



# Effects of prediction on timing and dynamics of vergence eye movements

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## Summary

Periodic square waves were used to generate predictable vergence eye movement responses. The timing and dynamic characteristics of vergence eye movement responses to predictable and non-predictable stimuli were compared. Results showed significant changes in timing characteristics along with a highly characteristic anticipatory movement in the early part of predictable vergence responses. This phenomenon is similar to that seen in saccadic eye movements and appears to influence the timing and dynamics of the subsequent vergence response. A model-based analysis of dynamics showed that the pulse width, pulse gain, and step gain of the motor command signal did not show major differences between predictable and non-predictable response. However, other model parameters related to the acceleration of the response showed a substantial decrease when the movements were predictive. © 2000 The College of Optometrists. Published by Elsevier Science Ltd. All rights reserved.

## Introduction

Prediction is an important strategy used by humans to improve their performance in reacting to the surrounding environment. In oculomotor research, the influence of prediction on saccades and smooth pursuit has been well studied (Dodge *et al.*, 1930; Dodge, 1931; Bahill and McDonald, 1983; Kowler and Steinman, 1979; Kowler, 1989; Barnes and Asselman, 1991; Barnes *et al.*, 1995). Dodge and his colleagues (Dodge *et al.*, 1930; Dodge, 1931) found that in smooth pursuit, the eyes were able to predict the future path of a target and track it more accurately. In saccades, it was found that anticipation could reduce latencies to near zero and initiate movement in advance of the stimulus (Kowler and Steinman, 1979). Kowler and colleagues (1979) also described a pre-saccadic drift in the direction of the expected target step associated with prediction. Their work provided strong evidence that

“expectations about a target’s future position always act as powerful inputs to the slow oculomotor (conjunctive) subsystems” (Kowler and Steinman, 1979).

Rashbass and Westheimer (1961) were the first to demonstrate prediction in vergence. They found that a vergence sinusoidal stimulus could be followed with little error and they postulated a predictive operator in the control system. However, the response to a step stimulus did not show prediction in their studies. Later, Krishnan *et al.* (1973) found that prediction substantially reduced the latency in vergence step responses, especially when the stimulus alternated at frequencies lower than 1 Hz. They did extensive research to investigate the optimal frequency and stimulus amplitude for prediction in terms of minimizing response latency. Later Erkelens *et al.* (1989) showed significantly reduced, often negative latencies when the target motion was controlled by the subject.

While the influence of prediction on latency is well known, no studies have been done on the influence of prediction on the dynamic details of the transient vergence response. The goal of this study is to describe quantitatively the effects of prediction on the dynamics of the vergence response to regularly repetitive (i.e. ‘predictable’) step stimuli. Response latency data will also be included to confirm the presence of prediction.

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## Methods

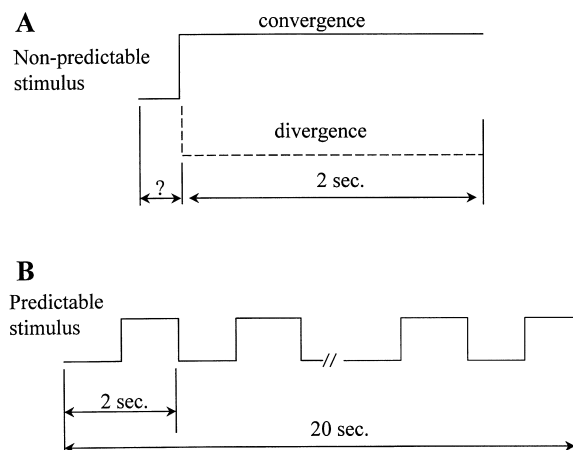
Four subjects, one male and three females, with normal binocular vision were involved in the experiments. One subject (JS) knew the goals of the experiment and was a very experienced subject while the other three subjects (YC, NG, and LA) were naïve to the goals of the experiment. The stimulus was generated by a pair of oscilloscopes (P31 phosphor and a bandwidth of 20 MHz) arranged as a haploscope to present two symmetrical vertical lines to the subjects. The stimulus device was calibrated by two physical targets viewed directly by the subjects. The movement of the target was controlled by a PC-type microcomputer. The responses of each eye were detected by a Skalar infrared eye movement monitor (Model 6500), which has a reported resolution of 1.5 min of arc, and a bandwidth of 200 Hz, well above the Nyquist frequency for vergence movements. Repeated three-point calibration studies have shown the linearity to be approximately 3% over a range of 25°. The horizontal position data for two eyes were digitized using a 12-bit A/D converter and stored on disk. Each eye was separately calibrated using a two-point calibration on every response trial. The vergence response was taken as the computed difference between the two eye movements. The velocity data were calculated using a two-point central difference algorithm (Bahill *et al.*, 1982) during off-line analysis. Data analysis was done using the MATLAB and AXUM software packages.

