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ANTICIPATORY SMOOOTH EYE MOVEMENTS ELICITED BY CUES

By

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## **ABSTRACT OF THE DISSERTATION**

### **Anticipatory smooth eye movements elicited by cues**

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Anticipatory eye movements are important when tracking the motion of a target because they help overcome inevitable sensorimotor delays. Understanding the processes that govern anticipatory eye movements can reveal how motion signals of a target and anticipatory signals are combined to produce a response that facilitates the tracking of moving objects. In order to determine whether the perceptual qualities of cues affect anticipatory eye movements, different types of cues were compared. Subjects pursued a disc that moved inside an inverted Y-shaped tube. Three cues were tested: (1) Natural: barrier that blocked the untraveled path; (2) Arbitrary/local: bar at the top of the tube indicated the path by being on the same side. (3) Arbitrary/global: color of the tube (red or green) indicated the path. (4) Symbolic cue: arrow pointing to the future direction of motion of the disc. Three experiments tested the sensitivities of the oculomotor system to cue properties, namely, effectiveness in overwriting past history of target motion, cue delay, cue removal, and cue validity. The barrier cue produced faster anticipatory eye movements than the arbitrary cues, and overwrite the effects of past history of target motion (Experiment 1). Delaying the presentation of the cue until the disc approached

the choice point decreased anticipatory eye velocity for all cues (Experiment 2). Removing the cues after the onset of target motion (so that only memory of the cue was available) had no effects with arbitrary cues, but reduced anticipatory pursuit substantially for the barrier cue. When the validity of the barrier cue was reduced so that the moving disc crashed through the barrier, the cue became ineffective (Experiment 3). The results of all three experiments indicate that the perceptual qualities of cues are important for anticipatory eye movements, even when the directional information conveyed is the same. This suggests different mechanisms are involved. One mechanism may depend on arbitrary associations that can be learned. Another mechanism evoked by naturalistic cues, such as the barrier, may be responsible for producing higher anticipatory eye velocities.

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I thank God for everything He has given me.

**Dedication**

I dedicate this dissertation to my family. I dedicate this dissertation to my mother and my father for being amazing parents and for everything they have done and continue to do for me. I dedicate this dissertation to my sister. Thank you for being so supportive and caring. I also dedicate this dissertation to my brother. Thank you for the time we spend together and the bond we share.

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## 1. General Introduction

Smooth pursuit eye movements are the relatively slow movements of the eyes that are used to track moving objects. Smooth pursuit can be considered to be under the control of the sensory motion signals from the stimulus since few people can initiate smooth pursuit in the absence of a moving target (Kowler, 2011). However, under predictable conditions, anticipatory smooth eye movements can be elicited in the direction of expected target motion before the onset of target motion (Kowler & Steinman, 1981; Kao & Morrow, 1994), before it changes trajectory (Kowler et al., 2014; Aitkin et al., 2013; Santos et al., 2012), or while it is momentarily occluded (Bennett et al., 2010). In addition to being found with predictable target motion, anticipatory eye movements can also be found in situations in which the direction of motion of a target is random (Kowler et al., 1984), or when its onset of motion is random (Badler & Heinen, 2006). Thus, anticipatory eye movements seem to be an integral part of smooth pursuit since they are not restricted to conditions in which the target moves predictably (Kowler & Steinman, 1981). Figure 1 shows an example of anticipatory eye movements (see red arrows). Anticipatory smooth eye movements are interesting because they are a clear example of how top-down processes influence behavior. But why are they important and how are they useful?

### *1.1. Why are anticipatory smooth eye movements important?*

Anticipatory smooth eye movements are important when tracking the motion of a target because they help overcome the inevitable sensorimotor delays estimated to be about 100 ms (Carl & Gellman, 1987). The significance of these delays becomes evident when the pursuit of a target whose trajectory is highly random is compared to the pursuit

of a predictable target. The pursuit of a target moving in a random trajectory is much poorer than the pursuit of a target moving in a predictable trajectory (Collewijn & Tamminga, 1984). Understanding the processes that govern anticipatory eye movements can reveal how motion signals of a target and anticipatory signals are combined to produce a response that facilitates the tracking of moving objects. Furthermore, this knowledge can shed light on how the motor system plans complex motor behaviors. Putting together a sequence of single movements requires the motor system to know what motor command needs to be executed next before it finishes executing a given motor command. Preparing for the execution of a future motor command allows the motor system to produce a sequence of movements that smoothly flow together to complete a task (Lu & Ashe, 2005).

In this Introduction I will first briefly describe how the initiation of smooth pursuit eye movements has been studied with repetitive target motion and symbolic cues. I will then focus on how cues can influence eye movements, and discuss some relevant behavioral and neurophysiological results. Finally, I will describe a set of experiments that aim to determine whether knowledge about the future direction of motion is the only factor that is important to trigger anticipatory pursuit or whether the physical properties of cues affect the magnitude of anticipatory eye velocity. Answering these questions can help to better understand how cues are processed and how they lead to the generation of anticipatory eye movements.

### *1.2. Anticipatory smooth eye movements: learning through repetitive target motions*

Anticipatory smooth eye movements were first observed in the presence of targets moving in a periodic motion. Westheimer (1954) examined eye movements in response

to different types of moving targets. When he compared the eye movements of a target that moved in sinusoidal pattern to the eye movements in response to a target that moved randomly, he found that the first trial of the sinusoidal motion was very similar to the random motion; the eye lagged behind the stimulus when there was a change in the direction of motion. However, after the observer viewed the target moving in a sinusoidal motion a few times, he noticed that eye began to change direction at the same time, or before, the target changed its direction of motion. Therefore, it was assumed that the learning that occurred after repeatedly pursuing the target moving in a sinusoidal target was producing the anticipatory pursuit. Other studies (i.e., Dallos & Jones, 1963) came to a similar conclusion, namely, that anticipatory pursuit occurs after we learn the periodic motion of a target. This conclusion seemed reasonable because anticipatory eye movements had only been observed during the tracking of repetitive motion.

### *1.3. Anticipatory smooth eye movements: influence of prior history*

As smooth pursuit began to be studied more in depth, it was found that anticipatory eye movements do not occur only during repetitive or periodic motion. The past history of target motion can also produce anticipatory eye movements even with non-repetitive motions (Kowler & Steinman, 1979b; Kowler et al., 1984; Badler & Heinen 2006; Yang & Lisberger, 2010). One study (Kowler et al., 1984) showing the effect of past history on smooth pursuit used a point target that randomly moved rightward or leftward. Subject showed anticipatory pursuit in the expected direction of motion and it was found that anticipatory eye velocity was higher when the direction of target motion was the same as in the previous trials. These results showed that periodic motion is not the only way to elicit anticipatory pursuit. Even though learning can still be

involved, learning a particular motion pattern does not seem to be essential. Rather, expectations about future direction of motion may be enough to produce anticipatory eye movements. These results also indicated that previous motion seems to be stored in memory and influence the speed of anticipatory pursuit. In another study illustrating effects of past history, Heinen, Badler and Ting (2006) examined the effects of expectations of the time of target motion onset on anticipatory pursuit. The onset of target motion was either 500 ms or 1000 ms after the target appeared on screen. Immediately after the pre-onset fixation period, the target would always move rightward at a constant velocity. Heinen et al. (2006) found that the onset of anticipatory pursuit was biased by the time of target onset of the previous trial. If the fixation period was long (1000 ms) in the previous trial, onset of anticipatory pursuit tended to happen later. Onset of anticipatory pursuit occurred earlier when the fixation period was short (500 ms). Tabata et al. (2005) examined the effect of prior history on smooth pursuit in monkeys. Monkeys were trained to fixate on a cross and to either make a saccade to target if it did not move, or to track its motion if it moved. The probability of target motion was blocked for 50 trials. In the sessions when the probability of target motion was 0, the monkey always made a saccade to the target and when the probability was 1, they always pursued its motion. Tabata et al. (2005) found that the mean eye velocity of the initial pursuit response (from 70 ms after target motion onset to 150 ms) increased as the probability of target motion increased. The influence of prior history on eye velocity of monkeys agrees with what has been found in humans (Kowler et al., 1984).

Even though there are similarities between the smooth pursuit systems of humans and monkeys, it has been found that the effect of prior history may not always be the

same for both species. For example, Yang & Lisberger (2010) designed an experiment with two learning conditions and one random condition. In the first learning condition the direction of motion of a target indicated the direction of motion of a second target: the direction of motion of the second target was the same as the first target. In this condition both humans and monkeys produced anticipatory pursuit in the direction that the first target moved when pursuing the second target. In the random condition the direction of motion of the second target could not be learned since the motion of the first target was not related to the motion of the second target. In this condition humans and monkeys pursued the second target poorly since the motion of the second target was random. In the second learning condition the direction of motion of the second target was always opposite to the first target (i.e., if the first target moved upward, the second target would move downward). Humans were able to generate anticipatory pursuit in the correct direction of motion when pursuing the second target, while monkeys tended to generate anticipatory pursuit in the direction that the first target moved. This implies that not all the anticipatory smooth eye movement research done with humans can be generalized to monkeys.

#### *1.4. Importance of studying cues*

Another way to elicit anticipatory pursuit is to use symbolic cues that indicate the future direction of target motion. Cues are important for the following reasons. Our environment has components whose predictability ranges from random to completely deterministic. There are elements of these components that are systematically related. We can learn these associations and behave in a reasonable way because our environment is generally structured (Palmer, 1975). However, our environment can also be very

complex and can demand more cognitive resources than we have available. Cues in the environment can help us make sense of our surrounding. In complex environments cues can direct our attention to areas of interest where there is information to be acquired (Reeves & Sperling, 1986; Kowler et al., 1995; Zhao et al., 2012). The newly acquired information can be used to make a coherent decision that can help us to complete a task or goal. Nevertheless, there are times when the information we acquire is not enough to make a decision, and we do not have time to gather and extensively process more information. It is in this type of situation in which a decision has to be made within a time limit that cues become even more essential to our decision making. In many situations in which we need to make decisions in short amounts of time with limited information, waiting until enough evidence is gathered to make a well informed decision is usually not an option. Thus, we are forced to make predictions about future events with the limited information we have, which usually includes cues since they are readily available and are generally easy to interpret. These predictions are important because they can be used to initiate predictive or anticipatory movements. One clear example of this is anticipatory smooth eye movements. Thus, there are three main characteristics that make cues interesting to study: (1) Cues are an important source of information naturally found in our environment; (2) Cues facilitate the identification of objects and events in complex environments; (3) Cues can help us make predictions, which influence our motor system and the commands we execute. These motor actions ultimately determine whether we can complete our goals and even survive in our environment.

### *1.5. Anticipatory smooth eye movements: cues*

Cues can trigger anticipatory pursuit in the direction of expected motion (Kowler et al., 2014; Aitkin et al., 2013; Ross & Santos, 2014; Kowler, 1989; Santos et al., 2012; Kowler, 2011; Heinen & Keller, 2003; Lisberger 2010; Eggert, Ladda, & Straube, 2009; Jarrett & Barnes, 2005). Kowler (1989) showed that expectations produced by cues are different from the learning that occurs through repetition of target motion. The target was a disc which traveled down a vertical path that split into left and right oblique pathways. There were two cues that indicated the future direction of motion that the target would take. The first cue was a line that blocked the untraveled path. The second cue was an auditory cue: the words “right” or “left” were played on a computer speaker. There was an uncued condition as well. There were clear anticipatory eye movements when the cues disclosed the path the disc would travel. Subjects showed slower anticipatory eye velocity in the uncued condition and they tended to anticipate in the direction that the disc traveled in the previous trials. However, further analysis demonstrated that the cues were able to override the sequential order effects of previous trials (i.e., the tendency for anticipatory pursuit to be in the same direction as the previous trial). These results showed that cognitive expectations play a more important role than past history. Cues seem to play a more important role than prior history because they can update or overwrite the tendency to generate anticipatory pursuit in the same direction as the previous trial (Kowler, 1989). These findings were confirmed by Jarrett & Barnes (2002) who used symbolic cues to indicate the direction of motion (left or right) with less- and more-than symbols or the speed of target motion with numerals. They found that eye velocity measured 100 ms after target motion onset was proportional to the cued velocity. This effect was observed regardless of whether the velocity and direction were



randomized or blocked, confirming that cues can overwrite the effect of prior history.

These findings showing the effects of cues on smooth pursuit show that it is possible to learn the associations between cues and target motion, and that this information can be used to modify behavior.

#### *1.6. Characteristics that make cues effective eliciting anticipatory pursuit*

Even though cues and anticipatory eye movements have been well researched for many years, there are still questions that have not been answered. Behavioral and neurophysiological studies have not been able to understand the mechanisms that process cues and in turn elicit anticipatory eye movements. There are neurophysiological results suggesting that different brain areas, such as the Middle Temporal area (MT) (Schlack & Albright, 2007) or the Supplementary Eye Field (SEF) (Heinen, 1995; de Hemptinne et al., 2008), might be responsible for eliciting anticipatory pursuit. This suggests that the mechanisms that process cues may be more complicated than previously thought, or that there are various mechanisms involved in the process. These neurophysiological results might be able to explain behavioral results (Kowler et al., 2014) showing that the anticipatory eye movements elicited by an arbitrary cue is considerably slower than the anticipatory eye movements elicited by a natural cue, such as a barrier that blocks an untraveled path (similar results were found by Eggert et al., 2009). Other studies (Santos et al., 2012) reported that a visual cue was more effective than an auditory cue producing anticipatory pursuit. The results of prior studies suggest that the interaction between a visual display and a cue might determine the effectiveness of a cue in eliciting anticipatory eye movements. Therefore, it is possible that different cues are processed by different mechanisms.

The present study aimed to determine what characteristics make different cues effective. In order to address this issues, different types of cues providing the same directional information, but with different perceptual qualities, were compared. The term “perceptual qualities” refers to the knowledge of how objects behave in the real-world. This particular knowledge is invoked by the physical properties of cues and the visual displays in which they are embedded. Most prior studies of anticipatory pursuit are concerned with whether there is an expectation about future direction of motion, regardless of how this information was delivered. In the present study, I investigated how the effectiveness of cues with different perceptual qualities depends on cue properties, namely, cue delay, cue duration, and cue validity. Such a comparison can shed light on mechanisms responsible for initiating anticipatory pursuit, and whether there is more than one way in which cues are processed.

