

Eye movements and imitation learning: Intentional disruption of expectation

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Over repeated viewings of motion along a quasi-random path, ability to reproduce that path from memory improves. To assess the role of expectations and sequence context on such learning, subjects eye movements were measured while trajectories were viewed for subsequent reproduction. As a sequence of motions was repeated, subjects' eye movements became anticipatory, leading the stimulus' motions. To investigate how prediction errors affected eye movements and imitation learning, we injected an occasional deviant motion into a well-learned stimulus sequence, violating subjects' expectation about the motion that would be seen. This unexpected direction of motion in the stimulus sequence did not impair reproduction of the sequence. The externally induced prediction errors promoted one-shot learning: During the very next stimulus presentation, their eye movements showed that subjects now expected the new sequence item to reappear. A second experiment showed that an associative mismatch can facilitate accurate reproduction of an unexpected stimulus. After a deviant sequence item was presented, imitation accuracy for sequences that contained the deviant direction of motion was reduced relative to sequences that restored the original direction of motions. These findings demonstrate that in the context of a familiar sequence, unexpected events can play an important role in learning the sequence.

Keywords: eye movements, memory, learning, motion—2D

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Introduction

Cognitive skills ranging from language and navigation to visually guided manipulation of tools and devices depend upon an ability to represent the sequential order of events. Such representations make it possible to develop increasingly accurate expectations about forthcoming sensory events (Summerfield & Egner, 2009) and are useful in preparing and guiding sensorimotor behaviors (Yu & Cohen, 2008). Moreover, whenever an expectation is disconfirmed, the resulting predictive error can be used to adjust expectations for future sequences. So, it is unsurprising that predictive errors occupy a central, beneficial place in theories of associative learning (e.g., den Ouden, Friston, Daw, McIntosh, & Stephan, 2009; Pearce & Hall, 1980; Schultz, 2006; Wills, Lavric, Croft, & Hodgson, 2007).

To examine the contribution of prediction errors to sequence learning (Kumaran & Maguire, 2007), we adapted an imitation task in which learning has been well characterized, behaviorally (Agam, Bullock, & Sekuler, 2005; Agam, Galperin, Gold, & Sekuler, 2007; Maryott & Sekuler, 2009) and electrophysiologically (Agam, Huang, & Sekuler, 2010; Agam & Sekuler, 2007). In our adaptation of this task, during repeated presentations of a

random sequence of motion directions, we measured (i) the eye movements that subjects made while observing the random motion sequence, as well as (ii) the fidelity with which subjects later reproduced that sequence from memory. Subjects' growing familiarity with each random sequence was reflected in both anticipatory eye movements and improved imitation fidelity. Occasionally, an unpredictable deviation was introduced into a motion sequence so as to intentionally disrupt subjects' expectations. This afforded us a unique, theoretically important opportunity to simultaneously assess dual consequences of such disruptions: their effect on (i) subjects' expectations for the sequence of motions the disk would subsequently follow, and their effect on (ii) the fidelity with which such deviant sequences were subsequently reproduced from memory.

Experiment 1

An established imitation-learning paradigm (Agam et al., 2005, 2007) was modified to capture practice-related changes in the eye movements that subjects made while viewing a motion sequence for subsequent imitation. The

motion sequences were sufficiently complex that several repetitions of a sequence were required before the fidelity of imitation approached asymptote. This made it possible to compare imitation accuracy and eye movements at distinct stages of learning and to measure parallel, practice-driven changes in the eye movements and in the quality of imitation.

As a stimulus' movements grow more familiar, there is a roughly parallel improvement in the quality of tracking eye movements and in the quality of imitation (Agam et al., 2007, 2010; Barnes, Barnes, & Chakraborti, 2000; Matarić & Pomplun, 1998). In fact, after multiple presentations of a motion sequence, tracking tends to become anticipatory so that the eyes actually lead the stimulus' motion (Barnes, 2008; Barnes et al., 2000; Boman & Hotson, 1992; de Hemptinne, Lefèvre, & Missal, 2008; Marcus, Karatekin, & Markiewicz, 2006). That is, subjects use previous experience to predict what will be seen (Barnes, 2008). By recording subjects' eye movements as they watched the stimulus disk, we hoped to understand subjects' expectations for the disks' movements and to relate those expectations to the accuracy of subjects' imitation.

We intentionally provoked errors in subjects' predictions of the disk trajectory. Occasionally, when a motion sequence was repeated, one component of the sequence was altered, thereby violating any expectation that might have been built up over preceding presentations of that sequence (Ferdinand, Mecklinger, & Kray, 2008; Kowler, 1989).

We assessed the degree to which smooth pursuit eye movements reflect learning of complex sequences of motions and whether error-induced changes in subjects' expectations alter those pursuit eye movements. We hypothesized that eye movements would become more accurate and anticipatory as subjects learned a specific sequence and that this accuracy would be disrupted by intentionally induced prediction errors. Finally, we examined whether induced errors improve imitation and whether such improvements are related at all to changes in smooth pursuit.

Methods

Subjects

Eleven young adults (9 females; ages 19–25) participated in this experiment. None had taken part in any previous experiments with this task; all had normal or corrected-to-normal vision.

Apparatus

A head-mounted eye tracker (EyeLink-II, SR Research) sampled the position of a subject's eyes at 500 Hz with an error of approximately 0.05° visual angle (estimated by the instrument's manufacturer and verified empirically by

the authors). The positions of both eyes were captured, time-stamped, and stored for offline analysis.

Experimental task

To assess imitation learning, we asked subjects to observe five repeated presentations of 112 different motion sequences and, after each presentation, to imitate from memory what they had seen. A single presentation of this task is represented schematically in Figure 1. A yellow disk (0.54° visual angle) moved along a pseudo-random path comprising a series of six connected linear motion segments. The luminance of the disk was 52.5 cd/m^2 , and it was presented on a dark gray, unstructured uniform background of 2.1 cd/m^2 . For five subjects, the disk appeared stationary for 600 ms before starting to move (Figure 1A); for the remaining six, the disk began to move immediately upon its appearance. This slight variation in experimental protocol likely does not affect the results reported here as our analysis disregards the initial motion segment, which is the segment that might have been affected. Moreover, we saw no systematic differences on subsequent segments in the eye movements made by subjects tested under the two protocols.

Each segment of the trajectory was 4.5° visual angle in length, and the disk moved at a constant speed of 9° visual angle/s, taking 500 ms to travel the length of each segment (Figure 1B). After each successive segment, the disk paused and remained stationary for 400 ms before resuming its motion, in a changed direction. After the sequence's completion, the yellow disk disappeared from view (Figure 1C). Then, after a 3.75-s retention interval, a new disk appeared, signaling the subject to move a handheld stylus over the surface of a graphics tablet ($31 \times 24 \text{ cm}$), reproducing from memory the sequence of disk motions that had just been seen (Figure 1D). During the imitation, the disk's motion was yoked to the movement of the stylus' tip on the graphics tablet (Figure 1E). No other feedback was provided. Note that neither the stimulus nor the imitation disk left a visible trail while moving across the computer display. As a result, any representation of the stimulus disk's complete path would have to be generated in the subject's mind's eye, and then maintained in short-term memory until imitation was called for (Geisler, Albrecht, Crane, & Stern, 2001; Jancke, 2000). During testing, a subject sat 65 cm from the computer screen with head supported in a chin rest.

Each trial's quasi-random sequence of six motion components was generated by an algorithm based on one described by Agam et al. (2005). The direction of a sequence's initial motion was chosen randomly from directions spanning 0 to 360° . Each successive motion component represented a change in direction of 30 to 150° relative to the immediately preceding direction.

These changes in direction could be clockwise or counterclockwise. The motions comprising any sequence were constrained by several rules. In particular, motion

