Anticipatory smooth eye movements with random-dot kinematograms

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Anticipatory smooth eye movements were studied in response to expectations of motion of random-dot kinematograms (RDKs). Dot lifetime was limited (52–208 ms) to prevent selection and tracking of the motion of local elements and to disrupt the perception of an object moving across space. Anticipatory smooth eye movements were found in response to cues signaling the future direction of global RDK motion, either prior to the onset of the RDK or prior to a change in its direction of motion. Cues signaling the lifetime of the dots were not effective. These results show that anticipatory smooth eye movements can be produced by expectations of global motion and do not require a sustained representation of an object or set of objects moving across space. At the same time, certain properties of global motion (direction) were more sensitive to cues than others (dot lifetime), suggesting that the rules by which prediction operates to influence pursuit may go beyond simple associations between cues and the upcoming motion of targets.

Keywords: anticipatory smooth eye movements, anticipatory pursuit, smooth pursuit, random-dot kinematogram, global motion, object motion, motion perception, expectations, eye movements


Introduction

Smooth pursuit eye movements maintain the line of sight on selected moving targets, allowing the retinal velocities of the targets to remain at levels that support clear vision. Considerable progress has been made over the past decades in understanding the nature of the motion signals that contribute to the control of pursuit, the neural pathways involved in transforming the motion signals to a pursuit motor command, and the contribution of high-level signals, including expectations and prediction, to the generation of the pursuit response (Barnes, 2008; Heinen & Keller, 2003; Kowler, 2011; Krauzlis, 2004; Lisberger, 2010; Spering & Montagnini, 2011).

Expectations and prediction are crucial to effective smooth pursuit because they help overcome inevitable delays in processing, thus avoiding large or unexpected mismatches between the motion of the target and motion of the eye (Collewijn & Tamminga, 1984; Dallos & Jones, 1963; Dodge, Travis, & Fox, 1930; Westheimer, 1954).

The role of expectations and prediction in the control of pursuit is shown by anticipatory smooth eye movements. Anticipatory smooth eye movements are smooth eye movements in the direction of expected future target motion that are observed either prior to the onset of target motion or prior to an expected change in the direction of motion (Badler, Lefèvre, & Missal, 2010; Boman & Hotson, 1988, 1992; de Hemptinne, Lefèvre, & Missal, 2008; Eggert, Ladda, & Straube, 2009; Heinen, Badler, & Ting, 2005; Jarrett & Barnes, 2002; Kowler, 1989; Kowler & Steinman, 1979a, 1979b; Ladda, Eggert, Glasauer, & Straube, 2007). Anticipatory smooth eye movements can be elicited by symbolic cues that disclose the direction of future motion (Badler, et al., 2010; de Hemptinne et al., 2008; Eggert et al., 2009; Jarrett & Barnes, 2002; Kowler, 1989; Kowler & Steinman, 1979a, 1979b; Ladda, Eggert, Glasauer, & Straube, 2007), or, in the absence of cues, by expectations derived from the prior history of target motions (Burke & Barnes, 2008; Collins & Barnes, 2009; de Hemptinne, Nozaradan, Duvrier, Lefèvre, & Missal, 2007; Heinen et al., 2005; Kowler, 1989; Kowler, Martins, & Pavel, 1984; Maryott, Noyce, & Sekuler, 2011; Yang & Lisberger, 2010). Neurophysiological studies in monkeys have linked anticipatory smooth eye movements to activity in the supplementary eye fields (SEF), pointing to SEF as a site that may be responsible for...
the initiation or control of the anticipatory movements (de Hemptinne et al., 2008; Heinen, 1995; Missal & Heinen, 2004).

The present study was done to determine whether representations of object motion are necessary to generate anticipatory smooth eye movements. The targets used in prior studies of anticipatory smooth eye movements were typically small targets moving against either uniform or structured visual backgrounds, much like the moving targets found in natural environments. Such stimuli convey the clear and sustained perceptual impression of an object moving across space. Are such representations of object motion necessary to generate anticipatory smooth eye movements? Given that anticipatory smooth eye movements are often described as a high-level phenomenon, it would be reasonable to assume that the expected motion would have to resemble the motion of natural objects in order to evoke an anticipatory response. Alternatively, any expected motion signal may be able to produce an anticipatory response.

Recent results by Montagnini, Spering, and Masson (2006) supported the view that signals representing object motion are needed to generate anticipatory responses and that other, more primitive motion signals are ineffective. This conclusion was based on their finding that anticipatory smooth eye movements in response to a tilted line moving horizontally could be evoked by expectations about the expected direction of object motion (i.e., 2D horizontal motion), and not by expectations about the direction of the more primitive 1D edge motion signals orthogonal to line orientation. Although transient responses to the 1D motion signals could be seen early in the vertical component of pursuit (see also Masson & Stone, 2002), these vertical movements were immune to anticipatory effects. The present study investigated whether representations of expected object motion are needed to generate anticipatory smooth eye movements. We eliminated representations of expected object motion by using targets that did not convey the perceptual impression of an object moving across space. Targets were random-dot kinematograms (RDKs) composed of moving, limited-lifetime elements that continually disappeared and reappeared in new locations. RDKs made with limited-lifetime dots generate global motion cues, but do not support representations of the motion of discrete objects over space because it is not possible to select and track an element or set of elements for longer than their brief lifetimes. Dosher, Landy, and Sperling (1989) studied 3D shape-from-motion perception using patterns with limited-lifetime dots for similar reasons, namely, to remove local cues to motion of individual elements. They found that the perception of 3D shape was unaffected by the brief lifetimes of the elements in the patterns.

