Closely Spaced, Fast Dynamic Movements in Disparity Vergence

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Alvarez, Tara L., John L. Semmlow, and Weihong Yuan. Closely spaced, fast dynamic movements in disparity vergence. J. Neurophysiol. 79: 37–44, 1998. Conflicting theories exist describing how symmetrical vergence responses, the inward or outward vergence, are mediated. Classical theories describe vergence control as mediated by visual feedback. Extensive experimental evidence indicates that two distinct control components comprise the vergence response, and a recent theory supports the concept that one of these components is not visually guided. Occasionally, saccadic eye movements will respond to a single step stimulus with two closely spaced saccades, a behavior that is indicative of its switching control structure. If a portion of the vergence response is controlled in a manner analogous to saccades, then occasional double fast dynamic components might be expected. During this study, eye movements were recorded in response to symmetrical vergence stimuli of 2, 4, 6, 8, and 10° steps. The left and right eye movements were subtracted to yield a net vergence response, and only convergent responses were investigated. Double fast dynamic components associated with high-velocity movements were observed in all four subjects studied. In double high-velocity component responses, the average peak velocity of both fast dynamic movements was always considerably less than the average peak velocity found when the response to the same stimulus was made with only a single component. Response amplitudes of single and double movements showed that if the primary component of a double response did not reach ≥80% of the stimulus amplitude, a secondary component would be generated to aid the movement. Plots of peak velocity as a function of response amplitude for both double and single movements followed the main sequence for vergence eye movements demonstrating that the first-order dynamic characteristics of all high-velocity components were the same. The time at which maximum velocity occurred (relative to stimulus onset) was also the same for both single component responses and the first component of double responses. The similarity in dynamics and timing implies that the high-velocity components were processed by the same controller mechanism. The existence of double high-velocity movements is indicative of an internal, switching mechanism similar to that found in saccades and is difficult to explain with theories that rely on visual feedback control alone.

INTRODUCTION

Vergence is the oculomotor system that aids in fusing images at varying depths in space by a symmetrical inward or outward turning of the eyes. A variety of stimulus modalities can induce or contribute to this response, but the primary stimulus is disparity of retinal images. Historically, vergence oculomotor control has been described in terms of a feedback system continuously guided by retinal information (Krishnan and Stark 1977; Toates 1974). Experiments performed since these early models indicate a more complex control structure. Several experiments show that the vergence system exhibits two quite different behaviors. Westheimer and Mitchell (1969) and Mitchell (1970) have shown that stimuli presented as a brief (200 ms) flash produced transient responses very similar to a stimulus of sustained duration, though in the former, the response eventually decayed to the baseline level. They also found similar results for nonfusible targets: for example, a horizontal line paired with a vertical line. Such behavior is difficult to explain based on classic feedback control and implies a two-stage process. Jones (1980) suggested that the vergence system be composed of a “fusion-initiating phase” and a “fusion-sustaining phase.” Semmlow et al. (1986) also found dichotomous behavior in responses to ramp stimuli. Slow ramps produced smooth tracking movement, whereas faster ramps produced step-like behavior. The dualistic nature of vergence control also is supported by neurophysiology evidence. Mays and colleagues have found midbrain neurons that code for velocity and other neurons that code for position (Gamlin and Mays 1992; Mays et al. 1986).

Findings of dualistic behavior coupled with dynamic considerations led to the development of the dual-mode theory of vergence control (Hung et al. 1986; Semmlow et al. 1986). This theory proposes a control system composed of two parts. The first is an “initial component” that is an internally guided control process similar to that used to drive saccades and also produces relatively high movement velocities. The second is a “slow component” mediated by a feedback control system that uses visual information to provide the fine tuning necessary to achieve the extraordinary accuracy of ocular bi fixation (Ogle et al. 1967). This research focuses on initial component dynamics and behavior.

The dual-mode theory for the control of vergence eye movements has not been widely accepted, and most contemporary vergence studies still tacitly assume a classic visually guided, continuous feedback control structure. Particularly controversial is the assertion that one of the components is not guided by visual feedback. For example, a recent theory of vergence control presented by Pobuda and Erkelens (1993) postulated a switched, multichannel control mechanism, but each channel operated under visual feedback control. The work presented here presents and examines behavior that supports, and is predicted by, the theory that a portion of the vergence eye movement response is controlled by a switching component.

