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Anticipatory eye movements evoked after active following versus passive observation of a predictable motion stimulus.

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Abstract

We used passive and active following of a predictable smooth pursuit stimulus in order to establish if predictive eye movement responses are equivalent under both passive and active conditions. The smooth pursuit stimulus was presented in pairs that were either 'predictable' in which both presentations were matched in timing and velocity, or 'randomized' in which each presentation in the pair was varied in both timing and velocity. A visual cue signaled the type of response required from the subject; a green cue indicated the subject should follow both the target presentations (Go-Go), a pink cue indicated that the subject should passively observe the 1st target

and follow the 2nd target (NoGo-Go), and finally a green cue with a black cross revealed a randomized (Rnd) trial in which the subject should follow both presentations. The results revealed better prediction in the Go-Go trials than in the NoGo-Go trials, as indicated by higher anticipatory velocity and earlier eye movement onset (latency). We conclude that velocity and timing information stored from passive observation of a moving target is diminished when compared to active following of the target. This study has significant consequences for understanding how visuomotor memory is generated, stored and subsequently released from short-term memory.

1) Introduction

Humans are able to produce predictive smooth eye movements to a moving visual stimulus that has been presented previously (Barnes and Donelan, 1999). However, they are unable to initiate and maintain smooth pursuit in the absence of either the target or expectation about the target re-appearance (Kowler and Steinman, 1979; Kowler et al., 1984; Kao and Morrow, 1994). More recently it has been discovered that humans are even able to produce anticipatory eye movements to a smooth pursuit stimulus after initially viewing, but not actually following, the target, even though the target moves progressively into the peripheral field during the initial presentation (Barnes et al, 1997). Barnes et al (1997) showed that stimulus information can be stored when the same smooth pursuit stimulus is repeated several times during passive viewing. A subsequent experiment revealed that subjects can even extract visual motion information from two stimuli when they are presented simultaneously but move with different velocity in the same direction in the horizontal plane (Poliakoff et al, 2005). The authors found that there was a slight detriment in scaling eye velocity 100ms after target onset (V100) to the target velocity if the subjects were not cued about which target to follow.

Cognitive cues have been used previously to elicit predictive smooth pursuit eye movements (Kowler, 1989; Jarrett and Barnes, 2002). These previous studies used a symbolic or verbal cue to indicate the direction and/or velocity of motion in the upcoming target. The experiment presented here does not provide any information about the direction/velocity of the target, and thus does not give a cognitive expectation of the target motion. Instead we use a colour-coded cue to instruct the subject to perform the required response (i.e. to follow the target) or not (i.e. to maintain fixation during target motion). In addition this cue indicates to the subject if the trial is predictable or random.

Numerous factors affect onset velocity of predictive smooth pursuit eye movements including: (a) the past-history effect where the target velocity of the preceding trial can influence predictive velocity of the present trial (Kowler, 1989; Poliakoff, 2005); (b) target direction (Burke and Barnes, 2007); (c) long delays between the first and second presentation of the target (Chakraborti et al, 2002). In the current experiment each trial incorporated two smooth pursuit velocity ramps presented in succession (stimulus pairs) and split by a variable delay. This paradigm extends previous work by addressing the following aims: (i) to establish if the predictive responses to a passively viewed or actively pursued stimulus are equivalent, (ii) to determine if there is any effect of past history from the previous trial on the anticipatory velocity or latency of the eye movement, (iii) to identify if the short-term storage of visual motion is equivalent in the vertical and horizontal directions of motion during passive and active viewing, and (iv) to determine any effects on prediction when using different delay periods between the first and second presentation of the stimulus, and (v) to ascertain if prediction can be elicited after only one presentation of a stimulus when using a novel cognitive cueing paradigm.

2) Results

Subjects were given 3 tasks to perform during the experiment (see Figure 1):

a) Go-Go task: This task consisted of a white fixation cue visible for 200ms that subsequently changed colour to green for a further 200ms before the screen went blank (gap) for 400ms. After the gap the green cue and a green target (T1) appeared, with the target displaced towards the direction of motion (6? or 12?). The target moved smoothly at either 15?/sec or 30?/sec for 800ms, in one of 4 directions (up, down, left or right) before being extinguished. A delay of either 2, 4 or 6 seconds was then included, in which only the fixation cue was visible, before the same cue and target presentations were repeated as above. The subjects were informed that they must follow the green moving target when it appeared and fixate the centrally positioned cues when present (see figure 1).

b) NoGo-Go task: This task mimicked the task described above; however, the white fixation cue changed to magenta instead of green in the first presentation indicating the subject must maintain fixation while a target would smoothly move in their peripheral field of view. Again a 2, 4 or 6 second delay was used which was then followed by the cue turning green indicating the subject to follow the preceding target in the second presentation (see figure 1).

c) Rnd task: This task was designed to be similar to the tasks above, but to elicit reactive responses to both presentations and thus discourage storage of target velocity information. Each presentation was cued with a green square with a black cross inside. However, this time, the duration of the gap was randomized (200-600ms) and also the velocity of the target between each of the two presentations in the pair. The subjects were instructed to simply follow the green target when it appeared (see figure 1).

