 16° , 12° , and 8° ; Figure 1B). The step disparity change was 4° because artifact-free responses are easier to attain than larger step disparities and still provide a reasonable signal to noise ratio. The most common artifacts are saccades and blinks. The data were compared using a within subject design.

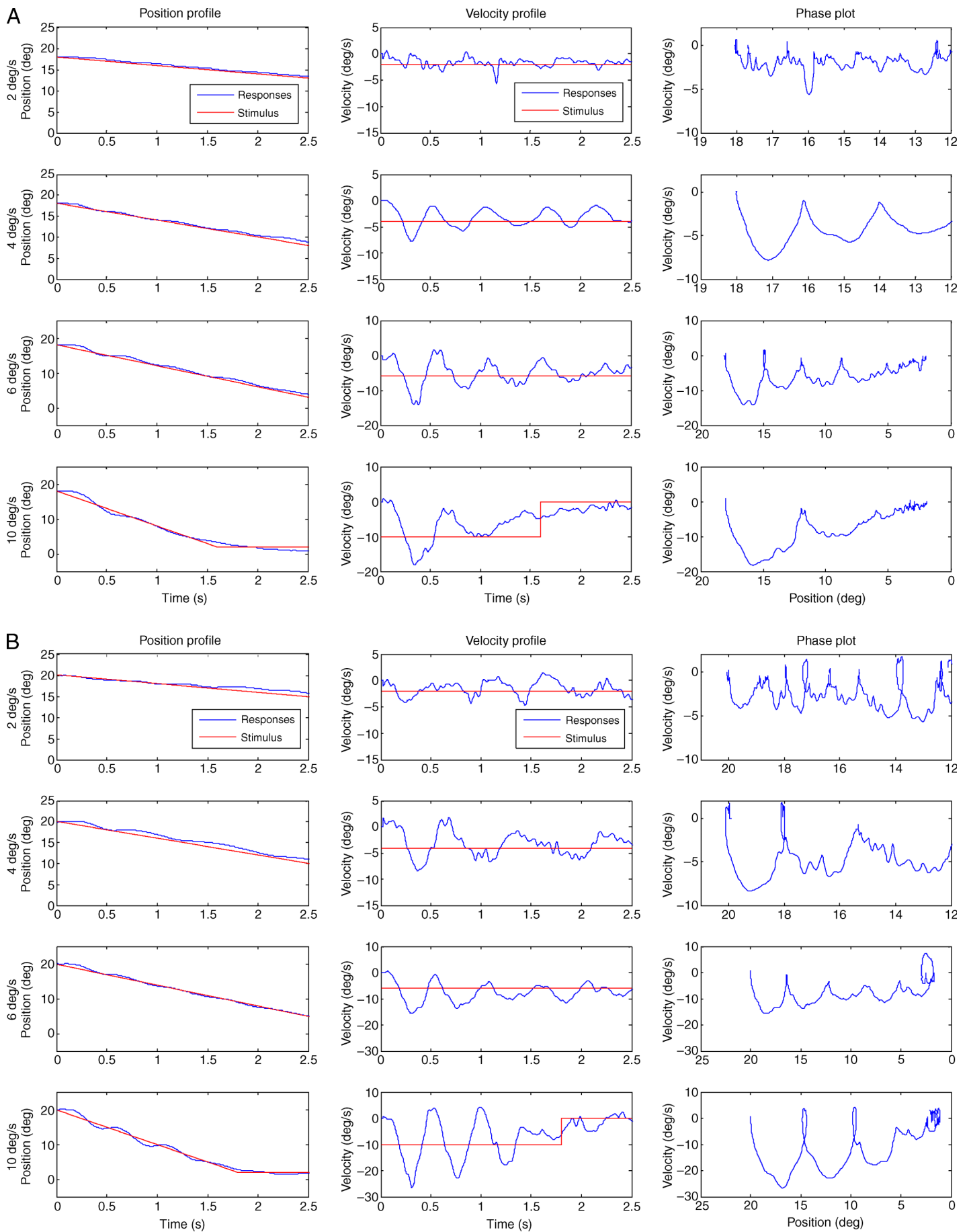
The second experiment compared the dynamics of steps with disappearing steps which were illuminated for 100 msec. Both the step and the disappearing step started at the subject’s near dissociated phoria position and diverged 2° , 4° , or 6° away from the subject. Near dissociated phoria was measured before the experiment using a Maddox rod. Subjects were carefully chosen to have similar phoria levels so that their data could be

compared. The phoria range used here was 4Δ esophoric to 4Δ exophoric, which corresponds to initial vergence angle position of 6.1° to 10.7° or a 4.6° range between subject stimuli, Figure 1D. The disappearing step dynamics were compared to 2° , 4° , and 6° step responses that had the same initial position. Figures 1C–1D show the stimuli for 4° movements. Divergence dynamics are known to be dependent on vergence initial position (Alvarez et al., 2005); hence, the stimuli should start at similar initial positions. To investigate if a preprogrammed element is present in divergence using a disappearing step protocol, the initial position must be the near dissociated phoria because when the target disappears the eyes will decay to the phoria level. Hence, it would be difficult to determine if the movement observed was due to phoria decay or due to disparity vergence. If a preprogrammed component is present, the hypothesis is that the eyes will begin the movement due to the disparity change and then decay back to the subject’s near phoria level. If a preprogrammed component is not present, then the hypothesis is virtually no change in the responses would be observed because the eyes are close to the subject’s phoria level.

The comparison of divergence and convergence responses to smoothly moving stimuli used ramps moving at 2, 4, 6, and $10^\circ/\text{s}$ for divergence compared to 6 and $10^\circ/\text{s}$ for convergence which investigates the second goal of this study. Slower moving convergence ramps were not investigated because they have been shown to exhibit typically smooth tracking that do not contain the fast dynamic behavior of interest here (Semmlow et al., 1986). Divergence ramp stimuli are summarized in Table 1 and Figure 1A. Convergence began at 2° and saturated at a maximum vergence position of 18° or 20° . The length of stimulation time varied per stimulus type because of the differences in vergence ranges. For example, over a 3-second duration, a ramp moving $10^\circ/\text{s}$ would move 30° which our subjects had difficulty fusing. Hence, the stimulus would saturate at the near point of convergence specified above. Furthermore, subjects were not asked to fuse targets beyond infinity. The degree position discussed throughout this research is the convergence necessary to point both lines of sight toward the target.

