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The temporal and spatial constraints of saccade planning to double-step target displacements

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Abstract

The double-step paradigm investigates the characteristics of planning and execution when the motor system must rapidly adjust for a new goal location. Studies have provided detailed temporal information based on the duration available for the motor system to prepare a new movement trajectory (here referred to as re-preparation time). However, previous work has largely examined single displacement sizes, limiting the spatiotemporal understanding of movement planning and execution. The lack of a description of this behavioral timecourse across increasing displacement sizes is true for saccades, rapid eye movements that redirect the fovea. Furthermore, during the double-step paradigm, the primary saccade often fails to accurately foveate the final target location and a secondary saccade brings the target onto the fovea. However, it is also unknown how this compensation is concurrently modified with the exposure duration and displacement of the movement goal. Here, we examined the amount of time required to change the initial saccade direction to a new target location for relatively small (20°, 30°, and 40°) and large (60° and 90°) target spatial separations. Interestingly, we found a clear relationship between the saccade direction and the amount of time allowed to redirect the movement; across separations, intermediate saccades occurred when approximately 60 to 140 ms was available to readjust the movement plan. Additionally, there was a consistent relationship between the timing of the secondary saccade and the re-preparation time across jump sizes, suggesting that concurrent movement correction planning was dependent on the amount of exposure to the final movement goal.

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Keywords

saccade; goal; planning; spatiotemporal; double-step

INTRODUCTION

The double-step paradigm has been used to determine the properties of movement target selection and planning when the target location is altered (Becker & Jürgens 1979; Aslin & Shea 1987; Ray et al. 2004; Camalier et al. 2007; Murthy et al. 2009; Hu & Walker 2011; Bhutani et al. 2012). When examining saccade planning (rapid eye movements that are used to reorient the fovea to objects of interest) this is accomplished by displacing a previously planned saccade target to a new location around the time the initial saccade is executed. The introduction of a new target location facilitates the creation of an eye movement plan that competes with the initial movement plan (Murthy et al. 2009; Hu & Walker 2011). One advantage of this method is the ability to estimate the properties of the evolving motor plan by measuring the saccade trajectory relative to the time the competing saccade target appears, referred to as reprogramming (Becker & Jürgens 1979) or re-preparation time (Haith et al. 2015). In both cases this represents the time available for the oculomotor system to adjust the initial motor plan and prepare an adjusted saccadic eye movement.

Early investigations using the double-step paradigm suggested competing saccades are processed in parallel (Becker & Jürgens 1979) and guided by a decision mechanism that continuously incorporates updated spatial information (Aslin & Shae 1987). Becker and Jürgens (1979) fit transition functions to the temporal changes in the saccade amplitude and examined the progression of change in the saccade amplitude from the initial location to the final location (in this case the target was displaced within the same plane as the movement, either towards the initial fixation location or farther away). The authors reported several temporal properties of interest. First was the modification time, or the point at which the transition function begins its slope (i.e., when the saccade amplitude is modified). This corresponds to the minimum time required for the second target location to influence the initial saccade amplitude (approximately 80 ms when the jump moved the movement goal back towards the original fixation location, and approximately 200 ms when the jump moved the movement goal farther away from the initial target location). The second temporal measure reported was the duration of the transition between the initial and final target locations, corresponding to the slope of the function (again ranging between 80–200 ms across subjects and conditions). This range is the time window in which saccade trajectories were no longer being directed to the initial goal location, but the movements had not yet compensated for the target displacement and are thus directed to an intermediate location between movement goals.

Based on the work of Becker and Jürgens (1979), Aslin and Shae (1987) adopted this paradigm but used a 45° radial target step. In this study it was reported that the midpoint of the transition function was approximately 175 ms after the target step. This suggests that around this time point the eye movements were being directed to the middle or average of the initial and final target locations (an averaging saccade). Additionally, the authors

reported that the duration of the transition from directing the saccade to the initial to final target location was between 30–80 ms. In a more recent study, Camalier et al. (2007) used target steps $\approx 90^\circ$ and defined a spatial range in which saccades were classified as compensating for the displacement (less than 1.5° from the final location). The authors reported that a duration approximately 240 to 300 ms after the target jump was required for subjects to make saccades to the final target location.

