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The time course of online trajectory corrections in memory-guided saccades

Brian A. Richardson · Anusha Ratneswaran · James Lyons · Ramesh Balasubramaniam

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Abstract Recent investigations have revealed the kinematics of horizontal saccades are less variable near the end of the trajectory than during the course of execution. Converging evidence indicates that oculomotor networks use online sensorimotor feedback to correct for initial trajectory errors. It is also known that oculomotor networks express saccadic corrections with decreased efficiency when responses are made toward memorized locations. The present research investigated whether repetitive motor timekeeping influences online feedback-based corrections in predictive saccades. Predictive saccades are a subclass of memory-guided saccades and are observed when one makes series of timed saccades. We hypothesized that cueing predictive saccades in a sequence would facilitate the expression of trajectory corrections. Seven participants produced a number of single unpaced, visually guided saccades, and also sequences of timed predictive saccades. Kinematic and trajectory variability were used to measure the expression of online saccadic corrections at a number of time indices in saccade trajectories. In particular, we estimated the minimum time required to implement feedback-based corrections, which was consistently 37 ms. Our

observations demonstrate that motor commands in predictive memory-guided saccades can be parameterized by spatial working memory and retain the accuracy of online trajectory corrections typically associated with visually guided behavior. In contrast, untimed memory-guided saccades exhibited diminished kinematic evidence for online corrections. We conclude that motor timekeeping and sequencing contributed to efficient saccadic corrections. These results contribute to an evolving view of the interactions between motor planning and spatial working memory, as they relate to oculomotor control.

Keywords Saccades · Feedback · Oculomotor control · Motor timing · Spatial working memory

Introduction

Saccadic movements of the eyes are among the fastest and most frequently occurring movements executed by humans. Satisfying both the speed and accuracy demands of oculomotor control is often quite difficult. As a result, the precision of saccades is imperfect, and few neural mechanisms exist to correct for spatial errors. To correct gaze position immediately following an inaccurate saccade, secondary corrective saccades toward the proper target location are made frequently (Prablanc et al. 1978). If a discrepancy between the target and gaze recurs consistently, future saccade plans are updated via gain adaptation (Noto and Robinson 2001). Recent work that investigated saccades on a finer timescale of error correction showed that the oculomotor system corrects for impending visual errors while the saccade is still being executed (Gaveau et al. 2003; West et al. 2009; Heath et al. 2010, 2011). These *online* changes to saccade trajectory resolve accruing spatial errors before

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movement termination. In the current experiment, we investigated the influence of motor timekeeping on the kinematics of online saccade corrections.

Saccadic eye movements are in a class of goal-directed actions that are directed toward a spatial goal. Often, goal-directed actions exhibit qualities that are invariant across effectors. For example, the relative kinematics observed in both manual aiming and saccading are remarkably similar. One methodology used for investigating the spatiotemporal dynamics of online corrective process in goal-directed actions involves a comparison of trajectory kinematics. It is commonly observed that spatial errors do not completely accumulate from movement onset to termination in rapid manual aiming (Khan et al. 2002) and saccading movements (West et al. 2009). When comparing repeated execution movements that have similar amplitudes, there is a large variability in effector position during early phases of the movement that is corrected for prior to arriving at the target. This leads to a characteristic and significant decrease in variability from mid-trajectory to the end. Online saccadic corrections are interesting phenomena since they occur at a fast rate, as early as 30 ms after the initiation of the saccade (West et al. 2009). Small amplitude saccades are completed in less time, so corrections are only observed in longer duration saccades.

Online saccadic corrections are expressed optimally when the movements are guided by a visible target. Memory-guided saccades are controlled differently since they are directed to a location where a target has previously been seen and is not visible when saccades are executed. When executing memory-guided saccades, the saccade motor command metrics are generated based on a target representation stored in spatial working memory (SWM). In the specific case of single memory-guided saccades, online corrections are implemented with decreased efficiency relative to visually guided saccades (West et al. 2009). This task involved showing a visual target only briefly, and saccades to the remembered location were made after a short delay.

Predictive saccades could also be considered as a class of memory-guided saccades when there is no visible target when they are initiated. Such predictive behavior is commonly observed in motor timekeeping tasks. For example, saccades arrive at target locations prior to the onset of target visibility when the movements are sequenced to periodic time intervals. Thus, predictive saccades provide a novel context in which to investigate online trajectory corrections. In the present study, we aimed to observe the expression of online corrections in predictive saccades. We hypothesized the expression of online corrections would be modulated by imposing a periodic motor timekeeping goal on sequences of saccades. One reason to predict that timekeeping will influence saccadic trajectories is that some models of timekeeping define an elementary overlap with

short-term memory resources (Staddon 2005). This is relevant to predictive saccades because their motor commands are parameterized by metrics stored in spatial working memory. Furthermore, it has also been demonstrated that repeated execution of a motor action contributes to potentiation of spatial working memory (Awh and Jonides 2001). It is possible that the aspect of sequencing in itself promotes ideas of greater cortical recruitment for anticipatory planning, which can even be done in parallel for consecutive goals (Heide et al. 2001; Baldauf et al. 2008). Consequently, with many possibilities for overlapping function, we reasoned that sequenced and periodic execution might facilitate online trajectory corrections in saccades.

Materials and methods

Seven undergraduate students (two men, five women, M age = 20.86 years, SD = 0.69, range 19–22 years) were recruited from the McMaster University student population. All participants gave informed consent to participate in the experiment and were naïve to the purposes of the study. All participants had 20/20 vision either naturally or corrected. The following experimental protocol was approved by the Research Ethics Board of McMaster University.

Apparatus

The data acquisition apparatus used in this study was the EyeLink II (SR Research, Osgoode, Ontario) eye-tracking system. We used this head-mounted system to sample gaze angle at a rate of 250 Hz. This system recorded gaze data with a dedicated host PC running proprietary DOS-based software. Experimental stimuli were presented using the Experiment Builder (SR Research) software on a display screen (CRT monitor, $640 \times 480@125$ Hz resolution) attached to a Windows XP (TM)-based PC. Saccading targets were presented on the computer screen as white circles, which subtended approximately 0.4° of visual angle (~ 5 mm). In order to cue saccades to predetermined amplitudes, participants sat with their heads located 65 cm from the display screen. The distance between saccade targets and the position of gaze direction was measured in degrees of visual angle.

Procedure

Participants made horizontal saccades to locations on the display screen, which were cued by visual targets in either a “control” condition or a “timed” condition. Saccades were executed to target amplitudes of 4° , 8° , 12° , 16° , and 20° of visual angle. To show the sequence of conditions visually, the following procedures are also illustrated in Fig. 1.