It is well known that saccadic eye movements are not under continuous visual guidance. The high velocity of these movements, coupled with the delays inherent to the visual system would lead to control instabilities if visual informa-
tion was required on a continuous basis. Early theories of saccadic control postulated that these movements were pre-programmed (Bahill and Stark 1979; Robinson 1964, 1973; Westheimer 1954) that is, under the guidance of internal open-loop processes that generated fixed neural drive signals in response to a given stimulus. More recent work has shown that while the saccadic signal does not use continuous visual feedback in its development, internal or “local feedback” guides the production of that signal (Keller 1974; Robinson 1973; Van Ginstergen et al. 1981; Zee et al. 1976). Several variations of Robinson’s original model have been developed (Jurgens et al. 1981; McKenzie and Lisberger 1986; Sparks et al. 1987), but they all share several features in common: an internal local feedback pathway that codes current saccadic position; a neural integrator that generates a step component from the pulse produced by the local feedback network; and a discontinuous operating mode that requires some form of a trigger signal for activation of the saccadic generator. It is the latter discontinuous, or switching, characteristic that ensures the stability of the local feedback circuit, despite the high gain of the saccadic generator (Jurgens et al. 1981; Van Ginstergen et al. 1981).

One of the many saccadic behaviors attributable to the switching control strategy is the finding of multiple closely spaced saccades (Bahill and Stark 1975). These responses are known as overlapping or double saccades and are found in response to a single step stimulus (Bahill and Stark 1975). If a switching control strategy also governs the vergence response, it would be expected that such double high-velocity movements would occasionally occur in these responses as well. The existence of such behavior would not be compatible with any control scheme based solely on continuous visual feedback: double fast dynamic components in response to a single step are characteristic of a switching system. This study reports vergence movements containing two high-velocity components and describes the basic features of these movements. This behavior occurs naturally in response to standard step stimuli.

METHODS

Experimental apparatus and stimuli

The stimulus display consisted of a pair of oscilloscopes (phosphor P31 with a bandwidth of 20 MHz) arranged as a haploscope. The stimulus from each oscilloscope was a vertical line, 0.15° in width and 5° in height. Because the stimulus display produced pure disparity stimuli and did not require the physical movement of an object to generate the stimulus, proximal vergence stimulation should be constant (Rosenfield and Ciuffreda 1991). In addition to the haploscope stimulus target, two real targets, positioned at set distances from the subject, were used to calibrate the stimulus display. Both stimulus generation and data acquisition were under computer control.

The stimuli consisted of 2, 4, 6, 8, and 10° step changes in pure disparity. Because prediction might influence the vergence response, stimuli were presented randomized in time. Experimental sessions usually lasted 15–20 min. After each session, a 5- to 10-min break was given before another experimental session began. Approximately 35–50 responses were recorded during an experimental session, and each subject participated in two to three sessions on a given day. Stimuli of the same amplitude were given in each session. As mentioned in RESULTS, it is possible that this repetition decreased the attentiveness of the subject and increased the likelihood of double responses.

The vergence eye movement responses were monitored using a limbus tracking system (Skintech Iris 6500). The eye movement monitor has a linearity of ±25° with a resolution of 1.5 min of arc. All movements were within the range of linearity. Left and right eye movements were recorded separately using a standard 12 bit A/D converter sampling at 200 Hz. Eye movements to known stimulus positions were recorded from each eye immediately before and after an experimental trial and served as calibration reference points. All associated parameters such as calibration and stimulus information were stored with the responses in a data file for later analysis.

Subjects

Four subjects participated in this study. Subject JS has been participating in vergence studies for a number of years and was aware of the aims of the study. Subjects CC, BS, and ML were all inexperienced subjects and naive to the goals of this research. These three subjects participated in one to two experimental sessions to become acquainted with the experimental apparatus before the study began. All subjects had normal binocular vision and had no difficulty with the experiment.

Data analysis

In the analysis program, the eye movement data were calibrated individually then subtracted to yield the net vergence response. Only convergent eye movements were investigated here, and convergence is plotted in the positive direction. Any responses that contained artifacts, such as blinks or saccades as described below, were omitted. The velocity of each movement was computed using a two-point central difference algorithm (Bahill et al. 1982). The peak velocity of each double response, and of each single response, was measured along with the time at which the peak velocity occurred, relative to stimulus onset. The analysis procedure described below used the Matlab software package (Waltham, MA).

Many investigators have studied the interaction of saccades and vergence, and several researchers have suggested that saccades aid in the execution of asymmetrical vergence responses (Collewijn et al. 1995; Enright 1984, 1986, 1996; Zee et al. 1992). In our case, symmetrical vergence stimuli were used, requiring equal and opposite movements. To eliminate any possible saccadic involvement, individual left and right eye movements were inspected for observable saccades, and records that contained saccades during the dynamic portion of the response were eliminated. Saccades were identified readily because they have much faster dynamics than vergence eye movements (Bahill and Stark 1979). Although vertical movements were not specifically measured, even very small vertical saccades were found to produce a distinctive artifact that was easy to identify. Because this investigation was interested in the faster transient portion of the vergence movement, records containing vertical or horizontal saccades during the later, steady-state portion of the response were analyzed.

