

Anticipatory smooth pursuit eye movements evoked by probabilistic cues

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Anticipatory smooth eye movements (ASEM; smooth eye movements in the direction of anticipated target motion) are elicited by cues that signal the direction of future target motion with high levels of certainty. Natural cues, however, rarely convey information with perfect certainty, and responses to uncertainty provide insights about how predictive behaviors are generated. Subjects smoothly pursued targets that moved to the right or left with varying cued probabilities. ASEM strength in a given direction increased with the probability level. The type of cue also played a role. ASEM elicited by symbolic visual cues tended to underweight low probabilities and overweight high probabilities. Cues based on memory (varying the proportion of trials with left or right motion) produced the opposite pattern, overweighting low probabilities and underweighting high probabilities. Finally, cues whose perceptual structure depicted the motion path produced a bias in ASEM in the depicted direction that was maintained across levels of cue congruency. The results show that the smooth pursuit system relies on a combination of signals, including memory for recent target motions, interpretation of cues, and prior beliefs about the relationship between the perceptual configuration and the motion path to determine the anticipatory response in the presence of uncertainty.

internal signals that are responsible for the anticipatory responses. In the case of anticipatory smooth eye movements, two central questions can be posed. First, what types of cues or signals generate anticipatory pursuit, and, second, how does the anticipatory response depend on both the type of cue and on the reliability and validity of the cued information? This study addresses both issues.

The ability of smooth pursuit to anticipate changes in the trajectory of target motion was first observed for pursuit of highly-predictable, sinusoidal target motions, when the eye was found to change direction either in time with, or slightly ahead of, the target (Dallos & Jones, 1963; Westheimer, 1954). The smooth pursuit system was assumed to be able to learn the pattern of repetitive motion (Dallos & Jones, 1963; Westheimer, 1954), or to include short-term memory for recent motions as part of the input signal (Barnes & Asselman, 1991). Repetitive motions, however, are not essential. Anticipatory smooth eye movements (ASEM), smooth eye movements in the direction of the expected future motion of a target (Boman & Hotson, 1992; Kowler & Steinman, 1979), do not require repetitive motion, and can be elicited by a variety of perceptual cues that disclose the future motion path (Aitkin, Santos, & Kowler, 2013; Badler & Heinen, 2006; de Hemptinne, Lefèvre, & Missal, 2006; Jarrett & Barnes, 2002; Kowler, 1989; Kowler, Aitkin, Ross, Santos, & Zhao, 2014; Ladda, Eggert, Glasauer, & Straube, 2007; Maryott, Noyce, & Sekuler, 2011; Medina, Carey, & Lisberger, 2005; Montagnini, Sperling, & Masson, 2006; Mrotek & Soechting, 2007; Orban de Xivry, Missal, & Lefèvre, 2008; Ross & Santos, 2014; Santos, Gngang, & Kowler, 2012), including on the very first exposure to the cue (Aitkin et al., 2013). ASEM produced by cues have been linked to neural activity in supplementary eye fields (de Hemptinne, Lefèvre, & Missal, 2008; Missal & Heinen, 2004;

Introduction

Smooth pursuit eye movements respond both reactively and predictively. Pursuit can be elicited by the motion of an attended target across the retina, and can also anticipate the path of future target motion (Barnes, 2008; Kowler, 2011; Pavel, 1990). The key challenge for understanding the predictive aspects of pursuit, as it is for anticipatory visuomotor behaviors more generally (Bosco et al., 2015; Wolpert & Landy, 2012; Zhao & Warren, 2015), is to characterize the

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Shichinohe et al., 2009; Yang, Hwang, Ford, & Heinen, 2010).

The ability of perceptual cues to elicit ASEM is a useful property. Cues that disclose the future motion path of objects are prevalent in natural environments, and many visuomotor behaviors depend on such cues to plan anticipatory responses (Bosco et al., 2015; Diaz, Cooper, Rothkopf, & Hayhoe, 2013; Zhao & Warren, 2015). Natural cues to motion include cues that call upon our knowledge of the physical structure of the environment, such as when observing objects rolling down hills or bouncing off surfaces (Badler, Lefèvre, & Missal, 2010; Land & McLeod, 2000; Regan, 2012; Sanborn, Mansinghka, & Griffiths, 2013; Souto & Kerzel, 2013), or cues that result from observing the actions of living things, such as when predicting the goal of a reaching movement from the initial trajectory of the arm (Kilner, Vargas, Duval, Blakemore, & Sirigu, 2004; Maranesi, Livi, Fogassi, Rizzolatti, & Bonini, 2014). Natural cues, however, rarely signal the path of future motion with perfect certainty due to inevitable fluctuations in the physical environment, or in the motion trajectories of living things. Thus, it is important to understand how smooth pursuit (and visuomotor behaviors more generally) responds to reductions in the level of certainty about the path of future motions.

Uncertainty by itself does not eliminate ASEM. ASEM are found when the direction, speed, or timing of the motion is selected at random in the absence of perceptual cues (Collins & Barnes, 2009; Heinen, Badler, & Ting, 2005; Kao & Morrow, 1994; Kowler & McKee, 1987; Kowler & Steinman, 1981; Kowler, Martins, & Pavel, 1984; Montagnini, Souto, & Masson, 2010). In these cases ASEM are determined by the motion presented in previous trials. Perceptual cues, however, can override effects of past history (Kowler, 1989), showing that ASEM are not determined exclusively by memory for recent motions. What happens when the cue itself conveys probabilistic information, a situation that is similar to that encountered with natural cues?

The present study examines ASEM elicited by different types of cues that convey probabilistic information about the direction of future motion. We address two main questions.

First, how does the strength of ASEM elicited by different types of cues vary with the cued probability of motion in a given direction? There are three classes of possible outcomes: ASEM elicited by cues may vary in proportion to the probability level (probability matching); ASEM elicited by cues may be reduced or abolished in the presence of uncertainty; or ASEM may conform to the most likely direction of motion, regardless of the probability level. Examples of each of these types of outcomes can be found in prior studies of

behavioral decision-making under uncertainty, with the results attributed to factors such as the way that the probabilities were represented, or the benefits and consequences of different responses (see Green, Benson, Kersten, & Schrater, 2010; Wu et al., 2009, for representative examples of effects of uncertainty on different types of decisions).

Second, do ASEM depend only on the objective probabilities of motion, or does the nature or the perceptual configuration of the cue play a role as well? Finding a role for the nature or the configuration of the cue opens up a role for factors other than a representation of objective probability, such as prior beliefs about motion paths derived from the perceptual structure of the cue (Kowler, Aitkin, Ross, Santos, & Zhao, 2014; Ladda et al., 2007).

We performed three experiments. Experiment 1 compared ASEM evoked by a visual cue to ASEM based solely on memory when the probability of motion in a given direction was varied. Experiment 2 was done to follow-up aspects of the results of Experiment 1 and examined effects of memory in the presence of high levels of certainty. Experiment 3 again used visual cues, but this time the cues bore a semantic or structural relationship to the motion path, and the level of congruency between the cued path and the actual path was varied probabilistically. The results showed that ASEM were preserved in the presence of uncertainty, with the strength of the ASEM depending on both the probability level and on the nature and configuration of the cue.