Different types of cues indicated the future direction of target motion as follows:

(1) Natural cue: A barrier that blocked the untraveled path. (2) Local arbitrary cue: Bar; filled or empty. Two kinds of bar cues were tested: deterministic, in which a filled red bar was always on the same side that the disc would travel, and probabilistic, in which the proportion filled corresponded to the probability of motion in a given direction of motion. (3) Global arbitrary cue; Color: red or green. A red tube indicated that the disc would move through the right-hand side path, while a green tube indicated that the disc would move through the left-hand side path. (4) Local symbolic cue: An arrow indicated the direction of motion by pointing to the path that the target would travel. These cues were used at least once across the three experiments described below.

## **2. Experiment 1: Effects of past history**

Experiment 1 investigated whether past history affects different types of cues similarly. A previous study (Kowler, 1989) showed that a natural cue, such as the barrier, can override most of the effects of past history on anticipatory eye movements, but not completely. Sequential effects were present: if the previous trial was rightward and the barrier cued rightward motion, the anticipatory velocity was slightly higher than when the previous trial was leftward and the barrier cued rightward. Will arbitrary cues, such as the bar, be as effective as the barrier cue in overriding the effects of past history on anticipatory pursuit? If past history affects both types of cues equally, then this can imply that past history is rooted in the system in a way that is not affected by the perceptual qualities of cues. On the other hand, if one cue is more effective than other at overriding sequential effects, then this would mean that there is an interaction between the directional information cues provide and their perceptual qualities. Perceptual qualities might be one of the factors that determine how easily the directional information of a cue can overwrite the effects of past history.

## **2.1. Methods: Experiment 1**

### *2.1.1. Subjects*

Four naïve subjects with normal vision participated in this experiment. They did not have prior experience with smooth pursuit studies and were naïve to the purpose of the experiment. Written informed consent was obtained from the participants before the experiment. The research protocol was approved by the Rutgers University IRB and is in accordance with the Declaration of Helsinki.

### *2.1.2. Stimuli*

The stimulus was displayed on a Viewsonic G90fb 19-in CRT monitor with a 60 Hz refresh rate, a resolution of  $1024 \times 768$  pixels, and located at a viewing distance of 118 cm. The paradigm used throughout this study included a line drawing of an inverted Y-shaped tube whose oblique paths were at a  $40^\circ$  from vertical and a disc with a 58.4 minarc diameter that was initially at the top, moved down at 263 min arc/s and then through one of the two paths at 170 min arc/s in the horizontal direction (Figure 2). This paradigm has been used previously to study anticipatory eye movements (Aitkin et. al, 2013; Kowler, 1989).

### *2.1.3. Procedure*

A black screen with a fixation cross at the top of the display appeared. Subjects started the trial by means of a button press when ready. After the button press, the fixation cross remained and the outline of the inverted Y-shaped tube appeared. Subject fixated on the cross about 10 ms. The cross was immediately replaced by a white disc, which stayed stationary for 1 s. After being stationary for 1 s, the disc began to move down immediately and into one of the two oblique paths. Instructions were to pay attention to the motion of the disc and not to try to use saccades to correct for errors if eye felt to be lagging behind.

### *2.1.4. Experimental conditions*

There were four conditions in this experiment. (1) Uncued condition. There was no cue indicating the direction of motion of the disc (Figure 2a). To study the effects of past history, the probability of rightward motion was blocked in sessions of 40 trials. The probabilities of rightward motion tested were 0, 0.25, 0.50, 0.75, and 1.0. Probability were announced at the beginning of each session. (2) Barrier cue, a line that blocked the

untraveled path was used to indicate the future direction of the disc (Figure 2b). Thus, subjects always knew which path the disc would travel. The probability of rightward motion was blocked in sessions of 40 trials for this condition. (3) Deterministic bars. A filled red bar was on the same side that the disc would travel. An outline of a red bar was on the side of the untraveled path (Figure 2c). The probability of rightward motion was also blocked for this condition. The cue always disclosed the direction of motion. (4) Probabilistic bars. In this condition subjects did not always know the upcoming direction of motion. Instead, the probability of rightward motion was randomly selected to be 0, 0.25, 0.50, 0.75, or 1.0 in a given trial. The proportion of filled red bar indicated the probability of rightward motion (Figure 2d).

Each experimental session was 40 trials long and each trial lasted 3.7 s. Subjects were tested in 19-25 sessions of the uncued condition and the cued conditions with different types of cues. The only exception to this was subject MP who was only able to run 7 sessions with the deterministic bar cue. The sessions tested with the barrier, with the probabilistic bar cue, and the uncued condition were randomly interleaved. The sessions with the deterministic bar cue were tested after the other three conditions were tested.

#### *2.1.5. Eye movement recording*

Horizontal and vertical movements of the right eye were recorded by a tower-mounted Eyelink 1000 (SR Research, Osgoode, Canada) with a sampling rate of 1000 Hz. Head was stabilized by a chin and foreheadrest. Viewing was binocular.

#### *2.1.6. Data analysis*

The onsets and offsets of saccades were determined offline by computing eye velocity during 13-ms samples, with onsets separated by 2 ms. Saccade onsets and offsets were detected using a velocity criterion that was determined and subsequently confirmed for each subject by examining a large sample of analog recordings of eye positions. Samples containing saccades or portions of saccades were removed.

## **2.2. Results: Experiment 1**

This experiment included three types of cues: barrier, deterministic bar, and probabilistic bar. The perceptual qualities of the barrier cue were different from deterministic bars, nevertheless, they both provided the same directional information. The deterministic bars were perceptually similar to the probabilistic bars, but they provided different type of information when the probability of rightward motion was 0.25, 0.50 or 0.75. In these conditions, the probabilistic bars indicated the most likely direction of motion. Finding differences and similarities between these cues will allow to determine whether directional information is more important than perceptual qualities when a cue is overwriting the effects of past history.

Figure 3 shows mean horizontal eye velocity over time averaged across all four subjects (mean of subject means) for the four conditions of Experiment 1. Time 0 on the x-axes represents the time the disc changed direction of motion when it reached the Y-junction. Negative velocities denote leftward velocities. The effects of past history are seen in the uncued condition (Figure 3a) and the probabilistic bar cue (Figure 3c). The fastest anticipatory eye movements occurred when the probability of rightward motion was either 1 or 0, and decreased as the direction of motion became less predictable. The effects of past history are less clear for the barrier (Figure 3b) cue and the deterministic

bar cue (Figure 3d) since there is clear anticipatory eye movements for all the probabilities of rightward motion.

Figure 4 shows index of anticipatory eye movements plotted against probability of rightward motion for the four experimental conditions. The index of anticipatory eye movements is the slope of the best fit line to samples within a 100 ms window ( $\pm 50$  ms) centered around the time of onset of horizontal motion divided by target velocity. This ratio has been used before as an index of anticipatory smooth eye movements before (Kowler et al., 2014). Figure 4A shows the index of anticipatory eye movements as a function of probability of rightward motion when the cue indicated rightward motion, while Figure 4B the same information for when the cue indicated leftward motion. The uncued condition shows the influence of past history on smooth pursuit eye movements. Anticipatory eye movements were clearest when direction of motion is always rightward,  $p(r) = 1.0$ , or always leftward,  $p(r) = 0.0$ . The velocity of anticipatory eye movements decreased as the direction of target motion became more random. This is expected because there is no other source of information that the subjects can use to anticipate the future direction of motion. The pattern of results for the probabilistic bar cue was very similar to the uncued condition. On the other hand, the barrier cue showed smaller effects of past history. There were clear anticipatory eye movements even when rightward and leftward motions were intermixed (probability of rightward trial = 0.5). The results for the deterministic bar cue had a similar pattern but the effects were smaller and the anticipatory eye movements were slower.

A two-way ANOVA (condition  $\times$  probability of rightward motion) on the index of anticipatory eye movements showed that the anticipatory eye movements elicited in

the four different conditions were significantly different [ $F(3, 6821) = 428.07, p < 0.0001$ ]. There was also a main effect of the probability of rightward motion [ $F(3, 6821) = 47.52, p < 0.0001$ ]. Tukey-Kramer post-hoc tests ( $p < 0.05$ ) revealed that the anticipatory eye movements elicited by the probabilistic bar cue were not significantly different from the anticipatory eye movements elicited by the uncued condition. This indicates that the probabilistic bar cue was not more effective than past history. Figure 4 shows that when the probability of target rightward motion was 0 or 1, anticipatory eye movements in the uncued condition were faster than anticipatory eye movements produced by the probabilistic bar cue. Post-hoc tests showed that these differences were significant, implying that past history can more effectively elicit anticipatory eye movements than a cue that provides probabilistic information. Post-hoc tests also showed that the barrier and the deterministic bar cues elicited anticipatory eye movements that were significantly different from the eye movements elicited by the uncued condition. This suggests that these two cues can overwrite most of the effects of past history. However, the anticipatory eye movements elicited by the barrier were significantly faster than the ones elicited by the deterministic bar cue.

### **2.3. Discussion: Experiment 1**

The effect of past history on three cues were compared in this experiment. A condition with no cue was included as well. Two of the cues, namely, the barrier and the deterministic bars, were able to effectively overwrite the effects of past history. The probabilistic bars, on the other hand, were not able to produce anticipatory eye movements that were significantly different from those of the uncued condition. This cue differed from the deterministic bar, not so much as in its perceptual qualities, but in the



information it provided. The probabilistic bars informed the subjects about the most likely direction of motion, not the actual direction, when the probability of rightward motion was 0.25, 0.50, and 0.75. Thus, it is possible that when the probabilistic bars informed the subject that the probability rightward motion was 0.75, for example, and the target moved leftward, the probabilistic bars may have been perceived no more useful than past history. Thus, the subject's strategy may have been to allow past history and the probabilistic information of the cue to influence the pursuit system similarly. These results imply that information conveyed about probability by either probabilistic cue or past history was equivalent.

### **3. Experiment 2: Effects of cue delay and cue removal**

Experiment 2 explored the temporal properties of cues. Three types of cues were tested (Figure 5). Two cues can be considered to be local since they are in a specific region of the inverted Y-shaped tube. The third cue was a global cue. This global cue would be available whenever it is presented in the display. Subjects would not have to shift attention from the moving target to the cue location. Thus, any differences should be due to the perceptual qualities of the cues, and not its location in the display.

The *cue delay condition* aimed to compare the anticipatory eye movements of different types of cues when the presentation of the cue is delayed relative to the event that the cues predict. Increasing the delay until no clear anticipatory eye movements are present can provide an estimate of how much processing time each cue needs before it stops producing clear anticipatory eye movements. Temporal properties of cues can be a good indicator of whether various types of cues are processed differently.

In the *cue removal condition*, the cue was removed so that only the memory of the directional information was present. If directional information is the only important factor to elicit smooth pursuit and perceptual properties are not, then effects of removal in anticipatory eye movements should be the same for the different types of cues.

### **3.1. Methods: Experiment 2**

#### *3.1.1. Subjects*

Four subjects with normal vision participated in this experiment. One of the subjects (SS) participated in Experiment 1. The other three subjects did not have prior experience with pursuit eye movement experiments.

#### *3.1.2. Stimuli*

The visual display for Experiment 2 was the same as in Experiment 1.

#### *3.1.3. Procedure*

The procedure this experiment was the same as in Experiment 1, except that the cues were either delayed or removed.

#### *3.1.4. Experimental conditions*

(1) Delay condition: the cue was presented at various times (900, 500, 300, and 100 ms) before the disc changed its direction of motion at the Y-junction (see top of Figure 6). Once the cues appeared, they stayed on the display until the end of the trial. A follow up of this condition was also conducted. This condition tested the same types of cues but with a finer time scale: the cues were presented 300, 250, 200, 150, 100 ms before the disc changed direction of motion.

(2) Removal condition: cues appeared at the same time that the disc appeared.

Cues were removed 800, 600, 400, and 0 ms before the disc changed direction of motion (see bottom of Figure 6).

### *3.1.3. Experimental sessions*

Each experimental session was 20 trials long and each trial lasted 3.7 s. Subjects were tested in 74-91 sessions in the delay condition with the coarse time scale, 75-92 sessions in the removal condition with the coarse time scale; 106-226 sessions in the delay condition with the fine time scale; and 41-67 sessions in the removal condition with the fine time scale. The condition (delay or cue removal) as well as the type of cue (barrier, bar or color) remained the same in a given session. The time at which the cue was removed, or the time it was delayed, were chosen randomly on each trial. The design of the experiment was the following: 5 delays/removal times  $\times$  3 types of cues  $\times$  2 directions of motion. Experimental sessions were randomly interleaved.

## **3.2. Results: Experiment 2**

### *3.2.1. Delay condition: coarse scale*

To investigate whether perceptual qualities influenced how cues are processed, the time needed to produce significant anticipatory eye movements will be compared for the three types of cues. A comparison of anticipatory eye movements elicited by different types of cues at different times relative to a predictable future event (i.e., change in direction of motion of a target) can determine whether the system responds in the same way to these cues at given points in time.

Examples of anticipatory smooth eye movements elicited by the three different of types of cue delays are in Figure 7. Figure 7 plots mean horizontal eye velocity over time

for each of the four subjects. In general, the later the cue was presented, the slower the anticipatory eye velocity. Even though this was true for all of the cues, delaying the barrier cue seem to have had the largest effect, which might be due to the fact that the barrier produces faster anticipatory pursuit than the other cues.

Figure 8 shows the trends more clearly. This graph shows an index of anticipatory eye movements as a function of the time the cue was presented relative to the change in direction of motion. Since subjects showed individual differences in their magnitude of anticipatory eye movements, the effects of the type of cue and cue presentation times were analyzed separately for each subject. Cue type had a significant effect on the anticipatory movements of all the subjects (BF:  $[F(2,1788)=151.8, p<0.001]$ , JA:  $[F(2,1827)=52, p<0.001]$ , SS:  $[F(2,1485)=43.87, p<0.001]$ , SK:  $[F(2,1528)=94.5, p<0.001]$ ). Tukey-Kramer post-hoc ( $P<0.05$ ) tests revealed that these difference were mostly due to fast anticipatory eye velocities elicited by the barrier cue at most cue delays. However, JA and SS did show consistent significant difference in the anticipatory eye velocity elicited by bar and color cues, but only when cue delay was 500 ms. The value of the cue delay also affected anticipatory eye movements of all subjects ([BF =  $F(3,1788)=49.27, p<0.001]$ , JA:  $[F(3,1827)=59.41, p<0.001]$ , SS  $[F(3,1485)=33.38, p<0.001]$ , SK:  $[F(3,1528)=30.16, p<0.001]$ ,).