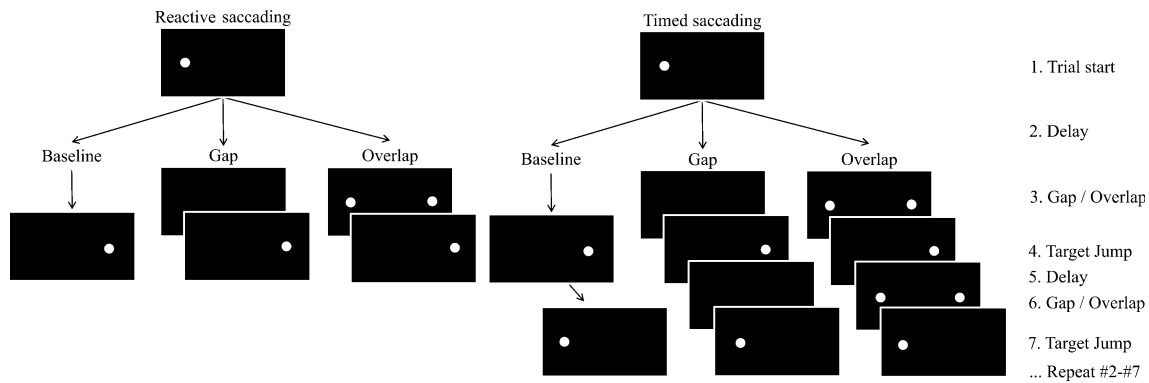


Fig. 1 Illustration of the procedure used in our experiment. Timed saccading cueing protocol is pictured on the *right*, and reactive saccading cues are presented in the control condition and pictured on the *left*. In the *baseline* condition, target jumps had no temporal gap or overlap and toggled visibility synchronously. Consequently, steps 3 and 6 do not apply to *baseline* trials. In reactive saccading trials, the delay at

step 2 was randomly set between 750 and 1,500 ms. After step 4, the reactive trials are terminated. In timed trials, delay in step 2 and 5 is represented by the duration of the inter-stimulus interval (ISI), at 500, 750, 1,000, and 1,500 ms. In these trials, targets were switched back and forth for 26 jumps total, then the trials were terminated

In the control condition, participants made reactive saccades in response to the onset of a visual target. Our control procedure was performed exactly using the specifications of the visually guided reactive saccading conditions used in previous research (see experiment 1; West et al. 2009). At the beginning of a trial, participants maintained fixation looking at a static target on the display screen. When the eye tracker detected a steady fixation for one second, a pseudorandom delay between 750 and 1,500 ms was imposed prior to the onset of the saccade target. This target would appear at one of the aforementioned amplitudes, either to the left or to the right of the fixation target. When participants saw the target appear, they quickly executed a saccade toward the target location and the trial was terminated shortly thereafter. Fifteen saccades were collected in both rightward and leftward directions, and data were collapsed for this factor in analysis.

In the timed saccading condition, targets were either visible on the left or on the right side of the screen. Pacing for saccades was cued by alternating the visibility of left and right visual targets at regular time intervals. Since saccades were made reciprocally in both directions, we referred to the fixation target as the location where gaze was fixated before a saccade, and the saccade target as the location to where each saccade is directed. In other words, during a sequence of movements, the saccade target of one saccade is effectively the fixation target for the next. Saccade cues were presented at 4 pacing rates (inter-stimulus intervals—ISI), 500, 750, 1,000, or 1,500 ms. These particular time intervals were chosen because they are associated with entraining periodic saccades to a rhythm such that initiation is accomplished by predictive timekeeping and not by visually guided reactive behavior (Joiner and Shelhamer 2006). We have used these techniques previously and replicated predictive responses using similar cueing methods

(Richardson and Balasubramaniam 2010). In the case of timed saccading alone, our analyses refer to *ISI* as the 4-level analysis factor within timed saccading trials. Our analyses instead use *pacing condition* when referring to the comparison of control condition reactive saccades against timed saccades. Each timed trial consisted of cueing 26 consecutive saccades in alternating directions, and data were collapsed across rightward and leftward directions.

We also manipulated target visibility using the gap paradigm (gap task) for both timed and reactive saccading tasks. Gaps in target visibility were used for manipulating the excitability of the oculomotor system in the time window immediately preceding saccade onset. When the eyes are not in motion, they are in fixation, and omnipause neurons are responsible for inhibiting activity in saccade-related burst neurons (Sparks 2002). Changing the visibility of a fixation target thus modulates the level of inhibition on saccade-related oculomotor output. The gap task manipulation had three conditions: in the baseline condition, the fixation target toggled synchronously with the saccade target. In other words, as the fixation target extinguished the saccade target appeared at the same instant. Here, the oculomotor system must increase activity in saccade-related burst neurons in parallel with decreasing the activity in omnipause neurons. In the gap condition, however, occlusion of the fixation target preceded the onset of the next saccade target by 200 ms. Similar gap conditions have been used in many experiments to demonstrate that active fixations are more quickly disengaged prior to onset of the saccade target, which leads to faster saccade latencies (Saslow 1967). In the overlap condition, the fixation target continued to be visible until 200 ms after the onset of the saccade target. Imposing this overlap in visibility directly opposes the intention of imposing a gap. An overlap is associated with longer response latencies, which are consequent to

extending the duration of inhibition on the saccade-related neurons. Previous research failed to demonstrate an influence of the gap effect on the trajectories of visually guided saccades (West et al. 2009). However, we included the gap, overlap, and baseline conditions to assess whether this manipulation influences oculomotor performance differently when saccades are initiated by means of internal sensorimotor timekeeping. Overall, the timed saccading trials consisted of 4 ISI \times 3 Gap Task \times 5 Target Amplitude factorial designs. Control saccading did not include the pacing rate factor, and data were acquired for a 3 Gap Task \times 5 Target Amplitude factorial model.