RDKs differ from conventional moving objects in other ways. Illusory stationary boundaries are produced at regions of the pattern where the motion trajectory changes, and it is not possible to smoothly pursue the local dot motions across the static boundary, showing that the global motion dominates local dot motion. Motion-defined boundaries are important for defining the contours of shapes (Regan, 2000), implying that systems that analyze the global motion of RDKs might be more concerned with supporting perceptual segmentation and shape perception than with generating representations of the motion of objects across space that may be crucial for driving pursuit.

Prior studies have examined pursuit of RDKs with either unlimited- (Heinen & Watamaniuk, 1998; Osborne & Lisberger, 2009; Schütz, Braun, & Gegenfurtner, 2009) or limited-lifetime patterns (Debono, Schütz, Spering, & Gegenfurtner, 2010; Krauzlis & Adler, 2001; Schraa-Tam et al., 2009; Schütz, Braun, Movshon, & Gegenfurtner, 2010), although none of these prior studies involved anticipatory smooth eye movements. Heinen and Watamaniuk (1998), for example, found that the gain of pursuit of unlimited-lifetime kinematograms increased with the size of the field, showing that the pursuit system is able to integrate motion cues across space. Using limited-lifetime RDKs of varying levels of coherence (i.e., varying ratios of signal-to-noise motion), Krauzlis and Adler (2001) found that both the direction of pursuit and of perceived motion could be biased in comparable ways by cues disclosing the likely direction of the global motion. These effects on pursuit could have involved expectations or, alternatively, could have been due to variations in the strength of selective attention to the signal dots. Schütz et al. (2010) found that pursuit of RDKs with limited-lifetime dots depends on the proportion of coherently moving dots, as well as on the ability to separately attend to the signal dots in the pattern.

Three experiments were done in this study, and all studied anticipatory smooth eye movements in response to expectations about the direction of future RDK motion for RDKs composed of limited-lifetime elements. In all experiments, the direction of future RDK motion was disclosed by symbolic cues. In Experiment 1 anticipatory smooth eye movements were examined prior to the onset of RDK motion. In Experiment 2 anticipatory smooth eye movements were investigated prior to a change in the direction of RDK motion. In both Experiments 1 and 2, different values of the dot lifetimes were tested in order to establish the generality of the effects. RDK patterns with unlimited lifetimes were also included as controls because such patterns support representations of the motion of discrete objects, i.e., it is possible to select and track the
sustained motion of one or more dots. Experiment 3 also used patterns with limited-lifetime elements and also used symbolic cues to disclose the direction of upcoming motion. Experiment 3 differed from the preceding two experiments in that the main purpose was to investigate effects of dot lifetime and cues to dot lifetime.

Experiment 1: Anticipatory smooth eye movements prior to the onset of motion of RDKs

Methods

Subjects

Eight subjects participated, all with normal vision, naïve to the purpose of the experiment, and none with prior experience in studies of smooth pursuit. The research protocol was approved by the Rutgers University IRB and is in accordance with the Declaration of Helsinki.

Stimuli

RDKs with brief lifetimes were displayed on a Dell P793 CRT monitor (Dell Corporation, Round Rock, TX) (13° × 12°; viewing distance 115 cm, 1.46 pixels/ minarc; refresh rate of 75 Hz, noninterlaced). Nine hundred small white squares (87 cd/m², size 4’ × 4’) moved coherently within a 9.9° × 9.9° square region (9 dots/deg²) against a black background. The velocity of a given dot was 150 minarc/s. The direction of motion (up, down, left, or right) was the same for all dots and was selected randomly before each trial.

There were two main conditions. In the cued-direction condition, the fixation cross was displaced 2° from center in the direction opposite to the future direction of motion (up, down, right, or left). Thus, the displacement served as a cue to indicate the direction of future motion (see Krauzlis & Adler, 2001 for use of a comparable cue). In the uncued-direction condition, the fixation cross was always at the center. Cued- and uncued-direction trials were run in separate 50-trial experimental sessions (Figure 1, top panel).

The lifetime of a dot is defined as the time a given dot remains on the screen before it is relocated to a new random location inside the display region. Three different brief lifetimes were tested: 4 (52 ms), 8 (104 ms), or 16 frames (208 ms). These lifetimes were sufficiently brief so that sustained pursuit of selected local elements would be precluded (Kowler & McKee, 1987). Displays with unlimited-lifetime dots were also tested. Reducing dot lifetime also introduced noise into the motion signal (see Appendix A for details).

Lifetime was chosen randomly prior to each trial. In order to ensure that all the limited-lifetime dots did not disappear at once on the same frame, the initial age of each dot was chosen randomly from values ranging from one frame to the maximum lifetime for that trial.

Procedure

Subjects fixated a stationary cross and started the trial by means of a button press when ready. The cross was then replaced by a field of static dots for 500 ms. Then, the motion began for either 1.5 s (uncued-direction condition) or 2.0 s (cued-direction condition). The subjects were instructed to pay attention to the motion of the dots and not to try to use saccades to catch up with the moving random dots if he or she felt that pursuit was lagging behind.

To test for the possibility that the displacement of the fixation cross by itself might induce drifts to display center (in the direction of the expected motion) in the cued condition, blocks of trials were run with the same stimulus used in the cued condition except that all dots remained stationary, thus no motion was expected. Under these conditions, no systematic drifts toward center were found.
Eye movement recording

Horizontal and vertical movements of the right eye were recorded using a Generation IV Double Purkinje Image Tracker (Fourward Technologies, Gallatin, MO) (Crane & Steele, 1978). The left eye was covered and the head was supported by a chinrest. The tracker’s voltage output was fed online through a low-pass 100 Hz filter to a 12-bit analog to digital converter (ADC). The ADC, controlled by a PC, sampled the eye’s position every 2 ms. The digitized voltages were stored for analysis. Changes in the pattern of motion on the screen (onsets, offsets, and direction changes) were recorded by the onsets and offsets of a small white square displayed out of the subject’s view. The white square was monitored by a photocell whose output was fed to a channel of the ADC and recorded along with the eye position to ensure accurate temporal synchronization between the analysis of critical changes in the stimulus display and the eye movements.