### Experimental design

Two different stimulus protocols were used to either encourage or discourage prediction, *Figure 1*. In the first experiment, the stimulus was unpredictable. In this experiment, each step stimulus was presented for two seconds. The subjects were told to push a button to start each trial, but the time between the button press and the onset of stimulus was randomized to be between 0.5 and 2 s. The amplitude of the stimulus was fixed at 4°; however, both convergence and divergence step stimuli were presented in a randomized sequence. Therefore, the subject did not know either the direction or the onset time of the next stimulus. While these techniques were expected to inhibit prediction, the presence or absence of prediction was confirmed by evaluation of response latencies.

In the second experiment, the stimulus was predictable: a 20-s square wave presented at a frequency of 0.5 Hz. Each of the ten convergence responses in a trial was analyzed separately. Based on the timing index as described below, the influence of prediction was always observed after the first several cycles in each of these trials for all subjects. It was easy to induce prediction without specific training in all subjects.

## Experimental Protocol



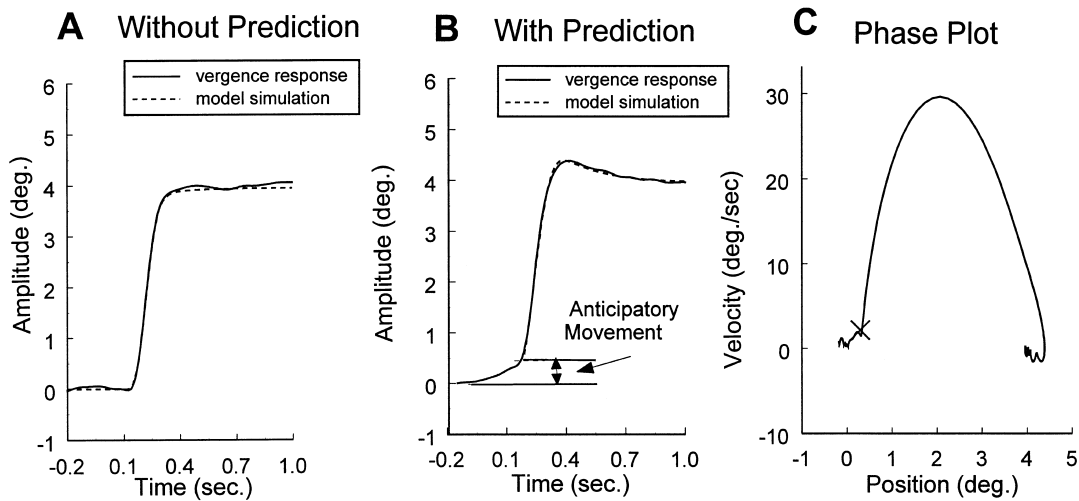
**Figure 1.** Stimuli presented to subjects. (A) In the first experiment, both convergent and divergent 4° stimuli were presented to subjects in a randomized sequence. In addition, the time period between button press and onset of stimulus was randomized to be between 0.5 and 2 s, as represented by “?”. (B) In the second experiment, a 20-s periodic square wave at 0.5 Hz was presented to subjects. Prediction was easy to induce after several cycles.