Data analysis

Data processing was carried out with in-house developed scripts written for MATLAB (Mathworks, Natick, MA). Gaze position, velocity, and acceleration time series were extracted for each trial. To better identify the gaze position at a finite time scale, MATLAB's *resample* function was used to upsample gaze data by a factor of four, which equated one sample to one millisecond. Similar interpolations have been used with the same intention in other research (van Beers 2007). Saccades were identified using velocity and acceleration thresholds. The onset of saccades was determined as the first sample to exceed both 30°/s and 8,000°/s². The termination of saccades was then marked by the first sample where velocity was less than 30°/s. Saccades were excluded based on one heuristic. When the saccade amplitude was greater than 2.75° visual angle error away from the cued amplitude, that saccade was excluded. This criterion is approximately the mean plus three standard deviations of the expected variability in saccade amplitudes as reported from saccades in previous research (West et al. 2009). The rate of exclusion was approximately 1 in 6 saccades and was consistent between both timed and control conditions. By definition, our inclusion criteria effectively constrain the analysis to accurate saccades. Since the intention of this experiment is to attribute the mid-saccade trajectory variability to corrective processes, we can only infer that variability is potentially representative of corrections if the saccade is accurate.

Each remaining saccade was examined using a kinematic analysis. Gaze position was extracted at five relative indices of movement completion: 20, 40, 60, 80% movement time (MT), and the endpoint. At these time markers, we computed the distance gaze had travelled from the location where the saccade was initiated. This was done for each saccade for ultimately comparing trajectory variability at all MT indices. For the variability analysis, kinematic data from the saccades in each trial condition were pooled for calculating the standard deviations of gaze distance traveled at each kinematic marker. Next, a regression anal-

ysis involved computing the proportion of explained endpoint variance as the square of the Pearson product-moment determined the strength of correlation between the gaze positions at all MT index and the eventual saccade endpoint. This process yielded the R^2 coefficient of determination, which describes how well mid-trajectory gaze predicts the locations where the saccades are terminated. High R^2 at early (i.e., 20, 40% MT) saccading indicates that the trajectory is largely ballistic thereafter. This implies that from that those time indices onward in time, the saccade proceeds deterministically to termination with no kinematic evidence of intervening processes. To the contrary, low R^2 are interpreted as evidence that saccadic corrections may be amending gaze trajectory. When values of R^2 are low at early MT, this implies the determinism of the trajectory is hampered because corrective processes affect the kinematics emerging at later phases of the movement. These R^2 data were also organized according to the time at which they occurred prior to saccade termination. In this format, an iterative outlier was used to estimate the minimum delay required to implement feedback-based corrections. The exact procedure will be described in the discussion.

Results

Descriptive statistics presented in Table 1 confirmed that participants performed the saccading tasks within the expected metrics. In the present data, there were no statistically significant effects or interactions when comparing saccade amplitude in all reactive and timed pacing conditions, and as a function of the gap task. A significant main effect of pacing condition ($F_{(4, 24)} = 5.67$, $P < 0.05$) was observed on movement duration, while there were no significant pairwise comparisons after applying Bonferroni corrections. These tests confirmed that saccadic accuracy and basic performance metrics were similar across all the experimental conditions. The remaining analyses focused on two main determinants of performance: temporal and spatial. To confirm that participants were successfully tracking the stimuli with predictive saccades, we measured the millisecond latency (i.e., asynchrony) between the initiation of saccades and the timing of onset of target visibility. Next, spatial analyses examined the kinematics of saccade trajectory to demonstrate evidence of online feedback-based corrections.

Saccading latency

Saccade latency indicated whether responses were initiated in anticipation of target onset, or instead as externally cued reactions toward the visual target. The absolute minimum latency for exogenously cued reactive saccade is approximately 80 ms. Thus, one can infer that responses executed

Table 1 Descriptive statistics of basic saccade metrics

Pacing interval	4°		8°		12°		16°		20°	
	M	SD	M	SD	M	SD	M	SD	M	SD
Amplitude										
500 ms	3.39	0.19	7.18	0.28	11.35	0.46	15.10	0.43	19.37	0.53
750 ms	3.49	0.28	7.37	0.24	11.41	0.36	15.32	0.49	19.26	0.52
1,000 ms	3.48	0.24	7.28	0.25	11.31	0.49	15.38	0.48	19.37	0.38
1,500 ms	3.34	0.21	7.11	0.32	11.17	0.41	15.13	0.55	19.32	0.60
Reactive	3.46	0.27	7.23	0.19	11.14	0.14	15.04	0.26	19.01	0.20
Movement time										
500 ms	27.67	2.04	42.73	4.84	53.64	6.21	61.15	7.37	68.68	8.22
750 ms	27.96	2.14	44.33	5.78	53.33	5.49	65.23	11.16	73.72	13.67
1,000 ms	28.25	2.97	44.60	6.97	55.49	7.25	65.61	13.18	74.30	16.10
1,500 ms	28.14	2.69	42.75	3.82	55.15	7.11	64.35	9.37	74.36	11.63
Reactive	25.42	1.65	39.22	4.73	48.76	4.58	56.10	5.54	62.84	4.90

with a shorter latency are made in anticipation of a stimulus through a voluntary motor plan. It is important to demonstrate predictive behavior in the current task because it implies that responses were guided to the target location by metrics stored in spatial working memory. A 5 Pacing condition (4 ISI + reactive saccades) \times 3 Gap Task \times 5 Saccade Amplitude repeated measures ANOVA was used to investigate trends in the latency data. Figure 2 shows the mean latency at all pacing conditions and saccade amplitudes. The main effects of pacing condition ($F_{(4, 24)} = 111.28, P < 0.001$) are quite clear, in that reactive saccades are well above the reference line for the fastest sensory reactions. This plot also confirms that saccade latency is representative of predictive tracking in all ISI levels of timed saccading.

There was also a significant main effect of saccade amplitude ($F_{(4, 24)} = 8.97, P < 0.001$) where saccade latency decreased at longer amplitudes. However, with Bonferroni corrections, there were only significant differences when comparing 4° saccades ($M = -0.84, 30.53$) against 12° ($M = -26.57, SD = 27.78, P < 0.005$) and 20° ($M = -32.86, SD = 34.20, P < 0.05$). While this effect demonstrates a modulation of saccade latency with the movement amplitude, we maintain that reactive saccades in the control condition were initiated in response to external sensory cueing, and saccades in the timed condition were predominantly initiated by means of sensorimotor prediction.

It is also expected that saccading latencies would vary according to the gap/overlap task. We confirmed a significant effect of gap task condition ($F_{(2, 12)} = 36.59, P < 0.001$). This effect is consequent to a facilitation of saccade onset latency during gap trials. Post hoc comparisons show that latency during gap trials ($M = -84.90, SD = 27.79$) is less than Baseline ($M = 13.21, SD = 29.54, P < 0.001$) and Overlap ($M = 7.92, SD = 46.38, P < 0.005$).