Tracker noise level was measured with an artificial eye after the tracker had been adjusted to have the same first and fourth image reflections as the average subject’s eye. Filtering and sampling rate were the same as those used in the experiment. Noise level, expressed as a standard deviation of position samples, was 0.40 for horizontal and 0.70 for vertical positions. Recordings were made with the tracker’s automatically movable optical stage disabled (auto-stage) and focus servo disabled during trials (Gersch, Kowler, & Dosher, 2004).

Experimental sessions and number of trials tested

Each experimental session was 50 trials long (cued trials lasted 2.5 s, and uncued trials lasted 2.0 s). Subjects were tested in 6–13 sessions of the cued condition and 8–13 sessions in the uncued condition.

Data analysis

Horizontal and vertical velocities were calculated from the eye positions. Each velocity sample is the slope of a regression line of 25 position samples separated by 2 ms within a sliding window of 50 ms. Samples containing saccades or portions of saccades were removed. The beginning and ending positions of saccades were detected offline by means of a computer algorithm employing an acceleration criterion to find saccade onset and velocity to find saccade offset. Acceleration was computed as the difference in velocity between two samples (duration 14 ms) with onsets separated by 2 ms. The value of the criterion (velocity differences 20–40/s) was determined empirically for individual observers by examining a large sample of analog recordings of eye positions.

The conventional algorithms for estimating pursuit latencies in response to the onset of target motion (e.g., Carl & Gellman, 1987; Krauzlis & Miles, 1996) were not useful for the present experiment because of the anticipatory responses. Thus, performance will be described with respect to the time of onset of the target motion.

Results

Examples of smooth pursuit of RDKs with two of the limited-lifetimes tested (52 and 208 ms) are shown in Figure 2. Anticipatory smooth eye movements in the cued direction can be seen before the onset of target motion. Pursuit reached velocities close to target velocity for both lifetimes shown, but slowed noticeably over time with the shorter lifetime dots.

Eye movements were analyzed by computing velocity during 50 ms samples (onsets separated by 2 ms; see Methods) and averaging responses over trials. Figure 3 shows an example of mean eye velocity (±1 SD) over time with both unlimited and short (52 ms) lifetimes. Anticipatory smooth eye movements in the direction of expected target motion could be seen before the onset of target motion when motion direction was cued. In addition, pursuit velocity (peak and steady-state) was slower for the shorter lifetime. The slower steady-state pursuit velocity with the shorter lifetime dots is expected since the motion signal gets noisier as the lifetime of the dots decreases (see Appendix A).

Anticipatory smooth eye movements can also be seen by comparing the responses as a function of the direction that was cued. Figure 4 (left column) shows mean horizontal eye velocities over time for 3 representative subjects (AS, ERC, and SS) when cues indicated that the motion would be either to the right (upper cluster of traces in each graph) or left (lower cluster of traces). The individual traces contained within each of the clusters show the responses for the different dot lifetimes. The cluster of traces representing eye velocities in response to the different cued directions (right vs. left) began to separate prior to the onset of target motion. The separation of the responses to the different cued directions suggests that the cues were effective in producing anticipatory smooth eye movements. By contrast, when motion direction was not cued in advance (Figure 4, right column), separation of the traces into two groups (one for target motion to the right and one for motion to the left) was not evident until after the onset of target motion. Results were similar for all subjects tested and also for vertical eye velocities when the cued direction of motion was either down or up (Figures S1 through S4).

A summary of evidence supporting the occurrence of anticipatory smooth eye movements for all subjects is
in Figure 5. The upper graph shows distributions of mean horizontal eye velocities (50 ms samples) taken at the onset of target motion when the cued direction of target motion was to the left or right, and the lower graph shows the distributions of mean vertical eye velocities taken at the onset of target motion when the cued direction of target motion was up or down (lower graph). Each entry in the distribution represents the mean eye velocity for a different subject, with the data for each subject pooled across all lifetimes. Figure 5 shows no overlap between the anticipatory eye velocities in response to the different cued directions (either left vs. right or up vs. down). Table 1 shows the results of t tests done to compare the distributions of eye velocities (whose means are in Figure 5) obtained for each subject and each cued direction. The results of the t tests indicate that the differences in the distributions of eye velocities in response to the cues were highly significant, with all but one p-value ($p = 10^{-6}$) less than $10^{-13}$.

Examination of the mean eye velocity traces (Figure 4 and Figures S1 through S4) indicates an additional characteristic of the pursuit response. The figures show that differences in pursuit as a function of dot lifetime appeared to take a long time to emerge. Differences in the average response as a function of lifetime would be expected to emerge eventually, as the pursuit response begins to be dominated by the actual, rather than the expected, signal. Specifically, pursuit should be slower for the stimulus patterns with shorter lifetimes because the target velocity signal is noisier (see Appendix A; Schütz et al., 2010). Examination of the mean eye velocity traces in Figure 4 and Figures S1 through S4, however, suggests that differences among the responses to the different dot lifetimes may not have emerged until eye velocity reached values at, or near, the velocity...
of the target. This finding is reminiscent of earlier results showing that effects of target speed on pursuit appear after relatively long delays when speed is unpredictable and uncued (Kowler & McKee, 1987; Rasche & Gegenfurtner, 2009).

Statistical analyses (one-way ANOVAs, where lifetime was a factor) were performed on the eye velocities for each subject, cuing condition, and direction of motion. Differences among lifetimes became significant \( (p < .001) \) an average of 204 ms after the onset of target motion \( (\text{SD} = 68, \bar{N} = 56; \text{see Table } S1 \text{ for individual values}) \). One subject (SS) was not included in this mean because SS either did not show effects of lifetime during the trial or did not show effects of lifetime until at least 1.5 s after motion onset.