### Data analysis

**Timing index.** *Figure 2* shows the time course of typical 4° response to: (a) non-predictable; and (b) predictable step stimuli. The timing index usually used to assess the presence of prediction is the response latency, defined as the period between the onset of stimulus and the onset of movement. However, the onset of the movement can be difficult to identify precisely, so in this study the time when peak velocity occurs, an easily identifiable point in time, was used as the second timing reference. Hence, the timing index used here to indicate prediction was the interval between stimulus onset and the time of peak velocity.

**Model-based dynamic indices.** The main sequence is a classical tool for the analysis of eye movement dynamics. With the main sequence, the ratio of peak velocity versus amplitude is used to estimate dynamics. Larger ratios indicate faster dynamics. However, since the main sequence ratio is determined only by two points, the maximum amplitude and peak velocity, many details of the response dynamics may be missed. Previous experiments have shown that the main sequence is not adequate to demonstrate the subtle dynamics found in vergence eye movements (Alvarez *et al.*, 1998; Yuan *et al.*, 1999).

The dynamic analysis used here is based on a model of vergence control processes. During simulations of the model, it is possible to adjust the model parameters so that the model output closely matches a particular response. If the match is fairly accurate, then the model parameters

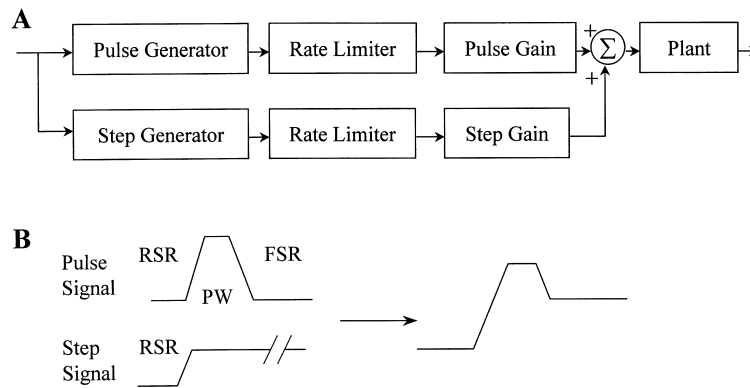


**Figure 2.** Time course of typical 4° step response to: (A) non-predictable; and (B) predictable stimuli. The solid line represents experimental data and the dashed line represents model simulations. It can be seen that the simulation matches experimental data quite well in both cases. A small pre-transient, labeled as “Anticipatory Movement” can be found in (B) and is typical of predictive movements. (C) Phase-plane plot of a response with prediction. There is a clear boundary, marked with an “x”, between the anticipatory movement and the normal transient movement.

constitute a concise description of the dynamic response. In theory, it is only necessary that the model provide a good representation of the response, but in practice it is also desirable that the model parameters have some meaningful relationship to the response dynamics or, alternatively, the underlying control signals.

The model used here was originally developed to study the influence of stimulus features on the motor command signal and to analyze movement-to-movement variability (Yuan *et al.*, 1999). It is based, at least approximately, on known features of the vergence control system. Mays and his colleagues found that the neural activity of convergence tonic cells was highly correlated with the coding of vergence position, while the firing rate of burst cells was closely correlated with the profiles of vergence velocity

(Mays and Porter, 1984; Mays *et al.*, 1986). This indicates that tonic cells encode position while burst cells encode velocity. These two signal components motivate the two signal pathways in our model, *Figure 3*. The lower pathway, as shown in *Figure 3*, represents the tonic cell contribution. It consists of a step generator which produces a step-like change in signal level, a nonlinear dynamic element that limits the maximum velocity of the step change, and a gain term. The upper pathway represents the burst cell signal and is similar to the lower pathway except that the step generator is replaced by a pulse generator and the gain term is different. Both signals feed a simple second-order process that represents the dynamics of the oculomotor neuromusculature. In this model, the rate limiters are nonlinear elements that shape the rectangular pulse and