Figure 8 shows that anticipatory smooth eye movements were weak at a delay of 100 ms. This implies that these cues need more than 100 ms to be processed. Post-hoc tests showed that for the barrier cue, the anticipatory smooth eye movements for a cue delay of 300 ms were significantly greater than for a cue delay of 100 ms for all subjects, except for SS. For SS a cue delay of 500 ms was significantly different than a cue delay

of 100 ms. Although anticipatory eye movements decreased for shorter delays for color, and bar cues, the effects did not reach significance for subjects BF, SS and SK. For JA, bar and color cues elicited anticipatory smooth eye movements that were significantly greater for a cue delay of 500 than cue 100 ms for subject JA.

In summary, anticipatory eye velocity were close to a value of 0 for all the subjects and all the different types of cues at a delay of 100 ms. This implies that these cues need more than 100 ms to be processed. When the cue presentation time was 300 ms before the change in direction of motion, the anticipatory eye movements elicited by the barrier were different from the other cues for most subjects. Cue delays at a finer scale between 100-300 ms were tested in the next condition. This was done to get a more precise estimate of cue processing time.

### 3.2.2. *Delay condition: fine scale*

The cue processing time of the three cues were compared at a fine time scale between 100 to 300 ms before the disc changed direction of motion. Figure S1 shows mean eye velocity over time for the four subjects and for the three types of cues tested. Figure 9 shows the index of anticipatory eye movements as a function of the time the cues were presented.

All subjects showed differences in the anticipatory eye movements elicited by the three different types of cues ([BF:  $F(2,3725)=92.67$ ,  $p<0.001$ ], JA:  $[F(2,4)=15.68$ ,  $p<0.001$ ], SS:  $[F(2,2502)=23.55$ ,  $p<0.001$ ], SK:  $[F(2,4502)=14.67$ ,  $p<0.001$ ]). Tukey-Kramer post-hoc tests ( $P<0.05$ ) indicated that the difference emerged because the anticipatory eye movements elicited by the barrier were significantly different from the bar and the color cue.

Cue delay had a significant effect on anticipatory eye movements for all the subjects (BF:  $[F(4,3725)=28.91, p<0.001]$ , JA:  $[F(4,2103)=6.81, p<0.001]$ , SS:  $[F(4,2502)=14.23, p<0.001]$ , SK:  $[F(4,4502)=26.1, p<0.001]$ ). Post-hoc tests ( $P<0.05$ ) indicated that for the barrier cue, the anticipatory smooth eye movements for a cue delay of 250 ms were significantly greater than for a cue delay of 100 ms for subjects JA, SK, and SS. For BF anticipatory eye movements for a cue delay of 200 ms were significantly different than when cue delay was 100 ms. Cue delay did not significantly affect the anticipatory eye velocity for the color cue. For the bar cue, subjects SK and BF showed anticipatory eye movements that were different from cue delay of 100 ms when the bar was delayed 300 ms.

In summary, to produce large effects the barrier cue needed about 200 ms of processing time. Effects of the bar and color cues were overall smaller, but in general, it seems like there was a reduction in the anticipatory eye velocity if there is less than 500 ms of processing time. A processing times of 300 – 500 ms are relatively long relative to the about 150 ms latency for smooth pursuit and saccadic eye movements. This points to the involvement of relatively slow central processing.

### 3.2.3. *Removal condition: coarse scale*

To further investigate the importance of directional information vs. perceptual qualities of cues on anticipatory eye movements, cues were removed at different times with respect to the time the disc changed direction of motion. Removing the cue separated the perceptual qualities of the cues from the directional information of the cues since subjects were now required to store the directional information of the cues in memory.

Figure 10 show mean eye velocity over time for four subjects and the same three types of cues used in the delay condition, namely, the barrier, the bar, and the color cue. Anticipatory eye velocity elicited by the color and the barrier cues did not seem to be affected when the cue was removed. However, for most subjects, removing the barrier cue before the disc reaches the Y-junction reduced the velocity of anticipatory eye velocity. The anticipatory eye movements produced by the barrier cue were reduced to about that of the other two arbitrary cues when it was removed.

Figure 11 shows index of anticipatory eye movements against the time cues were removed relative to when the disc changed direction of motion.

There was a difference in the anticipatory eye movement elicited by the various cues ([BF:  $F(2,1768)=3.38$ ,  $p<0.034$ ], JA: [ $F(2,1827)=14.39$ ,  $p<0.001$ ], SS: [ $F(2,1484)=26.04$ ,  $p<0.001$ ], SK: [ $F(2,1548)=31.12$ ,  $p<0.001$ ]). A Tukey-Kramer post-hoc test ( $P<0.05$ ) indicated that the barrier cue led to faster anticipatory eye movements than the other types of cues.

Some of the subjects showed some cue removal effects ([BF:  $F(3,1768)=3.23$ ,  $p<0.022$ ], SK: [ $F(3,1548)=5.82$ ,  $p<0.006$ ]), while others (JA: [ $F(3,1827)=1.58$ ,  $p<0.192$ ], SS: [ $F(3,1484)=2.16$ ,  $p<0.0913$ ]) did not show significant effects of cue removal. Tukey-Kramer post-hoc tests ( $P<0.05$ ) showed that, for all the subjects and for all types of cues, the anticipatory eye movements elicited by the barrier cue at a cue removal of 0 ms was significantly different from all other cue removals, except for the barrier removals of 400 and 600 ms of subject SS.

In summary, the barrier cue stops eliciting faster anticipatory eye movements than the bar or the color cue when it is removed 400 ms or more before the disc changed direction of motion.

There are two possible reasons for the decrease in anticipatory eye movements when the barrier is removed: (1) Directional information was not stored properly in memory and was lost over time. This possibility is unlikely because Figure 11 did not show any consistent pattern of anticipatory eye velocity increasing as the cue was removed closer to the time the disc changed direction of motion between 800 and 400 ms. (2) The perceptual qualities that facilitated the interpretation or processing of the barrier cue were absent, and thus it became as difficult to process as the other two cues. However, it is possible that if the barrier is removed close to when the disc changes direction of motion, the magnitude of anticipatory eye velocity will increase due to recent memory traces being able to, partially, make up for the physical absence of the perceptual qualities of the cue. To answer this question, the barrier cue was removed at a fine time scale between 0 to 400 ms before the disc changed direction of motion.

#### *3.2.4. Removal condition: fine scale*

The barrier cue was removed at a fine time scale between 0 to 400 ms before the disc changed direction of motion. The other two cues were not tested since anticipatory eye movements were not affected by the removal of the color and the bar cue. Figure S2 shows mean eye velocity over time for four subjects. The effects of barrier removal at the fine scale are more noticeable in some subjects (BF, and JA) than others.

Figure 12 shows the effect of barrier removal more clearly. The anticipatory index elicited by the color and bar cue in the previous condition when the cue was



removed 400 and 100 ms before the disc changed direction of motion are superimposed in these graphs. Superimposing these lines illustrates the difference of anticipatory eye movements elicited by the different types of cues.

The time of cue removal affected the anticipatory eye movements of most subjects (BF:  $[F(4,1259)=11.3, p<0.001]$ , JA:  $[F(4,734)=7.9, p<0.001]$ , SK:  $[F(4,1335)=3.61, p<0.006]$ , except SS ( $[F(4,809)=1.96, p<0.098]$ ). Tukey-Kramer post-hoc tests ( $P<0.05$ ) showed that, for BF, JA, and SK, anticipatory eye movements of a cue removal of 0 was different from cue removals of 200, 300, and 400 ms. Cue removals of 100 ms were not different from a cue removals of 0 ms for any of the subjects.

In summary, removing the barrier cue of as little as 200 ms before onset of horizontal motion reduced anticipatory eye movements.

### **3.3. Discussion: Experiment 2**

Experiments 1 and 2 showed that the barrier cue elicited the fastest anticipatory eye movements. They were about half the velocity of the target by the time the disc changed direction of motion. These results agree with the results of previous studies (Kowler et al., 2014; Eggert, Ladda & Straube, 2009), which also found differences in the anticipatory pursuit of different cues. Finding differences in the magnitude of anticipatory pursuit elicited by different types of cues was unexpected because all the cues provided the same directional information with 100% validity. They differed only in the way they conveyed the directional information due to their perceptual qualities.

The results of the delay conditions showed that the time needed to produce significant anticipatory eye movements for the barrier cue may have been shorter than for the the bar or the color cue. The time needed to produce significant anticipatory eye

movements with the barrier cue was more than about 200 ms, while this time was about 300 ms or more for the bar and color cue. This suggests that the way the barrier conveys direction of motion facilitates the interpretation of the cue or information processing since this cue requires less time to produce substantial anticipatory pursuit. The velocity of anticipatory eye movements elicited by the bar and color cue seem were about the same. The fact that the effects with the barrier were larger so that the effects of delays were more apparent, limits the conclusions that can be drawn from these results. It is possible that the anticipatory eye movements elicited by the bar and color cue became insignificant sooner than the barrier's because the effects of the color and bar cues were smaller to begin with.

The findings in the removal condition indicated that anticipatory eye movements elicited when the cue was present at the time the direction of motion occurs were not different than when was removed 100 ms before. However, when it was removed 200 ms or earlier, the velocity of anticipatory eye movements was slower. The barrier seems to become less effective when it is not physically present shortly before the disc reaches the Y-junction. This suggests that the perceptual qualities of the barrier cue is one of the factors that makes it effective, and memory is not an adequate substitute.

#### **4. Experiment 3: Effects of cue validity**

Experiment 3 systematically compares the anticipatory responses of different types of cues when their validity varied. If the directional information is the only important factor eliciting anticipatory pursuit, then cues should elicit similar anticipatory pursuit. However, if the perceptual qualities of cues bias the directional information they provide, then directional information is not the only factor that matters to the smooth

pursuit system. In other words, if perceptual qualities are important, the effects of varying cue validity might depend on the particular perceptual qualities of a given cue.

#### **4.1. Methods: Experiment 3**

##### *4.1.1. Subjects*

Three new naïve subjects and one subject who ran in Experiment 2 (BF) with normal vision participated in this experiment. The three new subjects were not familiar with the visual display or any of the cues. Thus, they could not be biased toward a particular type of cue or level of cue validity for the simple reason that they had more experience with it in the laboratory.

##### *4.1.2. Stimuli*

The visual display for Experiment 2 was the same as in Experiment 1.

##### *4.1.3. Procedure*

The experimenter explained to subjects what a valid and invalid trials were for each type of cue. This experiment used the same display as Experiments 1 and 2. Before beginning each session the experimenter would announce the validity of the cue. Thus, subjects knew the validity of the cue before the start of each session.

For three of the subjects (BF, AU, and EH) cue validity levels were as follow: 0, 25, 50, 75, and 100%. These subjects were tested with the barrier and arrow cue. The disc would travel down the unblocked path in a valid trial, and pass through the barrier when invalid (top of Figure 13). The disc would travel through path that the arrow was pointing in a valid trial, while in an invalid trial it would go through the path that was not being marked by the arrow.

##### *4.1.4. Experimental sessions*

Each experimental session was 20 trials long and each trial lasted 3.7 s. Subjects were tested in 24-48 sessions with the arrow cue, and 26-56 sessions with the barrier cue. All subjects ran in blocks of four consecutive sessions with the same cue and validity before running another combination of cue and validity. The blocks of four consecutive sessions were randomly interleaved. The design of the experiment for these three subjects was the following: 5 validities  $\times$  2 types of cues  $\times$  2 directions of motion.

Subject JW ran validities at a fine scale. Validities were 0, 17, 33, 50, 67, 83, 100%. This subject was tested in 34 sessions with the arrow cue, 34 sessions with the barrier cue, and 35 sessions with the bar cue. The design of the experiment for this subject was the following: 7 validities  $\times$  3 types of cues  $\times$  2 directions of motion.

#### **4.2. Results: Experiment 3**

In order to investigate how perceptual qualities of cues can influence or bias the directional information provided by different types of cues, the effects of the cues should depend on its perceptual qualities. Perceptual qualities might bias the directional information they provide independently of how valid its directional information is.

Figure 14 shows mean eye velocity over time for the four subjects. These graphs show that there is an effect of validity in the velocity of anticipatory pursuit.

Figure 15 shows the effects more clearly. These graphs show the index of anticipatory eye movements as a function of cue validity for four subjects and two types of cues for BF, EH, and AU. For JW it shows the effects of three types of cues.

For subject BF the type of cue [ $F(1,2319)=60.52$ ,  $p<0.001$ ] and cue validity ( $F(4,2328)=42.43$ ,  $p<0.001$ ) had significant effects on anticipatory eye velocity. Post hoc tests showed that the 0% and 25% validity of the barrier cue were significantly different

from the arrow. The pattern of results were similar for AU (cue type:  $[F(1,3509)=51.96, p<0.001]$ , cue validity:  $[F(4,3518)=45.48, p<0.001]$ ) except that the arrow cue was less sensitive to cue validity.

For subject EH, cue type was not significant  $[F(1,3910)=1.18, p=0.2783]$  and validity was marginally significant  $[F(4,3910)=2.46, p=0.043]$ .

For JW the anticipatory eye velocity elicited by the three different types of cues were significantly different  $[F(2,5321)=46.97, p<0.001]$ . JW also showed a significant effect of cue validity  $[F(6,5321)=29.73, p<0.001]$ . For subject JW, anticipatory eye movements elicited by the barrier cue were different than the bar and arrow cues when cue validity was 0, 17, and 33%.

The results show that when the validity of the barrier cue is low, the anticipatory eye movements elicited by the barrier are significantly slower than the anticipatory pursuit elicited by the other two types of cues tested. Lowering the validity of the barrier cues renders it ineffective. A cue that elicited the highest anticipatory eye movements than any other cue in almost all the conditions tested, now elicits the slowest anticipatory pursuit when its validity is low. The perceptual qualities of the barrier cue interfered with the directional information provided.

