A COMPARISON OF PREDICTIVE AND NONPREDICTIVE OCULAR PURSUIT UNDER ACTIVE AND PASSIVE STIMULATION CONDITIONS IN HUMANS

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Abstract — A technique has been developed for the comparison of predictive and nonpredictive ocular pursuit in human subjects, with the objective of estimating the contribution made by predictive processes to the normal pursuit response. Subjects were presented with a target moving at constant velocity in the horizontal plane and instructed to actively pursue the target or to passively stare at it. In the predictive mode (PRD), a step-ramp stimulus with velocity ranging from 12.5 to 50°/s was presented at regular intervals of 1.728 s, in alternating directions, with target exposure durations (PD) that varied from 80 to 640 ms. In the interval between presentations, subjects were in complete darkness. In the nonpredictive mode (RND), similar step-ramp stimuli were presented but with randomized direction and timing of target exposure. In the nonpredictive mode, during both active and passive stimulation, the smooth component of eye velocity was initiated after a mean delay of 125 ms. In the predictive mode, eye velocity started to build up well before target onset, even during passive stimulation. It was found that the time of initiation of this anticipatory response was closely associated with the time at which the target would have changed direction even though the target could not be seen at this time. Eye velocity measured 100 ms after target onset was negligible in the nonpredictive mode, whereas in the predictive mode, it progressively increased with target velocity, reaching a maximum of 18°/s when target velocity was 50°/s and PD was greater than 240 ms. Examination of the difference in the eye velocity trajectories for the predictive and nonpredictive modes indicated that the greatest contribution of prediction occurred approximately 150 ms after target onset and its effects were evident in the predictive response for at least 300 ms. This effect was reflected in the reaction time between target onset and the occurrence of peak eye velocity. In the nonpredictive mode, this progressively increased from 250 ms to 400 ms as PD increased from 80 to 640 ms, whereas in the predictive mode peak eye velocity occurred an average of 50 ms earlier for all values of PD. The results demonstrate the significant contribution that predictive processes make to normal ocular pursuit behavior and the importance of timing control in this process. They also indicate that this process is not dependent on voluntary control, but can be seen as an automatized response during passive stimulation.

Keywords — ocular pursuit; prediction; eye movement; anticipation.

Introduction

In previous experiments, we have used a number of techniques to reveal the characteristics of the predictive mechanisms of pursuit eye movements (1-3). These techniques have involved the deliberate repetition of similar transient target motion stimuli exposed for relatively brief periods of time (up to 320 ms). This has allowed the development of the predictive smooth eye movement pattern to be demonstrated. Subjects respond to the first presentation of the moving target with a delay of approximately
100 to 125 ms before initiation of smooth eye movement as demonstrated for random target presentation (4). However, with repetition, a pattern of anticipatory smooth eye movement builds up over the first 3 to 4 presentations, resulting in an increase in peak velocity and a shorter time to reach peak velocity. This technique allows high levels of eye velocity (up to 25°/s) to be generated in the dark period prior to target presentation when normally it would be impossible for subjects to produce a peak velocity of more than 4 to 6°/s in the absence of a moving target. Other authors have demonstrated such anticipatory eye movements (5–8), but these have generally been of low velocity. If such low velocity anticipatory movements were all that the system could produce, it would be difficult to explain their role in enhancing the phase during high velocity, high frequency sinusoidal pursuit. We have suggested, as have others before (for example, Rashbass [9]), that the system operates by storing information from prior visual stimulation and allowing the contents of this store to be released in such a way as to preempt the expected motion of the target (1,10). However, the crucial element in utilizing such stored information is that the pursuit system should have access to a relatively precise estimate of the time at which to release the predictive estimate, and in two experiments it has been demonstrated that this periodicity estimation process clearly exists (3,10).