Experiment 1: Memory-cues and visual cues of varying levels of reliability

Experiment 1 studied anticipatory smooth eye movements in response to a visual cue that signaled the probability of motion to the left or to the right. Performance was compared to that obtained when directional probabilities were derived solely from memory.

The target was a disc that moved vertically down an inverted Y-shaped outline tube, taking either the right or left oblique path (Figure 1). With such configurations, cues that disclose whether the target will enter the right or left path elicit horizontal ASEM before the onset of horizontal target motion, when the target first enters the cued path (Aitkin et al., 2013; Kowler, 1989; Kowler, Aitkin, Ross, Santos, & Zhao, 2014).

In the *memory-cue* condition the proportion of trials in which the target entered the left or to the right path varied across a block of trials, with the probability

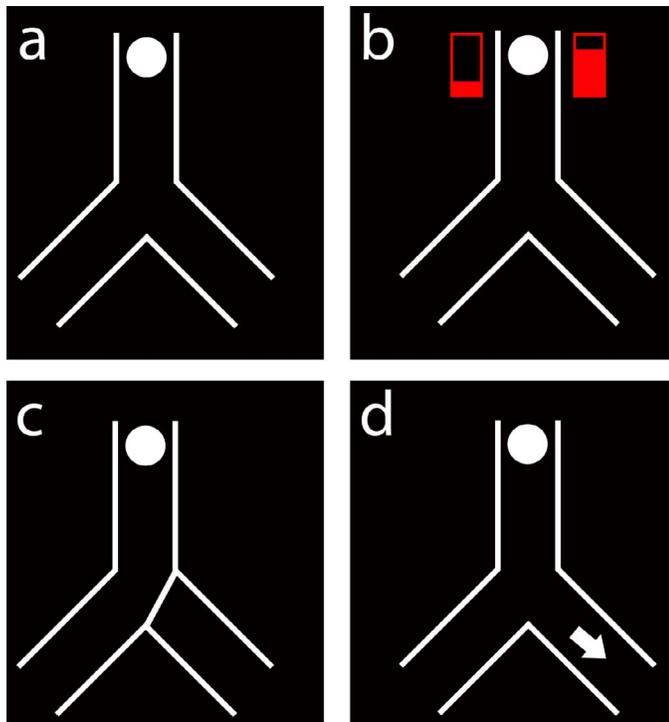


Figure 1. Illustrations of the experimental displays for the four types of cues. (a) Memory-cue: The proportion of trials in which the disc would move down the left or right oblique path varied across blocks of trials (Experiment 1); (b) Bar cue: The proportion of the bar filled in red indicated the probability that the disc would move down the left or right path on a given trial (Experiments 1 and 2); (c) Barrier cue: The disc moved down the unblocked path (congruent trials; Experiments 2 and 3) or the blocked path (incongruent trials), with the proportion of congruent trials varying across blocks (Experiment 3); and (d) Arrow cue: The disc moved down either the path indicated by the arrow (congruent trials) or the opposite path (incongruent trials) with the proportion of congruent trials varying across blocks (Experiment 3).

disclosed by a verbal message prior to each trial block (Figure 1a). Thus, the memory for the verbal message, as well as the memory for motions tracked in the preceding trials, provided information about the more probable direction of future target motion. In the *visual cue* condition, the probability of motion to the left or to the right was chosen randomly and independently on each trial, and was disclosed by a visual cue (a partially filled bar; Figure 1b).

Methods

Subjects

Six subjects participated in Experiment 1. Each had normal vision and did not wear glasses or contact lenses. All were naïve about 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.

Stimuli

The stimulus was displayed on a Dell U2413 monitor viewed at a distance of 60 cm, with a display area subtending 28.2° horizontally by 22.5° vertically, at a resolution of 1280×1024 pixels and a 60-Hz refresh rate.

The stimulus display consisted of a line drawing of an inverted Y-shaped tube (Figure 1). The walls of the tube were white, displayed on a black background. The oblique branches of the Y were at an angle of 40° from vertical. A 1° diameter-filled white disc, initially located near the top of the tube, moved downward for a vertical distance of 16.2° and then traveled down either the right or the left oblique branch.

Procedure

Before each trial a fixation cross appeared at the top of the display, at the position corresponding to the top of the tube. Subjects started the trial by means of a button press when ready. The inverted Y-shaped tube then appeared along with any cues that were to be used during the trial. As soon as fixation of the cross was verified by an online algorithm, the cross was replaced by the white disc. The disc remained stationary for 1 s and then began moving down the tube at $7.9^\circ/\text{s}$. The disc continued moving into either the left or right oblique branch of the Y. The horizontal component of the motion velocity in the oblique branch was $5.1^\circ/\text{s}$. Subjects were instructed to pay attention to the motion of the disc and to avoid using saccades to catch up to the target if the eye felt as if it were lagging behind (e.g., Kowler et al., 2014; Santos et al., 2012).

Experimental sessions

Trials were run in blocks of 40, with five blocks run each day for both the memory-cue and visual cue conditions. In the memory-cue condition, the probability of rightward motion (P_r) remained the same during each day of testing (200 trials/day). The order of testing of the five probability levels across days was randomly determined for each subject. In the visual cue condition the value of P_r was chosen randomly and independently on each trial. The probability level in the visual cue condition was indicated by the bars flanking the top of the stimulus, with the probability of motion in each direction indicated by the proportion of the bar filled with red (Figure 1b). Values of P_r were 0, 0.25, 0.5, 0.75, and 1.

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. The head was stabilized by a chin and forehead rest. Viewing was binocular.

Data analysis

Analyses were performed using custom developed Matlab software (MathWorks, Natick, MA). The onsets and offsets of saccades were determined offline by computing eye velocity during consecutive 13-ms samples, with onsets separated by 1 ms. Saccade onsets and offsets were detected using a velocity criterion that was determined and confirmed for each subject by examining a large sample of analog recordings of eye positions. The criterion was $22^\circ/\text{s}$ for five subjects and $13^\circ/\text{s}$ for one subject (subject SP).

Horizontal eye velocity was computed across 50-ms intervals with onsets of successive samples separated by 2 ms. Samples containing saccades, blinks, or portions of saccades or blinks were removed. Velocities were then averaged across time intervals relative to the start of the horizontal component of target motion (the entry of the disc into the oblique path). An index of ASEM strength was the mean eye velocity over a 100 ms interval, ± 50 ms around the onset of horizontal target motion. Once again, samples containing saccades, blinks, or portions of saccades, or blinks were removed. Slopes of the functions relating ASEM strength to probability of rightward motion were determined via a least squares fit using Matlab function `LinearModel.fit`. Five planned comparisons (t tests) were performed to (a) compare slopes over the three central probability values (0.25, 0.5, 0.75) to a value of zero (one-tailed) for the memory-cue and (b) the visual cue conditions; (c) compare slopes across the three central probability levels in the memory and the visual cue conditions to each other; (d) compare slopes across the three central probability levels to slopes across all five probability levels in the memory-cue and (e) visual cue conditions. The p value required for statistical significance, adjusted to reflect the Bonferroni correction based on the number of comparison ($n = 5$), was 0.01.