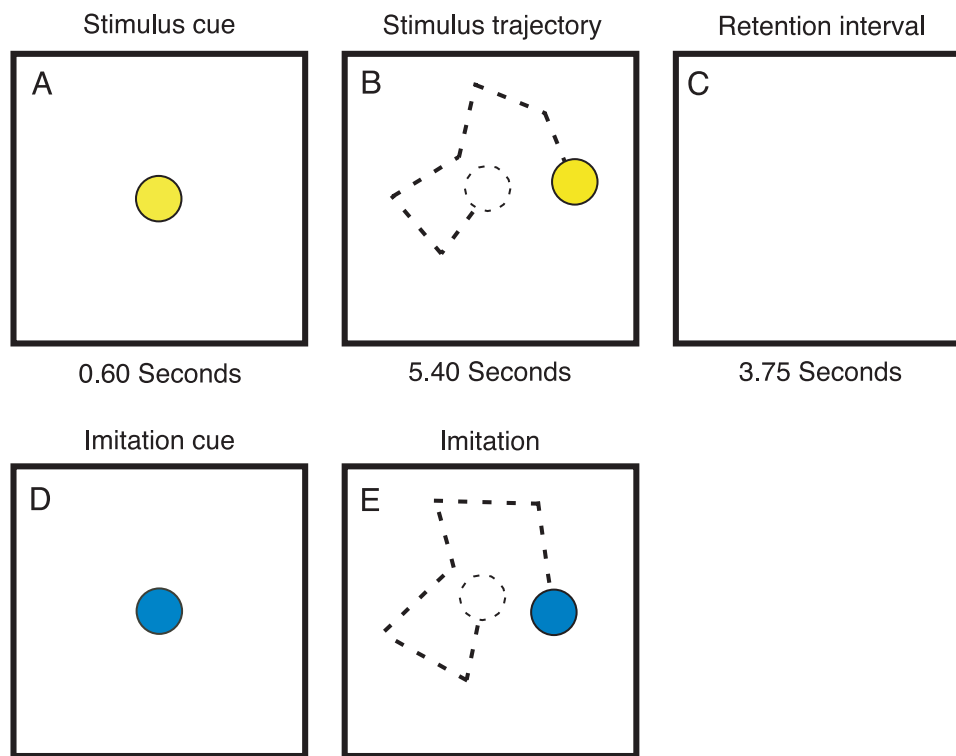


Figure 1. The sequence of events comprising one presentation within a trial in the experiment. At the start of each presentation, a yellow disk appeared at the center of the display (A) before beginning to move in a series of six, connected linear segments without leaving any visible trail (B). After enacting the six movements, the disk disappeared from view (C). After a retention interval, a colored disk appeared (D) signaling the subject to begin reproducing from memory the path that had been previously taken by the yellow disk (E). Each trial consisted of five such presentations.

segments could neither intersect, nor could they approach within one-half a segment length (2.25° visual angle) of one another, nor could they extend beyond the boundaries of the display area. These constraints produced a family of quasi-random motion sequences in which the directions of successive components differed on average by 80.82° ($SD = 34.36^\circ$).

Design and procedure

On every trial, that trial's unique sequence of motions was presented five times. A sequence comprised six linear, linked motion segments. Each set of five presentations constituted either congruent trials—on which all five presentations of a sequence were identical to one another—or incongruent trials—on which one motion component changed direction in the fourth presentation of the sequence. Of all the sequences that a subject saw, 64% were congruent trials and 36% were incongruent trials. Rows 1 and 4 in Figure 2 show examples of congruent trials. On the penultimate presentation of incongruent trials, the final component of the established sequence was replaced by a component in which the stimulus disk moved in the opposite direction. This 180° “flip” in direction is illustrated in Figure 2 (fourth column), in rows 2, 3, 5, and 6. On half the incongruent trials, the new direction

that the disk took on presentation 4 was maintained during the sequence's last presentation. Exemplars of these trials, which we call flip trials, are shown in rows 2 and 5 of Figure 2. On the remaining incongruent trials, the last component's original direction, which had been changed for presentation 4, was reinstated for the fifth and final presentation. Because on such trials the last component's direction “flips” on presentation 4 and then “returns” to its original direction on presentation 5, we term such trials flip–return trials. Exemplars of flip–return trials are shown in Figure 2 (third and sixth rows).

Every subject completed four 60-min sessions of 28 trials, with five presentations per trial. In each session, the first three trials were all congruent trials. This was intended to establish an expectation that successive presentations would be the same. The remaining 25 trials were distributed across blocks of five trials each; a block comprised one flip trial, one flip–return trial, and three congruent trials, in random order. Subjects were not informed that some trials would be incongruent trials. After the task had been explained, a subject practiced the task while not attached to the eye tracker. When the subject had become comfortable with the task, the eye tracker was secured to the participant's head and calibrated. Before each repetition of a stimulus sequence, the eye tracker calibration was checked and corrected for drift.

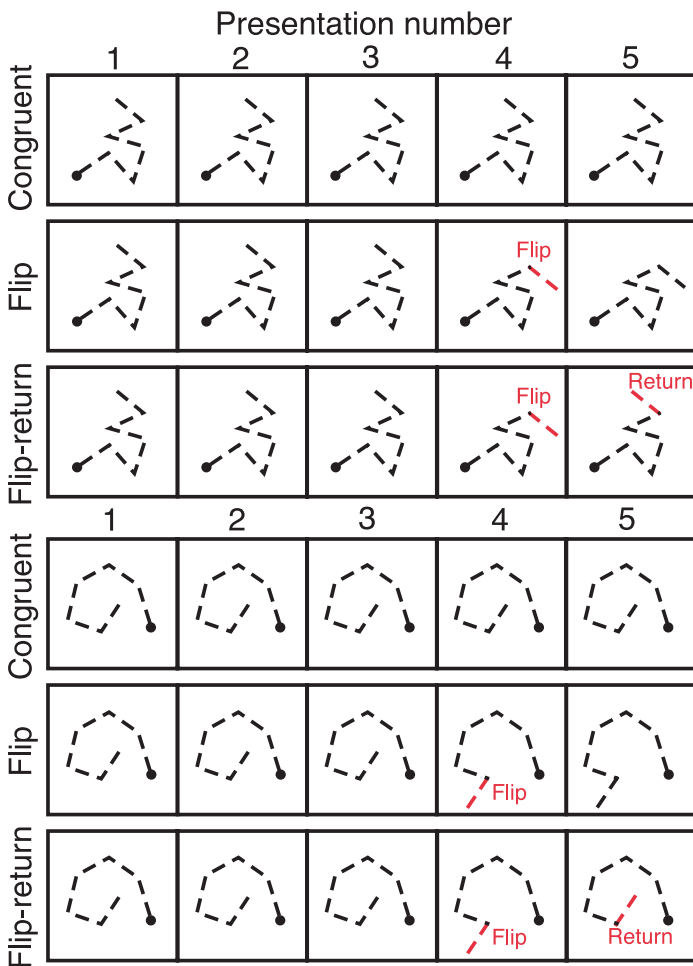


Figure 2. Exemplars of two motion sequences illustrating how a sequence could change over successive presentations. In each panel, the black disk represents the location from which the sequence began. Rows 1–3 illustrate the three types of trials for one exemplar motion sequence; rows 4–6 illustrate the three types of trials for a second exemplar motion sequence. Note that in the experiment, each trial’s trajectory (sequence of motion components) was unique; here, just two exemplars are given to illustrate differences among the three trial types. A motion component whose direction differed from that on the preceding presentation is shown in red. Rows 1 and 4: On congruent trials, the disk followed the same trajectory on each repeated presentation. Rows 2–3 and 5–6: On flip and flip–return trials, the first three presentations were identical, but then, on presentation 4, the final motion component was 180° flipped from its previous direction. These two trial types are collectively referred to as incongruent trials. Rows 2 and 5: On flip trials, the final motion component preserved its flipped direction for the fifth presentation. Rows 3 and 6: On flip–return trials, the final segment returned to its original, pre-flip direction for the fifth presentation.

Subjects were allowed to take breaks between trials to rest their eyes and head.

Subjects were instructed to track the stimulus disk as smoothly as possible during a stimulus presentation. This

instruction was meant to promote consistent smooth pursuit movement with short latency. In addition, eye movement records were monitored online by the experimenter; if a subject’s movements became jerky, or if the subject’s eyes ceased to track, the instructions were repeated. Subjects were not required to maintain smooth tracking while imitating the motion sequence that they had just seen.

Analysis of imitation

The fidelity of each imitation was quantified offline by means of a two-step algorithm that used spatial and temporal criteria to segment an imitation into components. The segmentation algorithm (Agam et al., 2005) estimated the orientation of each of an imitation’s components by fitting a line to its beginning and end points. Imitation accuracy was then defined by orientation error: the absolute angular difference between the orientation of a segment in the imitation and the orientation of the corresponding segment in the stimulus model. (We use absolute error rather than error relative to the preceding segment because although the latter measure shows similar patterns, it produces artificially high overall error levels, as Agam et al., 2005 demonstrated.)

More specifically, the segmentation algorithm’s first step used pauses and direction changes in the imitation in order to identify candidate component end points. The algorithm’s second step identified groups of points that were close together in both time (≤ 60 ms) and space ($\leq 1.125^\circ$ visual angle). The point nearest a cluster’s centroid was taken as the “best” of the group of points. To qualify as distinct motion segments, the angle between the lines defined by these end points had to exceed 5° .

As each stimulus model comprised six motion components, a trial was deemed to be invalid if the segmentation algorithm recovered either fewer or more than six components in an imitation. Invalid trials were excluded from further analysis. To minimize the number of invalid trials and maximize the precision with which segment direction could be determined, subjects were instructed to try to produce the same number of segments that had been in the stimulus (six) and to, insofar as possible, draw straight lines with pauses between them. These instructions allowed the segmentation algorithm to return over 90% valid trials.

When measuring average accuracy, we can distinguish between trials in which the subject is successfully reproducing the trajectory (in which the imitation direction is close to the model direction), versus those where the subject is guessing at random. In order to minimize the influence of a small number of high-error trials, we restricted some analyses to those trials in which the orientation error was 90° or less.