Effects of expectations about unpredictable properties of a stimulus, such as dot lifetime, can often be demonstrated by looking for evidence of sequential dependencies in which the response is influenced by the stimulus that occurred in the immediately preceding trial (Barnes & Collins, 2008; Kowler, 1989; Kowler et al., 1984; Luce, 1986; Yang & Lisberger, 2010). We looked for evidence of sequential dependencies for effects of lifetime by examining performance as a function of the lifetime on the immediately previous trial. We did not find sequential dependencies—that is, performance did not differ as a function of the lifetime on the previous trial (see representative example from one subject in Figure 6). Perhaps sequential dependencies were not found because too much time elapsed between the onset of motion on successive trials (0.5 s premotion interval + 2 s of motion + the intertrial time). Sequential dependencies in reaction time are known to diminish as a function of the elapsed time between trials (Luce, 1986). Sequential dependencies due to dot lifetime will be re-examined in Experiment 3 using displays with shorter time intervals between consecutive RDKs.

Figure 3. Experiment 1: Examples of mean horizontal eye velocities (50 ms samples, with onsets of successive samples separated by 2 ms) over time for subject LM tracking cued (left) and uncued (right) target motion with unlimited (top) or 52 ms (bottom) dot lifetimes. The shaded regions represent \( \pm 1 \text{ SD} \). The dotted line represents horizontal stimulus velocity. Each mean velocity function was the average of approximately 30 trials.
Discussion

Anticipatory smooth eye movements can be generated in response to expectations about the direction of global motion of random dot kinematograms. A representation of an object moving against a background is not needed to generate anticipatory smooth eye movements. In addition, effects of dot lifetime on pursuit emerged late, typically close to the time when pursuit reached peak or steady-state values.

Experiment 2: Anticipatory smooth eye movements prior to a change in direction of the RDK

In Experiment 1 the RDK patterns were stationary when the anticipatory smooth eye movements were generated. Experiment 2 examined anticipatory smooth eye movements prior to an expected change in direction of the RDKs, when pursuit was already underway. RDKs began by moving downward, after which the motion of the entire pattern changed direction to either down-left or down-right 0.5 s after an auditory cue signaled the direction of the motion change.

Methods

Stimuli and procedures were the same as in Experiment 1 with the following exceptions (see Figure 1). Before the start of the trial the fixation cross was located 2° above screen center and disappeared after the subject pressed the button to start the trial. Then field of dots appeared and began moving downward at 150°/s for 1.5 s, at which time the direction of motion changed to either down-right or down-left for another 1.5 s. The velocity of the horizontal component of motion was 106°/s. In the cued direction condition, an auditory cue (brief tone, 150 ms in duration) played through one of two sonalerters and was presented 0.5 s before the change in motion direction. Tone frequency and location (right...
or left of the subject) signaled the direction in which the target would move. Subjects were told about and asked to pay attention to the cues. There was no tone presented in the uncued direction condition.

Five of the subjects who participated in Experiment 1 (AS, ERC, MW, MP, and SS) were tested in Experiment 2. In the cued direction of motion condition, subjects ran 11–14 experimental sessions (50 trials per session). In the uncued condition they ran 9–14 sessions. Subjects MP and SS were tested in this experiment before running in Experiment 1.

Results

Average eye velocities over time when direction was either cued (left graphs) or not cued (right graphs) are shown in Figure 7 for the same three subjects whose results for Experiment 1 are shown in Figure 4. (Results from all five subjects are in Figures S5 and S6). Examination of the separation between the average eye velocity traces prior to expected target motion to the left and to the right suggests that anticipatory smooth eye movements were present for two of the depicted subjects (AS and ERC) but not for the third (SS).

To determine whether anticipatory smooth eye movements were present, the same analysis used in Experiment 1 was done. Specifically, the distributions of horizontal eye velocities obtained at the time of the change in direction were compared for the two different cued directions (right vs. left). Table 2 shows the mean eye velocities at the time of the change in direction along with the results of the $t$ tests comparing these distributions for all 5 subjects. Data for each subject were pooled across the three limited lifetime patterns (52, 104, and 208 ms). Differences between eye velocities for the different cued directions were found for three of the five subjects (AS and ERC, Figure 6; MP, Figure S5) and the differences were highly significant ($0 < p < 10^{-10}$). This indicates the occurrence of anticipatory smooth eye movements. The remaining two subjects (SS, Figure 7; MW, Figure S6) did not show significant differences between the eye velocities for the two cued directions (although the differences in the means were in the expected direction). Thus, three of the five subjects tested showed strong anticipatory smooth eye movements, while the other two did not show anticipatory smooth eye movements.

We also examined when significant differences among the pursuit responses to the different dot lifetimes emerged, as we did in Experiment 1. Differences among the lifetimes ($p < 0.001$) emerged on...
average 153 ms ($SD = 120, n = 20$) after the change in motion direction (see also Table 2). These average values were slightly but significantly earlier than the values ($mean = 204$) obtained for Experiment 1, $t(23) = 1.78, p = 0.044$.

Discussion

The results of Experiment 2 showed that anticipatory smooth eye movements can occur prior to an expected change in direction of the motion of RDKs. Anticipatory smooth eye movements were found in three of the five subjects tested. The two who did not show anticipatory smooth eye movements had shown them in Experiment 1. Perhaps some individuals cannot produce anticipatory smooth eye movements in response to expectations about the change in the direction of RDKs. Alternatively, the anticipatory response may have suffered because of lack of sensitivity to the auditory cues, which were tones delivered 0.5 s before the change in motion direction. This suggestion is plausible because prior work has shown that anticipatory smooth eye movements are more sensitive to visual cues embedded in the display than to auditory cues that are tangential to the display (Kowler, 1989).