2.1) Single Subject Response

Figure 2 shows a typical example of the eye and target displacement of a single subject performing each of the three tasks utilized in this experiment (i) the Go-Go task, (ii) the NoGo-Go task and, (iii) the Rnd task. The NoGo-Go task required subjects to inhibit a reflexive response towards the target during the 1st presentation of the target and if subjects failed to inhibit this response, the trial was subsequently excluded from further analysis (see data analysis section 4.4). We found the average error rate for all subjects to be 7.87% (mean = 3.8, range = 2 to 6 failed attempts) in the NoGo-Go trials.

2.2) Reactive Responses: V50 and Latency

Measures of eye acceleration and eye velocity 50ms after target onset (V50 and A50 respectively) were used to establish the magnitude of the predictive response. Reactive responses were obtained from both presentations in the Rnd task and the 1st presentation in the Go-Go task. There were 24 responses for each of these 3 reactive categories, giving a total of 72 responses. The only significant difference in V50 for the reactive responses was found in the 1st presentation of the NoGo-Go task (mean=-0.06?/s) when compared to the other (0.15?/s, 0.14?/s, and 0.13?/s) as in this condition fixation was actively maintained ($F_{(3,5)}$=23.524 and p=0.002) (see table 1). Note that in all four of these conditions, V50 was very low (<0.2 deg/s), as expected for reactive responses, thus indicating minimal prediction (see table 1). Latency for this experiment was defined as the difference between the time at onset of the target and the time at onset of the eye movement. No significant difference was found in latency between the 1st or 2nd presentation of the Rnd trial (1st mean=93.4ms and 2nd mean= 93.8ms), or the 1st presentation in the Go-Go task (mean=80.9ms) (see table 1).

2.3) Predictable Responses: V0, V50, A50 and latency

There were two categories of predictive response, i.e. those from the 2nd presentation of the Go-Go and NoGo-Go conditions. There were 24 responses within each category. To compare the values of V0 (the velocity at target onset), V50, A50 and latency 4-way ANOVAs were used in which the factors were task (Go-Go, NoGo-Go), velocity (15deg/s, 30deg/s), direction (L,R,U,D), and inter-presentation delay (2s, 4s, 6s). This analysis revealed significant effects of the main factors on all 3 variables, with significant interactions of task and velocity ($p<0.05$) and of task and delay ($p<0.05$). Results of the ANOVA will be presented for each of the factors separately below.

2.4) Comparison of Go-Go and NoGo-Go Task

There was a significant difference between the Go-Go and NoGo-Go tasks in V0, V50 and A50 (V0:$F_{(1,8)}$=7.604, p=0.025; V50:$F_{(1,8)}$=7.306, p=0.027; A50:$F_{(1,7)}$=12.276, p=0.01). Although significant, the differences were small; V50 and A50 were 11% and 14% less, respectively, in the NoGo-Go task than the Go-Go task. A significant difference was also found between the latency of the Go-Go and NoGo-Go task ($F_{(2,7)}$=12.556, p=0.005).

2.5) Effect of Delay (2, 4 or 6 seconds)

There was a significant effect of the inter-presentation delay on V50 for the Go-Go and NoGo-Go tasks (see table 1) ($F_{(2,7)}$=4.923, p=0.046), but no significant effect on V0 (F(2,7)=3.052), p=0.111) or A50. For both tasks (Go-Go and NoGo-Go) V0 and V50 were highest for the 4 second delay (see table 1). Simple contrasts confirmed that V50 for the 4s delay was significantly greater than for the 2s delay ($F_{(1,8)}$=5.309; p=0.05), whereas V0 exhibited a similar trend with a borderline significant difference between the 6s and 4s delay ($F_{(1,8)}$=4.919, p=0.057). However no significant difference was found between 2s and 6s in either V0 or V50. There was no significant effect of delay on the latency for the Go-Go or NoGo-Go tasks, although there was a trend for earlier onset at the 4 second delay ($F_{(2,7)}$ = 3.848, p=0.075). No significant task x delay interaction was observed.