Subjects were dark adapted for approximately five minutes. After the eye movement monitor was successfully

Figure 3. Typical divergence responses to ramp stimuli at various speeds from (A) Subject 1 (initial position of 18°) and (B) Subject 2 (initial position of 20°). The left and central columns show the position and velocity as a function of time respectively while the right column displays the phase domain plot (velocity as a function of position). Slower ramps elicit smoother tracking, whereas faster ramps exhibit more high-velocity responses. The peak velocity of each high-velocity component generally decreases as a function of initial position for divergence. Note the scales are different for the slower ramps of $2^\circ/\text{s}$ and $4^\circ/\text{s}$ versus the faster ramps $6^\circ/\text{s}$ and $10^\circ/\text{s}$.



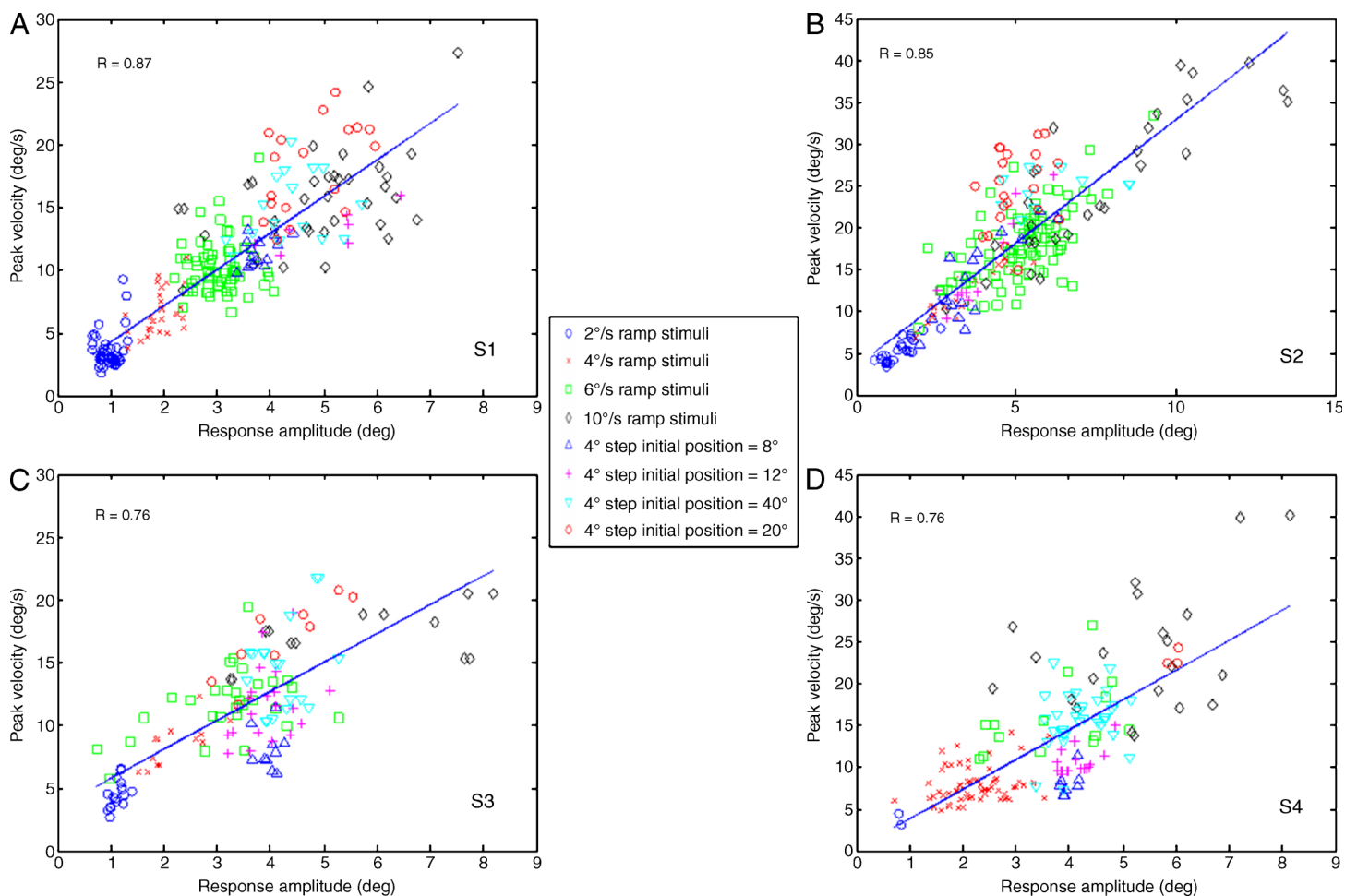


Figure 4. Main sequence analysis from Subjects 1 (A) through 4 (D) for high-velocity ramp responses with 4° step responses. Stimulus parameters are noted in the legend.

adjusted on the subject, he or she would initiate an experimental trial by depressing a button. Prediction was reduced using a randomized time delay of 0.5 to 2.0 seconds since prediction is known to alter vergence dynamics (Alvarez et al., 2002). After the random delay, a stimulus (ramp, step, or disappearing step) was presented. The subject could pause at any time to avoid fatigue and would then initiate another trial. Sessions lasted for approximately one hour.

Converging and diverging ramps and divergence steps at initial positions of 20, 16, 12, and 8° were recorded from Subjects 1 through 4. Divergence steps and disappearing steps with the same initial positions were recorded from Subjects 5 through 8.