Analysis of eye movement data

Offline processing removed blinks from the eye movement records, which were then passed through an 80 Hz,

first-order low-pass Butterworth filter. From successive samples of eye position, the eyes' velocity in the direction of the segment's motion was calculated; acceleration was calculated from successive velocity estimates. Saccades were identified by an absolute acceleration of $\geq 4000^\circ/\text{s}^2$ or an absolute velocity of $\geq 22^\circ/\text{s}$. These criterial values were chosen to distinguish saccades from smooth pursuit. Information about each saccade was stored for offline analysis, and the saccades were removed from the velocity records and replaced with linear interpolations.

To analyze de-saccaded eye movement data, we measured the degree of anticipatory acceleration during a window from 200 ms before each segment's disk motion onset to 50 ms after. We averaged eye movement data over trials, then fit a linear function to the velocity traces within this window to determine the degree of acceleration. To assess learning over presentations of congruent trials, we took the mean anticipatory acceleration preceding segments 2, 3, 4, and 5; to assess the effect of incongruent trials, we took the acceleration preceding segment 6 (Barnes & Donelan, 1999).

We had two reasons for choosing to analyze anticipatory eye movements during a time window that was defined relative to the onset of stimulus motion. First, the frequently used measure of pursuit onset described in Carl and Gellman (1987) requires defining a baseline period during which the eyes are not moving. Although the stimulus disk did pause briefly between its successive movements, that pause period did not provide a suitable baseline. For one thing, subjects' eyes tended to continue moving for some short time after the disk had paused; further, the subjects' eyes began to move again before the stimulus disk did. This left only a short, potential baseline period during which the eyes were not moving, and the timing of that period (that is, its onset and duration) varied with the subject's successive exposure to a motion sequence. Additionally, Carl and Gellman's (1987) metric for pursuit onset requires identifying a point three standard deviations away from the selected baseline, fitting a second line to the data in its vicinity, finding this line's intersection with the baseline, and defining that intersection to represent the onset of pursuit. In our data, this method entirely discounts the anticipatory eye movements that occur before disk motion onset, instead finding a point that occurs during the rapid acceleration that happens after the disk begins to move. Because we are primarily interested in using eye movements as an index of subjects' expectations, the loss of data regarding these anticipatory movements was unacceptable. We chose to instead measure eye acceleration during a time window that was fixed relative to stimulus motion rather than one that was defined relative to movements of the eyes. By measuring smooth eye movements made while the disk was actually stationary, we could identify eye movements that actually anticipated the disk's future motion, allowing us to tackle the cognitive questions that were our main interest.

We also measured the eyes' velocity at two theoretically significant times: before and after the time at which the actual direction of disk motion could affect eye movements. Specifically, 80 ms after the stationary disk began to move, the oculomotor system cannot yet respond to the disk's new direction of movement (Ball & Sekuler, 1980; Kowler, Martins, & Pavel, 1984). So, eye movements at that time are internally generated and provide a second measure of subjects' anticipation (Barnes, 2008; Barnes & Donelan, 1999). Measurements of eye velocity at 150 ms after disk motion onset, when the oculomotor system is responding to information about actual disk direction, allowed us to examine stimulus-motion-induced changes in eye movements (Barnes & Donelan, 1999).

Not surprisingly, the instruction to generate smooth pursuit movements in response to the stimulus did not suppress saccadic eye movements entirely. Because the disk accelerated abruptly from 0° to 9° per second at the start of each motion component, subjects often had to make a catch-up saccade in order to foveate the moving disk (de Brouwer, Yuksel, Blohm, Missal, & Lefèvre, 2002). Using the information about saccades that we captured during the de-saccading process, we found those saccades whose direction mirrored the direction of the disk, and which were made while the disk was moving. Of these, the single largest saccade whose distance did not exceed 5° visual angle was selected for analysis. We chose 5° as a cutoff because that value approximated the extent of a single motion component in the stimulus. A saccade greater than this value, or in a direction opposite the motion of the stimulus disk, was less likely to be a catch-up saccade than to reflect some momentary lapse of attention to the task.

Eye movements in response to the first segment of each trajectory are not included in our analyses.

Results

Three subjects failed to show improvement in imitation performance with successive repetition of stimuli. As such improvement was our index of learning, and as learning was the focus of our experiment, the data of those three, non-learning subjects were excluded from analysis.

Note that, except when stated otherwise, the first segment of each stimulus is ignored in these analyses. This segment had almost no anticipatory acceleration, and the sudden onset of the disk motion engendered a very large catch-up saccade, making eye movements to the first motion component quite different from eye movements to the remaining five.

Congruent trials

Our analysis of imitation performance began by focusing on congruent trials. We examined subjects' learning,

operationalized as improved fidelity of imitation as a motion sequence was repeated. We also examined possible parallels between learning-induced changes in imitation performance and changes in subjects' eye movements.

Imitation performance

With repeated presentations, subjects' error distributions shifted leftward (Figure 3A). Additionally, there was a decrease in the number of trials that qualify as "outliers," that is, trials on which imitation error exceeded 90° (Figure 3B). Because this cutoff value censored so few trials, particularly for later presentations, we decided to limit our later accuracy analyses to segments with error 90° or lower.

Figure 4 shows that within the data trimmed at 90° error, imitation on congruent trials improved as a stimulus sequence was repeated. This improvement was confirmed by a repeated-measures ANOVA, $F(4,28) = 106.49$; $p < 0.001$. However, the degree of improvement declined over successive presentations. From presentations 1 to 2, participants' accuracy on segments 2 to 5 improved by, on average, 4.77° (pairwise $t(7) = 10.30$, $p < 0.001$); from presentations 2 to 3, by 2.98° ($t(7) = 7.62$, $p < 0.001$); from 3 to 4, by 1.07° ($t(7) = 2.80$, $p < 0.05$); but from 4 to 5 by only 0.42° ($t(7) = 0.93$, $p = 0.39$).

Further, imitation fidelity varied with the serial position of an imitated component. As others found with a similar task (Agam et al., 2007, 2010; Maryott & Sekuler, 2009), imitation quality tended to be best for motion components

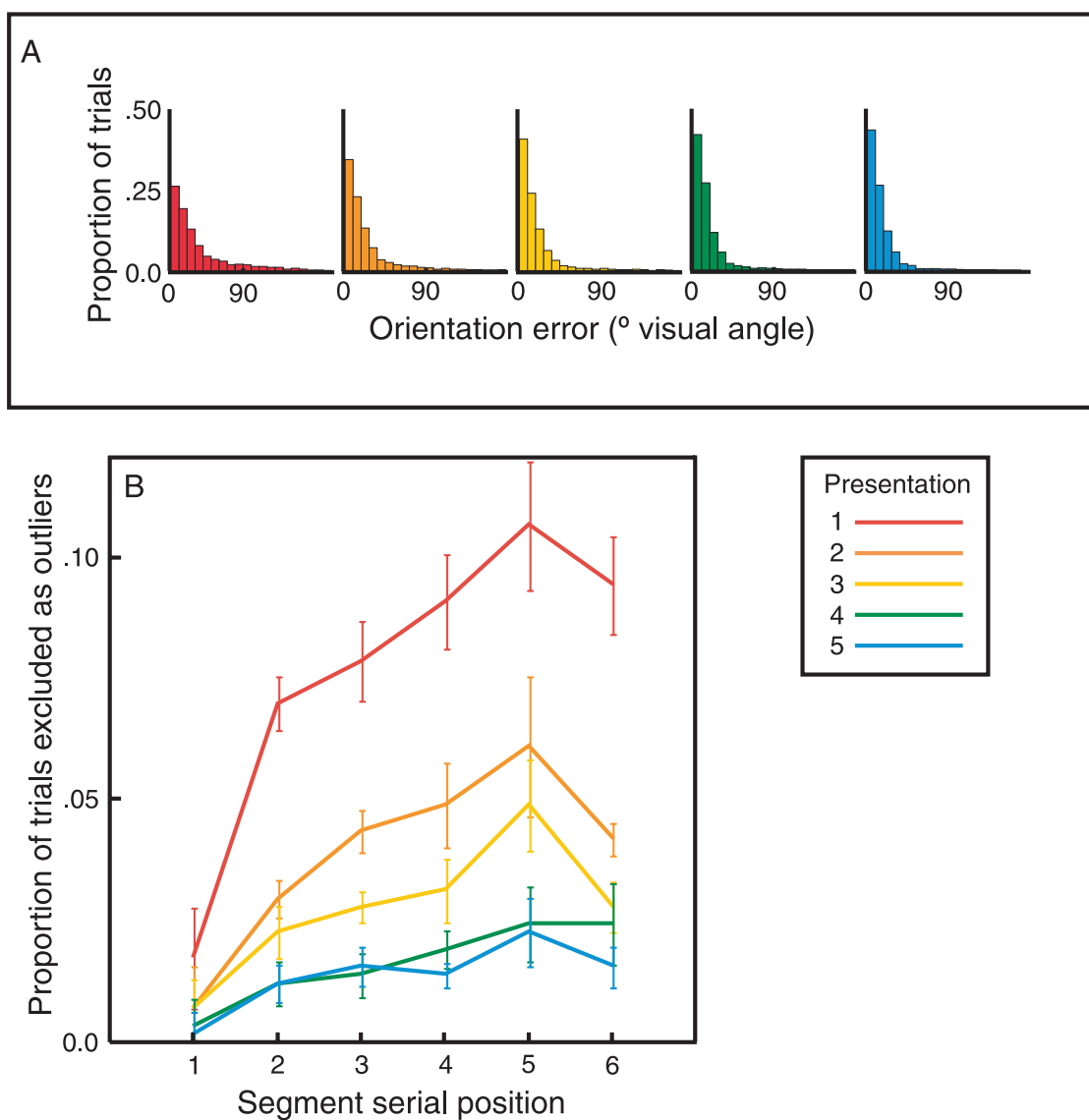


Figure 3. (A) Distribution of orientation error on congruent trials, over presentations 1 through 5, respectively. The distribution shifts leftward with successive presentations. (B) Proportion of trials excluded as outliers, by presentation and segment serial position. The five successive presentations are denoted by colors in spectrum order: red, orange, yellow, green, and then blue. Error bars are within-subject standard error, calculated independently for the data represented in each curve (Loftus & Masson, 1994).