**Figure 3.** (A) Model used to analyze the dynamics of the system. The pulse signal pathway represents the aggregate activity of burst cells while the step signal pathway represents the aggregate activity of tonic cells (Mays, 1984; Mays and Porter, 1984; Mays *et al.*, 1986). (B) The sum of the two pathways provides a pulse-step signal to drive the plant.

step signals by restricting their rate of change, i.e. maximum velocity, in rising and falling directions. Any signal with a slope beyond the limits set by the parameters will be constrained to those limits. The input to this system is the amplitude of a step stimulus. This input triggers the two signal generators, which then generate a pulse-step signal.

The two-pathway model has five adjustable parameters: pulse width (PW), rising slew rate (RSR), falling slew rate (FSR) for pulse signal, and rising slew rate for step signal (set equal to RSR in pulse signal pathway). Both pathways also have specific gain elements, SG for the step signal gain and pulse gain (PG) for the pulse signal gain. These five parameters are adjusted so that the model's simulated response matches the given experimental response. Two other parameters adjust the oculomotor time constants, but are fixed for all responses for any given subject.

The plant represents the mechanics of the ocular muscles and globe and is a simplified version of the plant model developed by Robinson (1965). In his work, the average value of the major time constant was 285 ms; however, the measured time constant varied between 200 and 400 ms. In the simulations used here, the major time constant was fixed at 200 ms for subject JS and 400 ms for the other three subjects. The minor time constant was fixed at 30 ms for all four subjects. Although some subjectivity was involved in the determination of the time constants, the values were set empirically for best fit between simulation and experimental data and are not very different from Robinson's results. While plant time constant can influence dynamic features such as peak velocity, if the plant time constants are held fixed for each subject, they exert a consistent influence so that all of the descriptive power is held in the five adjustable parameters.

The adjustable model parameters provide a concise quantitative representation of the transient dynamics and also have a well-defined relationship to the underlying motor command signal. In addition, the model parameters also relate to specific features of the response dynamics. Pulse gain is strongly related to the value of peak velocity while pulse width is directly related to the time when peak velocity is attained. The RSR is primarily influenced by the up-slope of the velocity curve (i.e. initial acceleration) while the FSR relates to the falling portion of the velocity curve, or deceleration, of the response. Step gain determines the final steady-state position and, hence, will be approximately the same as the stimulus amplitude. Thus the model provides a powerful tool for linking extended behaviors with the internal signal that produce those behaviors.

Simulations were carried out using MATLAB and plotted using AXUM. Each simulation was done by manually adjusting the parameters of the model until the simulation result was very close to the given experimental response. To avoid subjectivity in the parameter adjustment process, an optimization procedure was applied after preliminary manual adjustment. The optimization routine, a local minimizer,

was taken from the MATLAB software package (FMINS) and was based on the Simplex search method. This optimization routine was applied using the initial values obtained from the manual simulation and reduced the root mean square (RMS) error between the simulation and experimental response to less than 3% of the steady-state amplitude. This error was approximately the same as the measurement error. Since there was a response delay in the system, a latency element was added to the model. However, since the model did not contain a feedback pathway, the latency served as a time offset and had no other effect on response dynamics. The simulation was optimized in terms of the five adjustable parameters and the latency.