### **4.3. Discussion: Experiment 3**

Subjects were able to show relatively high anticipatory eye movements when the arrow cue was 0% valid. The perceptual qualities of the arrow cue did not interfere with the directional information it provided. It is surprising that the barrier cue did not elicit high anticipatory pursuit because subjects were informed before each session about the probability of the cue. They were able to interpret that when the arrow cue was 0% valid

it would cue the direction of motion by pointing to the side opposite to that which the disc would travel. It is reasonable for this cue to produce similar anticipatory eye movements at 0 and 100% validity since in this conditions, the future direction of motion of the disc is always known. However, that was not how subjects treated the information provided by the barrier cue. The anticipatory eye velocity elicited by the barrier cue was low when the cues was 0 and 25% valid. The perceptual qualities of the barrier cue were so strong that the knowledge that the disc would crash through the barrier in four consecutive experimental sessions was not enough to produce anticipatory eye velocities comparable to when the cue was 100% valid. Reducing the validity of the barrier cue rendered it cue ineffective.

## **5. General Discussion**

All the experiments in this study aimed to determine how the perceptual qualities of a cue influenced or biased the directional information it provides. Are the perceptual qualities of cues an important factor that can determine how the directional information they provide is treated by the system? Or, is the reliability of the directional information that the cue provides all that is important for the predictive mechanisms of the pursuit system? To answer these questions, and other questions that emerged, the anticipatory eye movements elicited by different types of cues were compared.

### *5.1. Past history*

Experiment 1 showed that the anticipatory eye velocities elicited by cues that provided deterministic information about the direction of motion were different from the anticipatory eye velocities produced by either past history or a cue that provided probabilistic information. Learning the probabilities of rightward motion from past

history was similar to getting the probabilities of rightward motion from the probabilistic bar cue.

### *5.2. Cue timing*

Perceptual qualities play an important role in the time it takes to interpret cues and produce clear anticipatory eye movements (Experiment 2). The barrier cue was able to elicit significant anticipatory eye movements about 200 ms before an upcoming change in direction of target motion, while other cues seem to require about 300 ms or more. This implied that cues that produce anticipatory eye movements vary in ease of interpretation and automaticity. Thus, there might be cues that are more effective producing anticipatory pursuit because they can be easier to interpret, which could suggest that the way that they deliver directional information facilitates anticipatory pursuit.

Experiment 2 also showed that when the barrier was removed, the anticipatory eye movements it elicited became very similar to arbitrary cues. One possible explanation for this is that the perceptual qualities of the barrier cue is responsible for the faster anticipatory eye movements that this cue usually elicits. By blocking the untraveled path at the time or near the time the disc changes direction of motion, the barrier cue may help to create a perceptual representation of the future target trajectory and this way facilitates the production of anticipatory eye movements. It is possible that the perceptual qualities of cues can momentarily be stored in memory to create a representation that can partially make up for the cues that is physically absent. Such representation seemed to be less effective than the physical cue, which might suggest that memory is not as effective as the perceptual signal.

Another possibility is that the transient created by removing the barrier cue affected the integration of the signals that guide pursuit. Experiment 2 was not set up to exclude this hypothesis. However, this can be tested by conducting another experiment in which an object that does not cue the direction of motion on the display is removed while the cues remain. For example, there can be two conditions. In the first condition a small square right below the Y-junction of the inverted Y-shaped tube can appear and disappear at a fixed time interval while the barrier is present throughout the length of the trial. The second condition is the same as the first condition, except that the square that the square does not disappear. If the anticipatory eye velocity is slower when the square is appears and disappear than when it is present the entire time, then this would indicate that removing a cue creates a transient that interferes with the production of anticipatory eye movements. It would also indicate that the perceptual qualities of a cue are do not affect the magnitude of anticipatory eye movements. However, even this experiment would not explain why removing the barrier cue affected anticipatory pursuit but not removing the color or the bar cues.

### *5.3. Cue Validity*

How do knowledge, learning, and the perceptual qualities of a cue interact? In Experiment 3, subjects were informed that the validity of the barrier cue was going to be 0% valid and thus it would always go through the barrier. The validity of a session was blocked and validities were ran in blocks of four consecutive sessions of 30 trials each. However, even after all of this information was available to the subjects, they were still not anticipating the future direction of motion. The barrier cue became ineffective. The barrier cue may become ineffective because the knowledge that an object cannot just



freely move through another interfered with the directional information it provides. Can people learn that the disc can actually move freely through the barrier? How many trials will it take, if it actually happens? What type of strategies will they develop to keep this higher level knowledge from producing anticipatory eye movements? Are there individual differences that might allow certain subjects to come up with the right strategy to be able to anticipate in the direction of the blocked path?

Many such questions remain unanswered. However, by examining all the results of this experiment, one can infer that cues are processed differently. Using different types of cues while not taking into account their perceptual qualities can bias the results of anticipatory eye movements. These results may be related to prior neurophysiological studies of anticipatory eye movements.

#### *5.4. Neural implications*

Various studies have attempted to determine brain areas where the associations between cues and direction of motion occur with the aim to understand the mechanisms that process this information and ultimately lead to anticipatory pursuit (de Hemptinne et al., 2008; Heinen and Liu, 1997; Li & Lisberger, 2011; Ilg, 2003; Krauzlis, 2005). Two candidate areas that have been investigated to determine if neurons can learn the association between cue and target motion are the supplementary eye field (SEF) and the middle temporal (MT) area (de Hemptinne et al., 2008; Schlack & Albright, 2007).

MT is known to be responsible for encoding motion signals (Newsome, Wurtz, Dursteler & Mikami, 1985), which are needed to initiate and maintain pursuit (Keller & Heinen, 1991). SEF is a decision area associated with goal directed saccadic eye movements and smooth pursuit (Schall, Morel & Kass, 1993). There are studies that

have found evidence showing that SEF and MT might be responsible for generating the signal that elicit anticipatory pursuit. A few of those studies are discussed below.

de Hemptinne et al. (2008) investigated whether SEF neurons could learn to associate the direction of target motion with an arbitrary color cue. To elicit anticipatory pursuit, monkeys were trained to associate the color of a fixation point with the future motion of a small disc. A yellow fixation point indicated that the target would move leftward. A red fixation point cued rightward motion, while a green fixation point was not informative because the target equal probability of moving right or left. Their results showed that SEF neurons can encode the direction of the future motion since these neurons became directionally selective in response to color cues before anticipatory pursuit eye movements and before the onset of target motion. Furthermore, de Hemptinne et al. (2008) found a strong correlation between the neural activity of SEF and anticipatory smooth eye movements: the higher the firing rate of SEF neurons, the faster the anticipatory smooth eye movements. Thus, the authors proposed that the directional selectivity of SEF neurons is responsible for anticipatory pursuit. However, this study did not compare different types of cues. It is unclear whether SEF can account for the effects of the barrier cue by processing information about perceptual qualities of cues.

Schlack and Albright (2007) conducted an experiment to test whether MT neurons can learn to respond to cues. Before any training monkeys were presented with patterns of moving dots. MT neurons, as expected, showed directional selectivity. Monkeys were later trained to associate the direction of motion of the pattern of dots with static arrows pointing in different directions (e.g., upward arrow was shown, pattern of dots moved upward). Note that there was no semantic link involved between the arrow

and the motion. Pairing of a downward arrow with upward motion was also effective. After learning the association, the neurons in area MT showed selectivity for the orientation of the arrow. This showed that MT neurons can learn the association between target motion and cue (even when it is static). These signals might be able to produce predictive signals that can lead to execution of motor commands such as anticipatory eye movements.

There are natural cues found in implied motion images that seem to influence MT. Images containing implied motion convey possible future trajectories of a static object. An fMRI study (Kourtzi & Kanwisher, 2000) found that the neural activity in MT/MST was higher when subjects were presented with implied motion images than when they were presented with images that did not imply motion. Neural signal seen in MS/MST in response to static implied motion cues might be able to trigger anticipatory smooth eye movements since these type of cues allow viewers to make inferences or predictions about the future trajectory of an object.

Finding evidence that multiple brain areas may be responsible for the generation of anticipatory pursuit is consistent with the possibility that cues are processed by different mechanisms, or perhaps by a combination of various mechanisms. For example, a natural cue, such as the barrier, might be by processed MT, or a combination of MT and SEF. The barrier cue can have an advantage over other cues because higher level knowledge about the physics of objects can allow subjects to naturally link the location of the barrier with the motion of the disc. The viewer can use the knowledge that an object cannot move through another and, therefore, the disc must travel through the unblocked path. By contrast, the perceptual qualities of the bar and color are

arbitrarily associated with the direction of motion. There is no natural way of reasoning why the disc must travel through the path on the right-hand side if the tube turns red or any other color.

Without changing cue delay, removal, or validity, an MRI study reveal which brain areas are more active when these different types of cues are being used to elicit anticipatory eye movements. For example, the results might show that there is a higher level of activation of area MT when the barrier cue is tested than when the color or bar cues are used.

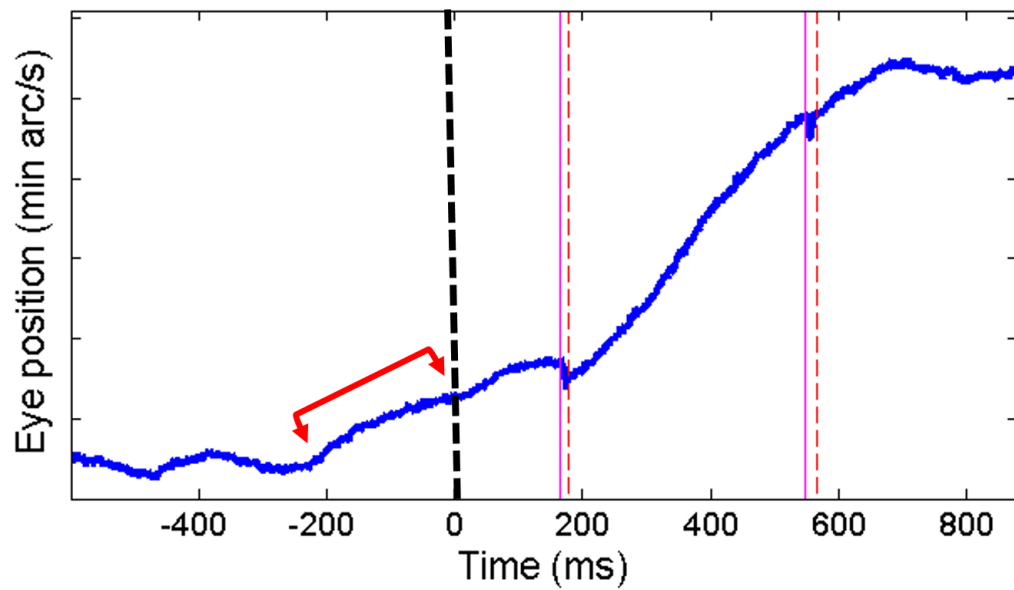
Another way to test how higher level knowledge about the physics of objects affect anticipatory eye movements is to use visual displays with implied motion. For instance, if the barrier is drawn slightly fragmented in the middle, as if it is broken, this might suggest to the viewer that the disc can break through the barrier and travel any path independently of where the barrier is located. The higher level knowledge that might influence anticipatory eye movements would be the following: a moving object with enough momentum can break through another whose constitution has been compromised.

### *5.5. Implications for anticipatory eye movement models*

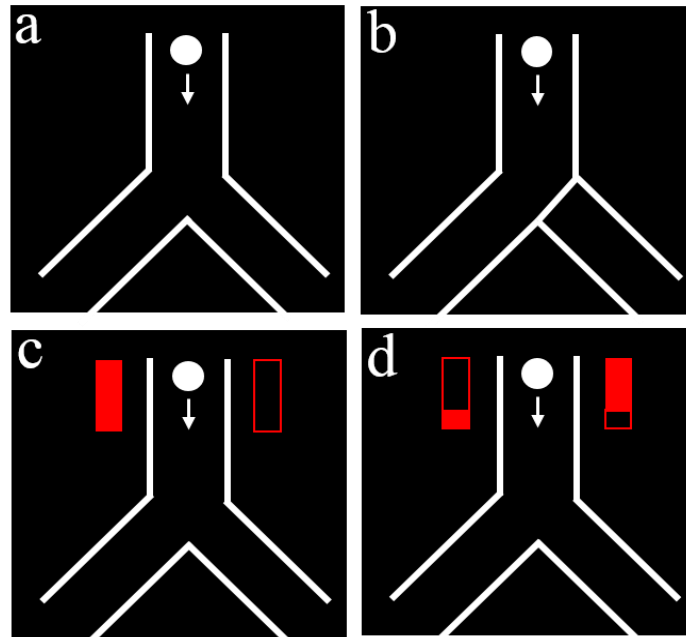
Current models (e.g., Barnes & Collins, 2008; Orban de Xivry, Missal, & Lefevre, 2008) of anticipatory smooth eye do not take into account some of the cue properties that I tested. Instead they assumed that past history determines anticipatory eye movements. A model would produce a better estimate of anticipatory eye velocity if it was to take into account that one type of cue may overwrite the effects of past history more effectively than others.

The barrier cue does not depend on trial-over-trial learning like other cues do. Anticipatory effects by the barrier cue are present in the first trial (Aitkin, et al., 2013; Kowler et al., 2014). Thus, current models based solely on learning cannot generate a good estimate of the anticipatory eye movements elicited by cues, such as the barrier.