The type of stimulus that we have used in the past is essentially identical to the step–ramp stimulus used first by Rashbass (9) and subsequently by many other authors (4,11), except that the target has only been presented during the ramp part of the target motion. In the majority of our previous experiments, we have used short-duration stimuli that appeared for periods of 40 to 320 ms. The very short durations of exposure do not allow the development of the full eye velocity within the period of exposure, and there arises the question of whether normal pursuit processes operate in such a paradigm. Other experimenters (8,12) have used longer duration target motion stimuli (typically >600 ms), which are clearly more closely related to normal pursuit. In the experiments described here, we have sought to investigate how the pattern of anticipatory eye velocity changes with increasing the duration of exposure up to 960 ms in order to obtain a clear idea of how anticipatory responses contribute to pursuit. We have also specifically compared responses to predictive and nonpredictive stimuli by randomizing the direction and timing of target motion stimuli. A preliminary report of this work was made previously (13). Kao and Morrow (12) have also recently described a similar technique, but in that study the target did not disappear after the ramp component.

Finally, we have also examined the difference between responses to active pursuit and to passive stimulation of the oculomotor system, a method used in a number of previous experiments (14–16). Here we have investigated both predictive and nonpredictive stimuli to establish the role of volitional control in the predictive process. Wyatt and Pola (17) have already shown that there is a significant difference between active and passive responses even during transient ramp stimulation, but no comparison was made between predictive and nonpredictive stimuli.

**Methods**

Subjects were seated in front of a circular screen (radius 1.5 m) with the head fixed by clamps to the side of the head. A visual display was presented on the screen and was made to move under the control of a motor-controlled mirror. Two types of display were used. During active pursuit, the display was a small target composed of a circle with superimposed crosshairs, subtending 50 minutes of arc at the eye. During passive stimulation, the display was larger, composed of horizontal stripes, and subtending 12° × 10° at the eye. Eye movements were recorded by an infrared limbus tracking technique (Skalar IRIS) and were sampled at intervals of 10 ms prior to storage on disc.

The target motion stimulus was a ramp of constant velocity that varied from 10° to 50°/s. The display was not continuously presented, but was illuminated for a pulse duration that varied from 80 to 960 ms in such a way that the center of the pulse coincided with the zero position of
Figure 1. Examples of eye movement responses evoked during (A) active pursuit and (B) passive stimulation of the oculomotor system for a predictive (PRD) pursuit stimulus. Target velocity = 37.5°/s; interpulse interval = 1.728 s; PD = 320 ms. Pulses indicate timing of target exposure (up = on). The broken vertical line indicates timing of eye velocity in relation to target onset. Examples of saccadic activity (sac) are shown circled; fast-phases have been removed from the eye velocity trace.
the ramp stimulus. In the predictive condition, the direction of target motion was alternated regularly to left and right with an interpulse interval of 1.728 s, as indicated in Figure 1. In the nonpredictive condition, the direction and timing of the ramp stimulus were varied at random, although the average interval between presentations was maintained at 1.728 s (Figure 2). During active pursuit, subjects were instructed to follow the target as well as possible during the exposure period, whereas in the passive stimulation condition, they were instructed to stare at the center of the horizontal stripe pattern and to attempt to maintain eye position near center. This was a demanding task, since there were no other static visual cues present that could be used as a reference for fixation.

A total of 3 experiments was carried out on a pool of 15 normal subjects. In the first, the responses of 10 subjects were examined in the predictive mode with active pursuit only. Pulse duration was varied from 160 to 960 ms in 6 steps, and 5 velocity levels were examined from 10° to 50°/s. In the second experiment, 11 subjects were examined during predictive and nonpredictive conditions for active pursuit at pulse durations of 80, 160, 240, 320, 480 and 640 ms. Four velocity levels were examined; 12.5°, 25°, 37.5°, and 50°/s. In the third experiment, responses to active and passive stimulation in both predictive and nonpredictive paradigms were examined in 8 subjects for pulse durations of 320 and 640 ms. Display velocity was varied from 12.5° to 50°/s.