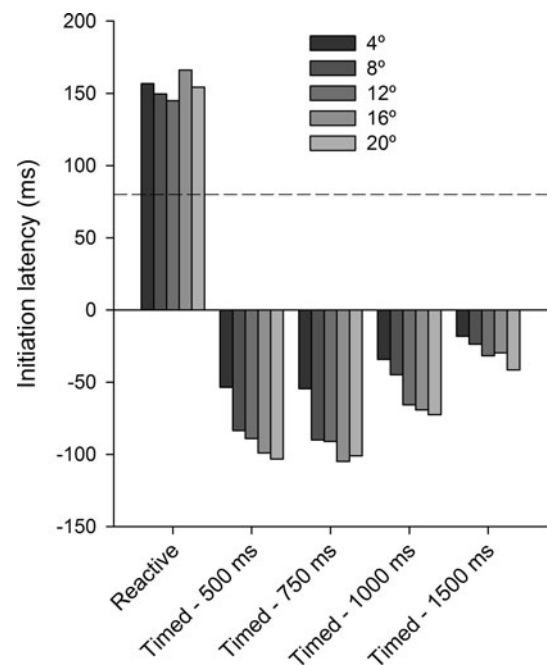


Fig. 2 Millisecond (ms) saccade latency as a function of all pacing conditions and saccade amplitude. Shortest possible latency for visually guided saccades is approximately 80 ms and is marked with a reference line. This plot confirms the predictive nature of saccades at all 4 ISI pacing rates

Since saccadic motor commands are actively inhibited during ocular fixation, the above effect of gap task indicates this inhibitory drive was reduced when the fixation target disappeared 200 ms prior to the onset of the saccading target. Here, we confirmed a perceptually mediated change in excitability of the saccadic oculomotor networks. Since predictive and reactive saccades are initiated by different means, we might also expect to see differences in the way

saccade kinematics are modulated by perisaccadic oculomotor excitability.

Lastly, saccade latency also interacted as a function of pacing condition and gap task ($F_{(8,48)} = 4.03$, $P < 0.05$). However, no consistent trends allude to conceptually important differences. In the context of our current investigation, it is solely important that we confirmed responses were predictive in all instances of timed saccades and reactive in all instances of control saccades. From this section of the analyses, we validate our intended classification of timed saccades as a predictive subclass of memory-guided saccades. This classification labels them as definitively different from reactive saccades made in the control saccading task.

Saccade trajectory variability

Next, we examined the data for evidence of online error corrections in the kinematics of saccade trajectories. To do this, gaze position at early and late phases of each saccade was examined in a variability analysis. Our experimental design comprised of one untimed control condition and 4 levels of timed conditions. Preliminary analysis of the control data aimed to replicate evidence for online corrections in reactive saccading trials. Subsequently, the same trends were demonstrated in the timed saccading data. Here, we were also concerned whether ISI pacing rates influenced the expression of online corrections. Lastly, we compare the expression of online corrections between reactive and timed saccades.

To corroborate our observations of trajectory kinematics in reactive saccades with those reported in related literature (West et al. 2009; Heath et al. 2010, 2011), we performed a 3 Gap Task \times 5 Saccade Amplitude \times 5 Percent MT repeated measures ANOVA on kinematic variability. Figure 3a is a plot of the significant interaction between saccade amplitude and percent MT ($F_{(16, 96)} = 11.13$, $P < 0.001$). Both factors also have significant main effects: saccade amplitude ($F_{(4, 24)} = 33.56$, $P < 0.001$) and percent MT ($F_{(4, 24)} = 25.50$, $P < 0.001$). This interaction successfully replicates a common observation that instantaneous trajectory variability increases continually from initiation to termination in saccades of short amplitude (4°). However, in longer amplitude saccades (12°–20°), the variability is maximal around 60% MT and significantly decreases as the saccades near termination. From this, we infer that some sensorimotor process operates in longer saccades—but not in shorter saccades—to resolve initial trajectory variability so that saccades end at a consistent target location.

The R^2 coefficient of determination measured from these reactive saccades also corroborates observations in the aforementioned studies. Values of R^2 approaching 1

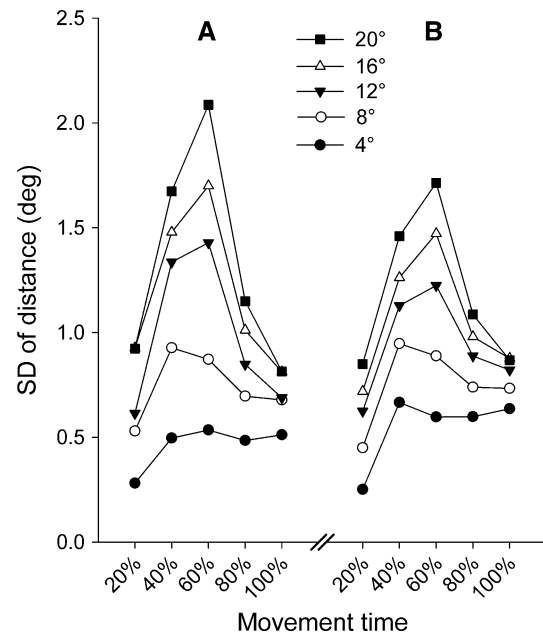


Fig. 3 Interaction plot for the variability of the gaze trajectory at all MT indices for saccades of all amplitudes. Data collected from reactive saccades in the control condition (a) and from timed saccade measures averaged across all ISI pacing rates (b). This plot demonstrates that shorter saccades generally increase in variability from their onset to termination, whereas larger saccades have a maximal variability measured at 60% MT that decreases significantly by the movement endpoint

indicate a high correlation between the gaze position at MT indexes and the saccade endpoints. These high values indicate a trajectory is ballistic, and values approaching zero are interpreted as evidence that sensorimotor processes intervene and alter the course of the movement. Main effects of the saccade amplitude ($F_{(4, 24)} = 14.59$, $P < 0.001$), percent MT ($F_{(3, 18)} = 326.81$, $P < 0.001$), and an interaction between these factors ($F_{(12,72)} = 10.42$, $P < 0.001$) all reached significance. Figure 4a is the interaction plot of these factors, which illustrates that small amplitude saccades are increasingly correlated with their movement endpoint beginning very early in their execution. Conversely, longer amplitude saccades do not become highly correlated with their endpoint until the latest phase of their execution, 80% MT. More importantly, the R^2 regression analysis supplements the variability analysis: the trajectory kinematics in longer saccades become deterministic in the same time window when variability in gaze position decreases. While the variability analysis cannot distinguish whether variability arises from different paths of ballistic trajectories, the regression analysis provides an account of the proportion of endpoint variance explained by gaze position earlier in the trajectory. Together, these findings replicate the expected evidence for a sensorimotor process that controls online corrections in reactive saccades.