The effects of dot lifetime appeared to emerge earlier in Experiment 2 than in Experiment 1. This would be consistent with the existence of effects of expectations about dot lifetime because in Experiment 2: (1) the lifetime of the motion before the direction change provided a reliable cue to lifetime after the direction change, and (2) the lifetime of the patterns before and after the change in direction of the target motion was the same. However, these observations about possible effects of expectations about lifetime on the basis of the findings in Experiments 1 and 2 are only provisional because neither experiment was explicitly designed to study effects of the value of the expected lifetime.

Experiment 3 was done to study the effects of expectations about dot lifetime and used both motion onsets (similar to Experiment 1) and direction changes (similar to Experiment 2) in a design that made it possible to determine both the effects of past history and the effects of visual cues to lifetime.
Experiment 3: Expectations about dot lifetime

Experiment 3 examined the effects of cues about dot lifetime that were delivered either before the onset of motion of an RDK (similar to Experiment 1) or before a change in motion direction (similar to Experiment 2).

In order to compare the role of cues about lifetime to the role of immediate past history, two consecutive RDKs (duration of each = 1.5 s) with limited-lifetime dots were shown in sequence. For the motion-onset

<table>
<thead>
<tr>
<th>Cue: left</th>
<th>Cue: right</th>
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<tr>
<td>Mean(SD), N</td>
<td>Mean(SD), N</td>
</tr>
<tr>
<td>AS</td>
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<td>ERC</td>
<td>−28.6(51), 199</td>
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<tr>
<td>MP</td>
<td>−1.9(43), 262</td>
</tr>
<tr>
<td>MW</td>
<td>−8.6(49), 281</td>
</tr>
<tr>
<td>SS</td>
<td>2.2(63), 224</td>
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Table 2. Experiment 2, cued directions: Mean eye velocities and results of t tests at the time of the direction change. Notes: Horizontal mean eye velocities, 50 ms samples, at the change in direction of target motion pooled over lifetimes of 52, 104, and 208 ms. Negative values represent leftward velocities. Auditory cues signaled motion direction.
condition, the first RDK was stationary (i.e., the velocity of the limited-lifetime dots was set to zero) and dots appeared to flicker rather than to move. For the direction-change condition, the first RDK moved downward at 150°/s. The second RDK moved either down and to the left or down and to the right (horizontal component of velocity = 106°/s).

The first RDK was used to provide a cue to dot lifetime. This was accomplished by setting the lifetime of the first RDK either to 4 frames (52 ms) or to 16 frames (208 ms). These values were sufficiently far apart that they were easily discriminable by the visible flicker of the dots, which could be seen in the first RDK regardless of whether it was stationary or moving.

There were three cuing conditions: (1) cued-same: the lifetime of the dots in the two RDKs was the same throughout a block of 50 trials; (2) cued-different: the lifetime of the dots in the two RDKs was different throughout a block of 50 trials; and (3) uncued: the lifetime of the dots in each RDK was selected at random and independently. Subjects were told before each 50-trial session which cuing condition was being tested. Motion-onset and direction-change trials were randomly interleaved in the same experimental session.

Analyses focused on the effects of the first RDK after pursuit of the second RDK was underway. If the first RDK acts as an effective cue to lifetime (as it may have done in Experiment 2), we expect to see higher eye velocities when the cue indicates that the longer lifetime will be present in the second RDK in both the cued-same and cued-different conditions, but not in the uncued condition. On the other hand, if effects of lifetime carry over from one moving pattern to the next, we would expect to see higher eye velocities when the first RDK has the longest lifetime in all three of the cuing conditions.

The direction of motion of the second RDK (down-right or down-left) was also cued by using the same technique that was effective in Experiment 1, namely, displacing the horizontal position of the initial fixation cross in a direction opposite to the future direction of horizontal motion.

Three new subjects were tested in 13–17 experimental sessions for each cuing condition. Subjects were naïve to the purpose of the experiments, and none had run in pursuit experiments before.

Results and discussion

The main result of Experiment 3 was that the pursuit of the second RDK was faster when the first RDK had a longer lifetime. This was found in all three cuing conditions. The influence of the first RDK was observed regardless of whether the first RDK was moving (direction-change condition) or stationary with flickering dots (motion-onset condition).

Figure 8 illustrates the influence of the first RDK on pursuit of the second RDK for 1 subject. The four graphs show results from the motion-onset condition (left), and the direction-change condition (right) when the lifetime of the second RDK was cued by the first RDK (bottom graphs) or not cued by the first RDK (top graphs). In each of the four graphs, the lifetime of the second RDK was 208 ms. The lifetime of the first RDK was either 52 ms (red lines) or 208 ms (green lines). Thus, for the cued condition (bottom graphs), the green line represents the results of the cued-same condition, and the red line represents the results of the cued-different condition.

In each graph, eye velocity by about 100 to 200 ms after the onset of target motion was faster when the lifetime of the first RDK was the longer of the two possible values. This pattern of results argues that the effects of dot lifetime carried over from one RDK to the next, regardless of the cuing condition. The pattern of results from the other 2 subjects was the same (Figures S7 and S8).

Carryover effects were verified by examining mean eye velocities for one representative temporal epoch, 200 ms after the onset of target motion or after the change in direction of target motion, when pursuit was underway. Figure 9 shows these mean eye velocities, with means averaged over subjects, as a function of the lifetime of the first RDK.