Data Analysis

Eye movements were analyzed off-line by first identifying and removing the fast phase components of the response in the eye velocity trajectory and using an interpolation routine to bridge the gaps in the eye velocity signal. As indicated in the examples shown in Figures 1 and 2, the fast phase movements were generally of small amplitude (<5°) and brief duration, making linear interpolation a simple and adequate method of waveform restoration. Various routines were then implemented on the derived velocity profiles to identify such features as the magnitude and timing of peak velocity in response to each ramp stimulus. The time of onset of the eye velocity in each direction was calculated by identifying the point at which eye velocity reached a threshold equal to 10% of peak eye velocity for a particular response, carrying out a linear regression on the next 100 ms of the velocity data and then extrapolating back to obtain the point at which the regression line crossed through zero. This was found to be a particularly reliable way of identifying response onset for the predictive responses, for which eye velocity exhibited only a gradual increase with time. Cycle-by-cycle averages were obtained for the response to a whole sequence of ramps by overlaying and averaging separately the left- and right-going responses. Statistical comparisons have been carried out using repeated measures analysis of variance.

Results

Qualitative Differences in the Predictive and Nonpredictive Responses during Active and Passive Stimulation

The simple technique of randomizing the timing and direction of successive target motion stimuli had a most profound effect on the oculomotor response during both active pursuit and passive stimulation, as demonstrated by the examples in Figures 1 and 2. In the nonpredictive (RND) mode, eye movements were not initiated until some time (100 to 150 ms) after target illumination, in accord with previous observations (4), and there was usually some saccadic activity within the eye movement trajectory. When all saccadic components were removed from the response, the eye velocity trajectory was observed to exhibit a rapid acceleration after target onset to reach target velocity. In contrast, in the predictive (PRD) mode there was little saccadic activity present, and inspection of the eye velocity trajectory showed a relatively slow build-up of eye velocity prior to target onset, with a more rapid acceleration occurring approximately 100 ms after target onset. However, although this pattern of anticipatory eye movement was evident in the steady-state response,
Figure 2. Examples of eye movement responses evoked during (A) active pursuit and (B) passive stimulation of the oculomotor system for a nonpredictive (RND) pursuit stimulus. See Figure 1 for details.
there were significant changes in the first 3 to 4 presentations of the target motion stimulus, which will be discussed later.

In the passive stimulation condition, the subjects found it very difficult to hold eye position during exposure of the larger moving display because of the strong optokinetic drive. As a consequence, a vigorous nystagmus was induced in both the predictive and the nonpredictive modes (Figures 1B & 2B).

Some inappropriate predictive eye velocity was generated in the nonpredictive condition during both active and passive stimulation. However, such movements were always of low velocity (<3°/s) and were frequently inappropriately directed.

Comparison of Eye Velocity Trajectories in the Predictive and Nonpredictive Modes

The contribution of the predictive mechanism to pursuit was assessed by comparing the averaged velocity trajectories in the predictive (PRD) and the nonpredictive (RND) conditions (Figure 3—active responses only). These trajectories represent the grand average across 10 subjects, and they serve to illustrate the general effects. All measures of velocity and timing discussed later are derived from the results of individual subjects, not from this grand average. Note, in particular, that the response to the 80-ms pulse duration in the nonpredictive condition was negligible compared to that which could be built up in the predictive condition and was initiated after the target had been extinguished. In contrast, that generated in the predictive condition was initiated well before target onset and reached a peak that was only a little less than that of the target. During the 640-ms pulse duration, subjects were able to attain target velocity in the nonpredictive condition well within the exposure period, and there was little difference in peak velocity from that in the predictive condition. Peak velocity sometimes exceeded target velocity (Figure 3 panels B and D) and normally reached its peak well before the target was extinguished for longer pulse durations (for example, Figure 3D). Note also that the anticipatory element of the predictive response was essentially very similar in form, though different in magnitude, for all durations of target exposure (PD) from 160 to 640 ms or even up to 960 ms in Expt I.

The remaining trace marked in each of the examples in Figure 3 represents the predictive residual (p.res), that is, the difference between the predictive and nonpredictive responses. This predictive residual should not be taken to represent the prediction component in isolation. It probably does so for the period up to 100 ms after target onset, but thereafter it will be modified by the effects of visual feedback. However, examination of this predictive residual does allow the conclusion that the predictive process makes its maximum contribution approximately 150 ms after target onset and continues to make a contribution for at least 300 ms after target onset, as indicated by the fact that the predictive residual is greater than zero until this time. Details of the magnitude and timing of responses will now be considered.