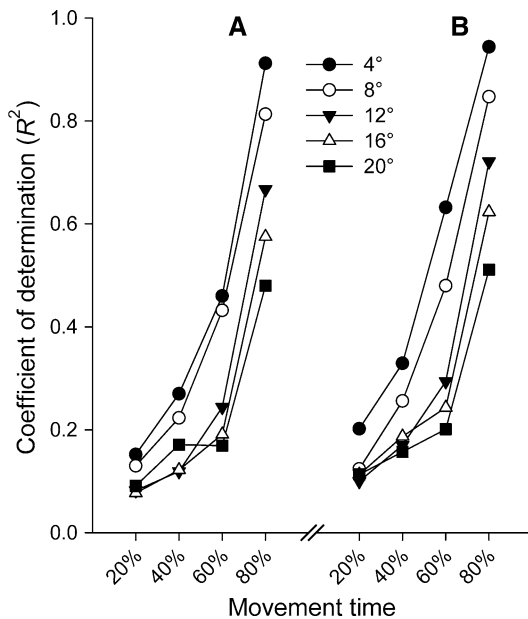


Fig. 4 Interaction plot for the coefficient of determination R^2 at all MT index for saccades of all amplitudes. Data from reactive saccading in the control condition are shown on the *left* (a) and from timed trials that were averaged across all ISI pacing rates on the *right* (b). R^2 is a measure of how well the position of the trajectory predicts the final endpoint. Higher R^2 is associated with an open-loop ballistic trajectory. This plot shows that small amplitude saccades raise quick from their onset to having large R^2 , which suggests the trajectory is mostly ballistic. Conversely, larger saccades do not increase to similar levels of predictability until later 80% MT. This reflects the intervention of online saccadic corrections mid-trajectory

Timed saccading

Within the timed saccading tasks, the same measures were analyzed with a 4 ISI \times 3 Gap Task \times 5 Saccade Amplitude \times 5 Percent MT repeated measures ANOVA. First, we consider timed saccades at all ISI pacing rates as representing a homogenous sample of predictive saccading behavior. In this case, when collapsed across the ISI factor because neither kinematic variability nor R^2 regression measures showed significance in main effects of or interactions involving the ISI pacing. Figure 3b illustrates data from all instances of timed saccading where the interactions between saccade amplitude and percent MT for kinematic variability ($F_{(16, 96)} = 5.04$, $P < 0.001$) reached significance. This interaction, main effects of saccade amplitude ($F_{(4, 24)} = 24.78$, $P < 0.001$), and percent MT ($F_{(4, 24)} = 17.49$, $P < 0.001$) replicate trends in trajectory variability that were observed during reactive saccading. These results reproduce the kinematics observed in reactive saccades, where only the kinematics in longer saccades decrease in variability from midway through their execution to the endpoint. Additionally, Fig. 4b shows that trajectories in timed

saccading also express evidence from R^2 regression analyses indicating that shorter saccades are highly ballistic and longer saccades are not. This is supported by main effects of saccade amplitude ($F_{(4, 24)} = 56.49$, $P < 0.001$), percent MT ($F_{(3, 18)} = 339.41$, $P < 0.001$), and an interaction between these factors ($F_{(12, 72)} = 20.97$, $P < 0.001$) all reached significance.

A result unique to the R^2 regression analysis in timed saccades is the significant main effect of gap task ($F_{(2,12)} = 5.88$, $P < 0.05$). This effect occurs such that mean R^2 in the baseline condition (synchronous target onset/offset) appeared to be lower than R^2 in overlap and gap conditions. However, applying Bonferroni corrections in post hoc pairwise comparison nullified this effect. Furthermore, the gap task conditions also interacted significantly with percent MT ($F_{(6,36)} = 3.36$, $P < 0.05$). Post hoc comparisons revealed that saccades made in the baseline condition had significantly lower R^2 than gap and overlap conditions only at the 40 and 60% MT markers (both $P < 0.05$). Here, we briefly revisit the topic that our investigations into saccade latency revealed that saccades in the gap condition had short latencies. This represents a more highly excitable state in the oculomotor system as compared with longer latency behaviors in baseline and overlap trials. We also hypothesized that changes in basic oculomotor excitability might interact with predictive saccading behavior in timed trials differently than in reactive saccading behavior observed in untimed control trials. Since gap and overlap task performance were equivocal in R^2 regression analyses, while baseline and overlap were equivocal in latency measures, we argue the mechanisms behind a modulation of saccade latency, and R^2 regression measures seem unrelated.

Untimed reactive saccading versus timed predictive saccading

Next, we collapse the timed data across all levels of ISI pacing rates and compare the reactive and timed saccading data to see if the kinematic evidence for online corrections is expressed differently. These data were tested in a 2 Pacing condition (reactive/timed) \times 3 Gap Task \times 5 Saccade Amplitude design. In reflection of the trends observed in both timed and reactive saccading data subsets, kinematic variability analyses revealed significant main effects for saccade amplitude ($F_{(4, 24)} = 37.22$, $P < 0.001$), percent MT ($F_{(2, 24)} = 22.51$, $P < 0.005$), and an interaction between these factors ($F_{(4, 24)} = 10.62$, $P < 0.005$).

Now that this interaction has been reported consistently in all instances of saccading, here we report post hoc tests. Interpreting this interaction is simplified when discussing it in terms of progression of a saccade from beginning to completion. To correct for multiple comparisons, we are

making only 4 comparisons per level of saccade amplitude: 20–40%, 40–60%, 60–80%, and 80% to the endpoint. At a corrected significance of $P < 0.013$, short 4° and 8° saccades increase consistently and significantly from 20% MT to their endpoint. All longer saccades between 12° and 20° increased in variability consistently and significantly only from 20% MT to 60% MT. These longer saccades also significantly decreased in kinematic variability from 60% MT to 80% MT and to the saccade endpoint.

A significant interaction between gap task and percent MT ($F_{(8, 48)} = 4.24$, $P < 0.018$) was also observed in the kinematic variability. Post hoc test significant at $P < 0.0167$ applies here, and the results indicate that kinematic variability measured at the saccade endpoint is significantly higher in gap trials ($M = 0.81$, $SD = 0.09$) than overlap ($M = 0.70$, $SD = 0.09$) and baseline ($M = 0.72$, $SD = 0.06$) trials. However, this is of little importance since the interaction between saccade amplitude and percent MT suggests that saccades in all instances of the gap task demonstrate evidence for online saccadic corrections.