Eye velocity was faster when the lifetime of the first RDK was longer, regardless of whether the first RDK was a reliable cue to lifetime (Figure 9, bottom graphs) or was not a reliable cue (top graphs), regardless of whether the first RDK was stationary (left graphs) or moving (right graphs), and regardless of the lifetime of the second RDK. Statistical analyses were carried out using the linear model described in Appendix B. Results, summarized in Table 3, showed that differences between eye velocities as a function of the lifetime of the first RDK were significant for all eight functions shown in Figure 9. Effects of the lifetime of the first RDK were highly significant in the cued condition, $t(4622) = 16.45, \ p < 10^{-15}$, and the uncued condition, $t(3671) = 14.08, \ p < 10^{-15}$. In addition, there were no significant differences in eye velocities as a function of the type of transition between the RDKs (motion onset vs. change in direction), $t(8295) = 0.783, \ p > 0.9$, and no significant differences depending on whether lifetime was or was not cued, $t(8295) = 2.02, \ p = 0.52$.

Finding effects of the lifetime of the first RDK, regardless of the information conveyed by the cue, argues for the existence of carryover effects of lifetime across the two consecutive patterns. The carryover of the effect of lifetime from the first to the second RDK occurred regardless of whether the subjects knew that
the lifetime of the second RDK would be the same as the first, different from the first, or not correlated with the first RDK.

Carryover effects could have contributed to the effects of lifetime observed in Experiment 2 because in Experiment 2 the lifetime did not change after the change in motion direction. Carryover effects (i.e., sequential dependencies) were not evidenced in Experiment 1, perhaps because the intervals between successive patterns, shown on successive trials rather than within a trial, were long enough so that any carryover may have dissipated.

Additional analyses, similar to those carried out for the results of Experiments 1 and 2, were done to confirm that visual cues to the direction of motion of the second RDK (see Methods) were effective (note that the direction of motion was cued on each trial). Differences in eye velocities at either motion onset or at the time of the change in direction, pooled across lifetimes, were highly significant for both motion-onset and direction-change conditions for each subject (see Table 4 for mean eye velocities and results of t tests).

General discussion

The results of all three experiments show that anticipatory smooth eye movements in response to symbolic cues about the direction of motion are found with patterns of global motion, specifically RDKs with limited-lifetime dots. These results show that the expectation of sustained motion of a discrete object, or a collection of objects moving together, is not necessary for the generation of anticipatory smooth eye movements. Expectations of global motion, such as that present in limited-lifetime RDKs, are sufficient. The present results extend previous findings of effective
pursuit of RDKs with either limited- (Krauzlis & Adler, 2001; Schütz et al., 2010) or unlimited-lifetime elements (Heinen & Watanmaniu, 1998; Osborne & Lisberger, 2009) by showing that such patterns can also support anticipatory smooth eye movements.

On the face of it, this conclusion might appear to be different from that drawn by Montagnini et al. (2006), who held that object motion was needed for anticipatory smooth eye movements. However, object motion referred to different characteristics of motion in the two studies. Object motion in Montagnini et al. (2006) referred to the 2D horizontal motion of a tilted line translating across space, which was different from the transient and more primitive 1D motion signals perpendicular to the orientation of the target line. They found that only the 2D motion, not the 1D motion, was associated with an anticipatory response. In our study, object motion referred to the representation of a discrete object that is seen as moving over space. The global motion created by the limited-lifetime RDKs is not object motion in the sense that there is no sustained moving object or objects that can be perceived, attended, and tracked as they move over space, yet these patterns can support anticipatory smooth eye movements. Thus, taking the two studies together, the results show that global motion can support anticipatory smooth eye movements, while primitive 1D motion cannot.

**Cues**

Although anticipatory smooth eye movements were found with RDK targets, not all cues to characteristics of the upcoming motion were equally effective. Consider the cues about direction. Visual cues about upcoming motion direction, such as those used in Experiments 1 and 3, were effective in all observers. However, the auditory cues in Experiment 2 were not effective for some observers. Perhaps the reduced
effectiveness of the cues in some observers is due to modality (visual vs. auditory signals) (Kowler, 1989; Winges & Soechting, 2011).

Cues signaling the dot lifetime of the pattern (Experiment 3) were not very effective in that there was a strong default preference to respond as if the lifetime seen in the recent past would continue. The default preference was similar regardless of whether the lifetime of the first RDK was or was not a reliable cue to the lifetime of the second. The default preference held even when observers could determine on the basis of past history that the lifetime of the first RDK would not carry over to the second RDK.

Taken together, the results of the three experiments show that anticipatory smooth eye movements can be elicited in response to expectations about the direction of global motion. However, cues about other properties of the global motion (e.g., dot lifetime) appear to be ineffective. What might account for this distinction in the effectiveness of cues?

Two general alternatives can be proposed. One holds that anticipatory smooth eye movements in response to cues occur only under conditions where the expectations are able to generate salient representations of the expected motion (see Krauzlis, 2004 for a similar proposal with respect to the difficulty of generating imagined motion signals). On the basis of our results, we suggest that salient representations of the expected direction of motion, sufficient to drive anticipatory smooth eye movements, may be generated either from expectations of the sustained motion of objects, or expectations of the global motion of limited-lifetime RDKs (but perhaps not for the direction of the primitive and transient 1D motions studied by Montagnini et al., 2006). Cues about the lifetime of the elements (lifetime controls the signal/noise properties of the stimulus; Appendix A), on the other hand, may be ineffective because expectations about dot lifetime might not be helpful in constructing a perceptually salient representation of the expected motion. The fact that neurons in regions associated with the generation of anticipatory smooth eye movements have strong directional selectivity (de Hemptinne et al., 2008) may be part of the reason that expectations about direction are effective, whereas expectations about properties such as lifetime are less effective.