Data and statistic analysis

All data analysis was performed with a custom program written in Matlab 7.0 (Waltham, MA). Left-eye and right-eye movements were first converted to degrees using the individual calibration data. The system has a high degree

of linearity, within 3% between $\pm 25^\circ$ horizontally (Hornig et al., 1998a, 1998b); hence, this study used a two-point calibration protocol. The left- and right-eye responses were calibrated separately and disparity vergence was obtained by subtracting the right-eye movement from the left-eye movement to yield a net vergence response where convergence is plotted as positive and divergence as negative. Blinks and saccadic eye movements were easily identified because of their fast dynamics compared to vergence. Responses with blinks at any point during the movement were omitted.

Dynamics were assessed using a two-point central difference algorithm to compute the vergence velocity response (Bahill, Kallman, & Lieberman, 1982). A main sequence analysis was used to compare the dynamics of different types of responses and is commonly used in saccadic and vergence analyses. The main sequence is a plot of the magnitude of peak velocity versus the response amplitude (Bahill, Clark, & Stark, 1975; Bahill & Stark, 1979). Figure 2 displays a plot of a typical divergence response to a 4° step in the phase plane (velocity as a function of amplitude). The response amplitude is easily

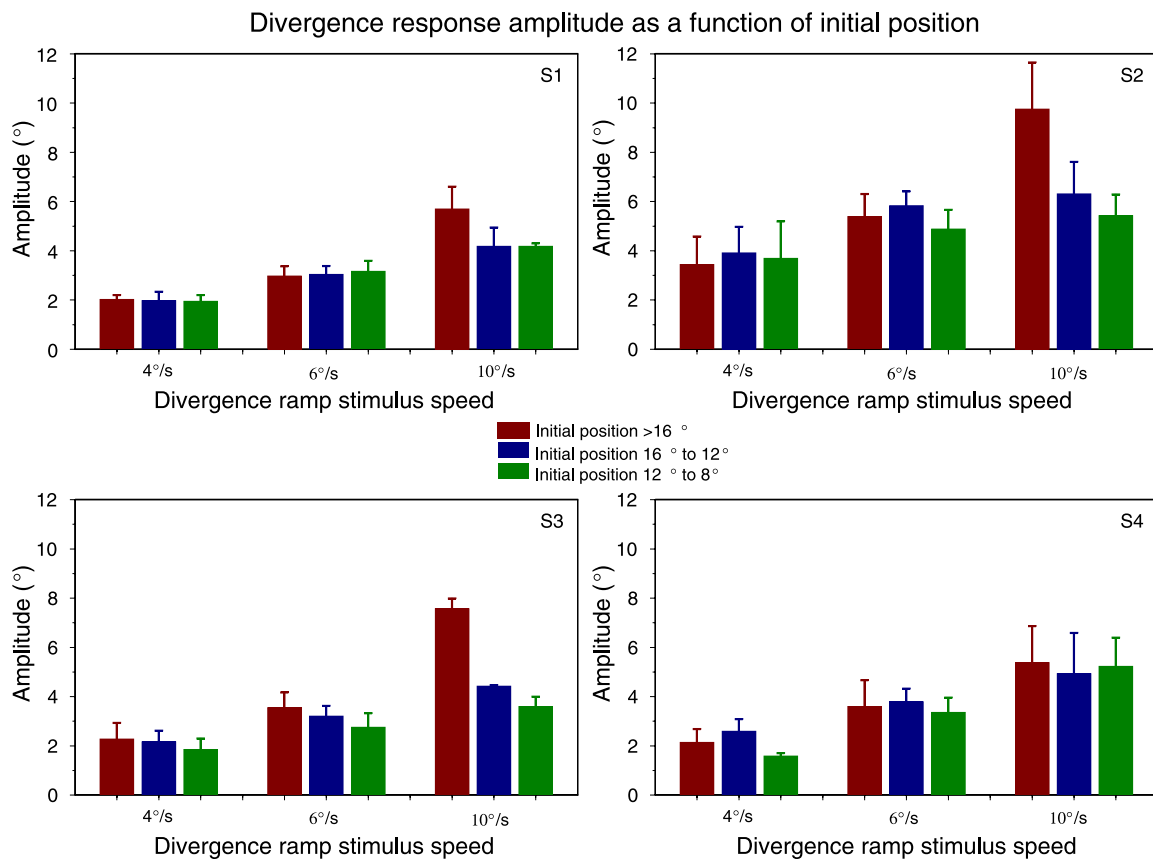


Figure 5. Average response amplitudes with standard deviation of high-velocity responses with different initial positions for the various ramp speeds for Subjects 1 through 4 who participated in this experiment. The legend specifies the initial position of where the high-velocity components began. The number of responses is denoted in Table 2.

measured for step responses (Figure 2) and is the amplitude when the velocity returns to approximately zero. However, it is more difficult to measure for ramp responses. The phase plane plot is useful for analyzing the dynamics of eye movement responses since it emphasizes the first-order dynamics (Alvarez et al., 1998; Yuan, Semmlow, Alvarez, & Munoz, 1999). To reduce subjectivity by the operator, an extrapolation method was used in the analysis which has been used previously (Alvarez et al., 1998). A second-order polynomial was fit to the increasing (denoted with “o” symbols in Figure 2) and decreasing portions (denoted with “x” symbols in Figure 2) of the response. The roots of the polynomial were calculated and plotted. The root for the increasing polynomial was selected as the initial position (denoted by an isolated “o” in Figure 2) of the high-velocity response while the root for the decreasing polynomial was chosen as the final position (denoted by an isolated “x” in Figure 2). The net response amplitude was the difference between the final and initial position of a high-velocity response, Figure 2 red line. This method was used for all responses for consistency.

Data were compared using a within subject three-way ANOVA where ramp speed (4°/s, 6°/s, and 10°/s), the peak

velocity of each high-velocity movement, and the response positions when the high-velocity component began (>16°, 16°–12°, and 12°–8°) were analyzed using the NCS2004 (Kaysville, UT) software package. The slowly moving ramps of 2°/s ramp were not included in the statistical analysis because high-velocity components were not always observed. Similarly, high-velocity components were not predominantly observed at positions less than 8°; hence, these were also not included in the statistical analysis.