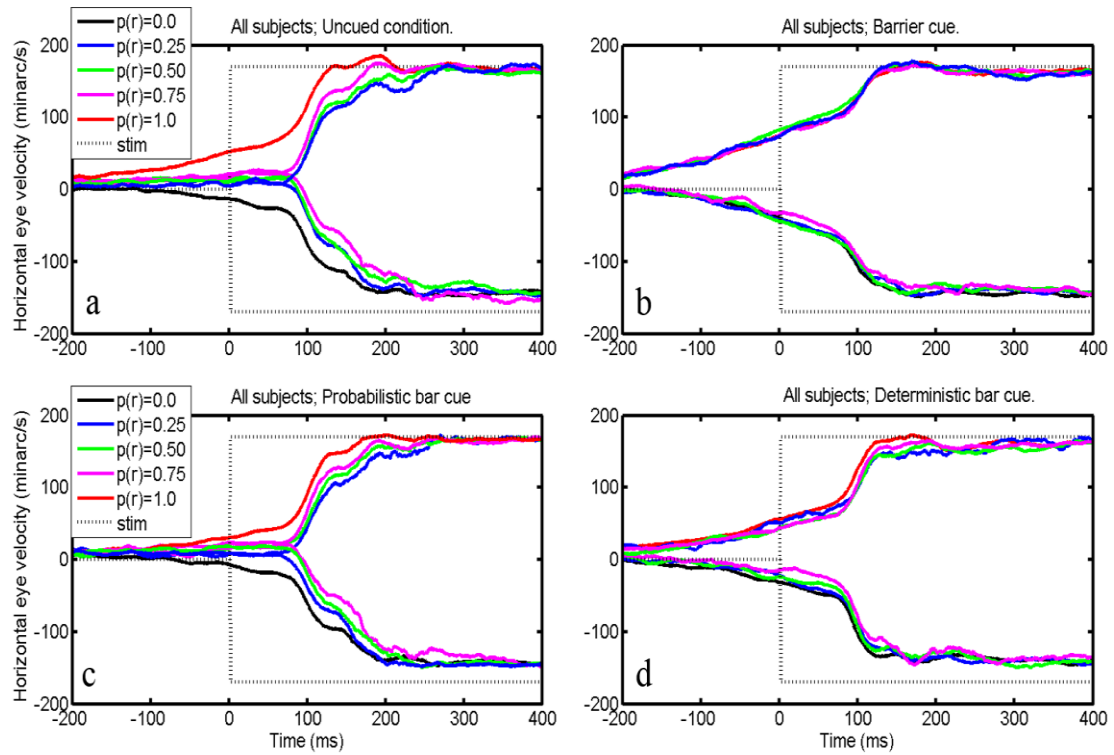
Models should also take into account the perceptual qualities of cues and the possible interpretations that they may trigger. For example, current models would not be able to predict the lack of anticipatory eye movements when the validity of the barrier cue is low. The influence of higher level phenomena like these is what makes anticipatory eye movements very difficult to model. However, at the same time it is one of the qualities that makes them interesting to study. Understanding anticipatory eye movements would allow us to expand the breadth of knowledge of the cognitive and perceptual process that allow us to interpret, and use cues to navigate and survive in our environment.



*Figure 1.* Representative eye traces of horizontal anticipatory smooth pursuit eye movements. The black dashed line represents the onset of horizontal target motion. Solid magenta line represents onset of a saccade. Dashed red line represents the offset of a saccade. Red arrows point at the change in eye position before the onset of horizontal target motion (anticipatory eye movements).

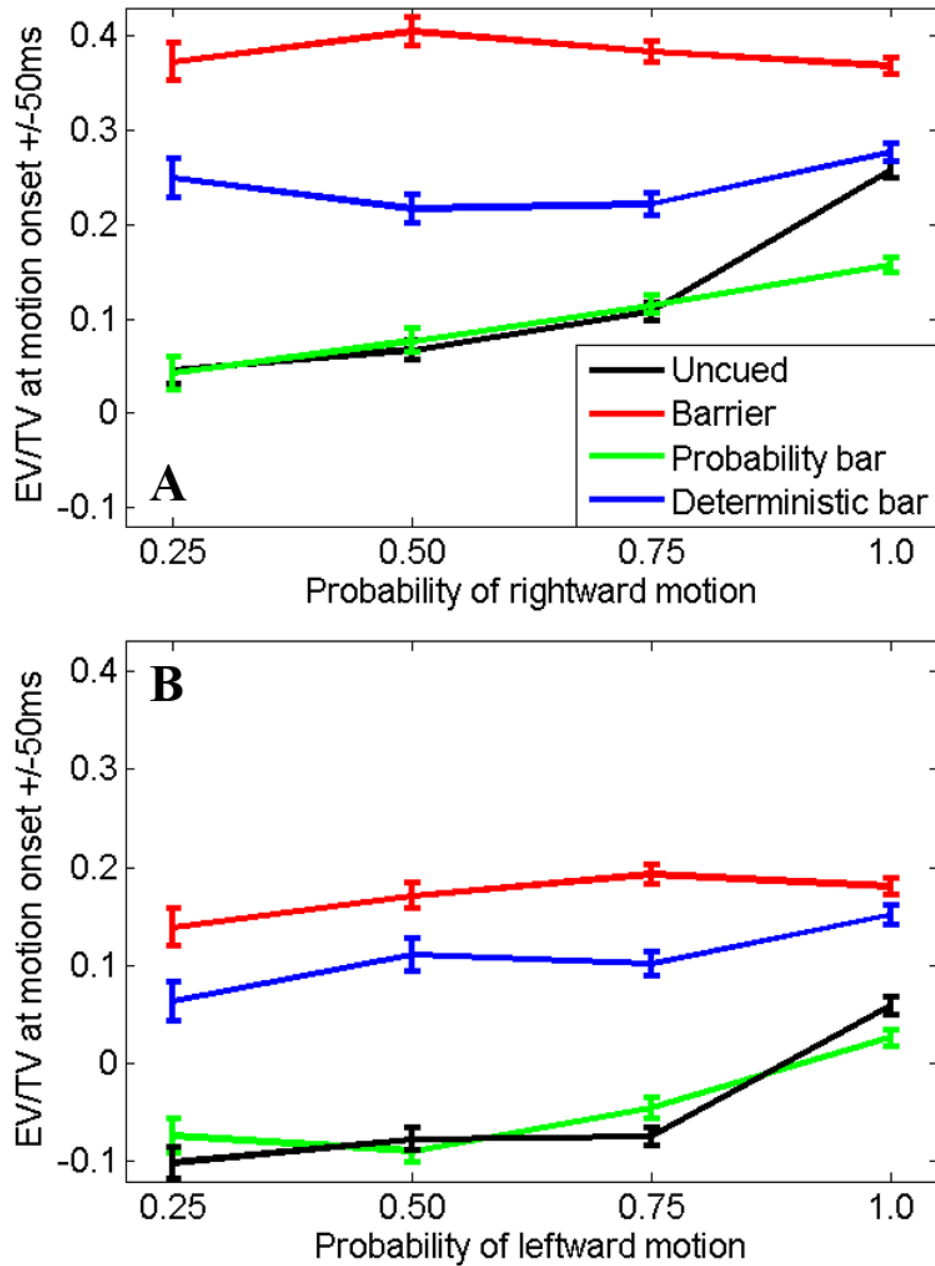


*Figure 2.* Stimulus display for Experiment 1. Inverted Y-shaped tube for experimental conditions. The disc moves down the tube and then travels down one of the two paths depending on the condition. (a) No cue indicates rightward or leftward motion. Probability of rightward motion was 0.5. (b) Disc travels down unblocked path. (c) Disc travels down the path on which the filled bar is. (d) Bars indicate the probability of rightward/leftward motion.

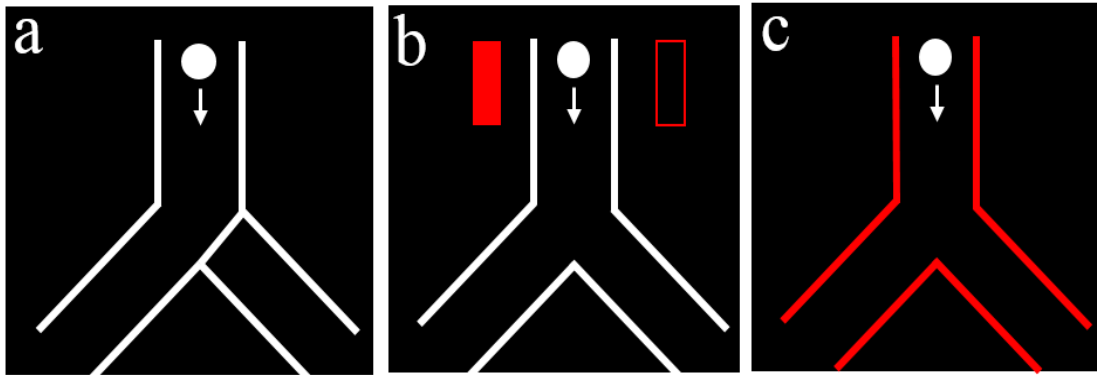


*Figure 3.* Mean horizontal eye velocity (50 ms samples, with onsets of successive samples separated by 2ms) over time averaged across subjects. Dotted line at time 0 ms represents onset of horizontal target velocity (time disc moved into one of the two paths of the inverted Y-shaped tube). Negative velocities indicate leftward eye velocities. (a) Uncued. (b) Barrier. (c) Probabilistic bars. (d) Probabilistic bars.

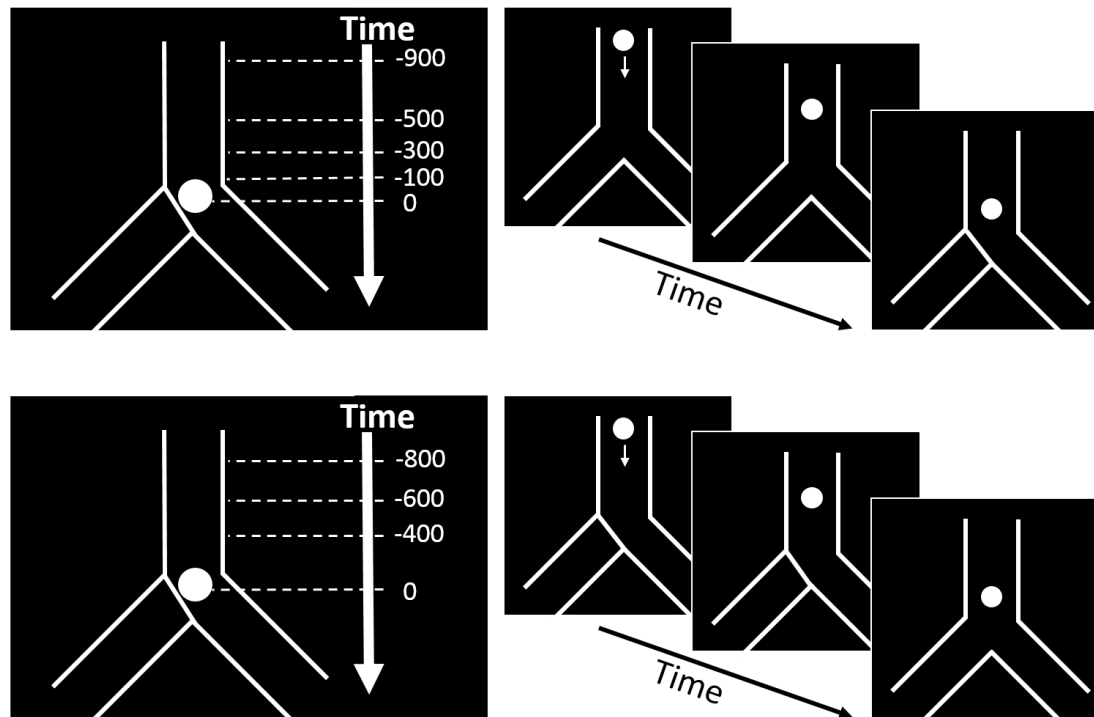




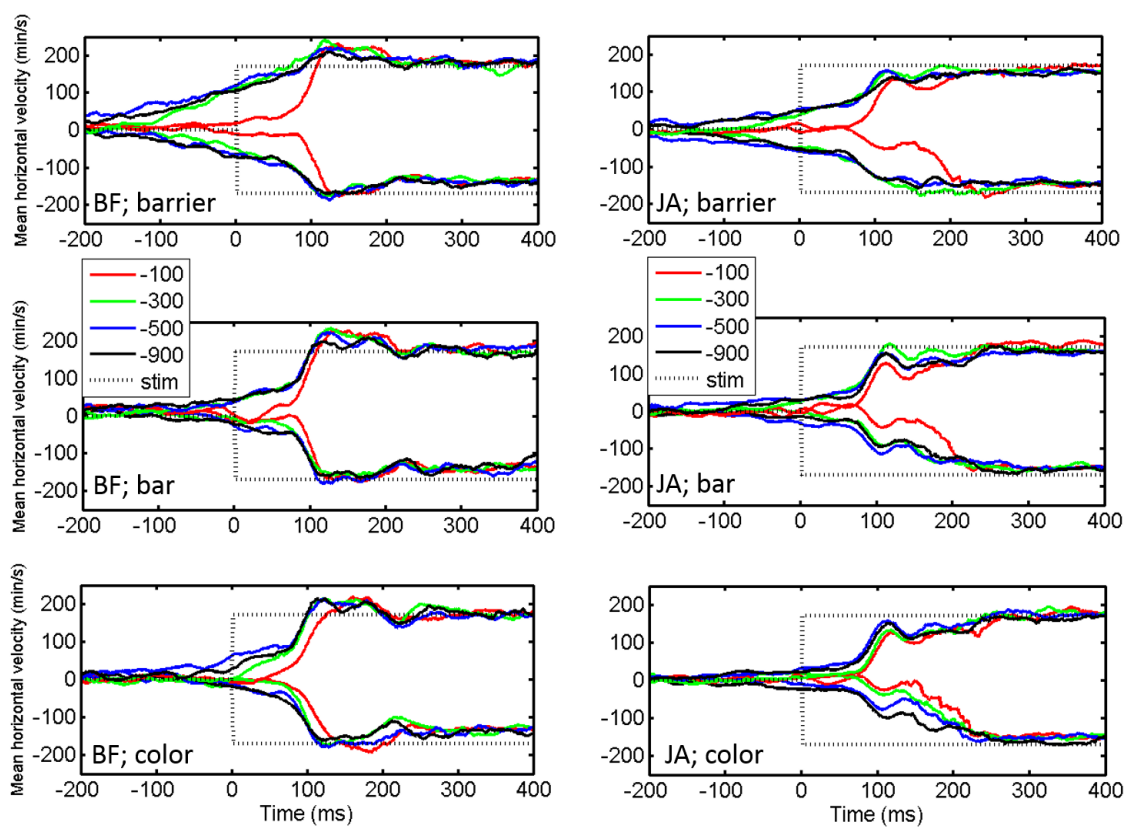
*Figure 4.* Graph showing the index of anticipatory eye movements as a function of the probability of rightward motion of the target (A). Graph showing the index of anticipatory eye movements as a function of the probability of leftward motion of the target (B). The index of anticipatory eye movements is the slope of the best fit line of position samples within a 100 ms window ( $\pm 50$  ms) centered around the time of onset of horizontal motion divided by target velocity. Error bars indicate  $\pm$  standard error.