Lastly, we observed a significant interaction between the 2 pacing conditions and the 5 percent MT indices ($F_{(4,24)} = 9.17$, $P < 0.001$). With only 1 pairwise comparison being made at each level of the percent MT factor, significance was maintained at the initial uncorrected $P < 0.05$. Post hoc tests reached significance at 60% MT where reactive saccades ($M = 1.32$, $SD = 0.34$) were significantly more variable than were timed saccades ($M = 1.18$, $SD = 0.36$). Interestingly, at the saccade endpoint, reactive saccades ($M = 0.70$, $SD = 0.06$) were significantly less variable than timed saccades ($M = 0.79$, $SD = 0.10$). Reactive saccades thus demonstrate a larger reduction in variability prior to saccade termination. However, the latent interaction between saccade amplitude and percent MT is the source of evidence for online saccadic corrections. The 3-way interaction between pacing condition, saccade amplitude, and percent MT factors narrowly missed significance when adjusting for sphericity with Greenhouse-Geisser corrections ($F_{(16,96)} = 2.09$, $P = 0.133$). Consequently, the failure of reaching significance in the 3-way interaction with pacing condition warrants caution when inferring whether the trends in the kinematic variability are different in reactive and timed saccades. The R^2 regression analyses were also examined for an effect of pacing condition. Saccade amplitude ($F_{(4, 24)} = 55.51$, $P < 0.001$), percent MT ($F_{(3,18)} = 437.98$, $P < 0.001$), and their 2-way interaction ($F_{(12, 72)} = 25.61$, $P < 0.001$) were all significant. This has been consistent in all instances of saccading, and here, we report post hoc comparisons. Mean R^2 data suggest that small saccades have a predictable trajectory (high R^2) from very early in the movement through to the end. At values above $R^2 = 0.3$, saccades are increasingly ballistic and 4° saccades surpass the R^2 value of 0.3 as

early as 40% MT ($M = 0.30$). Contrasting this, 8° saccades pass the R^2 value of 0.3 at 50% MT ($M = 0.46$), and 12° ($M = 0.69$), 16° ($M = 0.60$), and 20° ($M = 0.50$) saccades do not pass the said value until 80%. These data suggest the mid-trajectory variability in longer saccades is not a result of passive dynamics in variable ballistic saccades. This is inferred when considering that mid-trajectory variability is reduced prior to movement completion and also that R^2 values in the early phase of saccading are significantly lower as compared with R^2 nearing the movement endpoint.

We also observed significant differences in timed versus reactive saccading ($F_{(1, 6)} = 6.82$, $P < 0.05$). However, we interpret this with caution because of the very small changes in between the two marginal means. Reactive saccading trajectories ($M = 0.32$, $SD = 0.04$) had significantly lower R^2 than in timed saccading ($M = 0.36$, $SD = 0.05$). The observed power for this effect is only 59% at $\alpha = 0.05$. The mean difference of 0.04 is also quite small, especially compared with the experimental effects observed elsewhere (e.g., $\sim M_{\text{diff}} = 0.2$, see Heath et al. 2010). Another consideration is that R^2 is often equated between two conditions at very early and late percent MT indexes but is significantly different only at the middle 40–60% MT indices. Thus, truly robust effects between the timed and reactive saccading conditions would have been expected to express themselves with more power through an interaction with percent MT. Our data did not reach significance for this interaction ($F_{(3, 18)} = 1.95$, $P = 0.19$).

The distribution of R^2 values as a function of their time from saccade termination was also examined. This approach has been used in previous literature to estimate the minimum delay for implementing online corrections (West et al. 2009). The R^2 values are presented without distinction from what amplitude condition they were collected, only when they were measured relative to the saccade's end. Figure 5 plots these data for a few experimental conditions. The idea behind this analysis was to identify the time furthest preceding saccade termination at which R^2 could be measured and represent substantial predictability. Figure 5 illustrates the increasing R^2 as the measures near saccade termination. Here, an iterative outlier procedure compared each data point against the mean plus 2 standard deviations ($M + 2 \times SD$) of all previous points to determine the time at which saccades become increasingly correlated with their endpoint. This procedure was run separately for all gap task conditions in timed trials, in the control reactive saccades, and also separately for 1,500 ms ISI timed saccades. The distinction of the gap task was preserved in timed saccading data because of the aforementioned significant interaction between gap task and percent MT for R^2 in timed saccading. Furthermore, we chose to isolate data from 1,500-ms ISI trials, because they had the longest memory delay period between successive movements. This

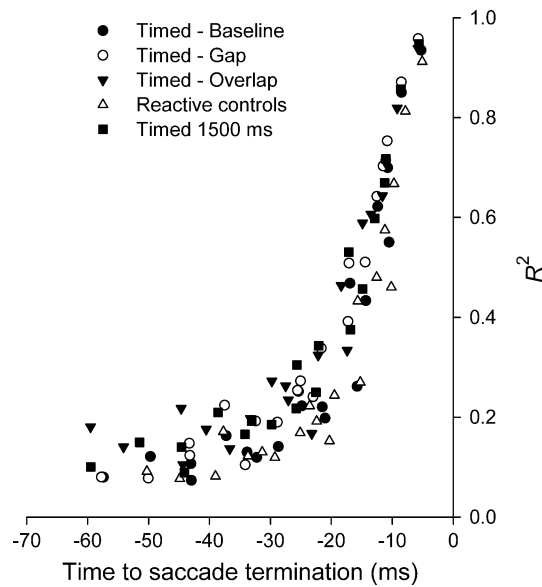


Fig. 5 Proportion of explained endpoint variance R^2 plotted as a function of the time before saccade termination. The iterated outlier procedure operates on this dataset and measures the point at which R^2 values first increase significantly as saccades approached their termination. Descriptive table of data that accompanies this plot is in Table 2

planned contrast was made to maintain consistency with previous research that has shown memory delays of this duration hinder the implementation of online saccadic corrections in single memory-guided saccades. Data for all conditions shown in Fig. 5 are provided in Table 2.