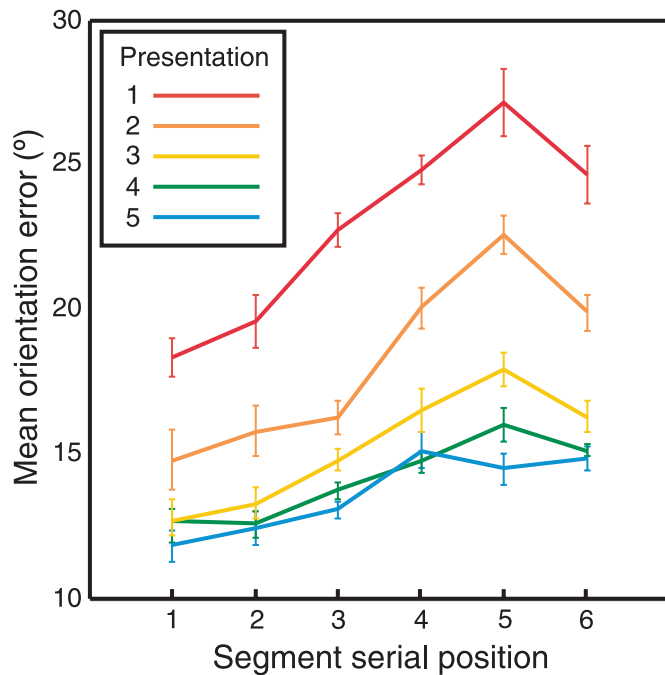


Figure 4. Mean orientation error on congruent trials across the six components in a motion sequence. Data are displayed separately for each of the five presentations of a sequence. Presentations are denoted by colors in spectrum order: red, orange, yellow, green, and blue. Note that imitation improved significantly over the first four presentations. Error bars are within-subject standard error, calculated independently for the data represented in each curve.

that occur early in a sequence and declined (that is, error grew) with serial position. This effect of serial position was confirmed by an ANOVA, $F(5,35) = 22.45$, $p < 0.001$. Finally, as also can be seen in both Figures 3B and 4, the pronounced serial position curve produced with a sequence's first presentations (red and orange curves) flattened out appreciably with subsequent presentations (yellow, green, and blue curves). This interaction between serial position and repeated presentation, which was confirmed by an ANOVA ($F(20,140) = 3.03$, $p < 0.001$), seems to reflect the fact that with repetition of a sequence, performance approaches an asymptote.

Smooth pursuit

Figure 5A shows de-saccaded eye velocity in the direction of stimulus motion for all subjects, and Figure 5C shows data for a single representative subject. The data have been collapsed across segments 2 through 5. The zero point on the figure's horizontal axis corresponds to the onset of disk motion. Note that traces corresponding to each presentation of a sequence exhibit a distinct leftward shift over successive presentations, with the degree of anticipation increasing over successive repetitions. Moreover, anticipatory acceleration in the direction the disk

will be moving can be seen beginning with the sequence's second presentation (Figure 5B). A series of post-hoc t -tests confirmed that the degree of anticipatory acceleration increased significantly with successive presentations from the first to the third ($p < 0.01$), as well as from presentations 4 to 5 ($p < 0.05$). The magnitude of this increase with repetition parallels the decline seen in imitation error. Both dependent measures show large changes from the first to second, and from the second to third presentations, followed by smaller changes thereafter. Moreover, similar changes are seen in eye velocity at 80 ms and at 150 ms after disk motion onset. Velocity increased with repetition ($F(4,28) = 43.22$, $p < 0.001$ at 80 ms; $F(4,28) = 47.54$, $p < 0.001$ at 150 ms), further confirming that smooth pursuit eye movements reflect learning over multiple presentations of the stimulus.

Saccades

The distance traveled by a catch-up saccade is a measure of the error in gaze position at the time that visual feedback becomes available to guide or correct eye movements. Figure 6A shows that on congruent trials, the average distance traveled during a catch-up saccade decreased with successive presentations ($F(4,28) = 118.02$, $p < 0.001$), with no effect of serial position ($F(3,21) = 0.58$, $p = 0.64$), which suggests that the amplitude of the catch-up saccade is similar for sequence components 2 through 5. Finally, the latency of catch-up saccades did not significantly change over repeated presentations ($F(4,28) = 2.66$, $p = 0.05$), and there was no consistent pattern of increase or decrease (Figure 6B).

Saccade amplitude reflects the quality of smooth pursuit. As the error and latency of smooth pursuit decrease, the distance that catch-up saccades need to travel also decreases. Therefore, these results are reassuring, but unsurprising.

Incongruent trials

Our analysis of flip and flip–return trials focused on the sixth and final component of a motion sequence. This is the component whose direction of motion flips (see Figure 2). Thus, unless stated otherwise, the following analyses are restricted to that sixth segment.

Smooth pursuit

Figures 7 and 8 show eye velocity traces for segment 6 alone on flip and flip–return trials, respectively. Presentations 1 through 3 (red, orange, and yellow) closely match those on congruent trials (Figure 5). On the fourth presentation (green), subjects made anticipatory eye movements in the direction the disk moved on previous repetitions, before correcting and moving their eyes in the direction the disk actually moved. On the fifth presentation

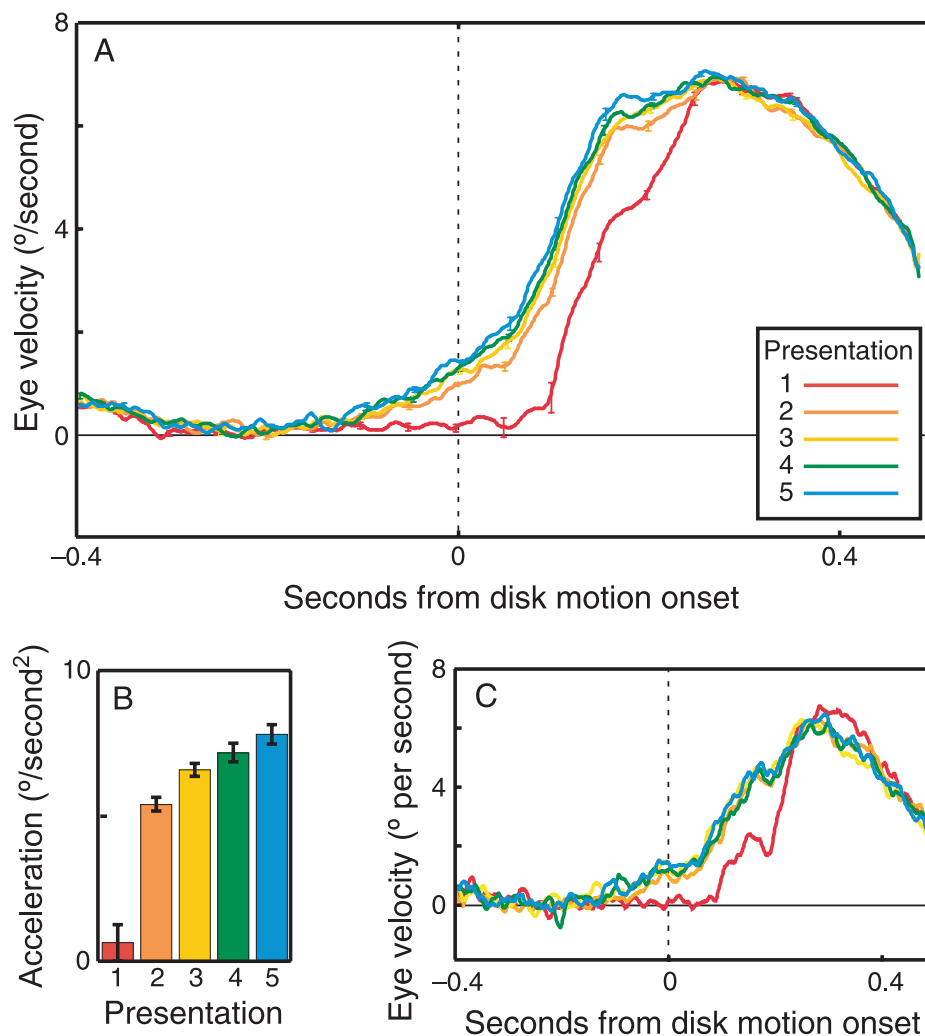


Figure 5. (A) De-saccaded eye velocity traces for congruent trials, averaged over subjects and motion segments 2 through 5, relative to onset of disk motion. Successive presentations are shown in spectral order (red, orange, yellow, green, and blue). Smooth pursuit movements began earlier with successive repetitions. Error bars are within-subject standard error calculated for each curve independently. (B) Anticipatory acceleration (degrees per second per second) for segments 2 through five, on congruent trials, by presentation. Acceleration was measured during a time window from 200 ms before disk motion onset to 50 ms after. (C) De-saccaded eye velocity traces by presentation for one representative subject, averaged over segments 2 through 5.