The dynamic characteristics of both double and single high-velocity movements were analyzed using the main sequence ratio: the ratio of peak velocity to response amplitude (Bahill et al. 1975). The main sequence ratio provides a quantitative description of the equivalent first-order dynamics of a movement. Although peak velocity could be easily determined from the velocity traces, amplitude was more difficult to measure, particularly in double responses where the second initial component might begin before the first component reached its final position. In these responses, an extrapolation procedure was used to determine the response amplitude. Essentially, a portion of the dynamic response was used...
The extrapolation method was validated by using the same method on single responses. The response amplitude of single high-velocity responses is generally easier to determine because the response usually is completed as indicated by the return of the phase trajectory to zero. For these responses, the falling portion of the phase trajectory (the points from maximum velocity to zero velocity as depicted by × in Fig. 1A) was used to extrapolate the final, zero velocity position, and this was compared with the actual zero velocity position. This extrapolated position (the isolated ×) was situated on the curve as seen in Fig. 1B and shows good correlation between the actual and extrapolated endpoint. Overall, errors in estimating amplitude were found to be <5% based on this comparative analysis.

Because the initial component is not visually guided, it is not always precise. In many vergence movements, the initial component responses were larger than that required by the steady-state position. This was particularly true for the second component of a response double (see Fig. 2). The analysis described above, based on the phase plane trajectory, will correctly identify the main sequence components irrespective of the error between the initial component and the required final amplitude.

**RESULTS**

Typical vergence double responses consisting of two distinct, high-velocity movements can be seen in Fig. 2, (left). Figure 2, (right), shows more typical step responses from the same subjects and stimulus conditions in which only a single high-velocity component is produced. Double responses were recorded from all four of the subjects that participated in this study.

The analysis examined three characteristics of both single and double responses: peak velocity, peak velocity to amplitude ratio, and peak velocity timing. In the high-velocity movements, peak velocity is an easily measured indicator of the magnitude of the response. Peak velocities for both double and single responses are presented in Fig. 3. The peak velocities for both movements in a double were always less than the peak velocity of a single response to the same stimulus as seen in Fig. 3. This was true for all stimulus amplitudes and for all subjects studied.

The main sequence ratio is a commonly used index to describe eye movement dynamics in both vergence and sac-
FIG. 2. Typical double and single responses. — position; ——, velocity trace. Convergence is plotted as positive. 

The main sequence is a plot of the peak velocity versus response amplitude and provides a quantitative measure of first-order dynamics. The main sequence plots of both singles and doubles are shown in Fig. 4. In Fig. 4, the solid symbols represent the primary responses from doubles, patterned symbols represent the sec-
FIG. 3. Maximum velocity of the first and second high-velocity components of doubles along with the maximum velocity of single component responses. Data of subjects JS, CC, and BS are from 8° step responses, whereas data from subject ML are from 6° steps. Average peak velocities of the doubles are always less than the peak velocities of singles. Note these are averages, at times the primary component may be as small as 20% of the stimulus amplitude, whereas at others, it would be as large as 80% of stimulus amplitude.

FIG. 4. Main sequence ratios (maximum velocity plotted as a function of response amplitude) for 2, 4, and 8° responses from subject JS and for 4, 8, and 10° responses from subject CC. Open symbols stand for single responses, the closed symbols represent the primary component in double responses and the patterned symbols represent the secondary components in double responses. Circles are for 2° responses, triangles are for 4° responses, diamonds are for 8° responses, and squares are for 10° responses.
The timing of peak velocities was measured for both single and double component responses. The time at which the peak velocity of the first double occurred relative to stimulus onset was, on average, the same as when peak velocity was attained during a standard, single initial component movement, as seen in Fig. 5. The timing for the second high-velocity response of a double was, on average, slightly less than twice that of the first, relative to stimulus onset.

To determine if a clearly defined threshold exists for the development of double responses, frequency histograms of movement amplitude were constructed. To compare the response to various stimuli, the response amplitudes were normalized by the stimulus amplitudes. Histograms for two subjects, shown in Fig. 6, indicate that a threshold exists. Specifically, if the primary component movement does not reach \( \sim 80\% \) of the stimulus amplitude, a second high-velocity movement will be generated. During double responses, the primary component amplitude ranged between 20 and 80\% of stimulus amplitude. In other words, some primary responses in a double contributed as little as 20\% to the overall response, whereas other primary components contributed \( \approx 80\% \) of the movement. Conversely, this plot demonstrates that responses with a primary component that reached \( \approx 80\% \) of the stimulus amplitude did not trigger a secondary component, but responses that were smaller needed a second effort to fixate the image.