2.6) Effect of Target Velocity (15?/s or 30?/s)

There was a clear effect of target velocity on V0 and V50 (table 1) in the predictable conditions, with the lower target velocity (15?/s) revealing a lower mean V0 and V50 than the 30?/s target velocity in both the Go-Go (V0:$F_{(1,8)}$=30.355, p=0.001; V50:$F_{(1,8)}$ = 8.821, p=0.018) and NoGo-Go tasks (V0: F(1,8)=11.937, p=0.009; V50:$F_{(1,8)}$=11.910, p=0.009). We also found a significant effect of target velocity on the acceleration (A50) during the Go-Go task ($F_{(1,7)}$ = 9.069, p=0.020), but this difference did not quite reach significance in the NoGo-Go task (see table 1). There was no significant effect of target velocity on latency in either the Go-Go or NoGo-Go task (table 1). This suggests that the difference in V0 and V50 in the Go-Go task was probably associated with a difference in the acceleration of the eye between the two target velocities rather than the latency. By contrast, in the NoGo-Go task both acceleration and latency seem to play a role in determining the level of V50.

2.7) Effect of Direction (Up, Down, Left and Right)

The results shown (see table 1) reveal V50 for each direction of the target movement (up, left, down and right). The analysis of variance indicated a significant difference in mean V50 as a function of target direction ($F_{(3,6)}$=6.126, p=0.029). Further post-hoc analysis revealed some significant differences between directions: the upward (U) direction revealed no significant difference to the leftward (L) (t=0.087, df=17; p=0.932), the L was significantly higher than the downward (D) (t=3.137, df=17; p=0.006), the D was significantly lower than the rightward (R) (t=-2.833, df=17; p=0.011), and no difference between U and R was found (t=1.240, df=17; p=0.232). Interestingly a similar trend in direction was also observed for V0 and latency, although the effects of direction did not quite reach significance (see table 1).

2.8) Past History Effect

An analysis was performed to investigate the effect of the previous task (Go-Go, NoGo-Go and Rnd) on the V50 and latency of the succeeding task. A statistical analysis of the data revealed that the preceding task had no significant effect on V50 or latency on the succeeding task during predictive responses. As previous studies have found that target velocity from the previous trial influences V50 (Kowler, 1989; Poliakoff et al., 2005), we also performed a past history analysis on target velocity. We found no significant effect in mean V50 of the subsequent trial (N) if the preceding trial (N-1) had either the same target velocity or a different target velocity indicating no significant past history effect for either task or target velocity.

3) Discussion

In the introduction we isolated four aims of the present study; the discussion will focus on addressing the outcome of these specific aims:

3.1) Are the predictive responses to passively viewed or actively pursued stimuli equivalent?

We have found greater prediction to the 2nd presentation in the actively pursued task (Go-Go) when compared to the passively viewed task (NoGo-Go). This difference between the active and passive conditions was clearly demonstrated by significantly higher eye velocity at target onset (V0) and 50ms after target onset (V50) in the active condition when compared to the passive, although the difference was small (i.e.V0=8% and V50=15% lower). As V0 and V50 measure eye velocity prior to any visual feedback of the actual target motion this measure may be classified as predictive (see table 1) (Burke and Barnes, 2006). In addition, we found that this higher initial eye velocity in the 2nd presentation of the active condition was associated with a significantly earlier onset of the eye movement (i.e. a shorter latency) when compared to the passive condition. Moreover, eye acceleration 50ms after target onset (A50) was also significantly higher in the active task. Given that anticipatory smooth pursuit exhibits fairly constant acceleration (Kao and Morrow, 1994), it is not surprising that earlier onset of the eye movement and higher eye acceleration should lead to higher V0 and V50 values in active conditions. This can be attributed to both an earlier onset of the eye movement and higher eye acceleration. Thus, storage of velocity and timing information appears to be enhanced when we actively follow a target as compared to passively viewing it.

This difference between passive and active conditions could be attributable to a number of sources, including attention. It may be the case that during the passive observation of the stimuli the subject simply did not attend to the stimulus as well as in the active condition. Indeed Kerzel et al. (2008) recently found that attending to a stationary background during active smooth pursuit resulted in reduced pursuit gain. As we observed a reduction in the magnitude of the velocity (V50) during the NoGo-Go task, this could provide evidence that increased attention to the target during the active (Go-Go) condition provides a better representation of the stored velocity information in the predictive response. Another possible explanation for the difference in V50 may arise from knowledge of results, and hence the differences between retinal and extraretinal visual information. In the context of pursuit, knowledge of results occurs when a subject is able to gain feedback about the accuracy of their performance by comparing the motor response with the target motion. In the Go-Go task such a comparison obtained from the first presentation could be used to adjust the response to the second presentation. Clearly, knowledge of results is not available in the first presentation of the No-Go Go task, since no motor response is made and the subject must rely on the retinal information alone.