Comparison of Peak Velocities in the Predictive and Nonpredictive Modes

As pointed out above, the velocity trajectories in the predictive and nonpredictive responses were quite different. In both conditions there was a steady and significant increase in the peak velocity attained as the duration of target exposure (PD) was increased (Figure 4A). For the longer pulse durations (>640 ms), peak eye velocity actually exceeded target velocity, started to decline well before the end of the exposure period, and was frequently much less than target velocity at the time that the target went off (Figure 3). As the velocity of the target increased, greater exposure times were required in order for peak eye velocity to reach or exceed target velocity. This minimum PD to reach target velocity was always less for the predictive response than for the nonpredictive response. Thus, for a target velocity of 12.5°/s, the predictive response reached and exceeded target velocity with a peak of 13.2°/s for PD = 160 ms, whereas a PD of 240 ms was required to reach target velocity in the nonpredictive task. Corre-
Figure 3. Comparison of averaged eye velocity trajectories for the predictable (PRD) and nonpredictable (RND) target motion stimuli in the following conditions: (A) $PD = 80$ ms, $V = 12.5°/s$; (B) $PD = 320$ ms, $V = 12.5°/s$; (C) $PD = 320$ ms, $V = 50°/s$; (D) $PD = 640$ ms, $V = 50°/s$. In each example, the predictive contribution to pursuit ($p.\text{res}$) was obtained by subtraction of the nonpredictive from the predictive response. Averages were obtained from 5 cycles of response in 10 subjects.
sponding values for a target velocity of 50°/s were 480 ms and 640 ms, respectively. But the results from Expt I showed that peak eye velocity continued to increase as PD was increased beyond these limits (Figure 4B). Peak velocity appeared to reach an asymptotic level about 5% to 10% greater than target velocity for PD > 640 ms, but then unexpectedly increased further for a PD of 960 ms.

The Timing of Eye Movement in the Predictive and Nonpredictive Conditions

Differences in timing of the responses to predictive and nonpredictive stimuli have been quantified by measuring the time at which the response was initiated (Figure 5A) and the time at which peak velocity occurred (Figure 5B). There was no significant effect of velocity on either of these latencies; the values shown in Figure 5A are from 2 velocity levels only (25°/s and 50°/s). In the nonpredictive mode smooth eye movements were initiated with a mean latency of 125 ms, and there was no significant effect of pulse duration on the onset latency.

In the predictive condition, pulse duration had a significant effect on latency to onset (Figure 5A, PRD-solid lines). For pulse durations below 240 ms, the eye movement was initiated well in advance of target onset, with a mean latency of ~636 ms. For longer pulse durations, eye movement occurred progressively less early in relation to target onset. Since all pulses were centered on the mid-point of the cycle (that is, the straight-ahead position), target onset occurred earlier in relation to the mid-point for longer pulse durations. When the latencies were recalculated as the time between eye movement onset and the mid-point of the pulse, there was found to be much less dependence on pulse duration (Figure 5A, PRD-broken lines), the mean

(A). Predictive vs. random - Expt II

(B). Predictive - Expt I.

Figure 4. Peak velocity of smooth eye movement as a function of the duration of target exposure (PD) and target velocity (V). (A) Pursuit of predictable (PRD) versus nonpredictable (RND) stimuli. Mean of 10 subjects +1 SEM. (Expt II). (B) Pursuit of predictable target motion stimulus. Mean of 11 subjects +1 SEM. (Expt I).
Figure 5. (A) Latency to onset of smooth eye movement in predictable and nonpredictable stimulus conditions. Solid lines represent latency referred to onset of target exposure, whereas broken lines represent latency referred to the center of the target pulse, which corresponds with the midline target position. Mean of 10 subjects +1 SEM. (B) Latency between onset of target exposure and occurrence of peak eye velocity as a function of the duration of target exposure (PD) and target velocity (V) in the predictable and nonpredictable conditions. Mean of 10 subjects +1 SEM.