An alternative view holds that the variation in the effectiveness of cues in producing anticipatory smooth eye movements can be understood, not by their structural links to the motion system, but by their

### Table 3. Experiment 3: Effects of the lifetime of the first RDK (52 ms vs. 208 ms)

<table>
<thead>
<tr>
<th>Condition</th>
<th>( t(df), p )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lifetime not cued Lifetime of second RDK = 52 ms</td>
<td>( t(893) = 4.9 \times 10^{-10} )</td>
</tr>
<tr>
<td>Direction change Lifetime of second RDK = 52 ms</td>
<td>( t(893) = 2.1 \times 10^{-8} )</td>
</tr>
<tr>
<td>Lifetime not cued Lifetime of second RDK = 208 ms</td>
<td>( t(926) = 3.8 \times 10^{-7} )</td>
</tr>
<tr>
<td>Direction change Lifetime of second RDK = 208 ms</td>
<td>( t(926) = 1.3 \times 10^{-10} )</td>
</tr>
<tr>
<td>Motion onset Lifetime of second RDK = 208 ms</td>
<td>( t(1169) = 1.4 \times 10^{-4} )</td>
</tr>
<tr>
<td>Lifetime cued Lifetime of second RDK = 208 ms</td>
<td>( t(1169) = 2.4 \times 10^{-15} )</td>
</tr>
<tr>
<td>Direction change Lifetime of second RDK = 208 ms</td>
<td>( t(1169) = 1.5 \times 10^{-4} )</td>
</tr>
<tr>
<td>Motion onset Lifetime of second RDK = 208 ms</td>
<td>( t(1167) = 2.4 \times 10^{-15} )</td>
</tr>
</tbody>
</table>

Notes: Mean velocities (± SD) are shown in Figure 9. The \( p \)-values were corrected using the Bonferroni method to reflect the 12 different tests conducted (eight tests shown in Table 3; see text, Experiment 3 Results, paragraph five for four additional tests). Tests were based on the linear model described in Appendix B.

### Table 4. Experiment 3, effects of directional cues: Mean eye velocities and results of \( t \) tests at the time of motion onset or direction change for the different cued directions

<table>
<thead>
<tr>
<th>Cue: left</th>
<th>Cue: right</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean(SD), ( N )</td>
<td>Mean(SD), ( N )</td>
</tr>
<tr>
<td>AT: motion onset</td>
<td>-4.8(41), 680</td>
</tr>
<tr>
<td>AT: direction change</td>
<td>-6.3(42), 707</td>
</tr>
<tr>
<td>KM: motion onset</td>
<td>-5.4(69), 726</td>
</tr>
<tr>
<td>KM: direction change</td>
<td>-6.8(64), 740</td>
</tr>
<tr>
<td>KH: motion onset</td>
<td>-33.0(59), 690</td>
</tr>
<tr>
<td>KH: direction change</td>
<td>-35.9(60), 627</td>
</tr>
</tbody>
</table>
expected value to pursuit (Pavel, 1990). According to this view, anticipatory smooth eye movements should be treated in the same way as other perceptual decisions (Yang, Hwang, Ford, & Heinen, 2010), in that the effectiveness of the cues depends on the prior probability that the cue is the source of a reliable prediction. Cues about the direction of upcoming target motion are likely to be the source of a reliable prediction (Blake & Shiffrar, 2007; Chouchourelou, Matsuka, Harber & Shiffrar, 2006; Pantelis et al., 2011). On the other hand, cues that disclose a more abstract property of a moving stimulus, such as the signal/noise properties of the global motion of an RDK, might be less informative because this property, unlike motion direction, is not connected to the motion of objects in real-world environments. De Hemptinne et al. (2007) made a similar argument when they concluded that anticipatory smooth eye movements represent the outcome of an optimal decision-making process that takes into account the statistical properties of previously seen motions. In the absence of effective cuing, anticipatory smooth eye movements may reflect the default preference to act as if the properties of recently seen or recently tracked motions will continue into the future (Burke & Barnes, 2008; Kowler et al., 1984). This appears to be a reasonable inference in the absence of reliable information to the contrary.

Summary

Anticipatory smooth eye movements were evoked by cues to the direction of global motion of RDKs with limited-lifetime dots. This result shows that neither representations of sustained motion of objects across space, nor the ability to select and pursue a set of identifiable elements, are necessary for the generation of anticipatory smooth eye movements. Expectations of global motion are sufficient. Cues to other properties of the global motion—namely, the lifetimes of the component elements—were less effective, as the system reverted to a default of responding as if the lifetimes in the immediate past would continue. These results show that prediction within smooth pursuit remains a pervasive option, but that the rules by which it operates transcend simple associations between cues and the upcoming motion of targets.

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### Appendix A

**Analysis of motion of random-dot kinematograms with limited-lifetime elements**

The motion signals produced by random-dot kinematograms (RDKs) has been modeled and quantified in the past (Barlow & Tripathy, 1997; Osborne & Lisberger, 2009; Schütz, Braun, Movshon, & Gegenfurtner, 2010). The strength of the motion signal of this type of stimulus often has been described in terms of the percent coherence since there are usually dots moving coherently in one direction and noise dots moving in random directions or velocities. In the
present paper, the coherence of the patterns was set to 100%, and the lifetime of the moving elements was varied. Reducing lifetime introduces noise into the pattern, similar to the reduction of coherence. The objective of this appendix is to quantify the noise introduced by reduction in lifetime.

In the motion algorithm used in the three experiments of this study, the dots were given a random lifetime in the first frame. After that, they died according to the lifetime for the particular experimental trial. This procedure avoided having all the dots die at the same time. All the dots moved at the same velocity until the end of their lifetime. When a given dot reached the end of its lifetime, it was “reborn” at a new, randomly-chosen location on the next frame. The rebirth introduced noise since each of the reborn dots can be considered to have moved in a random direction and at a random speed. Fourier analysis can be used to quantitatively model the strength of the motion signal and the strength of the noise of the RDKs used in this study.