Results

Typical divergence responses from Subjects 1 and 2 for various ramp stimuli are shown in Figure 3. Similar results were found for all subjects studied. The left and central columns display the position and velocity profile as a function of time respectively while the right column displays the phase domain plot. On average, smooth tracking behavior was observed in response to the slow ramp stimulus (2°/s), whereas smooth tracking combined

with some high-velocity behavior was observed in the faster ramp responses to the 4°/s, 6°/s, and 10°/s stimuli. Occasionally, a few of the 2°/s ramp responses contained both smooth tracking and high-velocity behavior. However, the 2°/s ramp responses were not included in the statistical analyses because the high-velocity behavior was not typically observed. In general, the peak velocities of the high-velocity responses decrease as the ramp stimulus moves away from the subject.

The dynamics were analyzed by plotting the main sequence, a plot of peak velocity versus response amplitude, for each high-velocity ramp movement with typical step responses (Figure 4). The regression line shown in Figure 4 is through all data plotted. Since the high-velocity components from ramps and steps fall along the same main sequence, their first-order dynamics are similar (Semmlow et al., 1986).

The response amplitude of the high-velocity components from 4°/s, 6°/s, and 10°/s is summarized for each subject in Figure 5. S3 shows a trend of the response amplitude decreasing as the target moved away from the subject. The other three subjects do not show a consistent trend with the amplitude of the high-velocity component being dependent on initial position.

The second experiment compared the dynamics of steps and disappearing steps for Subjects 5 through 8 where the initial position for both steps and disappearing steps during this experiment was set equal to the subject's near dissociated phoria level. Subject 5 was a 4Δ esophore. Subjects 6 and 7 were 4Δ exophores and Subject 8 was an orthophore. Figure 6 shows the main sequence of the initial dynamic response for steps and disappearing steps for the four subjects studied for 2, 4, and 6° disparity changes. A regression line (blue solid) is fit through only the step data with the corresponding 95% confidence lines (blue dotted) and then a separate regression line (red solid) is fit through only the disappearing step data with those corresponding 95% confidence lines (red dotted). There is overlap of the 95% confidence lines for all four subjects studied. The ratio of peak velocity to response amplitude for steps and for disappearing steps was compared using a Student *t* test. For the four subjects studied, there was no significant difference ($p > 0.1$). The first order dynamics were similar as depicted by the main sequence for the step and disappearing step responses.

The third experiment addressed the second goal and quantified the differences between convergence and

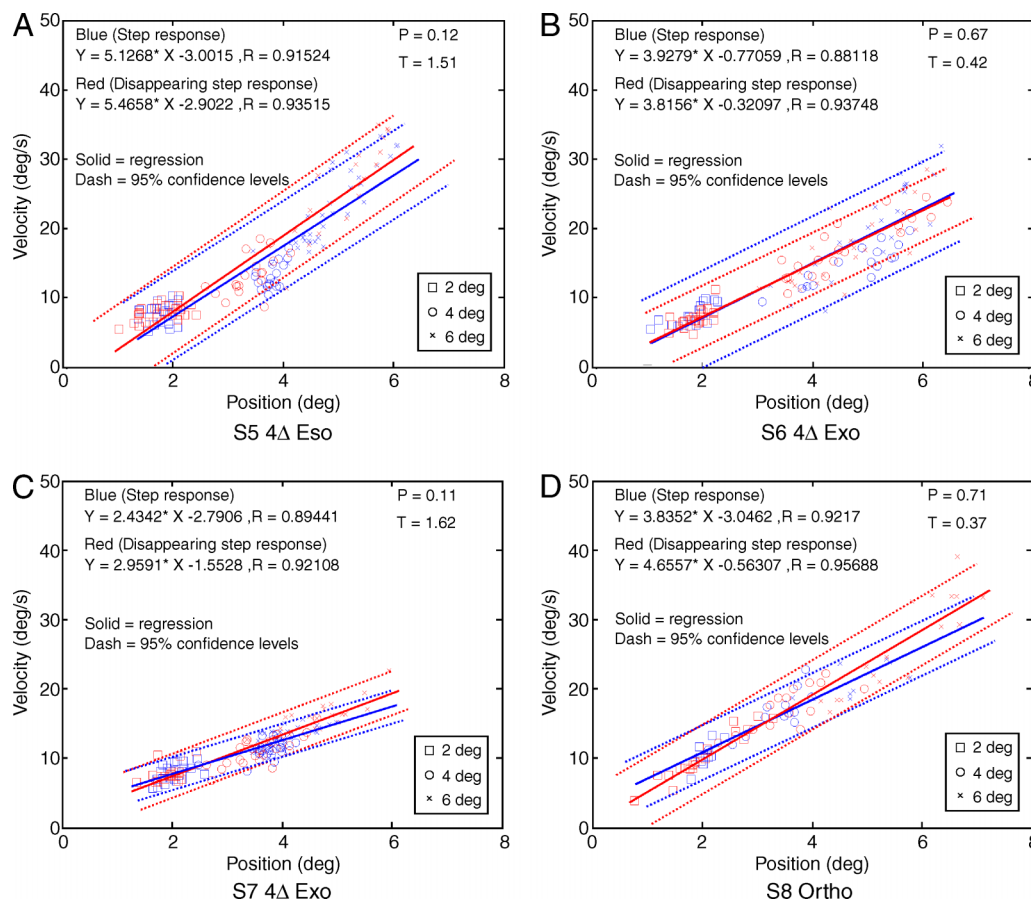


Figure 6. Main sequence of the responses to standard step and disappearing step stimulus of 2, 4, and 6° for Subjects 5 (A) through 8 (D) using the visual stimuli described in Figures 1C and 1D. The data distribution is similar under both conditions.