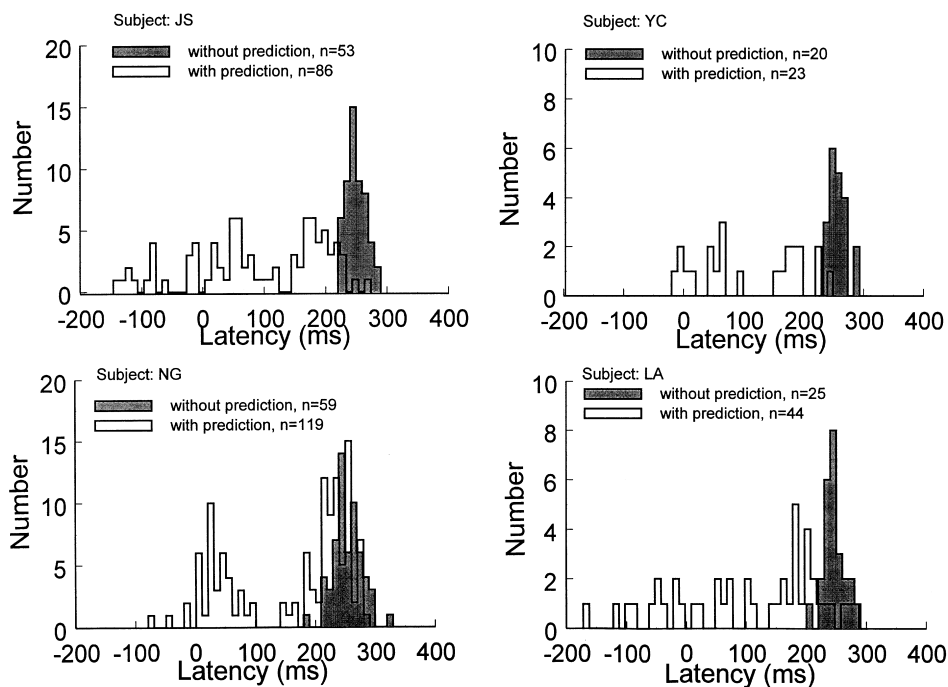
Figure 2A shows typical response by subject JS to non-predictable 4° convergence step stimulus. The solid line represents the time course of experimental data and the dashed line represents model simulation result. As seen in Figure 2A and B, the experimental data and model simulation fit with each other reasonably well. The RMS error between experimental and simulation was less than 3% of the steady-state amplitude.

Based on the work of Kowler and Steinman (1979) on saccadic prediction, we might expect to find small "anticipatory drifts" that proceed the initial transient portion of the response. We quantify such anticipatory movements in terms of their maximum amplitude as measured from the phase trajectory. In phase-plane plots, the velocity of the response (vertical axis) is plotted against position (horizontal axis) producing a graph that emphasizes the transient dynamics of a response. The phase-plane plot is useful in separating the anticipatory drift from the high-velocity transient. The anticipatory movement in the early portion of vergence response was found to be similar to a noisy ramp (i.e. constant velocity) response with small amplitude, Figure 2B. In the phase plot, this small movement appears as a horizontal line, sometimes with a slight curvature, Figure 2C. Following this small movement, the larger trajectory characteristic of a step response is seen, Figure 2C. An anticipatory vergence movement will be quantified in terms of the amplitude, or change from the baseline position, just before the onset of the step transient. For the response of Figure 2C, this occurs at the junction of the low velocity and high velocity trajectories as indicated by the "X" point in Figure 2C.

## Results

Figure 4 presents histograms that demonstrate the distribution of the timing index in responses to predictable and non-predictable stimuli. Comparing the timing index under the two conditions (Figure 4), we find that in responses without prediction the reaction time is tightly distributed with an average value for each of the four subjects at approximately 240–260 ms. The standard deviation of the timing index for unpredictable responses is less than