Latency to peak eye velocity increased significantly (p < 0.001) in the predictive than in the nonpredictive mode (Figure 5B). Thus, in the predictive mode, latency to peak increased from a mean of 190 ms to 365 ms as PD increased from 80 to 640 ms, whereas, in the nonpredictive mode, latency to peak increased from a mean of 268 ms to 400 ms. Thus, the effect of the anticipatory eye movement was to advance the average of 53 ms. In most instances, the earlier onset of eye velocity in the predictive mode simply allowed the eye velocity to reach and often exceed target velocity earlier, from which point eye velocity started to decline. However, in some examples, notably when PD was either 320 or 480 ms, eye velocity reached a peak that was less than target velocity and started to decline before the end of the pulse, even though time remained in which to increase eye velocity further before target extinction (for example, Fig-
Figure 3C). This was a strong indication that factors such as prediction of pulse duration (which was always constant within a single run) may have had a strong influence on the timing of response termination as noted previously (8,18).

**Velocity Characteristics of Anticipatory Eye Movements**

There is another way in which the effect of the anticipatory eye movement can be assessed. That is to examine the eye velocity achieved prior to the time at which the presence of the moving target is able to make a significant contribution to eye movement as a result of the effects of visual feedback. Such a comparison may be made at the time of target onset, but a more robust measure is obtained if the velocity is examined 100 ms after target onset (Figure 6A). It is evident from the latencies to eye movement initiation observed in the nonpredictive mode (Figure 5A) and from the observations of other authors (4,11) that visual feedback takes at least 100 ms to take effect. This is confirmed by the measures of eye velocity in the nonpredictive mode shown in Figure 6A, where there is negligible velocity (overall mean = 1.38°/s) 100 ms after target onset. In contrast, in the predictive mode, eye velocity was significantly greater than zero and increased with target velocity from a mean of 7.7°/s to 16.8°/s as target velocity increased from 12.5°/s to 50°/s. The anticipatory eye velocity increased with pulse duration up to 240 ms, as indicated by the velocity 100 ms after target onset (Figure 6A), but there was no further increase for longer PDs.

It is evident by inspection of the predictive residual (p.res) trace shown in Figure 3 that the difference in eye velocity between the predictive and nonpredictive modes actually persists for more than 100 ms after target onset. Figure

![Figure 6](image-url)

**Figure 6.** Mean eye velocity measured (A) 100 ms and (B) 200 ms after the onset of target exposure, as a function of target exposure duration (PD) and target velocity (V) for the predictive (PRD) and randomized (RND) conditions. Mean of 10 subjects ±1 SEM.
Predictive Compared with Nonpredictive Pursuit

6B shows values of eye velocity obtained 200 ms after target onset, a time that has frequently been referred to as representing the end of the open-loop phase of the response to a nonpredictive stimulus (4,11). For all values of PD and target velocity, the eye velocity 200 ms after onset was still significantly greater ($p < 0.001$) in the predictive mode than it was in the nonpredictive mode.

Changes in the Predictive Response Prior to Attainment of the Steady-state

It has been noted in previous experiments (1) that significant changes occur with repeated stimulation in the predictive mode; a significant build-up in peak velocity occurs over the first 3 to 4 presentations while, simultaneously, the response becomes progressively more predictive. However, in all previous experiments, only short durations of exposure ($PD < 320$ ms) have been examined. In the present experiment similar findings were made for the shorter pulse durations (80 to 240 ms). However, for the longer pulse durations a rather different picture emerged, as illustrated in Figure 7. When target velocity was 25°/s and PD was 80 to 240 ms (Figure 7A), there was a significant difference between the peak velocity attained in response to the first presentation and the mean level of peak velocity attained after the first 4 presentations. But for longer PDs, this was no longer true. In contrast, when target velocity was 50°/s (Figure 7B), there was a significant difference ($p < 0.001$) between the first peak velocity and the mean peak velocity for all values of PD.

It would be reasonable to expect that the response to the first target presentation of the predictive stimulus should be very similar to that observed during the nonpredictive stimulus. A comparison of the relevant peak velocities (Figure 7) revealed that this was true over a large range of PDs and target velocities. However,

(A). Target vel. = 25°/s.