Another source of difference between the active and passive conditions is that active pursuit uses central vision whereas passive observation relies more on peripheral vision. It has previously been found that central/retinal vision is more important than peripheral/extraretinal vision in manual tracking movements (van Donkelaar et al., 1994; Lawrence et al., 2006). Van Donkelaar and colleges (1994) found that restricting the subject's vision to fixating a central target while performing a hand movement resulted in an increase in latency (~24ms) of the response when compared to subjects being able to view their hand movement. Dubois and Collewijn (1979) established that the fovea is more potent than the periphery in eliciting optokinetic pursuit. This was confirmed in a number of subsequent studies (Barnes and Hill, 1984; Wyatt and Pola, 1988; Lisberger and Pavelko, 1989) in which it was demonstrated that the gain of smooth eye velocity decreases with increasing stimulus eccentricity. The peripheral location of the moving target in the first presentation of the NoGo-Go task could thus lead to a reduction in stored motion information and a reduced initial eye velocity (V50) when compared to the foveal tracking of that target in the Go-Go task.

Motor skill learning involves dynamic neural changes in a range of areas including cortical, motor and sub-cortical areas (Karni et al., 1995; Ungerleider et al., 2002; Wise et al., 1998). Generally it is thought that the acquisition of a motor skill is dependent on the amount of practice of the skill. Maquet et al (2003) have shown that subjects learning a smooth pursuit task for 5 minutes show an increased functional connectivity between the superior temporal sulcus and cerebellum and also between the supplementary eye fields and frontal eye fields when scanned prior to learning and then 3 days later. This reveals plasticity of the smooth pursuit eye movement system during even short periods of motor learning. In a recent paper, Frey and Gerry (2006) have isolated this effect further by showing that the passive observation of others' actions activates a similar network of brain regions associated with the actual performance of the task. A further experiment revealed that this network was activated to a lesser degree in the passive condition (Frey and Gerry, 2006). These results are in line with the behavioural findings reported here in that passive observation does result in prediction, but to a lesser degree than active following.

Finally, it should be noted that another source of difference in these results may be the general level of attention required to perform each task. Differences in the level of V50 could indicate that attention to the target in the NoGo-Go condition was less than that of the Go-Go condition. However, we found that the performance of this task needed a high level of attention throughout, due to the randomization of the timing between the 1st and 2nd presentation. In addition, inattention in this task would result in the subject making errors and as this rate was very low (i.e. ~3%) we are confident that the general level of attention was evenly maintained.

3.2) Does the previous trial have any effect on the current response i.e is there any a past history effect?

We investigated the past-history effect in order to establish if the previous task or target velocity had any effect on the current response and to establish if, for example, performing a Go-Go task prior to a Go-Go task would positively affect V50 or latency. We averaged V50 and latency of the previous task (N-1) and compared this to the current task (N) and found no effect in either V50 or latency. These findings are in accordance with the findings of Kowler (1989) in that they show that cognitive cues appear to override the motor habit generated by previous trials. This paper adds to this finding as we only provided cognitive information about the type of response required, and did not reveal any information about the velocity of the upcoming target. The information about the target was solely obtained from the 1st presentation of the stimulus and not a cognitive cue.

3.3) Is the short-term storage of visual motion equivalent in both the vertical and horizontal directions of motion during passive and active viewing?

We found a significant difference between the directions of motion in the second presentation of the stimulus in all conditions (Go-Go and NoGo-Go) at V50. There is a distinct pattern of asymmetry with the downwards direction revealing the lowest V50 value, followed by the leftward eye movement, then the upward and finally the rightward. No significant difference for direction was observed in the latency or V0 but a similar pattern of responses can be observed. A previous study has shown that asymmetries exist in different directions of motion with vertical smooth eye movements showing a detriment in prediction when compared to horizontal motion in a sequence learning task (Burke and Barnes, 2007). This previous study used repeated presentations of a four ramp sequence and not a single presentation (as in this study) and thus this provides further evidence of directional biases within subjects in both predictable and random presentations. As the directional asymmetries appear more potent for V50 than V0 and also slight trends in latency can be observed, this may suggest that the asymmetry is derived from the unequal storage of both velocity and timing information for different planes of motion. Further investigations into these asymmetries are required to resolve this issue.

3.4) Do different delay periods between the first and second presentation of the stimulus affect the ability to predict?