## Timing Index



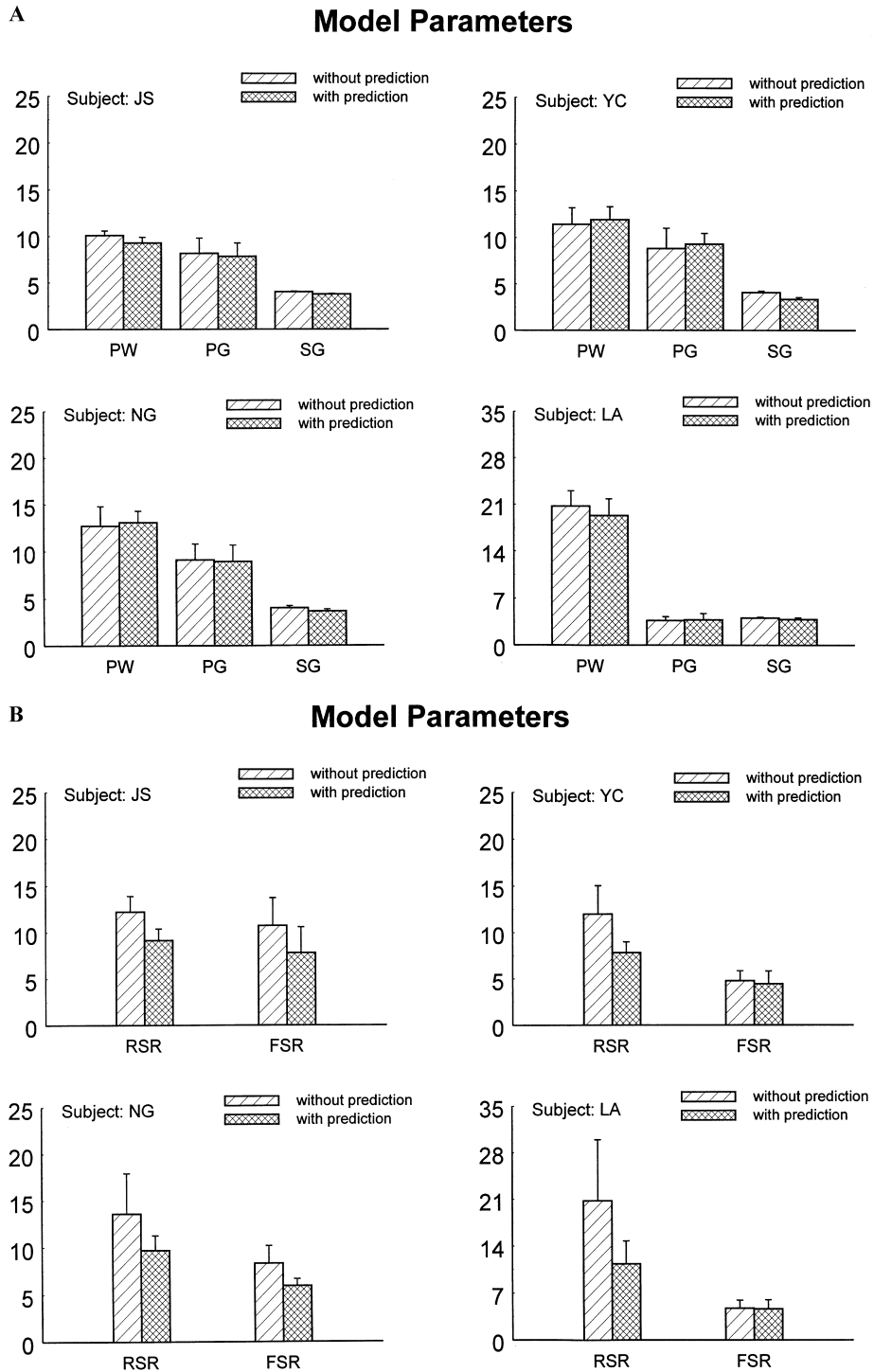
**Figure 4.** Timing index (response latency) comparison between responses to non-predictable and predictable stimuli shown as histograms. For all four subjects, response latency to non-predictable stimuli was distributed over a very narrow range with an average of approximately 200 ms. The response latency to predictable stimuli has a much wider distribution and a smaller average value.