(B). Target vel. = 50°/s

Figure 7. Changes in peak eye velocity between the first target presentation (○) and the mean level attained after the 4th presentation (△) of the target in the PRD condition as a function of PD (solid lines). Broken lines indicate the mean peak eye velocity attained in the RND condition. (A) Target velocity = 25°/s. (B) Target velocity = 50°/s.
there was a strong tendency to overestimate the velocity in the predictive mode for the shortest PD (80 ms) and to fail to reach the nonpredictive response level for the longest PD (640 ms).

**Comparison of Active and Passive Responses**

When subjects were required to stare passively at the moving target rather than pursuing it actively, the eye movements that were generated took a form distinctly different from those seen during active pursuit—the form of optokinetic nystagmus, in which fast phases acted in the direction opposite to that of the smooth movements (Figures 1B and 2B). However, when the fast phases were removed, the eye velocity trajectories could be seen to be very similar in form to those of active pursuit in both the predictive and nonpredictive modes (Figure 8). The major difference was that the peak velocities of the passive responses were always significantly less than those for the active responses, in both the predictive and nonpredictive modes (Figure 9A). The ratio of peak velocity in active

![Diagram](image_url)

**Figure 8.** Mean eye velocity trajectories for (A) active pursuit and (B) passive stimulation in the predictable (PRD) and nonpredictable (RND) conditions. The predictive residual (p.res) represents the difference between the PRD and RND conditions. Note that p.res reaches a peak approximately 150 ms after target onset.
and passive modes varied with target velocity, predictability, and PD, but active was typically 20% to 30% greater than passive.

The most important point is that the anticipatory response could still be observed during passive stimulation, indicating that this aspect of the response is not necessarily dependent on volitional control. This is clearly demonstrated by the velocity at 100 ms (Figure 9B), which was approximately half that for the active pursuit, but still had an appreciable level (for example, 14°/s at a target velocity of 50°/s for PD = 640 ms) that increased significantly (p < 0.001) with target velocity. Examination of the predictive residual for the passive responses (Figure 8) also confirmed that prediction was making a significant contribution to the predictive response for at least 300 ms, as it did for active pursuit. In addition the latency to the start of eye movement, when referred to the midpoint of the cycle, was approximately −750 ms for active and −700 ms for passive stimulation, indicating that timing of the anticipatory response was also being determined in a similar way, even though subjects were specifically engaged in a task other than that of mimicking the underlying target trajectory.

Discussion

A Specific Test for Comparing Predictive and Nonpredictive Function

One of the objectives of developing the tasks described in these experiments was to be able to make a specific comparison between the predictive and the nonpredictive control of eye movement. The technique presented appears to accomplish this successfully, although in subsequent experiments modifications have been made to improve the randomness of target presentation.
by varying the velocity as well as the direction and timing of the step–ramp stimuli, which reduces the incidence of inappropriate anticipatory eye movements. The results show quite clearly that there are two distinct elements to the response in the predictable mode: the anticipatory component that builds up relatively slowly and the visual feedback component that has a much more rapid acceleration. The visual feedback component has been studied in many previous experiments, and the characteristics that are demonstrated in our results are quite compatible with those published previously (4,11). The anticipatory component has also been examined previously (5–8,10,18). However, in most earlier experiments the anticipatory eye velocities generated were relatively low, and there has been no attempt until recently (1,12) to estimate the contribution that the anticipatory component makes to higher velocity responses. The results presented here show quite clearly that prediction enhances the response significantly for at least 300 ms after target onset in a way that would be of significance for continuous target tracking. In fact, the predictive response continues to exhibit a time advantage of approximately 50 ms on the nonpredictive behavior, right up to the point when peak velocity is attained (Figure 5B). This behavior was noted previously by Kowler and Steinman (7) for much lower velocity (1° to 2°/s) stimuli.