Ramp stimulus speed (°/s)	Initial high-velocity component position (°)														
	>16°				16° – 12°				12° – 8°				<8°		
	PV	Amp	n	PV	Amp	n	PV	Amp	n	PV	Amp	n	PV	Amp	n
Subject 1	2°/s	4.02 ± 0.89	0.94 ± 0.22	17	2.8 ± 0.37	0.98 ± 0.13	17	5.76 ± 0.77	1.95 ± 0.26	7	5.21 ± 1.09	1.52 ± 0.25	4	1.52 ± 0.25	4
	4°/s	8.88 ± 1.60	2.02 ± 0.19	16	6.36 ± 1.57	1.98 ± 0.36	9	8.74 ± 0.83	3.16 ± 0.43	19	8.18 ± 0.90	2.88 ± 0.78	4	2.88 ± 0.78	4
	6°/s	12.27 ± 2.32	2.97 ± 0.41	17	9.92 ± 0.98	3.04 ± 0.35	25	12.11 ± 2.01	4.18 ± 0.13	8	11.96 ± 3.11	4.74 ± 1.63	4	4.74 ± 1.63	4
	10°/s	18.24 ± 3.15	5.70 ± 0.91	18	13.92 ± 1.57	4.18 ± 0.77	6	11.29 ± 3.10	3.69 ± 1.51	4	8.96 ± 1.60	2.87 ± 0.75	4	2.87 ± 0.75	4
Subject 2	2°/s	5.63 ± 1.33	1.26 ± 0.54	11	5.54 ± 0.99	1.61 ± 0.42	10	14.36 ± 2.49	4.88 ± 0.79	22	13.90 ± 0.51	3.25 ± 0.99	3	3.25 ± 0.99	3
	4°/s	13.36 ± 2.65	3.44 ± 1.14	5	12.85 ± 2.84	3.91 ± 1.07	5	16.69 ± 2.65	5.43 ± 0.86	8	14.32 ± 5.6	4.11 ± 1.85	2	4.11 ± 1.85	2
	6°/s	20.36 ± 3.04	5.39 ± 0.92	34	19.05 ± 2.43	5.83 ± 0.59	21	8.61 ± 1.52	1.85 ± 0.45	3	7.75	1.78	1	1.78	1
	10°/s	33.37 ± 4.46	9.76 ± 1.90	13	22.23 ± 0.98	6.31 ± 1.30	3	8.18 ± 0.32	2.75 ± 0.58	5	5.77	0.98	1	0.98	1
Subject 3	2°/s	4.56 ± 1.08	1.13 ± 0.12	19	2.96 ± 0.53	0.98 ± 0.11	9	15.59 ± 2.23	3.60 ± 0.40	4	9.52 ± 1.00	5.93 ± 0.27	4	5.93 ± 0.27	4
	4°/s	10.84 ± 1.71	2.28 ± 0.66	15	10.17 ± 1.63	2.16 ± 0.46	4	8.81 ± 1.95	1.05 ± 0.13	4	3.75 ± 0.87	0.82 ± 0.02	2	0.82 ± 0.02	2
	6°/s	13.23 ± 2.10	3.55 ± 0.62	16	10.88 ± 0.74	3.21 ± 0.42	6	8.03 ± 1.96	2.14 ± 0.55	39	7.44 ± 1.22	2.59 ± 0.50	15	1.58 ± 0.13	3
	10°/s	19.81 ± 3.90	7.57 ± 0.42	8	15.22 ± 0.09	4.42 ± 0.05	4	19.64 ± 3.12	3.60 ± 1.07	12	12.88 ± 2.68	3.79 ± 0.54	10	3.36 ± 0.60	10
Subject 4	2°/s	8.81 ± 1.95	1.05 ± 0.13	4	3.75 ± 0.87	0.82 ± 0.02	2	28.39 ± 5.87	5.38 ± 1.49	10	18.62 ± 3.29	4.93 ± 1.66	6	5.23 ± 1.17	7
	4°/s	8.03 ± 1.96	2.14 ± 0.55	39	7.44 ± 1.22	2.59 ± 0.50	15	13.15 ± 1.99	5.23 ± 1.17	7	12.07 ± 2.44	5.18 ± 1.03	5	5.18 ± 1.03	5
	6°/s	19.64 ± 3.12	3.60 ± 1.07	12	12.88 ± 2.68	3.79 ± 0.54	10	9.65 ± 1.64	2.99 ± 0.49	11	9.65 ± 1.64	2.99 ± 0.49	11	2.99 ± 0.49	11
	10°/s	28.39 ± 5.87	5.38 ± 1.49	10	18.62 ± 3.29	4.93 ± 1.66	6	13.15 ± 1.99	5.23 ± 1.17	7	12.07 ± 2.44	5.18 ± 1.03	5	5.18 ± 1.03	5

Table 2. Peak velocity of divergence high-velocity responses from the four different ramp stimuli speeds. Mean peak velocity (PV) (°/s) with standard deviation, response amplitude (Amp) (°) with standard deviation, and number of samples.

Ramp stimulus speed (°/s)	Initial position (°)												
	>16°			16° - 12°			12° - 8°			<8°			
	PV	Amp	n	PV	Amp	n	PV	Amp	n	PV	Amp	n	
Subject 1	6°/s	10.22 ± 0.58	2.91 ± 0.88	2	11.18 ± 3.59	2.62 ± 0.96	3	9.55	3.66	1	13.14 ± 2.78	4.08 ± 0.63	8
	10°/s	14.52 ± 5.88	3.61 ± 2.27	2	18.6	1.52	1	18.32 ± 5.05	3.97 ± 1.75	4	19.69 ± 4.79	6.57 ± 2.64	8
Subject 2	6°/s	11.14 ± 2.72	2.64 ± 0.58	10	10.65 ± 2.42	3.12 ± 1.12	15	10.37 ± 2.26	3.21 ± 0.93	12	11.33 ± 2.17	3.42 ± 0.87	42
	10°/s	19.25	4.96	1	15.35 ± 2.94	4.12 ± 1.17	4	16.72 ± 4.00	5.46 ± 1.52	6	14.77 ± 2.31	5.86 ± 1.42	14
Subject 3	6°/s	17.72 ± 3.05	2.91 ± 0.92	9	15.85 ± 2.16	3.42 ± 0.39	6	17.52 ± 2.87	4.04 ± 1.17	5	19.91 ± 5.25	3.85 ± 0.77	15
	10°/s	21.53 ± 10.12	3.81 ± 1.66	4	19.90 ± 4.72	4.76 ± 1.20	10	16.27 ± 5.26	3.96 ± 1.27	9	24.11 ± 6.59	5.89 ± 1.49	21
Subject 4	6°/s	13.24 ± 2.71	2.27 ± 0.44	15	13.73 ± 3.22	2.68 ± 0.90	12	12.84 ± 3.25	2.71 ± 0.64	18	15.03 ± 5.36	3.59 ± 1.07	43
	10°/s	15.65 ± 2.74	3.03 ± 0.58	11	16.20 ± 3.07	3.74 ± 1.47	8	16.53 ± 3.41	4.27 ± 1.07	26	24.25 ± 4.87	6.34 ± 1.19	31