(blue), subjects' eye velocity remained low for approximately the first 100 ms after disk motion onset. After information about the direction of disk motion became available to the system, subjects' eyes accelerate to smooth pursuit speeds in the direction of actual disk movement (see Figure 10).

On presentations 1 through 3, the anticipatory acceleration seen on flip and flip–return trials was not significantly different from that seen on congruent trials. Figure 9 shows anticipatory acceleration associated with segment 6, by trial type and presentation. On presentation 4, subjects' anticipation was still similar across trial types, while on presentation 5, both flip and flip–return trials show anticipation in the new direction. This acceleration is significant (flip trials: $t(7) = -3.43$, $p < 0.05$; flip–return

trials: $t(7) = -5.8$, $p < 0.001$). After having experienced a sequence presentation on which a segment flipped, disconfirming expectations, subjects appear to expect the segment to remain flipped on the next presentation.

This difference in anticipation is confirmed by eye velocity measured at 80 ms and 150 ms after disk motion onset (Figure 10). As 80 ms is before visual information about the direction of disk motion is available to the eye movement system, the eye velocity at this time most likely reflects anticipatory eye movements. In contrast, velocity at 150 ms is after such information has become available and reflects subjects' corrections for unexpected disk motion.

The left panel of Figure 10 shows the eye velocity that is associated with segment 6 at 80 ms after disk motion

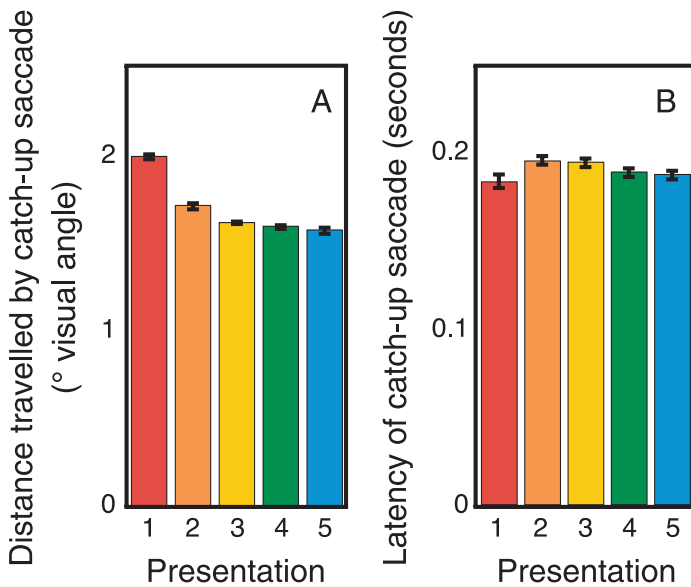


Figure 6. (A) Distance traveled by catch-up saccades on congruent trials, averaged across segments 2 through 5. This distance decreased significantly over the first four presentations. (B) Latency of catch-up saccades on congruent trials, averaged across segments 2 through 5. There were no significant changes in latency between successive presentations.

onset for the three trial types and for successive presentations. There are no differences across trial types for the first three presentations; notably, on presentation 4, subjects' eye velocity at 80 ms on flip and flip–return trials was the same as on congruent trials, even though the disk was traveling in the opposite direction. Because of the time it takes to determine a direction of motion (Ball & Sekuler, 1980), and because of lag in the oculomotor systems (Kowler et al., 1984), subjects' eye movements were not yet responding to the direction of disk motion. Note that on the fifth presentation, velocity at 80 ms was much smaller on both flip and flip–return than on congruent trials (paired t -test, $t(7) = 3.55$, $p < 0.01$ and $t(7) = 6.08$, $p < 0.01$, respectively). Nonetheless, this clearly confirms the expectation that the new component will again appear: the velocity of the eyes was significantly below zero (that is, in the direction of disk motion on the previous presentation) on both types of incongruent trials (flip: $t(7) = 3.07$, $p < 0.05$; flip–return: $t(7) = 5.32$, $p < 0.01$) but did not differ between them ($t(7) = 1.38$, $p = 0.210$).

The right panel of Figure 10 shows analogous data taken 150 ms after disk motion onset. Here, the smooth pursuit system has had time to respond to the direction of disk motion. On presentation 4, for both flip and flip–return trials, the eyes had stopped accelerating in the expected direction of disk movement and were accelerating in the actual direction of disk motion. (This is approximately the time at which velocity crossed zero as subjects reacted to the disk's unexpected trajectory.) On presentation 5, speed of eye pursuit on flip trials (on which

subjects' anticipatory eye movements were correct) was higher than on flip–return trials. The time required to correct for anticipation on flip–return trials led to reduced speed on those trials at 150 ms after disk motion onset.

Saccades

Catch-up saccades generated in response to segment 6 on the first three presentations were of similar amplitude across trial types. On presentation 4, catch-up saccades to congruent trials traveled a mean of 1.64° , those to flip trials traveled a mean of 2.64° , and those to flip–return trials traveled a mean of 2.65° . Distance traveled on the incongruent trials was significantly longer (paired t -test, $t(7) = 8.936$, $p < 0.001$ and $t(7) = 16.403$, $p < 0.001$, respectively). On presentation 5, catch-up saccades to congruent trials traveled 1.60° , those to flip trials traveled 1.86° , and those to flip–return trials traveled 2.31° . Catch-up saccades to congruent trials were shorter than those to flip trials ($t(7) = 4.602$, $p < 0.01$), which in turn were shorter

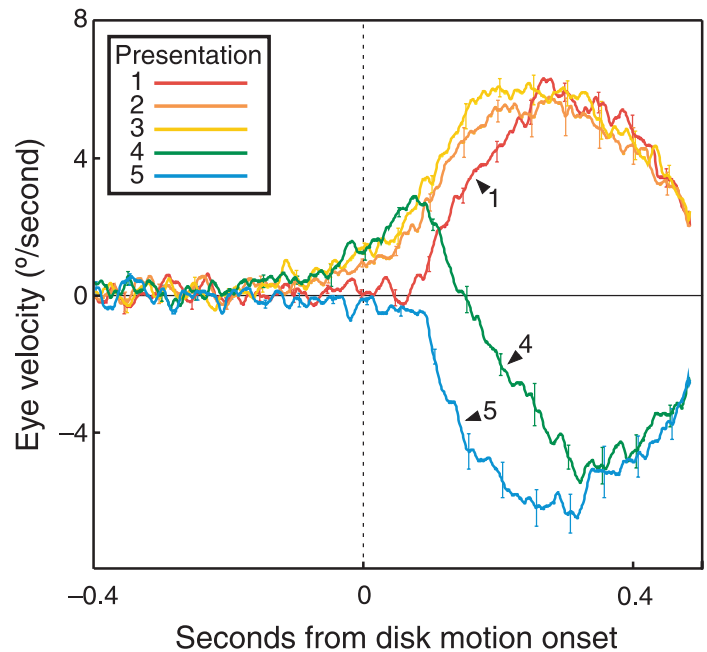


Figure 7. De-saccaded eye velocity traces for segment 6 on flip trials, averaged across subjects. Repeated presentations are shown in spectrum order (ROYGB). Note that on presentations 1, 2, and 3 (red, orange, and yellow traces), eye velocity was very similar to what was seen on congruent trials (Figure 5). On presentation 4 (green traces), anticipatory eye velocity was also very similar to that on congruent trials. However, at approximately 100 ms after onset of disk motion, subjects seemed to correct themselves and began to accelerate their eyes in the direction of the disk's actual motion. On presentation 5 (blue), subjects' anticipation was conservative but non-zero, with the eyes moving slowly in the direction the disk traveled on the previous presentation (Figure 9). Error bars are within-subject standard error, calculated independently for each curve.