The velocity achieved 100 ms after target onset is of particular significance because in the nonpredictive mode negligible eye movement is normally evoked before this time (Figure 6A). The demonstration that the velocity at 100 ms changes with stimulus velocity in the predictive mode (Figure 6A) clearly indicates that the anticipatory response does not just represent some default acceleration that can be produced in the absence of the target. Rather, it is based on the expectancy the system has of the ensuing target velocity. Moreover, the levels of eye velocity attained are considerably greater than those that could normally be developed in the absence of a moving target without prior exposure to the stimulus (10,12,19). The dependence of the magnitude of the anticipatory component on target velocity has now been demonstrated in a number of different experiments (1,5,8,18,20) and is clearly a fundamental aspect of the response. For the practical purposes of assessing the ability of subjects to generate a predictive response, the measurement of eye velocity 200 ms after target onset appears particularly useful. Since the eye velocity is normally well developed in either the predictive or the nonpredictive mode at this time, assessment of the difference in eye velocity between the two modes forms a very robust measure of the effectiveness of the predictive process (Figure 6B). It is evident that it would be possible to record such eye velocity levels quite easily with relatively insensitive recording techniques such as electro-oculography.

The Role of Attentional Mechanisms in Prediction

Anticipatory responses were also present during passive stimulation, but with peak velocities that were reduced compared with those of active pursuit. Although this confirms previous observations (1), it was somewhat surprising to find that it applied in circumstances where the interval between target presentations (1,728 ms) was considerably greater than that examined previously (720 ms) and that the anticipatory response started so early (700 ms) before target onset. The demonstration that a strong anticipatory response occurs even in the absence of volitional control indicates that it must be a fairly automatized process. This finding is compatible with that of Kowler and Steinman (21) in an experiment in which much lower eye velocities were examined. Kowler (22) has used the term motor habit to describe such behavior. A point of particular note is that passive stimulation gives a lower response for both predictive and nonpredictive stimuli. This is in accord with previous observations in which more conventional continuously presented stimuli have been used [14,16,23]). Taken together, these findings indicate that predictive mechanisms operate as a basic automatized process at a low level of attention; volition is not necessary for the simplest level of prediction, but serves to potentiate the eye movement response irrespective of whether it is predictive or reactive.
The Role of the Anticipatory Response in Normal Predictive Pursuit Behavior

In our own previous experiments (1), we chose to examine the anticipatory eye velocity in response to very brief target presentations in order to highlight its contribution in relation to the visual feedback component. However, the relevance of this technique to normal pursuit may not be immediately apparent. In the initial presentation, if the pulse duration is only very brief (for example, 80 ms, Figure 3A) the subject has no time to initiate a visually driven response before the target is extinguished. Because the target appears so briefly and only in the center of its trajectory, there is no real indication of the underlying displacement that the target is executing. Yet after 3 or 4 presentations, it is possible to build up a velocity that is much greater than can be achieved as a result of the visual feedback alone (Figure 7A) and greater than can normally be initiated and sustained in darkness. From the results presented in the experiments described here, it can be seen that even when the period of exposure is much longer (up to 960 ms) a similar pattern of anticipatory eye movement can be observed (Figure 3), thus supporting the original contention that the responses to brief presentation were representative of pursuit behavior. The anticipatory eye velocity trajectory is also similar to that described by other authors (6–8,12,18). The characteristic build up of velocity with repetition, noted previously, was not present with longer pulse durations (Figure 7A), except for high-velocity stimuli. This was largely because the subject was able to attain target velocity within the first exposure period. In fact, as noted in the Results section, peak velocity in the first exposure was often in excess of target velocity when target velocity was low (Figure 7A). It is likely that this represents a tendency to generate an initial guess that is close to the mid range of velocities presented within the experimental run. Such an effect was noted previously by Kowler and McKee (24), although at much lower velocities.

The importance of the results obtained with brief (<240 ms) pulse durations is that they reveal the action of a mechanism that would otherwise be concealed within the transient response to longer target exposures. An essential feature of the technique lies in the temporal separation of the brief transient motion stimuli. This separation allows the individual response to each target presentation to decay before the appearance of the next stimulus. There can therefore be no doubt that when the response velocity is observed to build up and to become more anticipatory, this is not the result of a simple summation of consecutive transient responses. Rather, it must represent the build-up of an internal store of velocity drive that can be replayed, with appropriate timing, as a predictive estimate of required eye velocity. The fact that the average peak velocity eventually attained after several presentations is a function of pulse duration (Figure 4A) suggests that the estimate that is stored is based on, and limited by, the afferent information received. It is therefore not a strict reconstruction of actual target velocity (25).

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