In comparison with previous delay estimates (West et al. 2009), our control data revealed a 37-ms delay for reactive saccades, ~ 7 ms slower than in comparison with the aforementioned study. It is not surprising to see an offset when comparing numbers from separate research groups. Our measures differ in two basic ways: our data were initially sampled at a lower rate and resampled to a finer timescale. Moreover, we performed the iterative outlier with more data points by including R^2 measures at 4 levels of percent MT, whereas previous work used only 3. The iterative outlier procedure seems partially responsible in itself, where the feedback estimate in the overlap condition is ~ 10 ms faster yet there is also a marked increase in the critical and threshold R^2 values. Using a $M + 2 \times SD$ heuristic seems to be less sensitive for these data. Since it is an absolute value

of R^2 that describes the nature of the trajectory as predictable, or not, consistency in the threshold R^2 value in turn determines the consistency of labeling what value of R^2 represents the time at which the trajectory becomes predominantly ballistic. As such, if we instead tested the iterated outlier using a manually imposed threshold of $R^2 = 0.16$ averaged from threshold values in the other timed saccading conditions, the estimate increases to ~ 33 ms. This value is closer to the estimates in the other saccading conditions. In ideal circumstances, an iterated outlier assumes stationarity in the data prior to the index at which a marked increase in value is to be identified. Since the initial stages of any movement would naturally be expected to have a lasting but small effect on the later phases of the movement, the data are inherently non-stationary. Future investigations could perhaps explore more accurate methods to identify a break point of a piecewise fit in data like these, which inherently show broad variability in short tails of the distribution.

Discussion

This study investigated the combined role of periodic timing and motor sequencing as they related to the implementation of online feedback-based trajectory corrections. We first confirmed that our participants were engaged in predictive visual tracking in the timed saccading conditions. By confirming anticipatory behavior, we concluded that saccades were initiated via internal sensorimotor planning whereby saccade metrics were parameterized by a task representation in spatial working memory. As expected, anticipatory behavior was preserved across all of the ISI, saccade amplitude, and gap task conditions. Importantly, this differed significantly from the large positive latencies observed in all variations in reactive saccading. These observed differences in temporal dynamics call for a separate classification of reactive and predictive saccades as visually guided and memory-guided behavior, respectively.

Subsequent analysis examined spatiotemporal dynamics of saccade kinematics. Kinematic variability in saccade trajectories results from compounded errors in sensory and motor functions (van Beers 2007; Khan et al. 2006). Without processes that make online corrections, such errors would

Table 2 Results from R^2 iterative outlier

	Reactive	Timed			
		Baseline	Gap	Overlap	1,500 ms
Threshold R^2 value	0.10	0.14	0.18	0.24	0.18
Critical R^2 value	0.17	0.16	0.22	0.27	0.21
Estimated implementation delay (ms)	37.71	37.24	37.52	29.75	38.59

accrue throughout the course of execution, leading to maximal movement variability measured at the endpoint (Messier and Kalaska 1999). As expected, we found evidence for online corrections in long amplitude saccades that were similar in reactive and predictive contexts: variability reached a maximum at 60% MT and decreased significantly at the endpoint. This observation replicates similar observations made in single visually guided and memory-guided saccading tasks (West et al. 2009; Heath et al. 2010, 2011). Further support for corrective mechanisms was corroborated with a regression analysis where we tested how accurately gaze position at MT indices predicted the endpoint. For larger amplitude saccades, the correlation between gaze position and endpoint was strong only at later phases of execution. This contrasts shorter saccades, where the coefficient of determination between MT indices and endpoint is high from early phases of saccading through to the endpoint. We observed similar trends in predictive and reactive saccades. This also led to an equivocal estimation of feedback delays in all instances of predictive and reactive saccading. In comparison with other literature, it is most relevant to contrast oculomotor behavior in 1500-ms ISI timed saccading with that in reactive saccading. Our estimate of the minimum delay to implement corrections is ~ 37 ms in both cases. Previous research (West et al. 2009; Heath et al. 2010) demonstrated that single memory-guided saccades exhibit slowly implemented (~ 50 ms delay) online corrections that also have reduced expression (higher R^2). From our observations, we infer that spatial working memory-related effects that hindered online corrections in single memory-guided saccades are mostly recovered when making predictive saccades in timed sequences.

In designing the methods, we made an explicit attempt to be consistent with other research that investigates spatial working memory. Accordingly, our tasks imposed memory delays between 500 and 1,500 ms, which are within a range commonly used in goal-directed motor tasks. Memory delays in this range provide ample time for spatial working memory to decay in the quality of metrics that are stored (Rolheiser et al. 2006) and also to exhibit a memory-related cortical recruitment (Brignani et al. 2010). In other words, our study provided visual cueing in the time window immediately prior to saccade onset that was similar to what participants would have seen in a typical single memory-guided saccading task. This lends support to the conclusion that timed sequencing is the only novel influence imposed in our task that is acting on the sensorimotor dynamics.

In sum, we concluded there are only negligible differences in the kinematic evidence for online trajectory corrections when saccades are performed reactively to visible targets or in timed sequences in anticipation of target onset. This led us to reason the combined processes of motor

timekeeping and sequencing were responsible for maintaining a fast and efficient mode of trajectory corrections. Despite periodic saccades being parameterized by metrics sourced in spatial working memory, online corrections to their trajectories operated as efficiently as was observed in visually guided reactive saccades. It is thus of particular importance that we tested control behavior in reactive saccades and then compared the measures in order to find appropriate evidence for online corrections in timed saccades.

General discussion and Neurophysiological implications

In order to understand the contribution of the present experiments to developing models of sensorimotor brain functions, one first requires a brief review of oculomotor networks and their putative online control systems. Saccadic motor efferents originate subcortically from the superior colliculus (SC) and the pontoreticular formation (PRF) in the brain stem (Sparks 2002). Feedback-based corrections are likely integrated near the source of motor output, in subcortical structures (Kato et al. 2006; Gaveau et al. 2003). The state of the oculomotor system is monitored using a combination of feedback modalities, all of which contribute to the registration of gaze position (Bridgeman and Stark 1991). Proprioception from extraocular muscles (EOM) (Weir et al. 2000), low latency visual afferents from the retina (Gaveau et al. 2003), and corollary discharge sourced from oculomotor control centers (Kato et al. 2006; Guthrie et al. 1983) are all mechanisms potentially contributing to saccade trajectory changes on a fast timescale. The coding of feedback via these pathways might contribute to the construction and integration of forward models of saccadic control, potentially implicating the cerebellum (Wolpert et al. 1998; Quaia et al. 2011). Subcortical oculomotor networks are also known to be tightly coupled with the thalamus and early sensory areas of visual processing, particularly the lateral geniculate nucleus (LGN) (Reppas et al. 2002). So, one or a combination of these networks could lend support to feedback (via sensory integration) or feed-forward (via corollary motor discharge) models of closed-loop online control. However, a complete understanding and parsing of modality-respective contributions to trajectory corrections remains elusive.