**DISCUSSION**

Multiple step behavior similar to the double high-velocity movements described here has been observed during vergence responses to open-loop step stimuli (Semmlow et al., 2002).
al. 1994) as well as fast moving ramps (Semmlow et al. 1986). Open-loop step stimuli ensure a constant disparity eliminating any influence from visual feedback. The investigation of vergence responses to open-loop steps sought to determine if the initial component was not under continuous visual guidance. The existence of multiple step-like behavior, under conditions that prevent feedback and the instabilities associated with feedback oscillations, implies a switching component in the vergence oculomotor control system. However, the open-loop stimulus condition is generated artificially, and the unnaturalness of this stimulus environment has left doubts regarding the generality of the resultant behavior. The multiple step-like movements reported here clearly indicate switching behavior, and they occur naturally in response to simple step stimuli.

With regard to the switching or trigger mechanism, the fact that the frequency and amplitude of these multiple steps found during ramp stimulation (Semmlow et al. 1986) increased with stimulus velocity suggests this mechanism is triggered by error between the stimulus and response. As demonstrated in Fig. 6, the occurrence of double initial component responses to a single step also seems to depend on an error-based trigger. This triggering could be based on error obtained from visual feedback or from an internal calculation based on an internal feedback signal such as suggested in some saccadic models (Jurgens et al. 1981). Ongoing studies are being directed to resolve this issue.

The value of the main sequence is its ability to compare the dynamic properties of a number of different responses. If the individual points (peak velocity vs. response amplitude) fall on a single line, these responses exhibit the same first-order dynamic characteristics. The response dynamics of all fast component movements, illustrated in Fig. 4, all fall close to the same curve irrespective of their context in a single or double response. This indicates that both the high-velocity components of a double have the same dynamic properties as those of a single movement and probably are created by the same or similar neural processes.

Our results clearly demonstrate the presence of a switching component in vergence control, an important control strategy that also is found in the saccadic system. Our experiments do not address the generation of the fast component, so that analogies to other saccadic control processes such as local feedback or pulse integration are speculative. However, there is neurophysiologic evidence to indicate that analogous control processes exist in the vergence and saccadic systems. Mays and colleagues have shown that midbrain neurons carry vergence velocity signals (Gamlin and Mays 1992; Mays et al. 1986). Gamlin and Mays (1992) further remark that signals in the midbrain and the medial rectus motoneurons serve to emphasize the similarities in control signal seen in the vergence and conjugate eye movement subsystems. As mentioned previously, theories based on local feedback have been used to describe the control theory for saccadic eye movements (Jurgens et al. 1981; Keller 1974; Robinson 1973; Van Gisbergen et al. 1981; Zee et al. 1976). A similar theory recently has been implemented to describe the control system of vergence eye movements. Zee and colleagues (1992) state that "...the premotor commands for vergence to step changes in the position of the target in depth derive from a neural network with a similar structure to that had been previously developed for the generation of saccades". This model includes burst neurons, which have been discovered in the midbrain (Mays et al. 1986) and in the medial rectus motoneurons (Gamlin and Mays 1992). These vergence burst cells were analogous to the medium-lead burst cells found in the saccadic system, and the roles of these cells were assumed to be similar despite differences in the dynamic appearance of the two systems (Mays et al. 1986).

Bahill and Stark (1975) suggested that fatigue was a factor in the production of closely spaced saccades. We also noted that double initial component responses occurred more often during the end of a run or during the second run of the day. However, subject reports tended to suggest that inattention, rather than fatigue per se, was a factor in the generation of vergence doubles.

Conclusions

The results presented in this study show that when the initial component of a vergence response does not bring the eyes close enough to the stimulus amplitude, a second high-velocity movement is generated. In such cases, the second response aids in the rapid repositioning of the eyes to the stimulus target. Analogous behavior is found in the saccadic system, as seen with overlapping and double saccades (Bahill and Stark 1975). A main sequence analysis showed that the dynamics of the primary and secondary component of a double response are the same as those of a standard single fast component response. The naturally occurring double component behavior cannot be explained by theories that are based solely on continuous visual feedback control but are typical of switching control strategies such as found in saccadic eye movements. Such behavior supports the dual-mode theory, which hypothesizes such a switching component, based on the dynamics of a disparity vergence eye movement.

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REFERENCES