Results

ASEM were found with both the memory-cues and the visual cues. Figure 2 shows an example of horizontal eye velocity (mean ± 1 SEM) over time for one observer for different levels of the probability of motion to the right (P_r). Results for each of the intermediate probability levels ($P_r = 0.25, 0.5, 0.75$) are

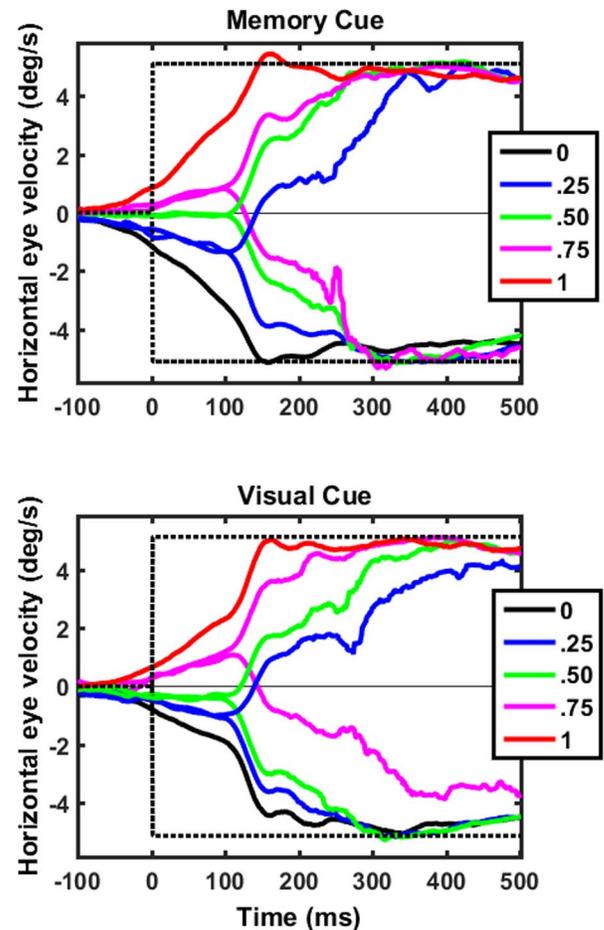


Figure 2. Experiment 1: Mean horizontal velocity over time ($^\circ/\text{s}$) (\pm SEM) for subject SP with memory-cues (top) and visual cues (bottom). Time 0 denotes the onset of the horizontal component of motion. Color indicates the probability of rightward motion (P_r), where $P_r = 0$ (black), 0.25 (blue), 0.5 (green), 0.75 (magenta), or 1 (red). The dotted line shows the horizontal velocity of the target. Each function is based on 173–200 observations. Positive values indicate motions to the right.

separated according to the actual direction of motion. The clear separations among the functions for the different levels of P_r , seen prior to the onset of the horizontal component of target motion with the memory-cues and with the visual cues, indicate the presence of ASEM. (See Figure S1 for examples of individual position traces for one subject when $P_r = 0$ and $P_r = 1$.)

Prior work with randomly selected target speeds (Kao & Morrow, 1994; Kowler & McKee, 1987) and computational models of anticipatory smooth eye movements (Bogadhi, Montagnini, & Masson, 2013; Orban de Xivry, Coppe, Blohm, & L efevre, 2013) suggest that anticipation should have consequences even after the onset of target motion. This can be seen in Figure 2, showing both the benefits and the costs of anticipation after the onset of the horizontal compo-

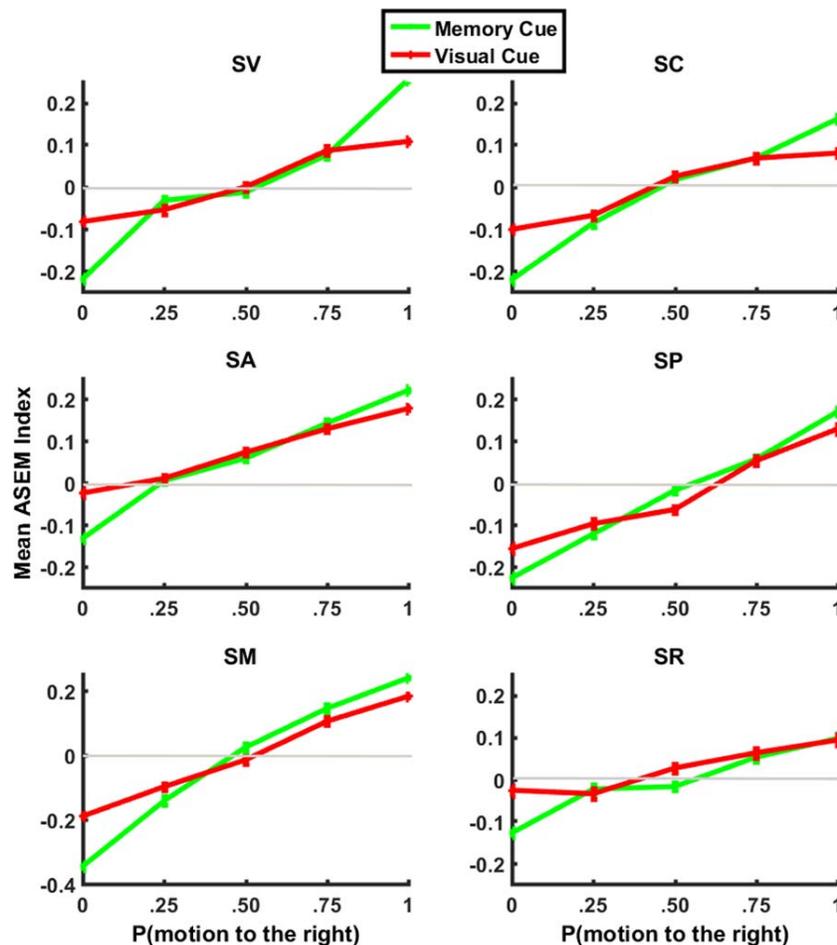


Figure 3. Experiment 1. Mean ASEM index (± 1 SEM) for the Memory-cue or the Visual Cue conditions for six subjects. The ASEM index was computed by dividing average eye velocity during the interval ± 50 ms around the onset of horizontal target motion by the velocity of the horizontal component of target motion ($5.1^\circ/\text{s}$). Each datum point is based on 150–200 observations. Positive values indicate motions to the right.

ment of target motion. When the actual direction of motion of the target matched the more likely direction (rightward target motion when $P_r = 0.75$, or leftward target motion when $P_r = 0.25$), eye velocity reached the velocity of the target by about 200 ms after the start of horizontal motion. However, when the target moved in the less likely direction (leftward target motion when $P_r = 0.75$ and rightward target motion when $P_r = 0.25$), the ASEM initially took the eye in the opposite direction. It took an additional 100–200 ms for the eye to turn around and for eye velocity to reach target velocity, illustrating the costs of anticipation.