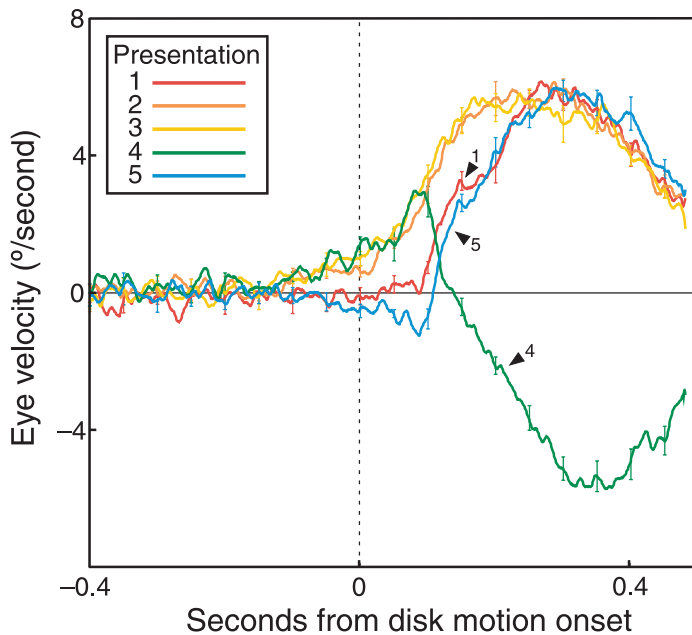


Figure 8. De-saccaded eye velocity traces for segment 6 on flip–return trials, averaged across subjects. Repeated presentations are shown in spectrum order (ROYGB). Note that on presentations 1, 2, and 3 (red, orange, and yellow traces), eye velocity was very similar to what was seen on congruent trials (Figure 5). On presentation 4 (green traces), anticipatory eye velocity was also very similar to that on congruent trials. However, at approximately 100 ms after onset of disk motion, subjects seemed to correct themselves and began to accelerate their eyes in the direction of the disk’s actual motion. On presentation 5 (blue), subjects’ anticipation was conservative but non-zero, with the eyes moving slowly in the direction the disk traveled on the previous presentation (Figure 9). Error bars are within-subject standard error, calculated independently for each curve.

than those to flip–return trials ($t(7) = 8.085, p < 0.001$). As is to be expected, this pattern of increased positional error resembles the pattern of eye velocity after feedback has become available and corroborates the hypothesis that subjects expected the final segment to remain flipped.

Imitation performance

Imitation performance on flip and flip–return trials is broadly similar to that on congruent trials. In particular, there is no effect of trial type on imitation for the first five segments of a sequence ($F(2,14) = 0.19, p = 0.83$), which justifies the decision to focus the present analysis on segment 6. The dark and light gray bars in Figure 11 show trimmed imitation performance on the sixth (final) segment of flip and flip–return trials, respectively; the corresponding performance on congruent trials is shown by the \diamond symbols. The general pattern of improvement (decreased error) seems to be approximately the same for all three trial types. In particular, on presentation 4 (when the flip occurred), there were no appreciable differences between

trial types. On presentation 5, there is a small difference between accuracy on flip trials and that on flip–return trials; we investigated this further in Experiment 2.

Discussion

As expected from previous behavioral studies with the task used here, when some particular sequence of movements was presented multiple times, there was a systematic increase in the accuracy with which the sequence was imitated. Here, this demonstration of learning was accompanied by increased anticipatory eye movements. Additionally, the distance traveled by any “catch-up” saccade decreased with repeated presentations, suggesting that subjects are able to produce smooth pursuit movements that more closely matched the motion of the disk, reducing the distance required for a saccade to restore foveation. In sum, our results show that repetition not only promotes learning in the imitation task itself, but also that the eye movements made by subjects reflect this learning.

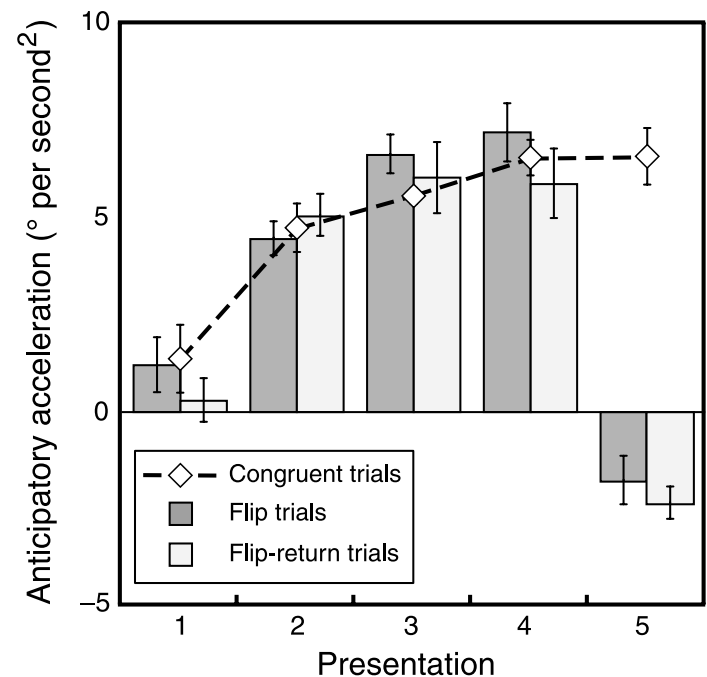


Figure 9. Anticipatory acceleration preceding segment 6, for congruent, flip, and flip–return trials. This is the degree of acceleration during a window from 200 ms before disk motion onset to 50 ms after. Acceleration on congruent trials is shown by the \diamond symbol; that on flip and flip–return trials is represented by the dark and light bars. On presentation 4, acceleration is similar across trial types; on presentation 5, acceleration suggests that participants anticipate that the flipped component will again appear. Error bars are within-subject standard error, calculated for each trial type independently.

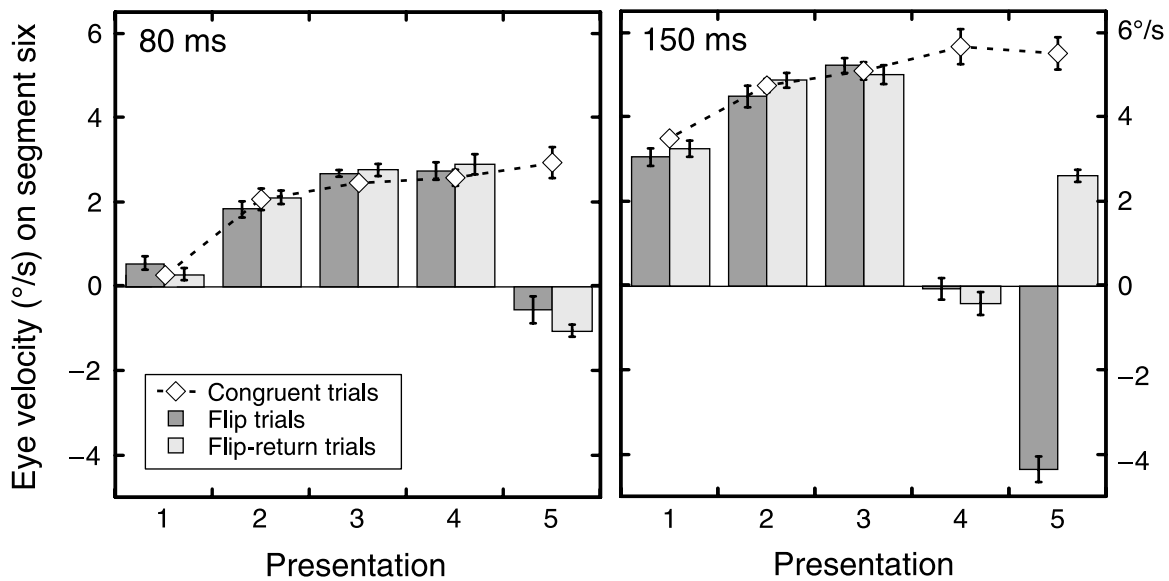


Figure 10. Eye velocity associated with the sixth (final) motion component in successive presentations of a stimulus sequence. The left panel shows tracking velocity at 80 ms after motion onset; the right panel shows tracking velocity at 150 ms after motion onset. Due to lag in the oculomotor system, these represent tracking velocity measured (left) just before and (right) just after visual information about the disk's direction of motion could guide a subject's eye movements. Mean tracking velocity on congruent trials is represented by the \diamond symbols. The bars within each panel represent tracking velocity for the two types of incongruent trials: dark bars for flip trials, and lighter bars for flip–return trials. Eye velocity at 80 ms after stimulus motion onset (left panel) confirms that on presentation 4, anticipatory eye movements are the same on incongruent trials as on congruent trials; however, because the disk actually moves in the opposite (unexpected) direction, this anticipatory movement is incorrect. On presentation 5, subjects appear to have been conservative in their anticipatory behavior but clearly moved their eyes in the direction in which the disk previously moved. Eye velocity at 150 ms (right panel) shows subjects' reaction to the direction of disk movement on presentation 4. Their eyes were accelerating in the correct direction (such that velocity at this time is near zero) but had not yet reached smooth pursuit speeds. On presentation 5, the early eye movement in the flipped direction resulted in eye speed at 150 ms being reduced on flip–return trials relative to flip trials. Error bars are within-subject standard error, calculated for each trial type independently.