We found that the 4 second delay resulted in a significantly higher initial eye velocity (V50) than the 2 and 6 second delay (see table 1). In addition, there was a trend for the eye to be initiated earlier in the 4 second delay condition, although this did not reach significance (see table 1). We found no such trend in the initial eye acceleration (A50). This finding is interesting as it suggests that the effects of a delay on predictive smooth pursuit may be more complex than originally thought. The results indicate that the stored velocity/timing information for generating prediction is optimal at around 4 seconds after the previous target has been exposed. This improvement may relate to increased expectation of the targets imminent arrival as time passes; however, the decrease observed in the 6 second delay contradicts this idea. A previous study has shown that delays of more than 7.2 seconds can result in a similar small reduction in V100 (velocity 100ms after target onset) possibly indicating a slow decay in the memory storage itself (Chakraborti et al, 2002). Taken together the results suggest that the stored information during prediction is non-linear and reaches a peak before the velocity store slowly degrades.

3.5) Can predictive responses be elicited after only one presentation of a stimulus by using a coloured visual cue?

The results of this study clearly show that by using colour-coded cues in predictive tasks, active following or passive observation of a moving target produces prediction of the subsequent target. Subjects are not only able to anticipate the onset and direction of the target motion but they are also able to scale their eye velocity to the target velocity. This study has shown that we can store visual motion information from passive stimulation in parafoveal vision to drive smooth pursuit, as shown previously by Barnes et al (1997) and Poliakoff et al (2005). In addition, we have shown that subjects are able to use the coloured visual cues in order to determine their response, and are

able to generate predictive responses even when the stimulus is only presented once. These findings add to the current literature on anticipatory smooth pursuit by suggesting that in addition to “building-up” an internal memory store (Wells and Barnes, 1998; Chakraborti et al., 2002) this store can be enabled after only one presentation and sustained for <6 seconds, providing the subject is cued that the subsequent target will be the same as the previous target. Chakraborti et al (2002) found the velocity store required around 3 presentations to be maximally charged, but in agreement with this study prediction was initiated on the second presentation when subjects were given predictable blocks of the same stimulus. This is not the first demonstration that cues can be used to initiate anticipatory movements. In a previous experiment by Kowler (1989) a voice or barrier cue signaling the direction of motion was sufficient to drive anticipatory smooth pursuit. Jarrett and Barnes (2002) extended this observation by showing that symbolic cues giving information about target velocity could also be used to scale the velocity of anticipatory pursuit. The cue used in the experiment presented here differs from previous cued response experiments in that the cue itself did not give information about the speed, direction or timing of the target, but about the type of response that was required.
One possible difference between the predictive responses generated after only one presentation compared to several may be the variability of the response. It is likely that multiple following of a stimulus generates a more stable and less variable motor plan via learning generated by a positive reinforcement system (Madelain and Krauzlis, 2003). This idea has recently been supported by fMRI studies that show visual motor learning is associated with decreased prefrontal-caudate activation and increasing cerebellar and basal ganglia activity (Floyer-Lea and Matthews, 2004).

3.6) Summary

This study found clear anticipation to a visual target from only one presentation of the stimulus, which was optimized after a 4 second delay. This provides evidence that decay of velocity storage information over time is non-linear. We also found that participants revealed a higher V50 and A50, and shorter latency to the 2nd presentation of the Go-Go condition when compared to the NoGo-Go condition. These findings suggest that the active condition utilizes additional velocity and timing information giving it a predictive advantage. Previous studies show a neural benefit to active motor rehearsal with an overall higher level of activation during active responses compared with passive (Frey and Gerry, 2006). In addition it seems that active following in hand tracking responses give a behavioural latency advantage over passive tracking. These behavioural findings form the basis of a subsequent fMRI study which will explore the neural differences between active and passive following of a smooth pursuit target.

4) Experimental Procedure

4.1) Participants

Nine participants (5 Females, 4 Males) took part in the experiment with a mean age of 31.5 years (range = 22-44 years). After the attainment of local ethics committee approval, full informed consent was obtained from each participant. All experimental testing was performed in accordance with the Declaration of Helsinki established in 1991. All subjects reported no neurological or psychiatric disorders, were right-handed with normal
or corrected to normal vision and were not colour blind.

4.2) Apparatus

Subjects were seated in a darkened room 1.5m from a flat, back-projection screen. Head immobilization was achieved with foam-lined ear clamps and a chin rest. Eye movements were recorded using a video-based eye tracking system (Chronos, Skalar Medical, BV) sampling at 200Hz with a spatial resolution of <0.1?. The targets were projected onto the screen using COGENT software (http://www.vislab.ucl.ac.uk/Cogent/index.html) running under MATLAB (Mathworks Inc., MA, USA). Custom-made MATLAB routines were used to generate the timing of the stimulus.