$\pm 30$  ms. On the other hand, the timing index for predictable responses varies considerably. The average value of the timing index for each of the four subjects was approximately 90–160 ms, with a standard deviation of approximately  $\pm 100$  ms. Since the normal delay between movement onset and peak velocity is approximately 100 ms, the eyes sometimes began to move before stimulus onset. This is similar to the findings of Krishnan *et al.* (1973). All of our four subjects' data showed similar differences in the timing index between predictable and non-predictable responses, *Figure 4*.

To investigate the influence of prediction on vergence dynamic properties, we simulated a large number of the responses to predictable and non-predictable step stimuli and determined the model parameters required to fit the simulation to the response as described above. *Figure 5* shows that, for all four subjects, there was no substantial change in either PW or PG under the two conditions. Step gain showed a small decrease that can be attributed to the contribution of the anticipatory movements since any anticipatory movement will reduce the amount of step required to attain the final vergence position. However, the two parameters that represent the response's acceleration dynamics RSR, and FSR, underwent a substantial decrease when the stimulus was predictable, particularly

for subjects JS and NG, *Figure 5B*. The decrease in FSR was small for subjects YC and LA, perhaps due to the already low values of this parameter. These unexpected results indicate that the dynamics of predictive movements were actually slower (i.e. have reduced accelerations and decelerations) than movements made without prediction.

The drifts that preceded the fast transient response (labeled "Anticipatory Movement" in *Figure 2B*) were much larger, occurred much more frequently, and were much more consistent in direction in predictable responses as compared to the non-predictable responses. To quantify this difference, we measured the amplitude of the pre-transient movement in responses with and without prediction using the methodology described previously. As seen in *Figure 6*, the amplitude of the pre-transient drift in responses without prediction had a very narrow distribution that was centered at  $0^\circ$ . Hence, pre-transient drifts for non-predictable movements were quite small and were as likely to be in a direction opposite to the step response as in the same direction. For the response under predictive stimulus conditions, the drift amplitude had a much broader distribution centered at  $0.3$ – $0.4^\circ$  and was in the direction of the stimulus. Occasionally, the drift could be greater than  $1^\circ$  in a  $4^\circ$  step response.



**Figure 5.** Comparisons of model parameters in response to non-predictable and predictable stimuli. (A) Pulse width (PW, in s/100), pulse gain (PG), and step gain (SG). (B) Rising slew rate (RSR, in  $^{\circ}$ /s) and falling slew rate (FSR, in  $^{\circ}$ /s).