In addition to examining the learning that came from repeated presentations of our stimuli, we intentionally promoted prediction errors on some random subset of trials (incongruent trials) by causing the last segment of stimuli on those trials to reverse (or “flip”) its direction on the penultimate presentation. Anticipatory eye movements can provide a sensitive assay of subjects' beliefs about an impending movement of a stimulus (Barnes, Schmid, & Jarrett, 2002; Kowler, 1989); by examining the eye movements associated with these flipped segments, we were able to probe subjects' expectations about the stimulus. On the penultimate (fourth) presentation, eye velocity traces suggest that subjects anticipated that the disk would travel in the same direction that it had taken on the previous three presentations. Subjects moved their eyes in the direction that the disk had traveled on previous presentations and did so at a time and with acceleration that was similar to that seen on congruent trials. That is, subjects had learned the sequence of movements and were acting upon the expectation that had been developed. Before the visual system had access to information about the disk's direction of motion, the eyes were already moving at more than 2.5°/s in the expected direction. By 150 ms after disk

motion onset, subjects were using visual feedback to correct for the unexpected motion, and their eyes were accelerating in the correct direction. The unexpected direction taken by the flipped motion segments also resulted in increased distance traveled by “catch-up” saccades, confirming that the positional error of the eye was larger for flipped segments than for unflipped segments.

By examining eye movements and imitation performance on the final presentation of a trial, we were able to investigate the consequences of exposure to an incongruent sequence. In our experiment, the two types of incongruent trials, flip and flip–return, occurred with equal frequency. Therefore, subjects had no basis to expect that a flip on the penultimate presentation would guarantee that the segment would remain flipped on the final presentation, rather than resuming its original direction of motion. Nonetheless, on the final presentation of both flip and flip–return trials, subjects moved their eyes in the flipped direction, that is, the direction in which the disk traveled on the previous presentation (see Figures 7 and 8). Further, these eye movements began well before the stimulus disk itself began to move. This result is consistent with previous demonstrations of one-shot learning in control of smooth eye

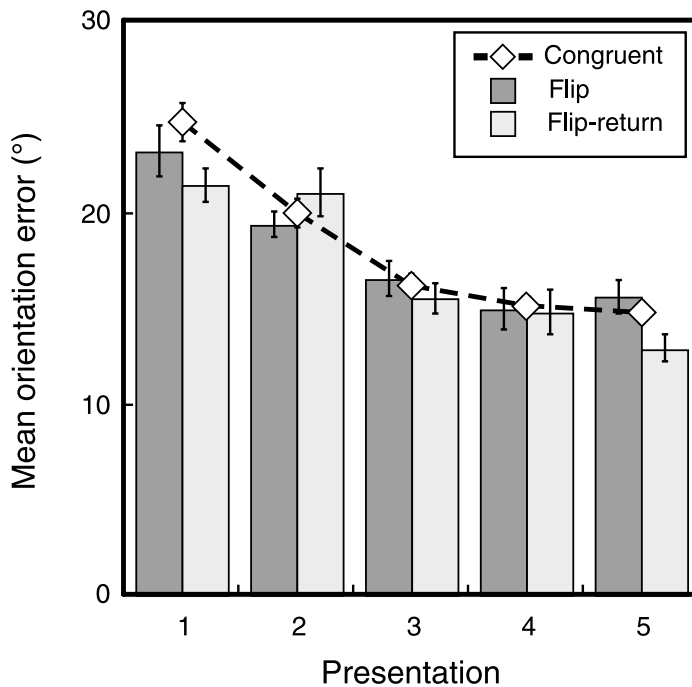


Figure 11. Mean orientation error in reproducing the sixth (final) motion component of stimulus sequences. Results are displayed according to trial type: congruent trials are represented by the \diamond symbol, dark bars represent results on flip trials, and lighter bars represent results on flip–return trials. Note that the general decrease in error is similar for all three types of trials, and especially that there is no appreciable effect of trial type on presentation 4, when the flip occurs. Error bars are within-subject standard error, calculated for each trial type independently.

movements (Barnes, 2008; Kowler, 1989). Recent work by Yang, Hwang, Ford, and Heinen (2010) suggests that the decision rules governing smooth eye movements are coded in the supplementary eye fields (SEF), which also play a role in anticipatory smooth pursuit (Missal & Heinen, 2004). It is not yet known, however, whether one-shot learning, such as we observed, results from some updating of SEF coding.

This indication that subjects expected the previously flipped segment to remain flipped is confirmed by quantitative measures. Eye velocity at 150 ms after disk motion onset was significantly lower on the final presentation on flip–return than on flip trials, and catch-up saccades traveled farther. This behavior on flip–return trials indicates that subjects incorrectly expected that the flip direction comprised a new direction that should be remembered. The result was that subject took longer to reestablish smooth pursuit. In contrast, on flip trials, subjects' expectation was correct, which resulted in shorter latency for smooth pursuit. Following a single presentation of a motion sequence containing an unexpected directional component, subjects' anticipatory eye movements show that they expect the novel component to reoccur. This

happens despite there being no statistical advantage to such an expectation. This bias in favor of a novel directional component suggests that events that had been unexpected have heightened salience for learning; after all, many errors that an organism makes are a sign that a change in behavior is in order when a similar situation next arises.

Finally, the effects that a flip had on imitation accuracy were small, possibly because the sequence had been well learned by the penultimate presentation, the one in which the flip occurred.

Experiment 2

In order to test the idea that performance on flip and flip–return trials differs on the presentation immediately after the original flip, and to see if ceiling effects influenced our original results, we conducted a second, behavioral experiment that presented the deviant sequence on the third, rather than the fourth, presentation.

Methods

Subjects

Eleven young adults (5 females; ages 19–23) participated in this experiment. None had taken part in any previous experiments with this task; all had normal or corrected-to-normal vision.

Experimental task

This experiment used the same task as that described for Experiment 1 (see Figure 1).

Design and procedure

As in Experiment 1, each trial's sequence of motions was presented five times, 64% of which were congruent trials and 36% of which were incongruent trials. Figure 12 shows examples of how congruent, flip, and flip–return trials changed over successive presentations. On the third presentation of incongruent trials, the final component of the trajectory was replaced by a component in which the stimulus disk moved in the opposite direction (Figure 12, rows 2 and 3). The incongruent trials were divided equally into flip trials, in which the new component appeared again on the fourth presentation, and flip–return trials, in which the fourth presentation included the original final component. On all trials, the fifth presentation was identical to the fourth presentation.

Each subject completed four 45-min sessions of 28 trials, with five presentations per trial. The first three trials of each session were always congruent trials, and the remaining 25 trials were distributed across blocks of five

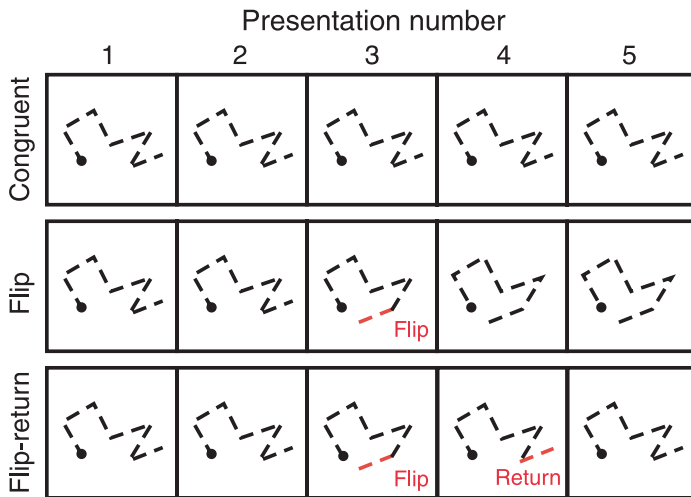


Figure 12. An exemplar of a motion sequence illustrating how a sequence could change over successive presentations. In each panel, the black disk represents the location from which the sequence began. Note that in the experiment, each trial's trajectory was unique; here, just one exemplar is given to illustrate differences among the three trial types. A motion component whose direction differed from that on the previous presentation is shown in red. Row 1: On congruent trials, the disk followed the same trajectory on each repeated presentation. Rows 2–3: On flip and flip–return trials, the first two presentations were identical, but then, on presentation 5, the final motion component was 180° flipped from its previous direction. These two trial types are collectively referred to as incongruent trials. On flip trials, the final motion component preserved its flipped direction for the fourth and fifth presentations; on flip–return trials, the final segment returned to its original pre-flip direction for the fourth and fifth presentations.

trials each; a block comprised one flip trial, one flip–return trial, and three congruent trials, in random order. Subjects were not informed that some trials would be incongruent trials.

Subjects' eye movements were not recorded during viewing of the stimulus sequence.

Analysis of imitation

The fidelity of each imitation was quantified offline using the algorithm described in Experiment 1. Again, to minimize the influence of a few high-error trials, we restricted some analyses to those trials in which the orientation error was 90° or less.

Results

One subject failed to show improvement in imitation performance with successive presentations of stimuli. As such learning was the focus of our experiment, the data of this non-learning subject were excluded from analysis.

Congruent trials

Figure 13 shows that within data trimmed at 90° error, performance on congruent trials improved over repeated presentations (repeated-measures $F(4,36) = 43.27$, $p < 0.001$). The degree of improvement tended to shrink with successive presentations, suggesting that participants are approaching a ceiling. From presentations 1 to 2, accuracy on segments 2 to 5 improved by, on average, 3.26° (pairwise $t(9) = 4.71$, $p < 0.01$); from presentations 2 to 3 by 2.59° ($t(9) = 3.73$, $p < 0.01$); but from 3 to 4 by only 0.75° ($t(9) = 1.75$, $p = 0.11$); and from 4 to 5 by only 0.85° ($t(9) = 2.97$, $p < 0.05$).