Table 3. Peak velocity of convergence high-velocity responses from the two different ramp stimuli speeds. Mean peak velocity (PV) (°/s) with standard deviation, response amplitude (Amp) (°) with standard deviation, and number of samples. Note, as the target moves toward the subject, it is less likely to observe a high-velocity component.

divergence to smoothly moving ramp stimuli. The magnitude of peak velocity of the high-velocity responses decreased when the ramp stimulus moved away from the subject (Figure 3). A dynamic analysis was conducted to determine if changes in dynamics occurred as the target moved in depth. The data were classified into four different groups according to the high-velocity component initial position (shown in Table 2 for divergence and Table 3 for convergence): greater than 16°, 16° to 12°, 12° to 8°, and less than 8°. The end point of 2°/s ramp stimulus was 12°; hence, no data were recorded beyond 12°. The peak velocity of each high-velocity response for the different initial positions decreased as the target moved away from the subject as demonstrated in Figure 7 for all subjects. These differences were confirmed by a significant effect of initial position, $F(2, 6) = 12.57$, $p < 0.001$. A post hoc Bonferroni test also specified that the peak velocity was significantly different for the different initial positions for all subjects who participated in this experiment.

Discussion

Behavioral evidence to support a preprogrammed component in divergence

The first goal of this study was to determine if divergence behavior exhibits support for a preprogrammed component as has been found in convergence behavior. Experiment 1 showed two results: (1) the existence of smooth tracking for slow ramp stimuli (2°/s) and the inclusion of high-velocity step-like movement for faster ramps (4, 6, and 10°/s), and (2) the high-velocity component observed in the faster responses fell on the same main sequence trajectory as divergence steps. This suggests that the first-order dynamics are the same. Hence, the high-velocity behavior was initiated by the same or similar neural mechanisms. Potentially, a preprogrammed element may be present.

The second experiment used a disappearing step stimulus initiated at the subject's near dissociated phoria level. The main sequence analysis comparing divergence steps and disappearing steps at the same initial position suggests that the transient portion of the responses was under the same or similar neural control. For step responses, the visual stimulus was present throughout the entire experiment, whereas it was only present for the initial 100 msec for the disappearing step responses. If divergence was strictly feedback controlled, then these responses should exhibit quite different behaviors because the error signal is different. Since the transient dynamics are similar, the finding suggests that a divergence transient response is similar between steps and disappearing steps lending support that a preprogrammed element may be present in divergence. Furthermore, the transient response could not

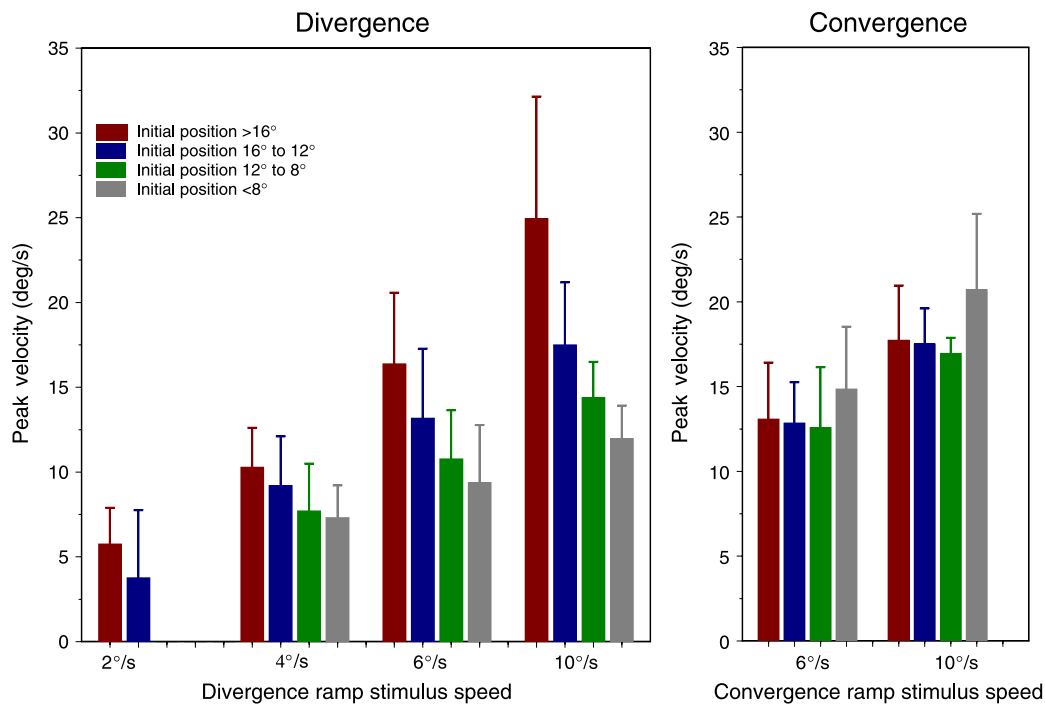


Figure 7. Average peak velocities with standard deviation of high-velocity responses with different initial positions for the various ramp speeds for Subjects 1 through 4. The legend specifies the initial position of where the high-velocity components began. The magnitude of peak velocity decreased as the stimulus moved away from the subject for divergence but not for convergence. The number of responses and the data for the individual subjects are denoted in Tables 2 and 3.

be due to phoria decay because the stimulus began at the subject's phoria level.