To quantify the effects of the directional probability on ASEM, we computed an index of ASEM, defined as mean eye velocity for the interval ± 50 ms around the onset of the horizontal component of target motion divided by the horizontal velocity (positive values denote rightward movements of the eye or target). Figure 3 shows the ASEM index as a function of P_r for both types of cues.

ASEM depended on the probability of motion in each direction for both the memory-cues and the visual cues. This can be seen by the increase in the ASEM index as a function of P_r in Figure 3. Slopes of the functions related the ASEM index to P_r were greater than zero for the central three probabilities: $P_r = 0.25$ – 0.75 ; memory-cues, $t = 5.3(5)$, $p = 0.0016$; visual cues, $t = 9.7(5)$, $p = 10^{-4}$ (Table 1), showing that ASEM were present with both types of cues in the presence of uncertainty. Slopes for the central three probability levels were not significantly different for the memory-cues and the visual cues: $t = 0.96(5)$, $p = 0.38$.

Prior work on ASEM in the absence of cues reported sequential dependencies in which the ASEM in a given trial depended on the motion in the preceding trial (Collins & Barnes, 2009; Heinen et al., 2005; Kao & Morrow, 1994; Kowler, Martins, & Pavel, 1984; Santos et al., 2012; Yang & Lisberger, 2010). We confirmed that sequential dependencies occurred with the memory-cues, i.e., ASEM were typically biased in the direction of motion that was shown in the previous trial

Subject	Memory-cue: slope across five levels of P_r	Memory-cue: slope across central three levels of P_r	Visual cue: slope across five levels of P_r	Visual cue: slope across central three levels of P_r
SV	0.42	0.22	0.21	0.28
SC	0.36	0.31	0.20	0.27
SA	0.34	0.28	0.21	0.24
SP	0.39	0.36	0.29	0.30
SM	0.59	0.57	0.38	0.41
SR	0.21	0.15	0.13	0.19
Mean (SD)	0.385 (0.123)	0.314 (0.145)	0.237 (0.085)	0.282 (0.071)

Table 1. Experiment 1. Slopes of the functions of the index of ASEM strength versus the probability of motion to the right (P_r).

(see Figure S2). The sequential dependencies were most evident in four of the six subjects (SM; SC; SP; and SR). A repeated measures analysis of variance performed on results for the central three probability levels ($P_r = 0.25, 0.5, \text{ or } 0.75$), with probability level, prior direction of motion (right or left) and subjects ($n = 6$) as factors, showed marginally significant effects of prior direction, $F(1, 5) = 7.0, p = 0.046$, and a significant interaction between prior direction and subjects, $F(5, 10) = 13.4, p = 0.0004$. For the visual cues, where the directional probability was cued on each trial, sequential dependencies were weaker. This is as expected, given that the cue is providing information about the directional probabilities, independent of the prior trials. With the visual cue the effects of the direction on the prior trial were not significant overall, $F(1, 5) = 2.2, p = 0.2$, but there was a significant interaction between prior direction and subject, $F(5, 10) = 9.6; p = 0.0014$, due to the larger effects of prior direction in two of the six subjects (SM and SR; see Figure S2).

Although the slopes of the functions relating ASEM strength to P_r were similar for the visual cues and the memory-cues in the presence of uncertainty ($P_r = 0.25, 0.5, 0.75$; Figure 3), there were differences due to the type of cue at the highest levels of certainty. With the memory-cues, slopes across the central three probability levels were slightly smaller than the slopes across all five probability levels in each of the six subjects (binomial test, $p = 0.016$; Table 1), although the magnitude of the differences did not reach significance, $t = 2.49(5), p = 0.05$. For the visual cues, slopes across the central three probability levels were steeper than slopes across all five probability levels for all six subjects (binomial test, $p = 0.016$; Table 1) and significantly steeper overall, $t = 4.14(5), p = 0.009$. From Figure 3 it can also be seen that ASEM strength was greater at the highest levels of certainty with the memory-cues than with the visual cues. The differences between the memory-cues and visual cues at high levels of certainty led us to perform Experiment 2 in which we varied the proportion of trials with motion in a given direction while cuing the direction prior to each trial.

Experiment 2: Effects of repetition under high levels of certainty

Experiment 2 investigated the dependence of ASEM on the proportion of trials with motion in a given direction when the contribution of uncertainty was reduced by cuing the direction of motion with perfect certainty on each trial. This manipulation preserved the variation in the proportion of trials with motion in a given direction that was present with the memory-cues in Experiment 1, while removing objective uncertainty about future motion. Two types of visual cues were tested: (1) the filled bar used in Experiment 1 (Figure 1b), and (2) a barrier blocking the untraveled path (Figure 1c). Both cues conveyed the same information, but only the barrier cue provided a perceptual depiction of the motion path, as can be seen in Figure 1c.

Methods

Four subjects, all participants in Experiment 1, were tested. A visual cue presented before the trial disclosed the direction of motion with probability = 1. Two types of cues were tested: a barrier cue (Figure 1c), a line that blocked the untraveled path; or the bar cue used in Experiment 1 (Figure 1b), a filled red bar located on the side of the path in which the disc would travel. An unfilled bar was drawn on the other side. The proportion of trials with rightward motion, P_r , was set to 0, 0.25, 0.5, 0.75, or 1.0 during each 40 trial session. The value of P_r was kept the same for four consecutive experimental sessions. The index of ASEM strength was computed as in Experiment 1. Two planned comparisons (one-tailed t tests) were performed to compare slopes to a value of zero for the (a) bar cue and (b) barrier cue. The p value required for statistical significance, adjusted to reflect the Bonferroni correction based on the number of comparisons ($n = 2$) was 0.025.