Imitation accuracy varied with serial position, showing a strong primacy effect ($F(5,45) = 12.66$, $p < 0.001$), similar to that seen in Experiment 1 and as seen in other experiments using a similar task (Agam et al., 2007, 2010; Maryott & Sekuler, 2009). As well, the dramatic serial position curve of presentation 1 tends to flatten with successive presentations ($F(20,180) = 6.34$, $p < 0.001$).

Incongruent trials

Again, imitation performance on flip and flip–return trials is broadly similar to that on congruent trials. In particular, there is no effect of trial type on imitation for

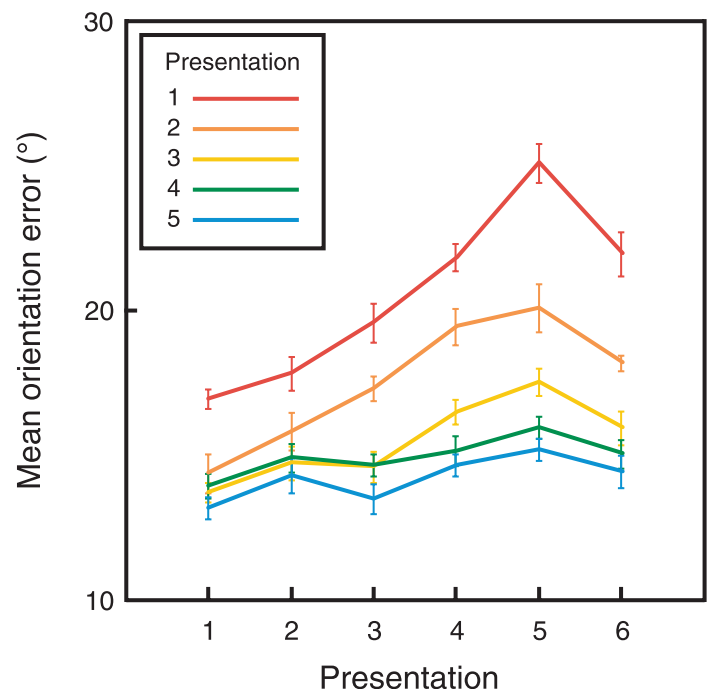


Figure 13. Mean orientation error on congruent trials with 90° error or less, shown across the six components in a motion sequence. Data are displayed separately for each of the five presentations of a sequence. Error bars are within-subject standard error (Loftus & Masson, 1994), calculated for each curve separately. Note that improvement over presentations includes a flattening of the serial position curve.

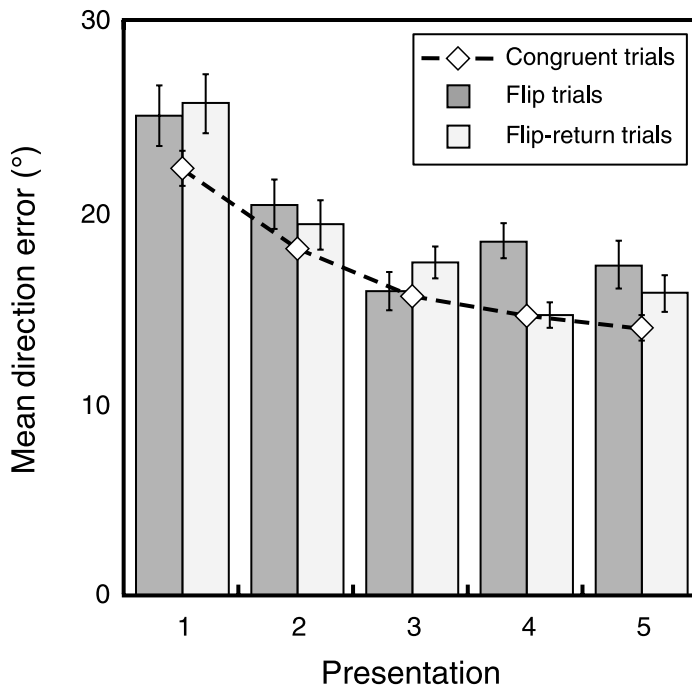


Figure 14. Mean orientation error in reproducing the sixth (final) motion component of stimulus sequences. Results are displayed according to trial type: congruent trials are represented by the \diamond symbol; dark bars represent results on flip trials, and lighter bars represent results on flip–return trials. The general decrease in error is similar for all three types of trials. Note particularly that although there was no effect of trial type on presentation 3, accuracy on flip trials was significantly worse than on flip–return trials on presentation 4. Error bars are within-subject standard error, calculated independently for the data from each trial type.

the first five segments of a sequence ($F(2,18) = 2.57, p = 0.10$), so we focused our analysis on segment 6.

Figure 14 shows imitation performance on the sixth and final component of each trial type. We again see the general pattern of decreasing error over presentations 1 and 2, and on presentation 3, when the flip occurs, there is no appreciable effect of trial type. On presentation 4, imitation accuracy decreases on flip trials ($t(9) = 2.52, p < 0.05$) but increases on flip–return trials ($t(9) = 2.51, p < 0.05$). In fact, on this (fourth) presentation, imitation accuracy on flip trials is significantly worse than on flip–return trials ($t(9) = 3.25, p < 0.01$). No trial type showed significant changes in accuracy from presentations 4 to 5.

Discussion

In order to assess subjects' performance on incongruent trials, we can compare their imitation of the novel segment (seen on the third presentation of a trial) to their imitation of the corresponding segment on the very first presentation (when the whole stimulus was novel). Performance on flipped segments was considerably better

than on that first presentation. In fact, performance was not appreciably different from that on the comparable segment during the third presentation on congruent trials. This equivalence could reflect the fact that the prediction error led to improved learning for the novel segment (as in den Ouden et al., 2009; Frank, Worocho, & Curran, 2005; Laurent, 2008), bringing imitation accuracy to the near-ceiling level on congruent trials' third presentation. Another possibility is that, by the third presentation, the rest of the sequence was sufficiently well learned that subjects had additional resources to devote to encoding the novel component. Further, as the flipped segment always changed direction by 180° subjects might have registered and then exploited that regularity in order to aid encoding of the novel segment. That could have decreased task difficulty and produced better memory for the novel segment (Agam & Sekuler, 2007). However, these later two hypotheses do not entirely explain the discrepancy between performance on flip and that on flip–return trials on the presentation after a flip. In short, these data show that an unexpected item in the context of a familiar sequence leads to improved learning for that item.

General discussion

The results of our experiments are consistent with previous demonstrations that error-induced learning can strengthen associative memory (e.g., den Ouden et al., 2009; Schultz, 2006; Wills et al., 2007) and with demonstrations of one-shot learning in episodic memory (e.g., Kumaran & Maguire, 2006, 2007) and in a target-reaching task (Thoroughman & Shadmehr, 2000). Note that the associative learning literature has generally described errors that occur when a subject gives an incorrect response, i.e., endogenous errors. Our study, on the other hand, describes exogenous errors that arise when we add unexpected deviant components to a well-learned sequence, causing subjects' predictions to be incorrect. Nonetheless, the similarity of event-related potentials to deviant sequences and those to task errors (Ferdinand et al., 2008; Rüsseler, Hennighausen, Münte, & Rösler, 2003; Schlaghecken, Stürmer, & Eimer, 2000) suggest that both exogenous and endogenous errors may lead to stronger learning for mispredicted events, either as a source of neural signals that promote learning directly, and/or as a modulator of selective attention. A fuller understanding of the mechanisms responsible for error-induced learning could come from future work that directly investigates the neural response associated with such mispredictions. Additionally, important questions remain about the way in which induced errors and sequence learning are related. A future study might examine whether unbalanced exposure to flip and flip–return trials, which here were equally likely, would alter what seems to be the subjects' expectation that, once a

stimulus changed, that change would be preserved on its next occurrence. If, as generally found in studies of episodic memory, the most recent experience exerts a disproportionately strong influence on expectation (Kumaran & Maguire, 2006), it would be theoretically valuable to know how this effect might be modulated by the statistical distribution of trial types.

In summary, we have shown that an imitation-learning task can be useful as an arena within which to track the evolution of subjects' memory-based representations of complex, time-varying visual stimuli. The task can also be useful for examining how such representations are influenced by cognitive factors, particularly violations of the expectations that subjects acquire over repeated presentations. Additionally, our results reveal how learning and expectation can affect the tracking and saccadic eye movements that subjects make while viewing a complex stimulus. Although some compatible results have been reported with simpler stimuli, such as horizontal and vertical motions (Burke & Barnes, 2007), our study is the first to combine directionally complex stimuli with intentionally provoked errors in order to examine subjects' memory-based representation of the stimulus. Finally, our results demonstrate that errors, in our case, externally induced ones, can lead to strong, error-induced learning.

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