4.3) Procedure

Each subject was given the same instructions, which included a verbal description, a diagram illustrating the coloured cues and verbal instructions on how to perform the task prior to performing the set of tasks listed below. Subjects performed 3 blocks in a single experimental session consisting of 48 pairs of presentations (i.e. 144 pairs in total for each of the 9 subjects), taking around 40 minutes. Each pair within each block was pseudo-randomly chosen from the three conditions outlined below (Go-Go, NoGo-Go and Rnd tasks) with equal probability, and the velocity of the target was also pseudo-randomized between pairs for all 3 conditions. Overall, this resulted in a balanced design with equal repetitions of each task. Each pair of presentations was given in either a predictable or randomized manner, in which either the first and second presentations were matched in time and velocity, or the two presentations had randomized time and velocity. The fixation cue was a white square that subtended ~1 dva on the eye and changed colour in order to indicate which of the conditions (detailed below) the subjects would subsequently perform (see figure 1). The target diameter again subtended ~1 dva on the eye and was a coloured disk that moved up, down, left or right at either 15 or 30 degrees per second. All experiments took place in a dark room devoid of any external light source.

The subjects performed 3 experimental paradigms during the experimental session; two predictable paradigms (Go-Go and NoGo-Go), and one non-predictable (Rnd). The predictable paradigms presented the same smoothly moving target twice with each presentation separated by a random delay period (2, 4 and 6s), whereas the non-predictable condition presented two different targets separated by a random delay. The target could move in one of 4 directions (up, down left and right), at one of 2 velocities (15 and 30?/s) resulting in 72 individual conditions. As each condition was performed twice, this resulted in two *attempts* by each subject and thus totaled 144 conditions for each subject.

4.4) Analysis

The eye movement data were analyzed offline by capturing the pupil and subjecting the horizontal and vertical eye displacements to a range of pre-processing steps. These steps included: low-pass filtering with a zero-phase digital filter at 30Hz, blinks were identified by the Chronos software and removed, and the removal of fast-phase intrusions was achieved by using an acceleration threshold of 1000?/s^2 and bridging the gap with a linear interpolation. Velocity was calculated using a 2-point central difference of the displacement, and acceleration a two-point difference of velocity. Velocity and acceleration 50ms after the target onset (V50 and A50 respectively) and velocity at target onset (V0) were calculated by taking a mean of 3 data points before and after each point for both vertical and horizontal results. Any trials in which a saccade was detected during the period of V0 or V50 measurement were omitted from further analysis. This procedure ensured intrusive saccades would not affect our findings.

It was important for this experiment to isolate trials in which subjects incorrectly followed the first target during the NoGo condition. This was done automatically by selecting trials where eye velocity was > 3?/s in the 1st presentation during the NoGo-Go trials and plotting the data to ensure the subjects had made an incorrect response by following the target. This data was removed and the numbers of errors was then summated for each subject. Latency was calculated using a procedure described previously (Burke and Barnes, 2007), which involved identifying the time at which 20% of peak target velocity was attained and performing a linear regression from this point back to the ordinate axis. Visual inspection of the data at this point ensured the algorithm identified the correct eye movement onset time. The time at which the eye velocity crossed the abscissa (i.e. y=0) was then subtracted from the time at which the target became visible (target onset) to obtain latency. All data were tested for normality using the Shapiro-Wilk statistic, and significant differences were assessed using a repeated-measures analysis of variance (ANOVA) in SPSS. Due to the clear differences in V50 and latency between reactive and predictive conditions these conditions were separated into two ANOVA's performed on: 1) ***reactive*** responses only which included both 1st and 2nd presentations of the Rnd trial, and the 1st presentation of the Go-Go and NoGo-Go trials, and 2) ***predictive*** responses which used responses to the 2nd presentation of the stimulus in both the Go-Go and NoGo-Go trials. Finally, in order to investigate the past history effects of the trial type (Go-Go, NoGo-Go and Rnd) we calculated mean V50 responses for each subject for the current trial (N) and compared this to V50 in the previous trial (N-1) using a T-test. Likewise this process was also used to investigate the effect on V50 of the previous target velocity (15°/s and 30°/s), when the current target velocity was either the same or different. This past history analysis has been described previously in detail by Kowler (1989).