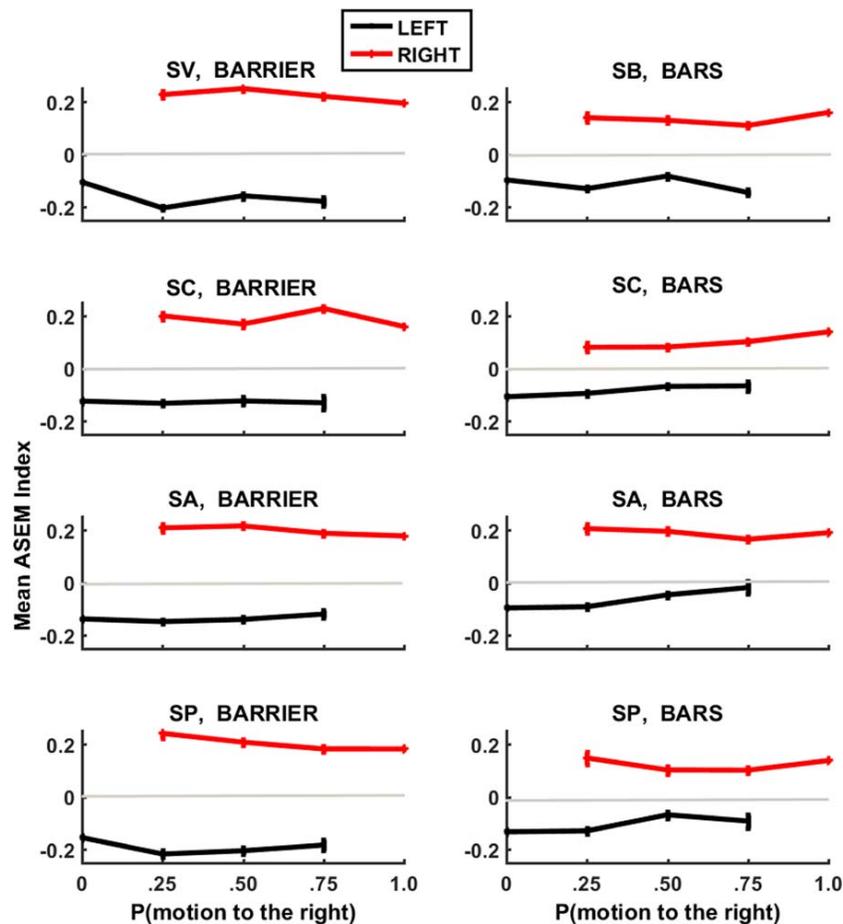


Figure 4. Experiment 2. Mean ASEM index (± 1 SEM) for four subjects when the direction of horizontal motion was cued by either the barrier (Figure 1c) or bar cue (Figure 1b) with the direction of motion always corresponding to the direction indicated by the cue. The abscissa shows the proportion of trials with motion to the right in a given block of 40 trials. The ASEM index was computed by dividing average eye velocity during the interval ± 50 ms around the onset of horizontal target motion by the horizontal velocity of target motion. Each datum point is based on 30–200 observations. Positive values indicate motions to the right.

Results and discussion

Both the bar and barrier cues produced strong ASEM, as shown by the separation between the functions for each cued direction (Figure 4). The barrier cue produced stronger ASEM than the bar cue, as shown by the larger separation of the functions. Thus, the information conveyed by the cues clearly dominated any effects of the proportion of trials with motion in a given direction.

Despite the dominance of the cues, the effects of trial proportions were not completely abolished for the weaker bar cue. Slopes of the functions for the bar cue (Figure 4) were shallow, but significantly greater than zero, $t = 2.675(7)$, $p = 0.016$ (Table 2). The ASEM for the stronger barrier cue were not influenced by the trial proportions: slopes of the functions in Figure 4 were not greater than zero; $t = -2.35(7)$, $p = 0.974$ (Table 2).

Although effects of trial proportions are consistent with sequential dependencies, we did not find signif-

icant differences between ASEM as a function of the direction of motion in prior trials (Figure S3): bar cue, left, $F(1, 3) = 1.1$, $p = 0.38$; bar cue, right, $F(1, 3) = 1.1$, $p = 0.37$; barrier cue left, $F(1, 3) = 4.12$, $p = 0.14$; barrier cue right, $F(1, 3) = 1.21$, $p = 0.35$.

Subject	Barrier cue: motion to left	Barrier cue: motion to right	Bar cue: motion to left	Bar cue: motion to right
SV	-0.161	0.0007	-0.04	0.06
SC	-0.008	-0.052	0.10	0.14
SA	0.0201	-0.045	0.16	-0.025
SP	-0.1024	-0.044	0.130	0.043

Table 2. Experiment 2. Slopes of the functions of ASEM strength versus the proportion of trials with motion to the right (P_r) for barrier cue and bar cues signaling that the motion would be to the left or to the right. Notes: Barrier cue: Mean slope (SD) = $-0.049(0.059)$, $N = 8$; bar cue: Mean slope (SD) = $0.071(0.075)$, $N = 8$.

These results show that the experience of tracking the same motion repeatedly can increase the strength of ASEM with a relatively weak cue. The effect of the repetition found for the bar cue may be similar to the stronger ASEM found with $P_r = 0$ or $P_r = 1$ for the memory-cue of Experiment 1. In each case ASEM could reflect either a passive process that remembers and repeats recent responses, or an effect of repetition on the salience of the expectations about future motion direction (Collins & Barnes, 2009; Kowler et al., 1984; Yang & Lisberger, 2010). Such tendencies, however, were largely overridden by cues, either the visual bar cue of Experiment 1, or the bar and the barrier cues of Experiment 2.

Experiment 3: Effects of the level of congruency between the perceptual structure of the cue and the motion path

Experiment 3 tested the consequences of introducing uncertainty using cues that had clear semantic or perceptual links to the motion path. This was done by varying the proportion of trials in which the motion of the target was congruent with the motion path depicted by the cue.

Two types of cues were tested, a barrier blocking one path (Figure 1c), or an arrow pointing to one path (Figure 1d). In the congruent trials the target either moved along the unblocked path or moved in the direction pointed to by the arrow. In the incongruent trials the target either crashed through the barrier, or moved opposite to the direction signaled by the arrow. Thus, incongruent trials created a conflict between the direction of motion depicted by the cue and the direction of motion that would be expected on the basis of recent past experience or knowledge of the level of congruency. The key question is whether manipulations of the proportion of congruent trials would override any longer term prior perceptual or semantic interpretations of the cues. Previous studies demonstrated differences between the effects of totally congruent or incongruent cues on ASEM (Kowler et al., 2014; Ladda et al., 2007), but did not introduce uncertainty between the perceptual structure of the cue and the motion path.

Methods

The stimulus was the same as in Experiments 1 and 2 except that the following two types of cues were

tested, either a barrier blocking the untraveled path (Figure 1c), or an arrow pointing to one of the paths (Figure 1d). The path of motion of the target was either congruent or incongruent with the path of motion depicted by the barrier cue or pointed to by the arrow cue. The proportion of trials in which the motion path was congruent with the semantic or perceptual aspects of the cue remained constant across blocks of 120–240 trials and was announced prior to each block. The proportion of trials with congruent motion was 0, 0.25, 0.5, 0.75, or 1.0, except for one subject (SJ), for whom the proportions were 0, 0.17, 0.33, 0.5, 0.67, 0.83, or 1.

Two subjects (SR and SV) were tested using the same experimental display apparatus as in Experiment 1. SR ran in Experiment 3 prior to Experiment 1; SV ran in Experiment 3 after running in Experiments 1 and 2. Five additional subjects were tested using a Viewsonic G90fb 19 in CRT display with 60-Hz refresh rate, resolution of 1280×1024 pixels, located at 118 cm from the eye. The display area subtended 16.2° horizontally by 12.3° vertically. The horizontal velocity of the target within the oblique portion with this display was $2.8^\circ/\text{s}$. This group of five included subject SA, who ran in Experiment 3 prior to running in Experiments 1 and 2.