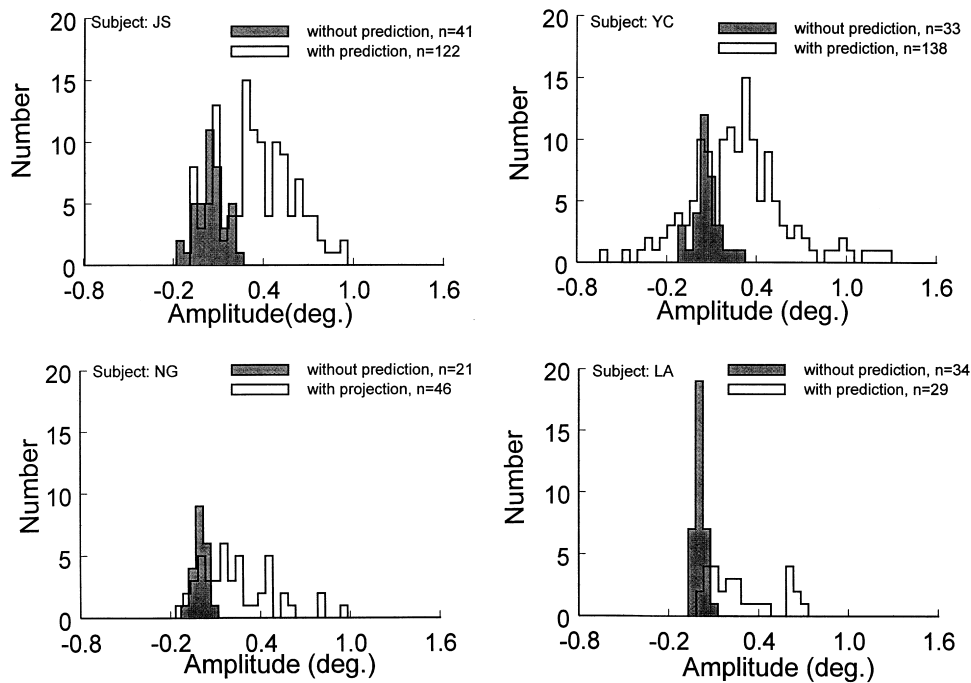
## Discussion

Examination of the fine details of vergence responses to predictable stimuli shows that an anticipatory response generally preceded the fast transient movement. This

response had an amplitude of up to  $1^{\circ}$  in a  $4^{\circ}$  step response. The anticipatory movements usually started well ahead of the target movement despite the fact that they would produce an initial retinal error.

Original expectations regarding the dynamic parameters,

## Anticipatory Movement



**Figure 6.** Histograms of anticipatory movements. For all the subjects, the distribution of the anticipatory movement to non-predictable stimuli is very narrow and centered at zero. The distribution of the anticipatory movement to predictable stimuli is centered between 0.3 and 0.4° and has a broader range of values.

RSR and FSR which described the acceleration and deceleration of the movement, were that these parameters would increase in responses with prediction. This was based on the assumption that the system would be able to generate a faster dynamic response when it knows the future of the stimulus. However, the model-based dynamics analysis showed the opposite result: the acceleration and deceleration dynamics decreased in predictive responses in all four subjects. This result might represent some sort of interactive influence of the anticipatory movement on the central control processes that generate the motor command signal. For example, some neural cells that generate the motor signal may be recruited in the very early portion of the vergence response to produce the anticipatory movement. The use of these neurons to produce an anticipatory movement may reduce the number of neurons available to the neuronal pool to generate the high-velocity initial component control signal. From *Figure 2B* and *C*, a clear boundary can be observed between the anticipatory movement and the normal initial transient. However, it is conceivable that the anticipatory movement continues into the fast transient movement and interferes with its production. The substantial decrease of RSR and the less consistent decrease in FSR indicate that this influence is strong during the early portion of predictive movements, but has less effect during the latter portion of the response.

The process that gives rise to the anticipatory movement is unknown. A possible explanation is that this is a low-level adaptive process where the oculomotor command itself is modified based on the memory of recent motion. In this case, adaptive processes would operate at the level of the brain stem and would not involve higher, cortical functions. A second possibility is that prediction is a high level cognitive and/or voluntary process. This latter hypothesis is supported by new evidence from functional magnetic resonance imaging (fMRI) studies (Munoz *et al.*, 1999). Munoz *et al.* (1999) found that areas 8 and 9 of Brodman in the superior frontal and prefrontal cortex were activated solely by the effort to predict vergence responses. These neural centers are close to those that mediate prediction in saccades. Based on these preliminary findings, we speculate that the neural centers involved in saccadic and vergence prediction are cortically-based and are similar. This suggests that vergence prediction might be a high-level cognitive process such as found in saccades (Kowler, 1989).

### Conclusions

We found substantial changes in the timing index in vergence responses to predictive step stimuli. As shown previously, prediction significantly reduced the average delay time and also made it much more variable. We also

found that a predictive stimulus commonly gave rise to large pre-transient drifts in the same direction as the subsequent response. These “anticipatory movements” were similar to those found prior to predictive saccades. Finally, prediction leads to a decrease in dynamics (i.e. reduced acceleration and deceleration) of the step response as indicated by a model-based dynamic analysis. This may be due to neuronal interactions associated with the anticipatory movement and those of the high-velocity transient.

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