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Task	Condition		V0(°/s) Mean (± SE)	V50 (°/s) Mean (± SE)	A50 (°/s^2) Mean (± SE)	Latency (ms) Mean (± SE)
Go-Go	Target Velocity	15	2.82 (0.08)	3.59 (0.26)	156 (49)	-254 (16)
		30	3.07 (0.10)	4.89 (0.35)	163 (46)	-261 (18)
	Direction	Down	2.07 (0.13)	3.26 (0.32)		-240 (21)
		Left	2.13 (0.12)	4.05 (0.39)		-246 (23)
		Up	2.67 (0.16)	4.65 (0.45)		-254 (19)
		Right	2.47 (0.15)	5.01 (0.35)		-291 (21)
	Delay	2	2.40 (0.11)	4.13 (0.29)		-266 (15)
		4	2.49 (0.05)	4.48 (0.28)		-272 (14)
		6	2.36 (0.12)	4.13 (0.25)		-234 (16)
NoGo-Go	Target Velocity	15	2.20 (0.06)	3.09 (0.27)	108 (45)	-219 (13)
		30	2.38 (0.10)	4.39 (0.36)	120 (50)	-223 (13)
	Direction	Down	2.06 (0.14)	2.87 (0.31)		-189 (13)
		Left	2.10 (0.14)	3.66 (0.14)		-239 (17)
		Up	2.63 (0.14)	4.05 (0.47)		-229 (18)
		Right	2.35 (0.11)	4.47 (0.43)		-220 (17)
	Delay	2	2.29 (0.07)	3.46 (0.27)		-203 (10)
		4	2.44 (0.08)	4.26 (0.30)		-233 (13)
		6	2.41 (0.10)	3.50 (0.26)		-226 (11)
Rnd	Rnd (1)			-0.15 (0.12)		93 (8)
	Rnd (2)			-0.14 (0.17)		94 (6)
	Go-Go (1)			-0.13 (0.13)		81 (5)

Table 1: The above table reveals the means and standard errors from the mean (in brackets) for eye velocity at target onset (V0), 50ms after target onset (V50, Eye acceleration 50ms after target onset (A50) and latency for each of the different experimental conditions.

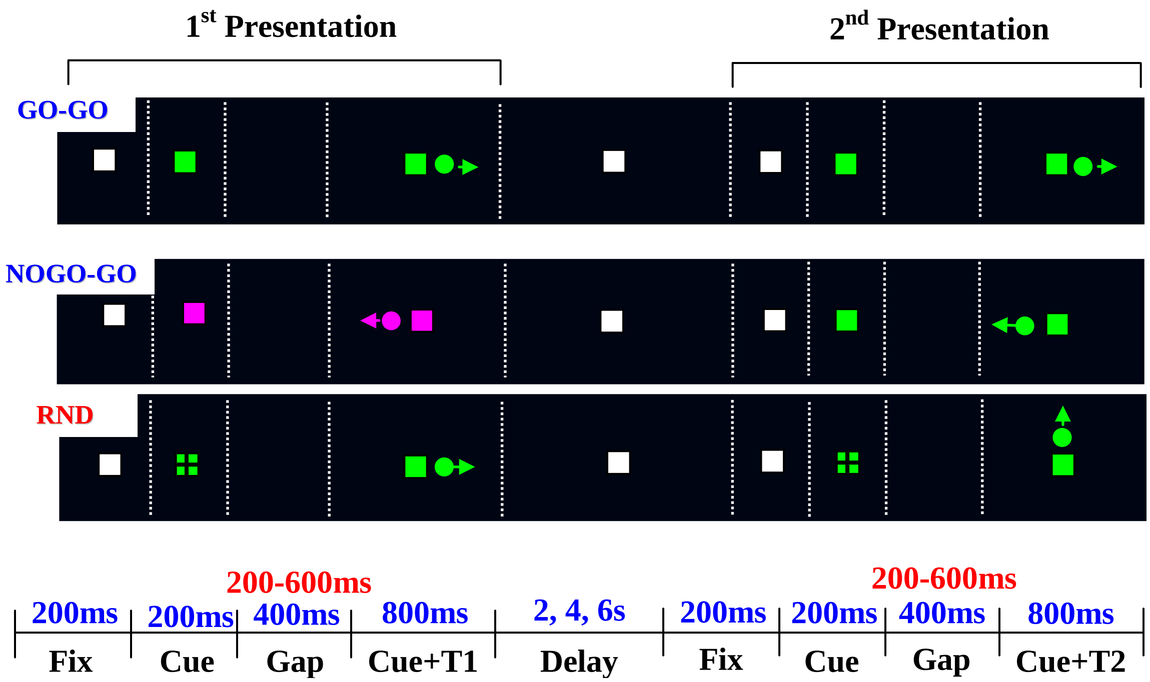

Figure 1: A timeline diagram of the 3 tasks: (i) the top diagram shows the Go-Go condition in which the subject follows the 1st and 2nd presentation of the target and both targets are the same, (ii) the middle diagram shows NoGo-Go task in which the subject must maintain fixation during the 1st presentation of the stimulus and follow the repeated target on the 2nd presentation of the stimulus, and (iii) the bottom diagram shows the Rnd task in which the subject follows the 1st and 2nd presentation of the stimulus and cue indicates that the targets in each presentation are not the same. The timings for the predictive tasks (Go-Go and NoGo-Go) are shown in blue and the random task (Rnd) is shown in red. The colored arrows indicate the direction of motion of the target.