Analyses were the same as in Experiment 1. The following eight planned comparisons (t tests) were performed: (a) comparisons of slopes of ASEM index versus congruency level (one-tailed t test) to a value of zero for the barrier cue and (b) for the arrow cue conditions; (c) comparisons of slopes over the three central congruency levels (0.25, 0.5, 0.75; one-tailed t test) to a value of zero for the barrier cue and (d) for the arrow cue conditions; (e) comparisons of slopes across the three central probability levels to slopes across all five probability levels for the barrier cue and (f) the arrow cue conditions; (g) comparisons of ASEM strength in the completely congruent ($P = 1$) and completely incongruent ($P = 0$) conditions for the barrier cue and (h) the arrow cue conditions. The p value required for statistical significance, adjusted to reflect the Bonferroni correction based on the number of comparison ($n = 8$) was 0.006.

Results

If ASEM depend solely on the motion path depicted by the cue, independently of the proportion of congruent trials, the functions relating ASEM to the proportion of congruent trials for each cued direction (left or right) would be flat and separated by an amount that reflects the influence of the cue. Alternatively, if the level of congruency is the only factor that determines the anticipated path of future

target motion, then the ASEM would be strongest at both extreme levels of congruency (equivalent to highest levels of certainty) and the functions for the two cued directions would intersect when the proportion of congruent trials is 0.5.

The outcome depended on the type of cue. With the arrow cue, ASEM depended on the level of congruency, with little effect of the semantic aspects of the cue. The slopes of the functions relating the ASEM index to cue congruency were greater than zero (Figure 5 and Table 3): $t = 9.20(13)$, $p = 2 \times 10^{-7}$, including across the central three congruency levels, $t = 3.52(13)$, $p = 0.002$. Slopes across the central three congruency levels were shallower than slopes across all five levels, $t = 3.87(13)$, $p = 0.002$, showing a reduction in ASEM due to uncertainty (similar to what was found for the memory-cues of Experiment 1). The strength of ASEM, assessed by the difference between ASEM for cued motion to the right and to the left, was about the same for the totally congruent cues, mean = 0.24, $SD = 0.12$, and totally incongruent cues, mean = 0.21, $SD = 0.09$, $t = 0.65(12)$, $p = 0.53$, and the functions for cues to motion to the right and to the left intersected at a congruency level near 0.5. These results showed no evidence for an effect of the semantic aspect of the arrow cue on the ASEM.

ASEM with the barrier cue, on the other hand, depended on both the perceptual attributes of the cue and on the level of congruency. Effects of congruency were shown by the slopes of the functions relating the ASEM to the congruency level (Figure 5; Table 4), which were significantly greater than zero, $t = 9.12(13)$, $p = 3 \times 10^{-7}$, including across the central three congruency levels, $t = 5.19(13)$, $p = 9 \times 10^{-5}$ (Table 4). Slopes across all five congruency levels and central three congruency levels were not different; $t = 1.38(13)$, $p = 0.19$. In contrast to the findings with the arrow cue, the difference in the ASEM index for the two cued directions was much larger for totally congruent cues (mean = 0.44, $SD = 0.16$) than totally incongruent cues, mean = 0.12, $SD = 0.12$, $t = 4.32(12)$, $p = 10 \times 10^{-4}$ (similar to Kowler et al., 2014; Ladda et al., 2007), with the functions for the two cued directions intersecting at congruency levels near 0.25.

The pattern of results with the barrier cue shows that the strong effects of the perceptual and structural attributes of the barrier cue added to the modulations in ASEM strength due to variations in congruency. Thus, with a compelling perceptual cue, the direction of motion depicted by the cue continued to influence ASEM despite the reductions in congruency. The barrier induced a strong bias in ASEM strength in the cued direction that persisted across all the tested levels of congruency.

General discussion

The present study examined anticipatory smooth eye movements evoked by different types of cues that conveyed probabilistic information about the direction of future motion. The main findings were (a) uncertainty does not abolish ASEM elicited by cues, (b) the strength of ASEM depended on the probability of motion in a given direction, and (c) objective probabilities alone did not determine the results. The strength of ASEM also depended on the nature of the cue.

The dependence on the probability of motion to the right or left is a rational strategy. Pursuit gets a head-start in the majority of cases, when the target moves in the more probable direction, while minimizing the negative consequences (higher retinal velocities) when the target moves in the less probable direction. The dependence on probability was found regardless of whether the probability of motion in a given direction was given by the memory for the directions of recent motions coupled with an initial verbal message (Experiment 1), by a visual cue depicting directional probabilities (Experiments 1 and 2), or by memory for the level of perceptual congruency between the cue and the motion path, coupled with an initial verbal message (Experiment 3).

We also found that the relationship between ASEM and the probability levels changed in systematic ways depending on the nature of the cue that signaled the likely direction of motion. The effects of the nature of the cue suggested that other factors, beside objective probability, are influential. These factors include the way in which probabilities are represented or remembered, and prior beliefs about the direction of motion depicted by the cue. These additional factors will be discussed below.

Memory-cues versus visual cues

With the memory-cues (Experiment 1), ASEM depended on probability levels. Departures from strict probability matching were found at the highest levels of certainty about the future direction of motion ($P_T = 0$ or 1), where ASEM were stronger than would be predicted by a strictly linear relationship between probability and ASEM strength. These effects, though small, were found in all observers. The stronger ASEM under the highest levels of certainty could be due to the reduced levels of monitoring required when the same direction of motion was tested repeatedly, or, alternatively, to a passive processes that may remember and repeat the target motions of the recent past (Collins & Barnes, 2009; Kowler et al., 1984; Santos et