Neurophysiologists have also observed different burst-tonic cells in the midbrain encode for divergence and convergence (Mays et al., 1986). The burst-tonic cells could be interpreted as having a preprogrammed control structure where researchers report that the burst activity was faster and longer for large disparities. Similar arguments have been observed for convergence using ramps (Semmlow et al., 1986) and disappearing steps (Semmlow et al., 1993) where researchers concluded that the behaviors observed for convergence lend support for a dual control composed of preprogrammed and feedback elements.

Similar to convergence, these results potentially suggest that the transient component was triggered by the error between visual stimulus and current eye position. With slower moving ramp stimuli, the error signal is small; hence, smooth tracking is observed. However, if an error signal begins to increase beyond a threshold, a high-velocity component is triggered to facilitate binocular vision and maintain fusion. This behavior could also be described as oscillatory where vergence is alternately speeding up and slowing down in order to keep the target near the fovea at least some of the time. Figure 5 quantifies the response amplitude as a function of initial position. For Subject 3, a trend does exist where the amplitude of the high-velocity components decrease as the target moves away from the subject which could suggest motor learning or the

system improves tracking over time. However, this trend is not as apparent with the other three subjects studied.

Divergence is a distinct system and not merely negative convergence

The second goal of this study was to compare convergence and divergence by quantifying differences between the systems. The results from this study suggest commonality in the control systems where behavioral evidence supports the existence of a preprogrammed and feedback element for convergence and divergence. However, the results from this study also showed divergence dynamics decreased as the visual stimulus moved away from the subject for smoothly moving ramp stimuli. Different cells fire for convergence and divergence so there is no reason for the systems to be identical (Mays et al., 1986). Other behavioral results support differences between convergence and divergence. For step responses, Alvarez and colleagues (2005) showed that the dynamics of divergence steps were dependent on stimulus initial position where convergence was not. Investigating only a single ramp speed, researchers have also shown that divergence dynamics decrease as the targets move away from the subject (Alvarez, Semmlow, & Pedrono, 2007).

The cause for the initial position dependence is unknown. The dependence could be dependent on the extraocular muscles or differences in the controller or

perhaps an adaptation to the visual environment. Further investigation is needed to understand why divergence has an initial position dependency.

Conclusion

This study lends behavioral support that divergence eye movements contain a preprogrammed component similar to convergence which was tested by comparing various ramp dynamics to step dynamics and by comparing dynamics of steps and disappearing steps initially viewed at a subject's near dissociated phoria position. Differences between divergence and convergence are also documented where divergence responses to smoothly moving targets exhibit a dependence on initial position, whereas convergence movements did not. These findings have implications on the basic neural control of divergence by highlighting differences between vergence systems. This information could ultimately be useful in the diagnosis and care of individuals with divergence dysfunctions such as divergence insufficiency.

Acknowledgments

This work was supported in part by a CAREER award from the National Science Foundation (BES-0447713) to TLA. The authors appreciate the comments from John L. Semmlow and the anonymous reviewers.

Commercial relationships: none.

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References

- Alvarez, T. L., Semmlow, J. L., & Pedrono, C. (2005). Divergence eye movements are dependent on initial stimulus position. *Vision Research*, *45*, 1847–1855. [[PubMed](#)]
- Alvarez, T. L., Semmlow, J. L., & Pedrono, C. (2007). Dynamic assessment of disparity vergence ramps. *Computers in Biology and Medicine*, *37*, 903–909. [[PubMed](#)]
- Alvarez, T. L., Semmlow, J. L., & Yuan, W. (1998). Closely spaced, fast dynamic movements in disparity vergence. *Journal of Neurophysiology*, *79*, 37–44. [[PubMed](#)] [[Article](#)]
- Alvarez, T. L., Semmlow, J. L., Yuan, W., & Munoz, P. (2002). Comparison of disparity vergence system responses to predictable and non-predictable stimulations. *Current Psychology of Cognition*, *21*, 243–261.
- Bahill, A. T., Clark, M. R., & Stark, L. (1975). The main sequence: A tool for studying eye movements. *Mathematical Biosciences*, *24*, 191–204.
- Bahill, A. T., Kallman, J. S., & Lieberman, J. E. (1982). Frequency limitations of the two-point central difference differentiation algorithm. *Biological Cybernetics*, *45*, 1–4. [[PubMed](#)]
- Bahill, A. T., & Stark, L. (1979). The trajectories of saccadic eye movements. *Scientific American*, *240*, 108–117. [[PubMed](#)]
- Busettoni, C., Fitzgibbon, E. J., & Miles, F. A. (2001). Short-latency disparity vergence in humans. *Journal of Neurophysiology*, *85*, 1129–1152. [[PubMed](#)] [[Article](#)]
- Busettoni, C., Masson, G. S., & Miles, F. A. (1997). Radial optic flow induces vergence eye movements with ultra-short latencies. *Nature*, *390*, 512–515. [[PubMed](#)]
- Busettoni, C., & Mays, L. E. (2003). Pontine omnipause activity during conjugate and disconjugate eye movements in macaques. *Journal of Neurophysiology*, *90*, 3838–3853. [[PubMed](#)] [[Article](#)]
- Busettoni, C., Miles, F. A., & Krauzlis, R. J. (1996). Short-latency disparity vergence responses and their dependence on a prior saccadic eye movement. *Journal of Neurophysiology*, *75*, 1392–1410. [[PubMed](#)]
- Ciuffreda, K. J., & Tannen, B. (1995). Vergence eye movements. In K. J. Ciuffreda & B. Tannen (Eds.), *Eye movement basics for the clinician* (pp. 133). New York: Mosby.
- Coubard, O., Daunys, G., Kapoula, Z., (2004). Gap effects on saccade and vergence latency. *Experimental Brain Research*, *154*, 368–381. [[PubMed](#)]
- Gamlin, P. D., & Mays, L. E. (1992). Dynamic properties of medial rectus motoneuron during vergence eye movements. *Journal of Neurophysiology*, *67*, 64–74. [[PubMed](#)]
- Gamlin, P. D., Yoon, K., & Zhang, H. (1996). The role of cerebro-ponto-cerebellar pathways in the control of vergence eye movements. *Eye*, *10*, 167–171. [[PubMed](#)]
- Hornig, J. L., Semmlow, J. L., Hung, G. K., & Ciuffreda, K. J. (1998a). Dynamic asymmetries in disparity convergence eye movements. *Vision Research*, *38*, 2761–2768. [[PubMed](#)]
- Hornig, J. L., Semmlow, J. L., Hung, G. K., & Ciuffreda, K. J. (1998b). Initial component control in disparity vergence: A model-based study. *IEEE Transactions on Biomedical Engineering*, *45*, 249–257. [[PubMed](#)]