Figure A1 shows space–time plots corresponding to RDKs with different lifetimes. This analysis was performed over a field of 225 dots moving horizontally at a speed of 150°/s within a 5° × 5° field (dot density = 10 dots/deg²) for 8 seconds. The space–time plots overlay the positions of the dots appearing in a 5.0° × 0.01° window, which was arbitrarily selected for the purpose of the Fourier analysis. The long lines with negative slopes on the upper left panel of Figure A1 (unlimited lifetime) represent the signal motion and indicates the velocity of the dots. The lines are shorter when lifetime is reduced in the remaining panels of Figure A1, indicating an increase in the noise in the stimulus.

Figure A2 shows the results of analyzing the energy spectrum in the spatial and temporal domains and shows the energy in the layer with no vertical frequency component (Schütz et al., 2010). Note that the motion energy of the dots with shorter lifetimes is scattered across a larger range of spatial and temporal frequencies, showing the additional noise that was introduced when lifetimes were shortened. Thus, poorer steady-state pursuit with a shorter lifetime is expected due to the degraded, noisier motion signal, in the same way...
that pursuit becomes poorer with decreasing motion coherence (Schütz et al., 2010).

### Appendix B

There were 16 testing conditions for Experiment 3, which were specified by using a categorical variable (Table B1). Using a categorical variable to represent each of the 16 conditions avoided using the first and second random dot kinematograms (denoted as RDK1 and RDK2) as independent variables. This design was also balanced since the combinations of lifetimes for RDK1 and RDK2 were the same for the cued and uncued conditions and the same regardless of whether a motion onset or a change in direction of motion was involved.

The eye velocities were fitted with a linear model

\[ V_{ij} = \mu + \beta_i C_i + \sigma_j S_j + \epsilon_{ij}, \]

\[ i = 1, \ldots, 16, \quad j = 1, \ldots, 3. \]  

(1)

![Spatiotemporal frequency plots for the three lifetimes tested and the RDK with unlimited lifetime. White bands represent motion energy.](Image)

Table B1. Testing conditions of Experiment 3. Note: RDK = random-dot kinematogram.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Cuing condition</th>
<th>Pursuit type</th>
<th>RDK1 lifetime (ms)</th>
<th>RDK2 lifetime (ms)</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \beta_1 )</td>
<td>uncued</td>
<td>direction change</td>
<td>52</td>
<td>52</td>
</tr>
<tr>
<td>( \beta_2 )</td>
<td>uncued</td>
<td>direction change</td>
<td>52</td>
<td>208</td>
</tr>
<tr>
<td>( \beta_3 )</td>
<td>uncued</td>
<td>direction change</td>
<td>208</td>
<td>52</td>
</tr>
<tr>
<td>( \beta_4 )</td>
<td>uncued</td>
<td>direction change</td>
<td>208</td>
<td>208</td>
</tr>
<tr>
<td>( \beta_5 )</td>
<td>uncued</td>
<td>motion onset</td>
<td>52</td>
<td>52</td>
</tr>
<tr>
<td>( \beta_6 )</td>
<td>uncued</td>
<td>motion onset</td>
<td>52</td>
<td>208</td>
</tr>
<tr>
<td>( \beta_7 )</td>
<td>uncued</td>
<td>motion onset</td>
<td>208</td>
<td>52</td>
</tr>
<tr>
<td>( \beta_8 )</td>
<td>uncued</td>
<td>motion onset</td>
<td>208</td>
<td>208</td>
</tr>
<tr>
<td>( \beta_9 )</td>
<td>cued</td>
<td>direction change</td>
<td>52</td>
<td>52</td>
</tr>
<tr>
<td>( \beta_{10} )</td>
<td>cued</td>
<td>direction change</td>
<td>52</td>
<td>208</td>
</tr>
<tr>
<td>( \beta_{11} )</td>
<td>cued</td>
<td>direction change</td>
<td>208</td>
<td>52</td>
</tr>
<tr>
<td>( \beta_{12} )</td>
<td>cued</td>
<td>direction change</td>
<td>208</td>
<td>208</td>
</tr>
<tr>
<td>( \beta_{13} )</td>
<td>cued</td>
<td>motion onset</td>
<td>52</td>
<td>52</td>
</tr>
<tr>
<td>( \beta_{14} )</td>
<td>cued</td>
<td>motion onset</td>
<td>52</td>
<td>208</td>
</tr>
<tr>
<td>( \beta_{15} )</td>
<td>cued</td>
<td>motion onset</td>
<td>208</td>
<td>52</td>
</tr>
<tr>
<td>( \beta_{16} )</td>
<td>cued</td>
<td>motion onset</td>
<td>208</td>
<td>208</td>
</tr>
</tbody>
</table>
In this model $V_{ij}$ represents eye velocity in condition $i$ (where $i$ ranges from 1–16; see Table B1) for subject $j$; $\mu$ is the intercept, $C_i$ indicates the effect of the condition, $S_j$ denotes the effect of subject, and $\varepsilon$ is the error term. The linear combination of the estimated coefficients for the testing condition, $\hat{\beta}$, and the estimated coefficient for subject, $\hat{\alpha}$, give us an estimate of the eye velocity. Eye velocities were collapsed across direction of motions.

The fitted model provided the estimated coefficients, which can be used to perform general hypothesis testing for linear models, as described by Bretz, Hothorn and Westfall (2008) and Hothorn, Bretz, and Westfall (2008). The general null hypothesis is expressed as $H: c^T \beta = 0$. The matrix $c$ indicates the hypothesis in question and $\beta$ represents the coefficients to be tested. The $t$ test statistics for each comparison were computed as proposed by Genz and Bretz (2002).

Using the coefficients given by the fitted model described above, we tested 12 hypotheses, which are described in the text (four tests; see Experiment 3 Results, paragraph 5) and Table 3 (eight tests). Since the 12 hypotheses were tested on the same coefficients, the $p$-values were corrected using the Bonferroni method.