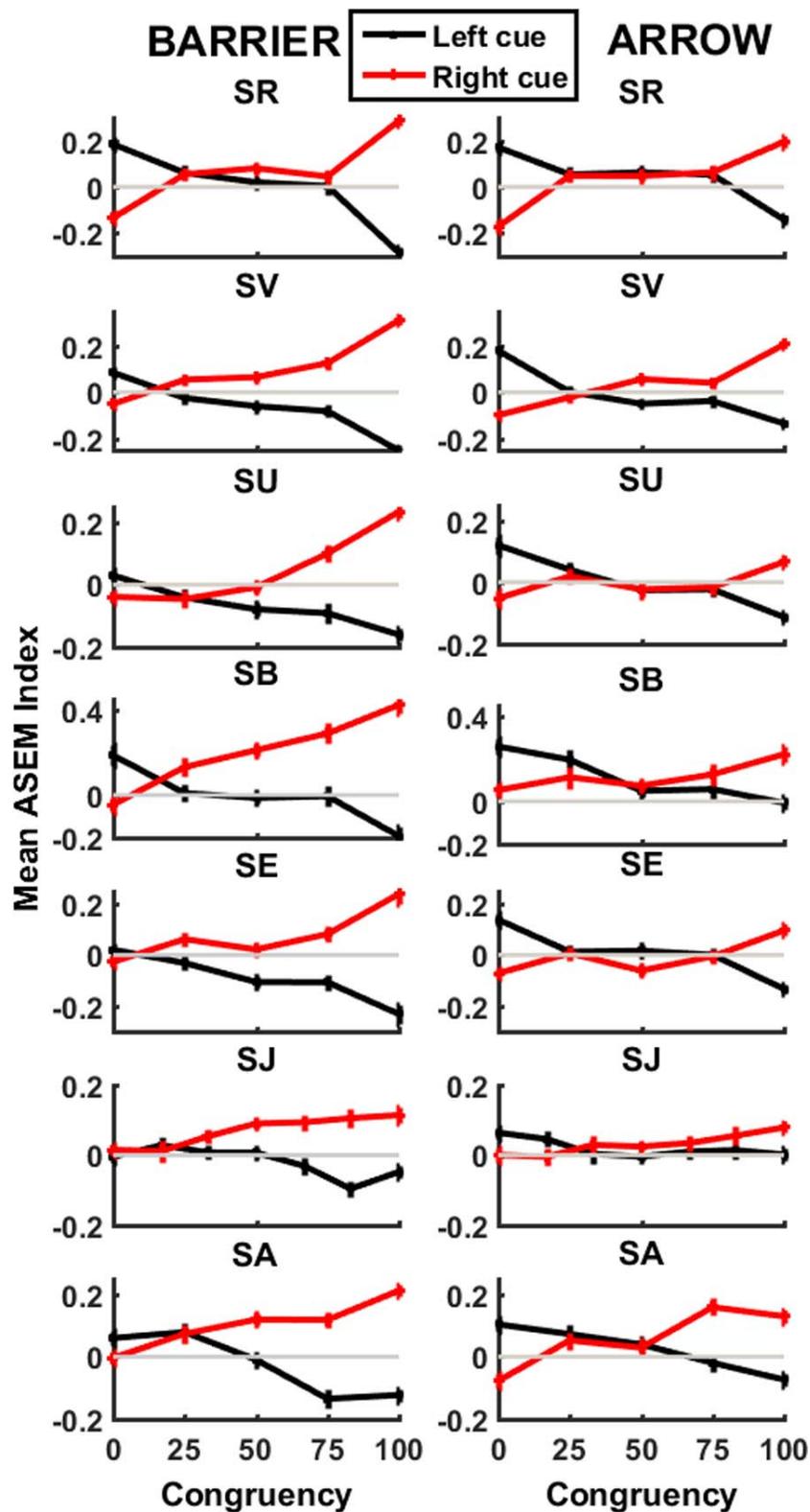


Figure 5. Experiment 3. Mean ASEM index (± 1 SEM) for seven subjects. The barrier cue (left) (Figure 1c) or arrow cue (right, Figure 1d) signaled motion to the left (black lines) or to the right (red lines). The abscissa shows the percentage of trials in which the actual motion direction was congruent with the cued direction. The ASEM index was computed by dividing average eye velocity during the interval ± 50 ms around the onset of horizontal target motion by the horizontal velocity of target motion. Number of observations/datum point as follows: SR, 57–93; SV, 76–104; SU, 97–174; SB, 49–135; SE, 59–253; SJ, 55–103; SA, 94–126. Positive values indicate motions to the right.

Subject	Arrow cue, motion to left: slope across five levels of congruency	Arrow cue, motion to left: slope across central three levels of congruency	Arrow cue, motion to right: slope across five levels of congruency	Arrow cue, motion to right: slope across central three levels of congruency
SR	−0.20	−0.22	0.24	0.16
SV	−0.15	−0.04	0.15	0.07
SU	−0.21	−0.12	0.08	−0.07
SB	−0.27	−0.28	0.14	0.03
SE	−0.18	−0.03	0.10	−0.03
SJ	−0.05	−0.03	0.08	0.07
SA	−0.18	−0.18	0.21	0.21
Mean (SD)	−0.18 (0.07)	−0.13 (0.11)	0.14 (0.06)	0.06 (0.10)

Table 3. Experiment 3. Slopes of the functions of ASEM strength versus the proportion of trials in which the motion of the disc was congruent with the motion depicted by the Arrow Cue when the arrow cue signaled motion to the right or to the left. *Note:* Positive values indicate rightward motions, as in Figure 5.

al., 2012; Yang & Lisberger, 2010). Either process is consistent with the observed pattern of sequential dependencies for the memory cues of Experiment 1, or the small effects of directional proportions found for the weaker bar cues under high levels of certainty in Experiment 2.

The same pattern, relatively stronger ASEM under the highest levels of certainty, was also found for the arrow cues in Experiment 3, where ASEM were stronger for the extreme levels of congruency (0 or 1) than would be expected from a strict linear relationship between congruency level and ASEM. Memory played a role with the arrow cues in that the level of congruency between the cued path and the actual path was varied across blocks of trials, and thus was monitored using memory, rather than explicitly signaled by a perceptual cue on each trial. In the case of the extreme levels of congruency, however, unlike the extreme probabilities of motion in a given direction in Experiment 1, the role of any passive processes that may remember and repeat the directions of target motions of the recent past would not be helpful because the congruency level (0 or 1), not the direction, remained constant across blocks of trials.

A dependence on directional probability was also observed when probabilities were signaled on each trial by a visual cue in Experiment 1. In the visual cue condition of Experiment 1, probability level was selected randomly and independently on each trial and the cue (a partially filled bar) signaled the probability before the trial. With the visual cues of Experiment 1, sequential dependencies on the direction of motion in the prior trial were weaker than with the memory-cue of Experiment 1. This result shows that cues override effects of recent past history on ASEM even when there is uncertainty about future motion direction.

The main difference between performance with the memory-cue and visual cue of Experiment 1 was that the increase in strength of the ASEM under high levels of certainty found for the memory-cue was not observed for the visual cue. Instead, a different pattern was observed with the visual cues. The difference between ASEM strength for the two probability levels that favored rightward motion ($P_r = 0.75$; $P_r = 1$) was smaller than the difference between ASEM strength for $P_r = 0.75$ and $P_r = 0.5$. Similarly, differences in ASEM between $P_r = 0$ and 0.25 were smaller than differences in ASEM strength between $P_r = 0.25$ and 0.5. This

Subject	Barrier cue, motion to left: slope across five levels of congruency	Barrier cue, motion to left: slope across central three levels of congruency	Barrier cue, motion to right: slope across five levels of congruency	Barrier cue, motion to right: slope across central three levels of congruency
SR	−0.33	−0.39	0.28	0.25
SV	−0.16	−0.06	0.17	0.08
SU	−0.16	−0.10	0.28	0.30
SB	−0.28	−0.04	0.42	0.32
SE	−0.20	−0.15	0.17	0.04
SJ	−0.09	−0.17	0.11	0.13
SA	−0.24	−0.42	0.19	0.09
Mean (SD)	−0.21 (0.08)	−0.19 (0.15)	0.23 (0.11)	0.17 (0.11)

Table 4. Experiment 3. Slopes of the functions of ASEM strength versus the proportion of trials in which the motion of the disc was congruent with the motion depicted by the barrier cue when the barrier cue signaled motion to the right or to the left. *Note:* Positive values indicate rightward motions, as in Figure 5.

finding suggests a role for how the visual cues were interpreted. Cues indicating that motion in a given direction was likely may have been treated in similar ways, without as precise a distinction as the objective probabilities would warrant. Distinctions between equal and unequal probability levels (0.5 vs. 0.25; 0.5 vs. 0.75), on the other hand, may have been drawn more sharply.