One might suppose our protocol lends support for corrections based on fast visual feedback networks: it stands to argue that predictive saccades were partially guided by low-latency visual information when targets became visible in the perisaccadic time window. Such an argument would follow a notion that target onset may have occurred during the course of the saccade. According to observations made by Gaveau et al. (2003), changes in target visibility during a saccade was often perceived and resulted in online correc-

tions prior to termination of the saccade. However, data from this study do not support the idea that transient visual feedback is used for trajectory guidance in our tasks. For example, the movement time of 20° saccades is approximately 70 ms. When executed in the 500-ms ISI condition, saccades of this amplitude had a mean latency of approximately –100 ms. Consequently, we ascertain that saccades in this condition were terminated prior to the onset of target visibility. However, 20° saccades in the 1,500-ms ISI condition had a mean latency of approximately –40 ms, and target onset would have occurred while the saccade was in mid-flight. Importantly, we observed a significant main effect of ISI on latency, but no effect of or interaction involving ISI in the kinematic variability and regression analyses of timed saccading. This led us to refute that a transient visibility of visual targets was at least not solely responsible for the online corrections.

An important factor to consider when discussing candidate oculomotor feedback integrators is the speed of neuronal signaling. The rate of afferent propagation from the retina to the central nervous system limits the likelihood that the neocortex integrates online performance feedback for mediating efferent signals. Yet the latent possibility of a top-down cortical source of online saccadic corrections is not excluded. From a behavioral standpoint, cognitive manipulations in our current study and other seminal works (West et al. 2009; Heath et al. 2010, 2011) modulate online oculomotor corrections. With regard to the contributions of cortical and subcortical networks, the following sections are a non-exhaustive discussion of possible explanations for task-dependent changes in oculomotor behavior.

Task representation in the cortex

When saccades are directed toward visible targets in our immediate environment, the “real-time” hypothesis (Westwood and Goodale 2003) suggests that dorsal stream visual processing is specialized for integrating object metrics into the motor system. In the other case that saccades are directed to memorized locations, the movement goal is no longer parameterized directly from this real-time percept. Instead, saccade metrics must be first translated from a non-metric qualitative memory in the ventral visual-processing stream (Haffenden and Goodale 2000). West et al. (2009) postulated this ventral representation is used less efficiently for feedback-based corrections as compared with a native dorsal representation. This is supported by the fact that reciprocal and single memory-guided saccades are more variable in their execution than are visually guided saccades (Rolheiser et al. 2006).

This reasoning is founded in the perception–action model of visual processing (Goodale and Milner 1992), a limitation of which is the absence of a neurophysiological

distinction for motor parameterization by planning or by real-time visual integration. Predictive saccades observed in our study were guided by a short-term, spatial working memory (SWM) representation of the target and did not show a characteristic performance decrement associated with single memory-guided saccades. Less efficient online corrections in single memory-guided saccades were explained by a delay of ventral stream interpolation of target metrics. Interestingly, the perception–action model fails to explain how predictive saccades can rely on SWM yet be equivocal in their performance to reactive saccades. It is therefore possible that saccades operate outside the classical behaviors used to construct the perception–action model.

Our study is not alone in elucidating motor behavior in goal-directed tasks that is at odds with the perception–action model (Glazebrook et al. 2005). A more favorable approach for applying theoretical sensorimotor processing models to the current study is situated in the planning–control model (Glover 2004). In addition to the specialized dorsal and ventral visual processing streams, the planning–control model also incorporates a “third stream.” This model is more compatible with the current behavioral results because the third stream accounts for differences in the neuroanatomical correlates implicated in motor planning and online control processes. These two processes are distinguished as separate functions of the inferior parietal lobule (IPL) and superior parietal lobule (SPL), respectively. Using this framework, one can easily adapt the model to the results of our current study. One supporting example suggests that it is important to consider the role of the IPL because this area has been ascribed functions related to saccade planning and maintenance of memorized spatial coordinates (Brignani et al. 2010; Schluppeck et al. 2005). The planning–control model also accounts for a source of collateral projections to the motor system from the IPL and SPL. In the case of memory-guided saccades, it is possible to account for differences in the performance of single and repetitive saccades if SWM integrates differently into sequence planning via these networks.

These arguments have been framed with the assumption that SWM is established equivocally between the short-interval timed saccades in our study and other single memory-guided saccades. From an alternative standpoint, it is possible that motor planning was unrelated, and instead, the act of repeating movements in a sequence enhanced the representation of saccade metrics in SWM through habituation. In this case, the quality of memorized saccade metrics would decay in quality at a slower rate, thus contributing to improved execution and online control. The entrainment of sensorimotor networks with repetitive movements has been shown to persist based on prior context, including selective activity in the posterior parietal cortex (Jantzen et al. 2004).

This might reflect neural activity related to the maintenance of task goals. If modulation of memory habituation is the source of the observed differences in memory-guided saccading behaviors, and this is fundamentally different from distinguishing the contribution of planning movements in a sequence. Recent work in this field (Heath et al. 2010, 2011) has distinguished between effects of response suppression and vector inversion in anti-saccading. Future studies could be targeted at isolating the differential role of SWM maintenance and sequence planning in their contribution to online corrections in saccades.

Task representation in subcortical regions

As mentioned in the previous paragraph, the entrainment dynamics of repetitive movements have a lasting effect on cortical recruitment. There are also similar entrainment effects noted in subcortical structures including the thalamus, which also has known roles for integrating corollary discharge of saccade motor commands (Bellebaum et al. 2005). It is likely that other subcortical areas might be responsible for the observed enhanced performance in timed saccading. When making saccades to predictable locations, as the probability of specific locations of visual stimuli increases, there is a priming effect on the activity of neuronal activity in the SC (Basso and Wurtz 1998). Enhancement effects of the kind noted here reflect some level of potentiated task parameters, possibly reflecting the role of neurons in the SC. Determining whether low-level responses are caused locally through interaction with other subcortical networks or reflect top-down modulation is a general question we pose and hope to see solved in future research.

Conclusions

We hypothesized that some form of functional overlap in task-relevant resources—between spatial working memory, sensorimotor timekeeping processes, and sequence planning networks—would lead to differences in saccadic corrections. We have provided evidence that imposing a temporal expectation structure on repetitive saccades facilitates the integration of task-relevant sensorimotor information for online oculomotor control. More specifically, we have demonstrated that repetitive motor timekeeping in saccade sequences influences the fundamental operations of the oculomotor control system. This was based on observations that predictive saccades expressed enhanced online corrections when compared with suboptimal behaviors exhibited in untimed single memory-guided saccades.

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