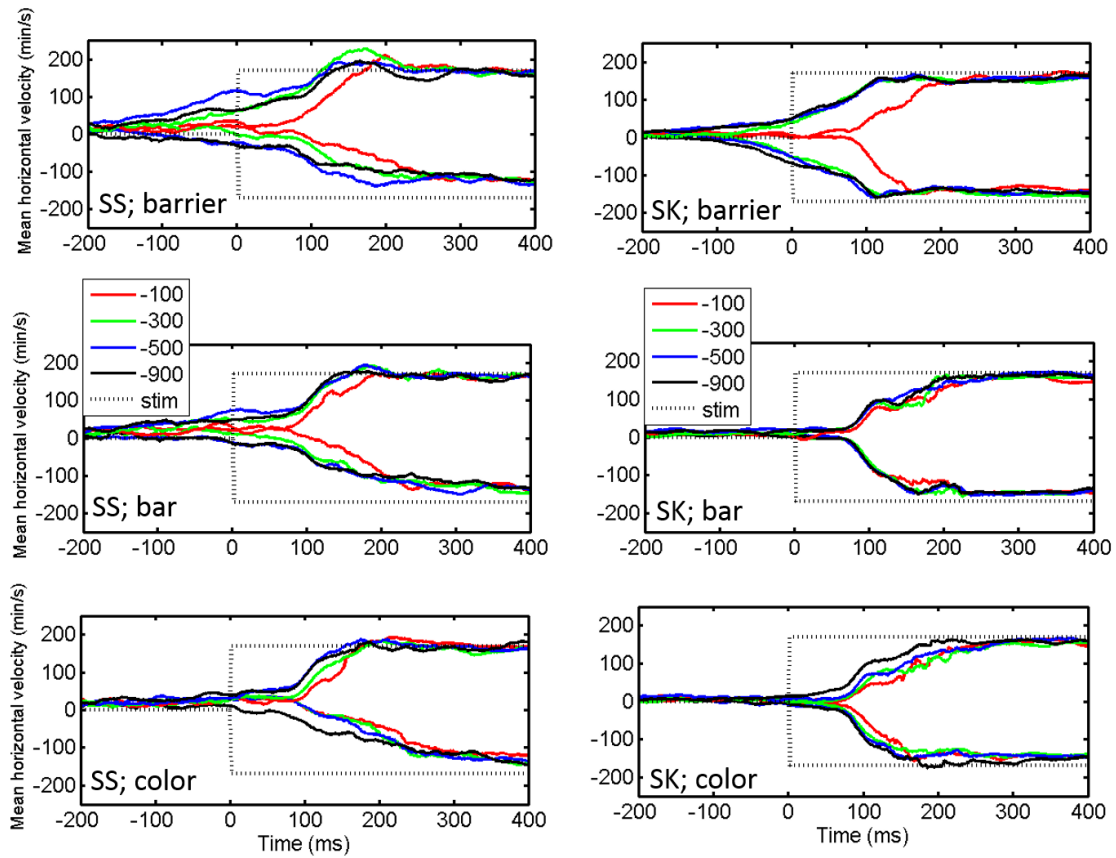


*Figure 5.* Stimulus display for Experiment 2. Inverted Y-shaped tube for experimental conditions with different types of cues. The disc moves down the tube and then travels down the path indicated by the cue: (a) Barrier indicates direction of motion by blocking untraveled path. (b) Disc travels down the path on which the filled bar is. (c) Red tube indicates rightward motion. Green tube indicates leftward motion.

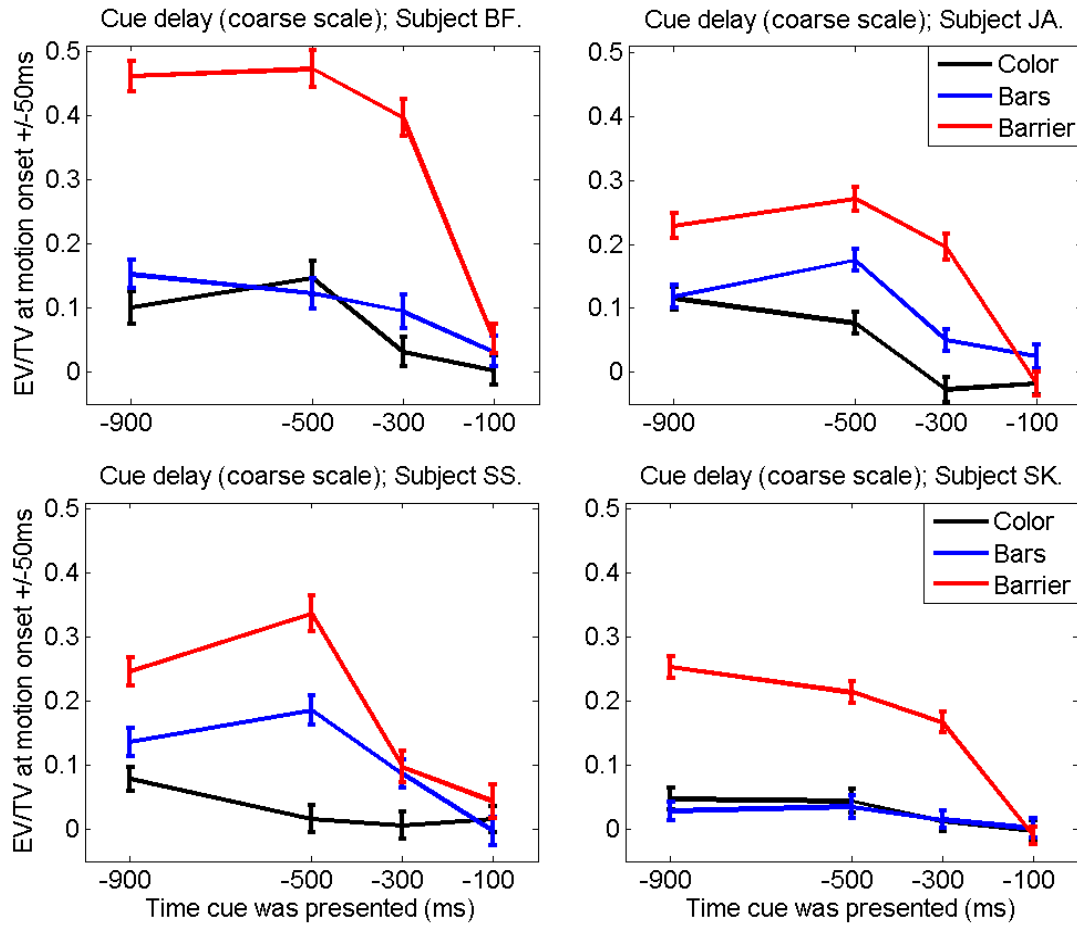


*Figure 6.* Sketches showing the sequence of events for Experiment 2. Top: delay times for Experiment 2. Cue was delayed 100, 300, 500, and 900 ms before the disc changed direction of motion at the Y-junction (time 0 ms). Bottom: removal times for Experiment 2. Cue was removed 800, 600, 400 and 0 ms before the disc changed direction of motion at the Y-junction (time 0 ms).

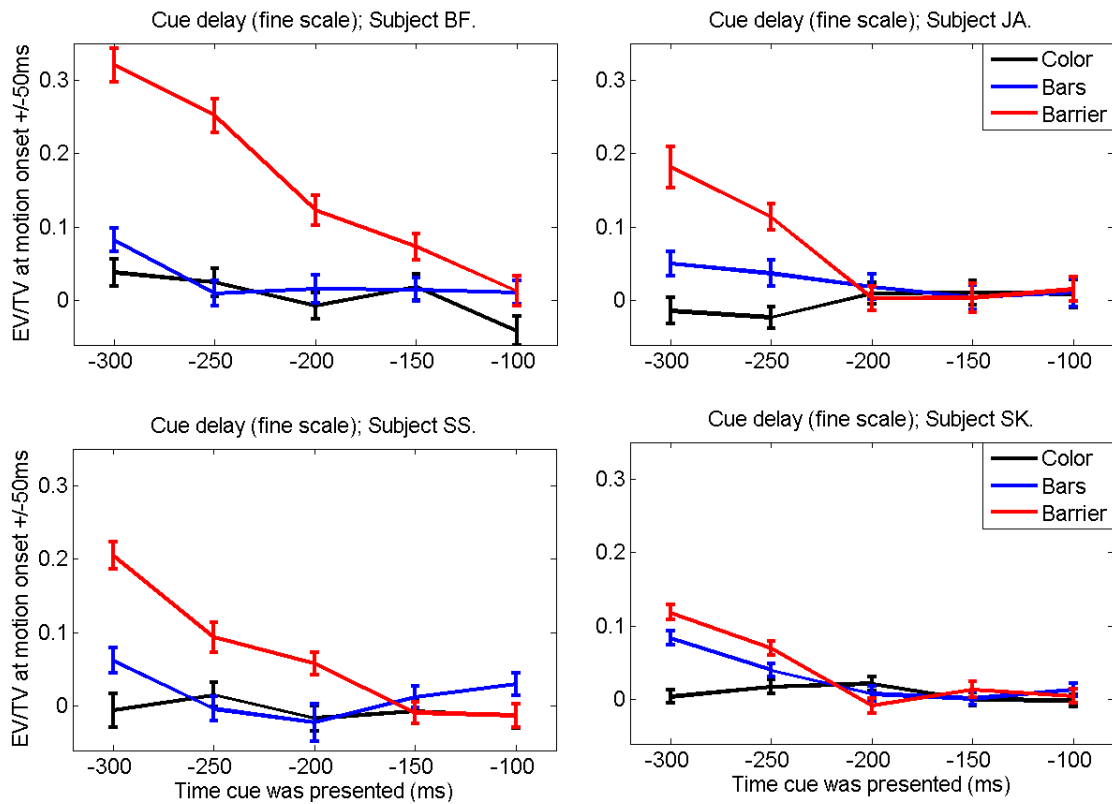




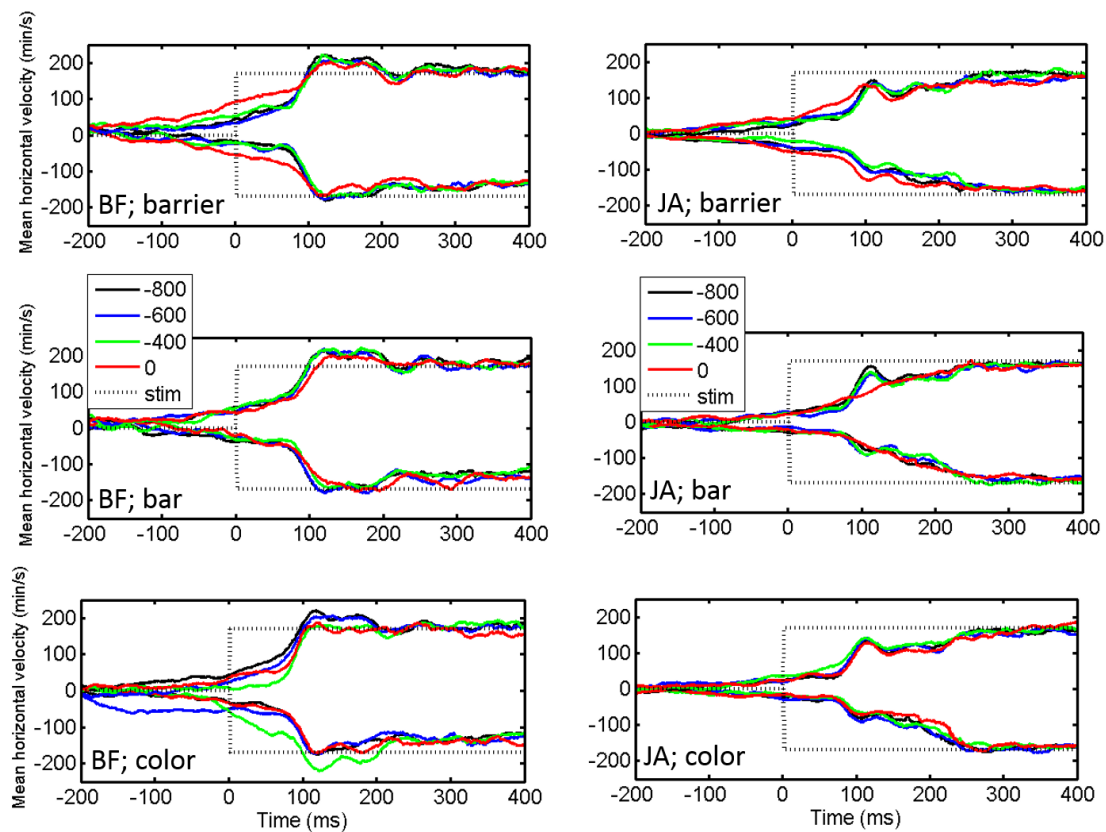
*Figure 7.* Mean horizontal eye velocity over time velocity (50 ms samples, with onsets of successive samples separated by 2ms) for each of the four subjects who participated in the delay condition of Experiment 2 (coarse scale). Dotted line at time 0 ms represents time onset of target horizontal velocity into one of the two paths of the inverted Y-shaped tube. Negative velocities indicate leftward eye velocities. Each subject ran in the delay condition with the barrier, bar, and color cue.