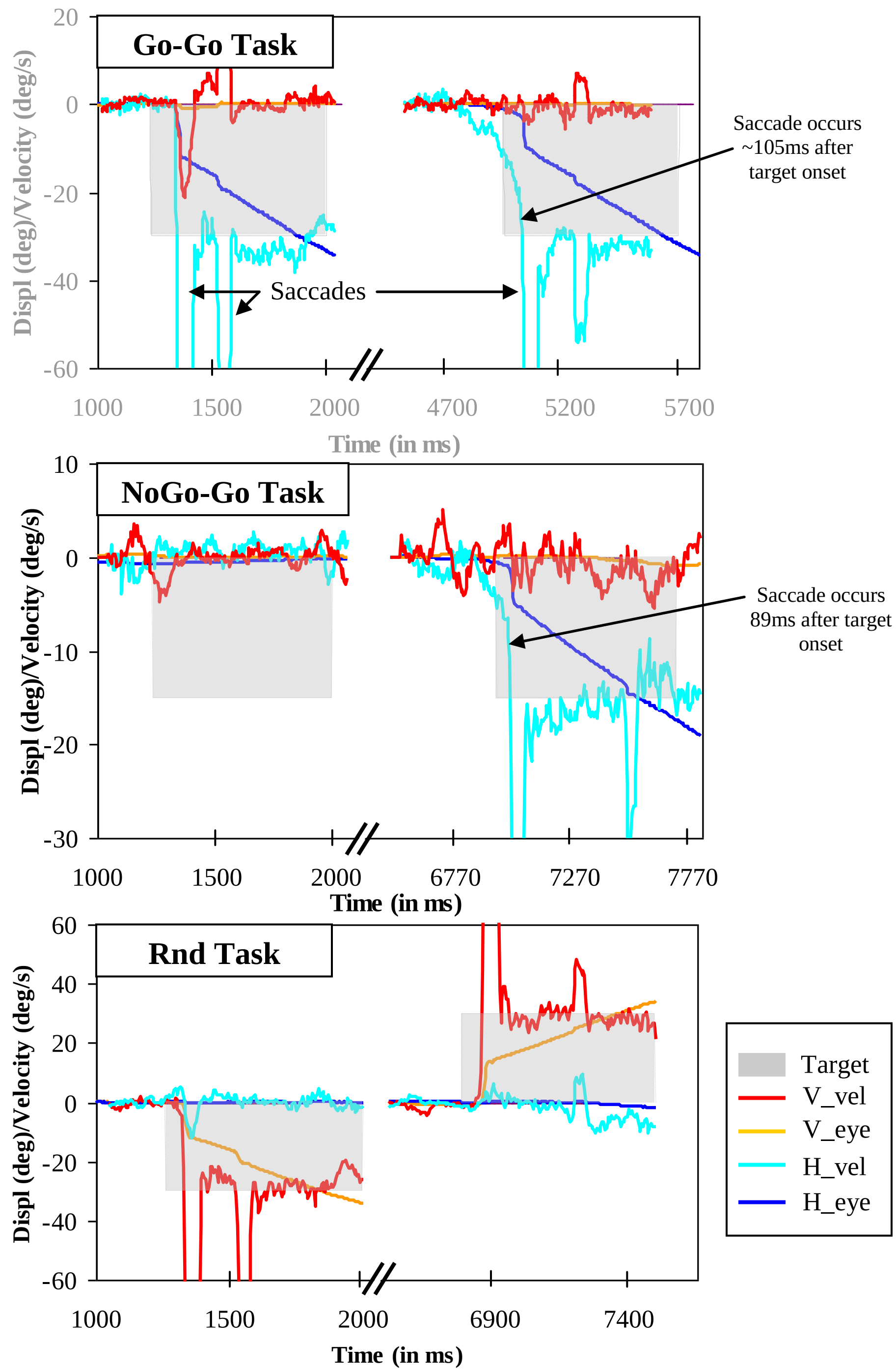

Figure 2: Examples of the horizontal and vertical eye movements made to each of the three tasks (Go-Go, NoGo-Go and Rnd) used in the experimental protocol. The blue line is horizontal eye displacement and the cyan line horizontal eye velocity, the red line is vertical eye displacement and the pink line vertical eye velocity. The grey bar indicates the time at which the target was visible. Eye displacement is presented on the left ordinate axis and eye velocity on the right ordinate axis with time (in ms) presented on the abscissa.