- Hung, G. K. (1998). Dynamic model of the vergence eye movement system: Simulations using MATLAB/SIMULINK. *Computer Methods and Programs in Biomedicine*, *55*, 59–68. [PubMed]
- Hung, G. K., Semmlow, J. L., & Ciuffreda, K. J. (1986). A dual-mode dynamic model of the vergence eye movement system. *IEEE Transactions on Biomedical Engineering*, *33*, 1021–1028. [PubMed]
- Hung, G. K., Zhu, H., & Ciuffreda, K. J. (1997). Convergence and divergence exhibit different response characteristics to symmetric stimuli. *Vision Research*, *37*, 1197–1205. [PubMed]
- Jones, R. (1980). Fusional vergence: Sustained and transient components. *American Journal of Optometry and Physiological Optics*, *57*, 640–644. [PubMed]
- Jones, R., & Stephens, G. L. (1989). Horizontal fusional amplitudes. Evidence for disparity tuning. *Investigative Ophthalmology & Visual Science*, *30*, 1638–1642. [PubMed] [Article]
- Kumar, A. N., Han, Y., Dell’osso, L. F., Durand, D. M., & Leigh, R. J. (2005). Directional asymmetry during combined saccade-vergence movements. *Journal of Neurophysiology*, *93*, 2797–2808. [PubMed] [Article]
- Maxwell, J. S., & King, W. M. (1992). Dynamics and efficacy of saccade-facilitated vergence eye movements in monkeys. *Journal of Neurophysiology*, *68*, 1248–1260. [PubMed]
- Mays, L. E. (1984). Neural control of vergence eye movements: Convergence and divergence neurons in midbrain. *Journal of Neurophysiology*, *51*, 1091–1108. [PubMed]
- Mays, L. E., & Porter, J. D. (1984). Neural control of vergence eye movements: Activity of abducens and oculomotor neurons. *Journal of Neurophysiology*, *52*, 743–761. [PubMed]
- Mays, L. E., Porter, J. D., Gamlin, P. D., & Tello, C. A. (1986). Neural control of vergence eye movements: Neurons encoding vergence velocity. *Journal of Neurophysiology*, *56*, 1007–1021. [PubMed]
- Nitta, T., Akao, T., Kurkin, S., & Fukushima, K. (2008). Involvement of the cerebellar dorsal vermis in vergence eye movements in monkeys. *Cerebral Cortex*, *18*, 1042–1057. [PubMed] [Article]
- Patel, S. S., Jiang, B. C., White, J. M., & Ogmen, H. (1999). Nonlinear alteration of transient vergence dynamics after sustained convergence. *Optometry and Vision Science*, *76*, 656–663. [PubMed]
- Radisavljevic-Gajic, V. (2006). Slow-fast decoupling of the disparity convergence eye movements dynamics. *Annals of Biomedical Engineering*, *34*, 310–314. [PubMed]
- Rambold, H., Neumann, G., Sander, T., & Helmchen, C. (2006). Age-related changes of vergence under natural viewing conditions. *Neurobiology of Aging*, *27*, 163–172. [PubMed]
- Rambold, H., Sander, T., Neumann, G., & Helmchen, C. (2005). Palsy of “fast” and “slow” vergence by pontine lesions. *Neurology*, *64*, 338–340. [PubMed]
- Rashbass, C., & Westheimer, G. (1961). Disjunctive eye movements. *The Journal of Physiology*, *159*, 339–360. [PubMed] [Article]
- Schor, C. (1988). Influence of accommodative and vergence adaptation on binocular motor disorders. *American Journal of Optometry and Physiological Optics*, *65*, 464–475. [PubMed]
- Semmlow, J. L., Hung, G. K., Horng, J. L., & Ciuffreda, K. (1993). Initial control component in disparity vergence eye movements. *Ophthalmic & Physiological Optics*, *13*, 48–55. [PubMed]
- Semmlow, J. L., Hung, G. K., & Ciuffreda, K. J. (1986). Quantitative assessment of disparity vergence components. *Investigative Ophthalmology & Visual Science*, *27*, 558–564. [PubMed] [Article]
- Semmlow, J. L., & Yuan, W. (2002). Adaptive modification of disparity vergence components: An independent component analysis study. *Investigative Ophthalmology & Visual Science*, *43*, 2189–2195. [PubMed] [Article]
- Westheimer, G., & Mitchell, A. M. (1956). Eye movement responses to convergence stimuli. *AMA Archives of Ophthalmology*, *55*, 848–856. [PubMed]
- Yuan, W., Semmlow J. L., Alvarez, T. L., & Munoz, P. (1999). Dynamics of the disparity vergence step response: A model-based analysis. *IEEE Transactions on Bio-medical Engineering*, *46*, 1191–1198. [PubMed]
- Zee, D. S., Fitzgibbon, E. J., & Optican, L. M. (1992). Saccade-vergence interactions in humans. *Journal of Neurophysiology*, *68*, 1624–1641. [PubMed]
- Zhang, H., & Gamlin, P. D. (1998). Neurons in the posterior interposed nucleus of the cerebellum related to vergence and accommodation. I. Steady-state characteristics. *Journal of Neurophysiology*, *79*, 1255–1269. [PubMed] [Article]
- Zhang, Y., Gamlin, P. D., & Mays, L. E. (1991). Antidromic identification of midbrain near response cells projecting to the oculomotor nucleus. *Experimental Brain Research*, *84*, 525–528. [PubMed]