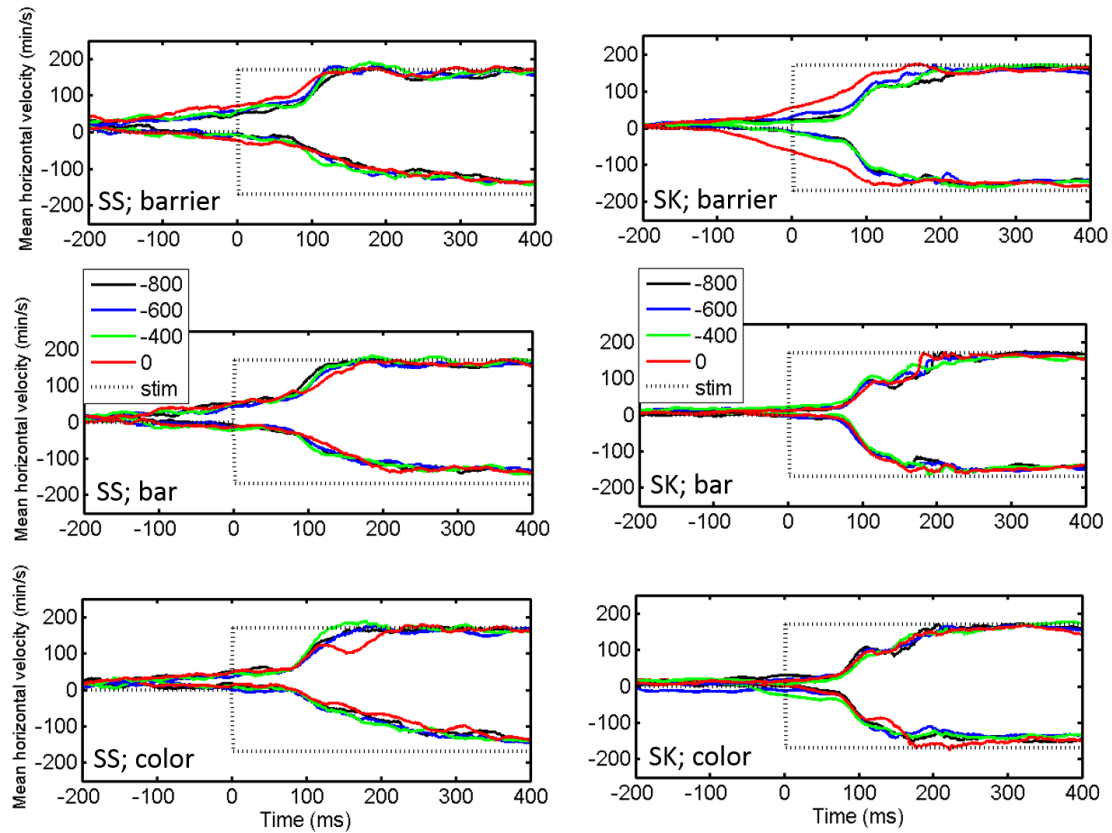
*Figure 8.* Graphs showing the index of anticipatory eye movements as a function of delay times for each of the subjects. The index of anticipatory eye movements is the slope of the best fit line of position samples within a 100 ms window ( $\pm 50$  ms) centered around the time of onset of horizontal motion divided by target velocity. Error bars indicate  $\pm$  standard error. These graphs are for the delay time condition of Experiment 2 tested with the coarse scale.



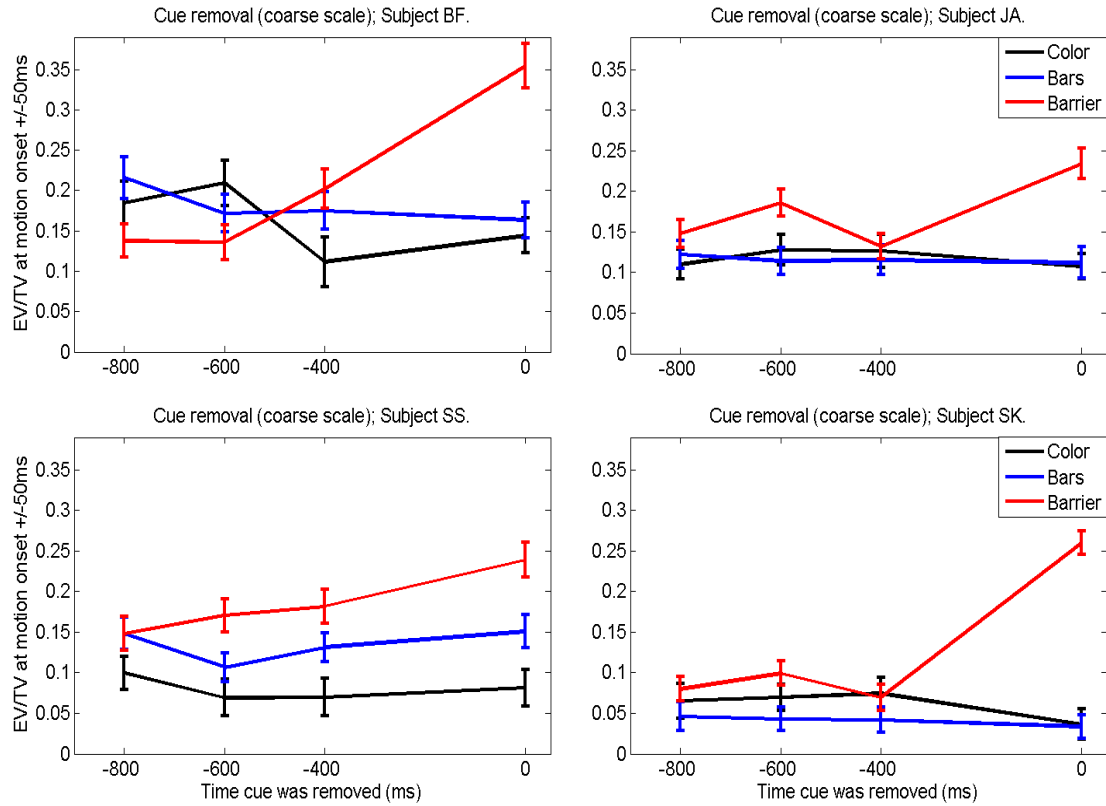
*Figure 9.* Graphs showing the index of anticipatory eye movements as a function of delay times for each of the subjects. The index of anticipatory eye movements is the slope of the best fit line of position samples within a 100 ms window ( $\pm 50$  ms) centered around the time of onset of horizontal motion divided by target velocity. Error bars indicate  $\pm$  standard error. These graphs are for the delay time condition of Experiment 2 tested with fine time scale.



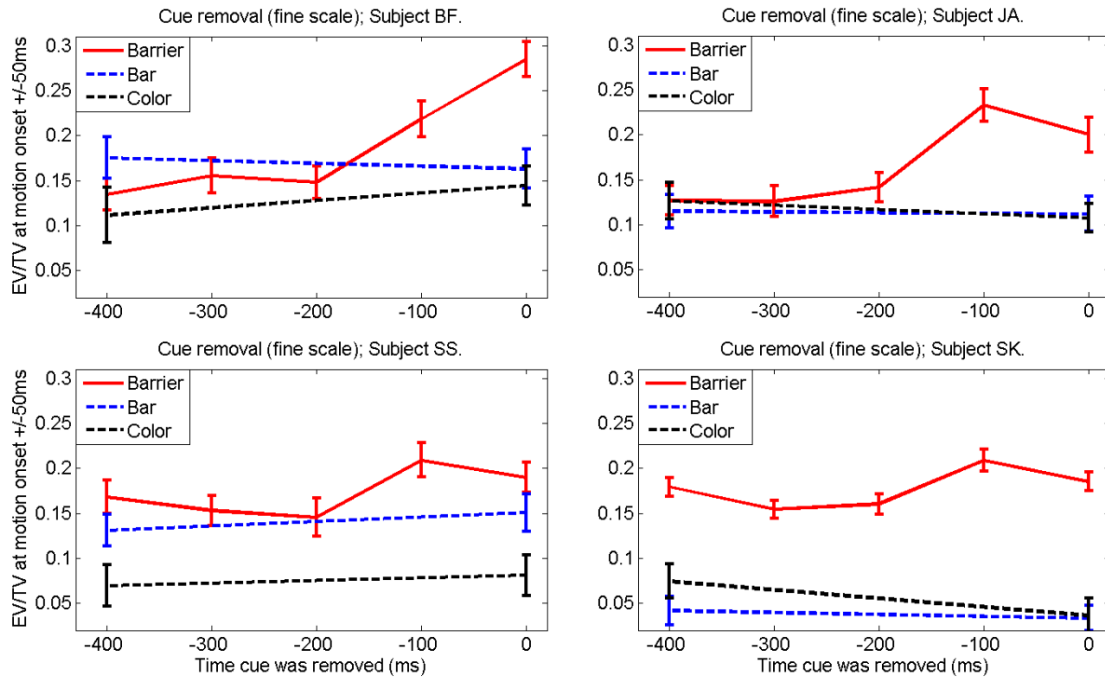




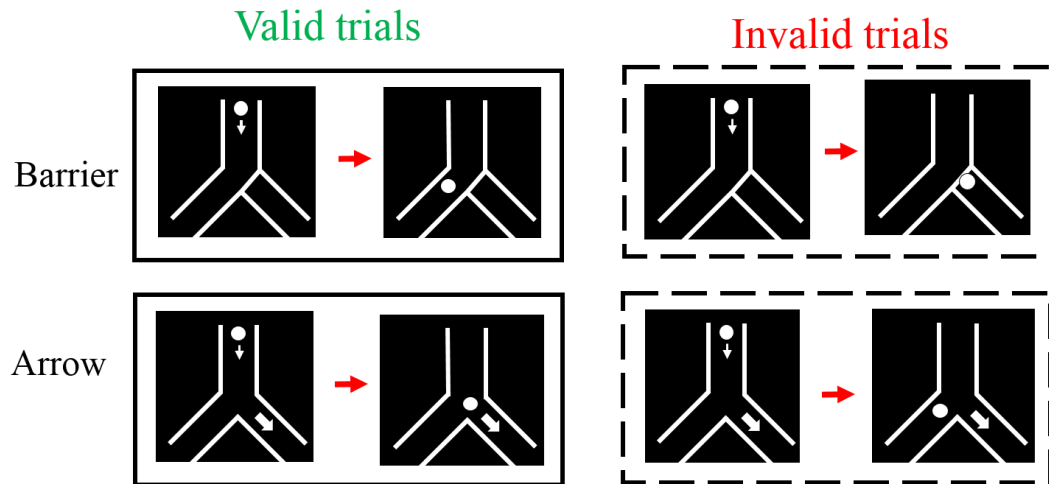
*Figure 10.* Mean horizontal eye velocity (50 ms samples, with onsets of successive samples separated by 2ms) over time for each of the four subjects who participated in the removal condition of Experiment 2 (fine scale). Dotted line at time 0 ms represents time onset of target horizontal velocity into one of the two paths of the inverted Y-shaped tube. Negative velocities indicate leftward eye velocities. Each subject ran in the delay condition with the barrier, bar, and color cue.



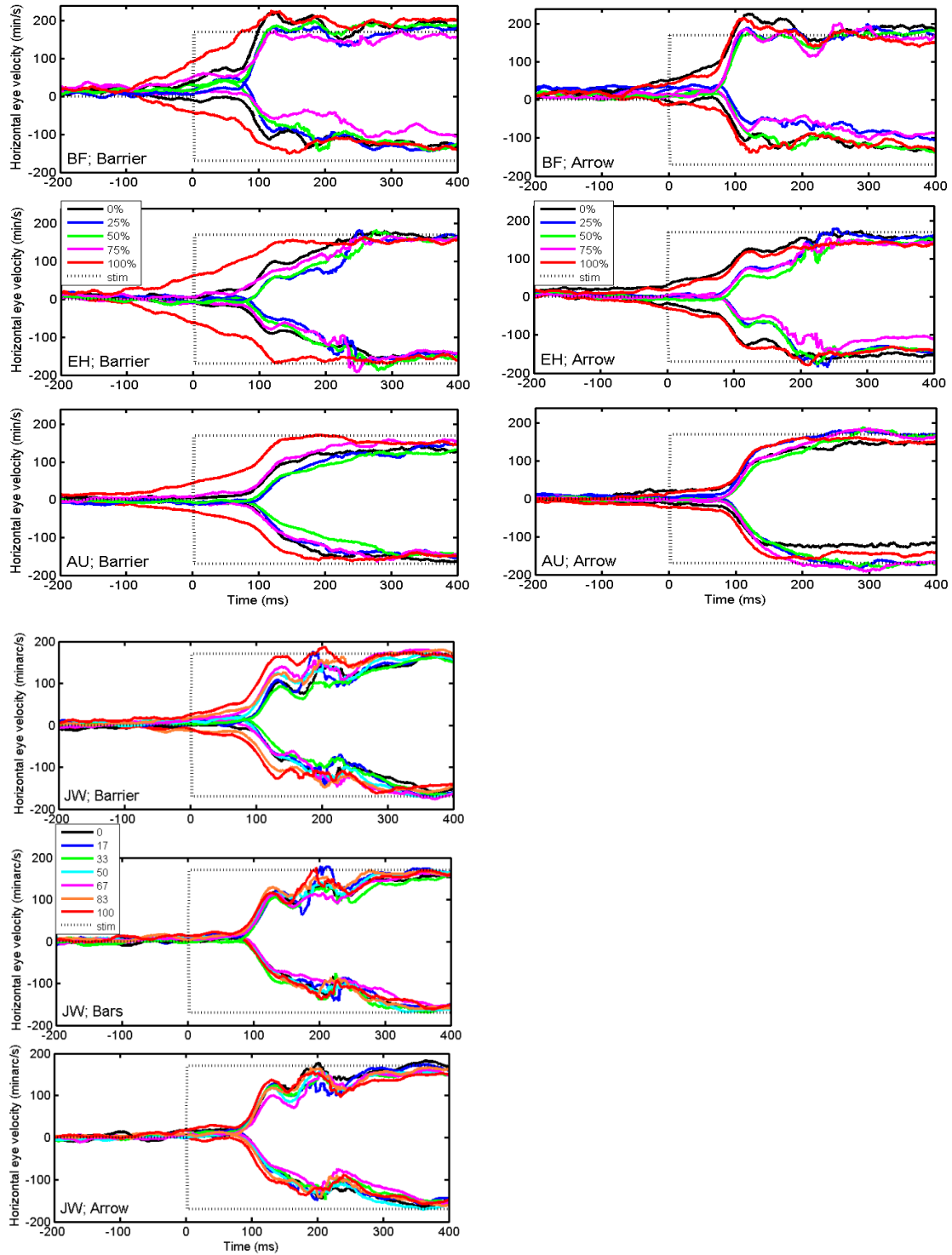
*Figure 11.* Graphs showing the index of anticipatory eye movements as a function of removal times for each of the subjects. The index of anticipatory eye movements is the slope of the best fit line of position samples within a 100 ms window ( $\pm 50$  ms) centered around the time of onset of horizontal motion divided by target velocity. Error bars indicate  $\pm$  standard error. These results are for the removal time condition of Experiment 2 tested with the coarse scale.