The ways in which ASEM strength departed from a strictly linear relationship with probability levels for either the memory-cues or the visual cues, summarized above, may be compared to prior work on effects of probabilities on decisions. Wu et al. (2009) found that for decisions based on explicit presentations of probability levels, the probability levels were typically represented in ways similar to what we found for the memory-cues, namely, functions relating representations of probability levels to objective probabilities were flatter in the central portion (i.e., overweighting low probabilities and underweighting high probabilities). Wu et al. (2009) also found that for decisions based on implicit representations of probability, derived from knowledge of one's own motor variability in a pointing task, probability levels were typically represented in ways more similar to what we found for the explicit visual cues, namely, functions relating representations of probability levels to objective probabilities were typically steeper in the central portion (i.e., underweighting low probabilities and overweighting high probabilities).

This comparison of results across the two studies suggests that the key factor that determines the relationship between performance and probability levels may not be whether the information about probability is given implicitly or explicitly (see also Trampenau, Kuhtz-Buschbeck, & van Elmeren, 2015). However, comparing these studies is not straightforward. Wu, Delgado, & Maloney (2009) tested verbal reports of decisions and used these reports to estimate the representations of probability levels. We measured motor activity. Representations of probability may differ across these two very different types of tasks and measures. In addition, it is possible that our results reflected processing stages downstream from stages that represent probabilities. Finally, it is important to note that subjects had considerable discretion in how they chose to approach the visual cues, including the need to notice and interpret the cue on each trial; thus, variations in any of these stages of processing could have affected performance. Nevertheless, it is interesting that the same types of departures from a strictly linear relationship with probability levels that are found for decisions are also found in smooth eye movements, and that these relationships depend on task characteristics.

The congruency between the cue and the motion path

The strong effects of the perceptual structure of the cues that were found in Experiments 2 and 3 provided another way in which the observed ASEM did not depend strictly on objective probability levels, but also depended on the type of cue.

Cues that had a clear structural link to the motion path, namely, the barrier cue tested in Experiments 2 and 3, produced a strong bias of ASEM in the direction depicted by the cue. In Experiment 2 the effect of the barrier cue was strong enough to override an influence of the proportion of trials with motion in a given direction. By contrast, the proportion of trials with motion in a given direction affected the ASEM with the weaker bar cues in Experiment 2.

Effects of the structural properties of the cues were even more apparent in Experiment 3. There, ASEM were biased to occur in the direction depicted by the structural barrier cue even when the level of congruency between the cued path and the actual path was reduced (see also Kowler et al., 2014; Ladda et al., 2007). The strong effects of the motion path depicted by the barrier cue are similar to other reports of effects of the pattern of motion implied by visual cues on smooth pursuit (Badler et al., 2010; Souto & Kerzel, 2013).

The bias in ASEM induced by the barrier cue may be analogous to the way in which strong prior beliefs about the configurations of natural scenes influence perceptual judgments. Long-standing prior beliefs, acquired due to evolution or during years of life experience, may be resistant to modification by short-term laboratory experiments (Serriès & Seitz, 2013; Ma, 2012). Studies of perceptual judgments or motor behaviors have shown that cues and prior beliefs tend to combine in proportion to their relative reliabilities (Knill, 2005; Kording & Wolpert, 2004; Seydell, Knill, & Trommershauser, 2011). In this framework the compelling depiction of the motion path created by the barrier cue constitutes a strong prior that would allow the depicted path to receive a high weight relative to other available cues, such as retinal image motion or memory for previous motions. The extent to which prior beliefs and other cues (memory, image motion) combine in statistically optimal ways to determine ASEM remains an area for further investigation.

The benefits and costs of anticipatory smooth eye movements

The utility of anticipatory smooth eye movements, like that of anticipatory movements more generally,

would appear to be clear: to reduce processing delays and achieve a better overall outcome. For anticipatory motor behaviors involved in, for example, intercepting moving targets, the desired outcome is a higher rate of interception (Bosco et al., 2015; Zhao & Warren, 2015).

Anticipatory smooth eye movements, however, are found without any defined behavioral goals other than to attend to and track the moving target. It is not necessary to intercept the target or to evaluate its visual properties. Why anticipate? Any negative consequences of failures to anticipate, such as additional retinal image motion, or lags of eye position relative to target position, are not reflected in any concrete behavioral outcome other than the pursuit itself. The additional image motion due to processing delays following the onset of target motion is transient, and any positional lags of the eye behind the target can be compensated for by saccades. Moreover, any benefits due to anticipation would have to be balanced against the potential costs of the increase in image motion prior to the onset of target motion due to the anticipatory smooth eye movements. All these considerations point to need for a more complete understanding of the potential benefits of anticipatory smooth eye movements, and the nature of the costs that a failure to anticipate might incur.

The present results, showing that anticipatory smooth eye movements depend on the level of uncertainty and the type of cue used to signal upcoming motion, have implications for understanding the potential benefits of anticipatory smooth eye movements. The argument has been made that one benefit of anticipation in perception is that by taking advantage of cues or redundancies, it is possible to reduce the load attached to analyzing incoming sensory signals (Bar, 2004; Kok, Jehee, & de Lange, 2012). Such arguments may be particularly relevant to pursuit. By taking advantage of cues, long-term prior knowledge of likely motion trajectories, probabilistic information and memory for recent motions (information that is also relevant to ongoing motor or perceptual processing), a pursuit response can be determined that represents the most likely pattern of future target motion with less dependence on costly, moment-by-moment sensory analyses.

The efficiencies of processing that may result from programming pursuit on the basis of beliefs about future target motions, available cues, prior knowledge, and memory needs to be taken into account when seeking to understand the benefits of anticipation in fulfilling the overall objectives of smooth pursuit eye movements, either when pursuit is performed alone or in conjunction with other behavioral tasks.

Summary and conclusions

We found that anticipatory smooth eye movements (ASEM) could be elicited by perceptual cues that conveyed probabilistic information about the direction of future motion. ASEM were found with all three types of cues tested: (a) cues based on memory for prior motions coupled with a verbal message disclosing probabilities prior to each block of trials; (b) cues that symbolically indicated the probabilities on each trial; (c) cues whose perceptual structure depicted the motion path, with the level of congruency between the depicted and actual path varying probabilistically. The strength of ASEM depended on both the probability levels and the type of cue. The dependence on the type of cue points to a role for how different types of cues are represented or interpreted.

The results contribute to the growing body of evidence that smooth pursuit uses multiple factors, including perceptual cues, memory for the recent past, and prior beliefs, to anticipate the future motion path. The present results show that uncertainty about the information conveyed by these cues does not prevent them from contributing to the anticipatory response. Anticipatory pursuit can reduce retinal image motion due to processing delays, and may reduce the dependence of pursuit on costly moment-by-moment sensory analysis.

Keywords: anticipatory smooth eye movements, anticipatory pursuit, anticipation, smooth pursuit, eye movements, smooth eye movements, motion, decisions, representations of probabilities, expectations

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