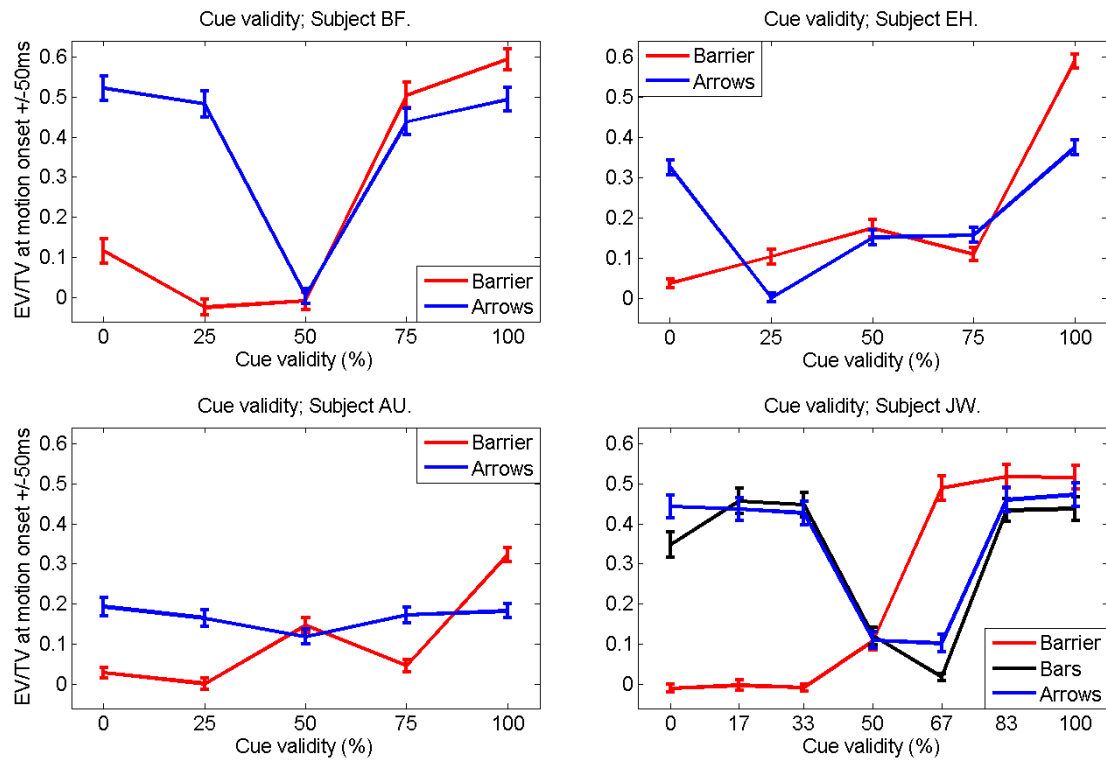
*Figure 12.* Graphs showing the index of anticipatory eye movements as a function of removal times for each of the subjects. The index of anticipatory eye movements is the slope of the best fit line of position samples within a 100 ms window ( $\pm 50$  ms) centered around the time of onset of horizontal motion divided by target velocity. Error bars indicate  $\pm$  standard error. These results are for the removal time condition of Experiment 2 tested with the fine scale.



*Figure 13.* Stimulus display for Experiment 3. Inverted Y-shaped tube for experimental conditions. The disc moves down the tube and then travels down the path indicated by the cue in valid trials. (a) Left-hand side: Display for a valid trials of the barrier (top) and arrow cue (bottom). Right-hand side: Display for invalid trials of the barrier (top) and the arrow (bottom).

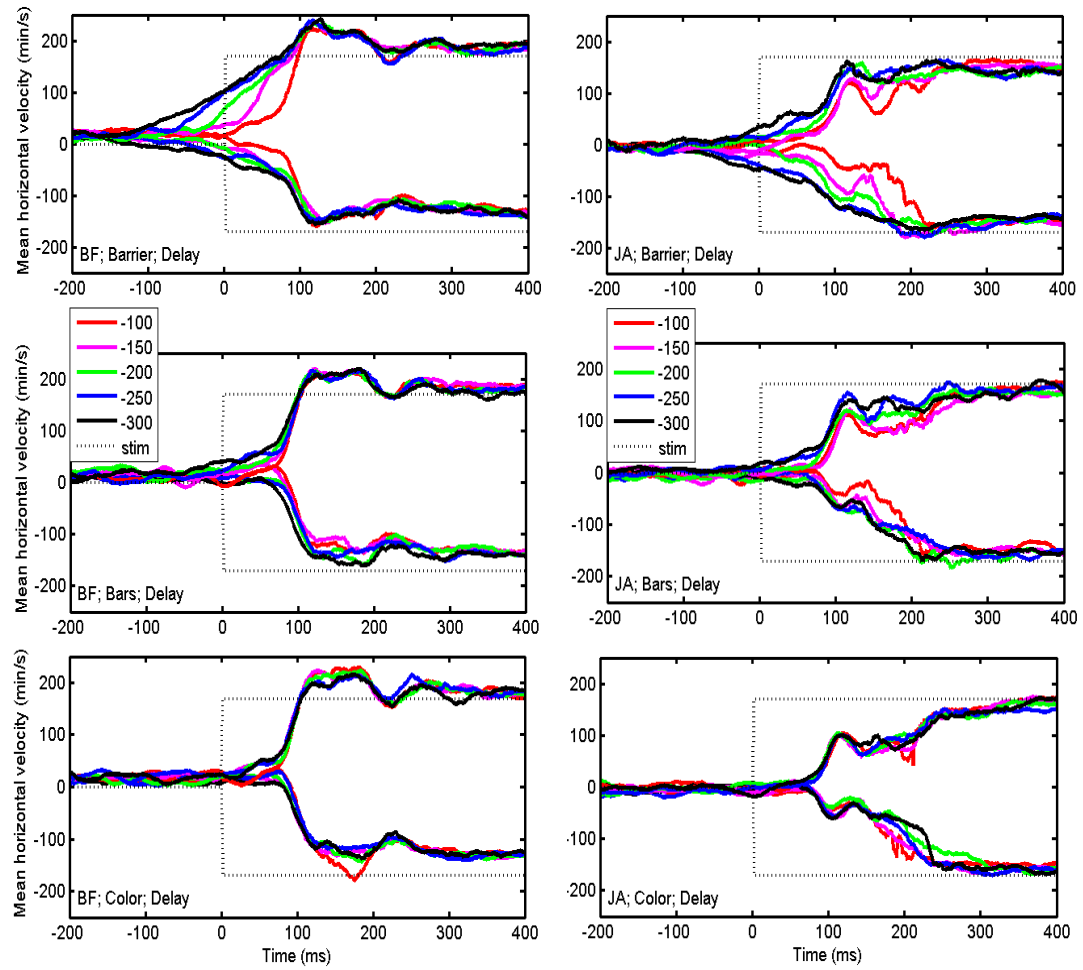


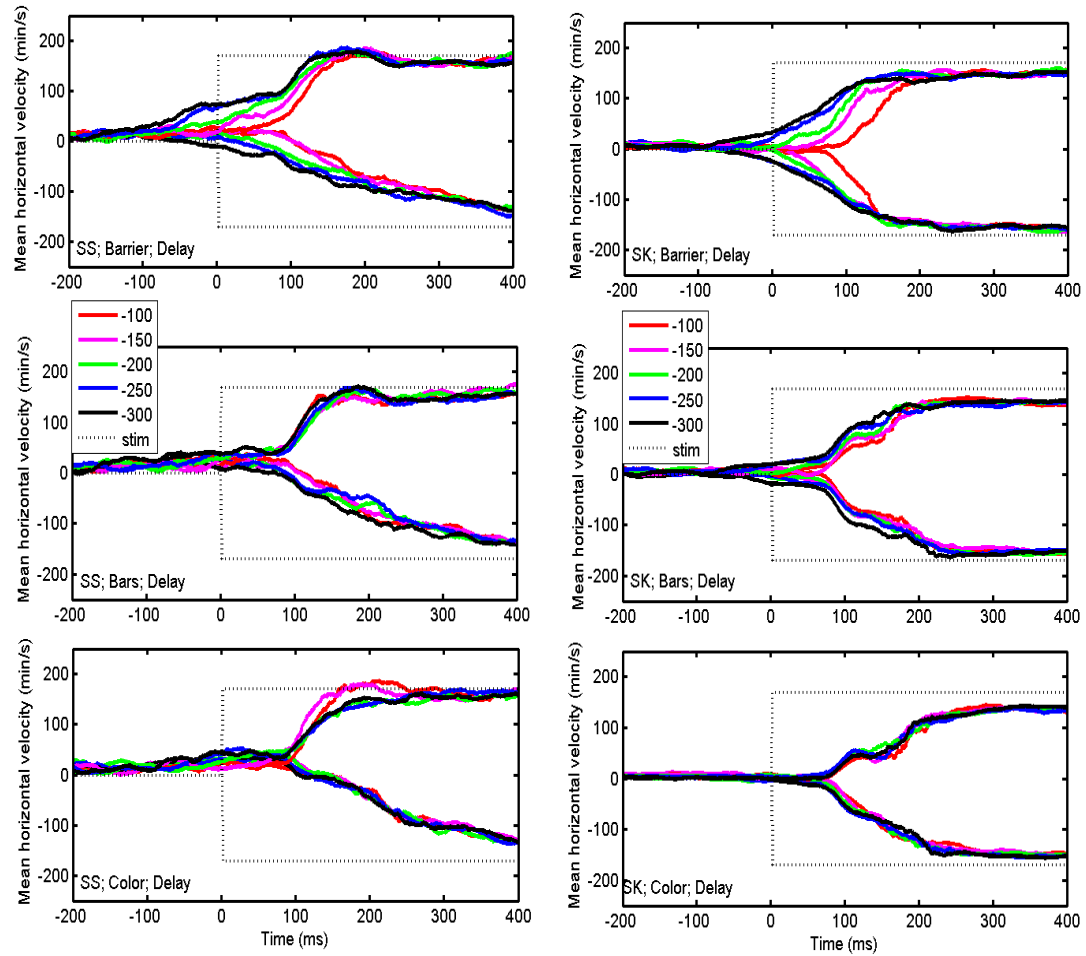
*Figure 14.* Mean horizontal eye velocity (50 ms samples, with onsets of successive samples separated by 2ms) over time for each of the four subjects who participated in Experiment 3. Dotted line at time 0 ms represents onset of horizontal target motion. Negative velocities indicate leftward eye velocities.



*Figure 15.* Graphs showing the index of anticipatory eye movements as a function of removal times for each of the subjects. The index of anticipatory eye movements is the slope of the best fit line of position samples within a 100 ms window ( $\pm 50$  ms) centered around the time of onset of horizontal motion divided by target velocity. Error bars indicate  $\pm$  standard error. These results are for the Experiment 3, cue validity.

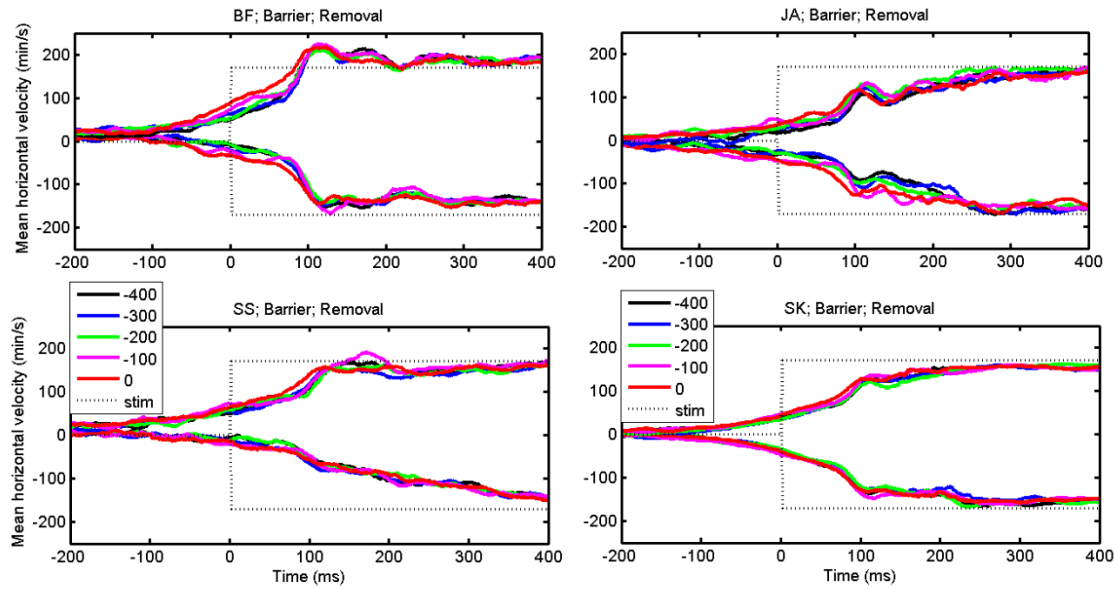
## Appendix





*Figure S1.* Mean horizontal eye velocity (50 ms samples, with onsets of successive samples separated by 2ms) over time for each of the four subjects who participated in the delay condition with a fine time scale of Experiment 2. Dotted line at time 0 ms represents time onset of target horizontal velocity into one of the two paths of the inverted Y-shaped tube. Negative velocities indicate leftward eye velocities. Each subject ran in the delay condition with the barrier, bar, and color cue.





*Figure S2.* Mean horizontal eye velocity (50 ms samples, with onsets of successive samples separated by 2ms) over time for each of the four subjects who participated in the removal condition with a fine time scale of Experiment 2. Dotted line at time 0 ms represents time onset of target horizontal velocity into one of the two paths of the inverted Y-shaped tube. Negative velocities indicate leftward eye velocities. Each subject ran in the removal condition with the barrier, bar, and color cue.

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