Based on the above results, the double-step paradigm is well suited for examining the temporal metrics that characterize saccade planning, competition and execution (Aslin & Shea 1987; Bhutani et al. 2012). However, because these previous studies mainly employed single target displacements, it is largely unknown how this timecourse changes across varying displacement amplitudes. That is, are there concurrent changes in the temporal properties of saccade planning when the spatial properties of saccade targets are simultaneously manipulated? Here, we use a modified double-step paradigm to determine the concurrent temporal and spatial influences on the saccade trajectory. Certain aspects of the current double-step paradigm were influenced by a recent study by Haith and colleagues (2015) that examined intermediate movements during a time-restricted visually guided reaching task. Subjects made reaching movements to one of several peripheral target locations. On a random number of trials, prior to the go-signal (an auditory cue) the target location jumped to a different location with variable angular separation amplitude and direction. Similar to the double-step paradigms above (Becker & Jürgens 1979; Aslin & Shae 1987; Camalier et al. 2007; Bhutani et al. 2012), the time from the target jump to the reach onset was defined as the re-preparation time available for the sensorimotor system to compensate for the ambiguous movement goal between the initial and new target location. With low re-preparation time (<150 ms), the reaches were directed to the initially cued target. However, with increasing re-preparation time (150 to 275 ms), intermediate reaching movements were observed, and with enough time (> 275 ms) the subjects were able to completely compensate for the location change and execute a movement to the new target. Additionally, the separation of the targets played a role in the movement trajectory; increasing the separation led to a decrease in the occurrence of intermediate movements and a change in slope of the transition function. That is, there was a decrease in the temporal window that the target change influenced the saccade trajectory as the separation between the two target goals increased.

We applied this control of the reaction time in a double-step saccade task in order to examine the timecourse of saccade target selection. We show that with small jump separation (20° to 40°), intermediate movements began as early as 60 ms of re-preparation time. However, similar to the arm reaching study (Haith et al. 2015), the temporal range in which intermediate movements occurred (re-preparation times between 75 and 175 ms) decreased with increasing stimuli separation ($\approx 60^\circ$). In addition, we found that as jump size increased, the number of intermediate saccades decreased, suggesting a decrease in saccade averaging once the two target locations were separated by a sufficient distance.

Recently, Bhutani et al. (2017) used a double-step task to investigate the properties of saccades executed in a sequence. Having a target jump on a majority of trials (60%), these authors found that the secondary saccade in the sequence increased in amplitude in order to

compensate for the target displacement. This finding, as well as those of several others, suggests that the oculomotor system does not need to wait for one saccade to end before beginning to plan another (concurrent processing: McPeck et al. 2000; Hu & Walker 2011; Mokler & Fischer 1999). Until now, it was unknown whether the timecourse of concurrent processing is affected by the size of a target displacement. It was also unknown how the duration of target exposure affects the timing of the secondary saccade. We report that, along with increasing target displacement size, we found an increasing negative correlation between the re-preparation time and the timing of the secondary saccade (the inter-saccade interval, ISI) following the intermediate movements. The relationship between the two timing measures indicates that concurrent planning of the primary saccade and correction (characterized by a short ISI) required sufficient exposure to the final movement goal location. As the exposure duration (re-preparation time) decreased, the ISI increased suggesting that subjects transitioned to a visually-guided secondary movement to bring the fovea to the new movement goal.

METHODS

Subjects

We recorded the eye movements of 20 healthy individuals (13 female, mean age = 21 years). Subjects had normal, or corrected to normal vision and were naïve to the purpose of the study. The Institutional Review Board of George Mason University approved experimental protocols, and informed consent was obtained from each subject. Subjects completed one practice and three experimental sessions over the course of three days.

Materials

Subjects were seated in a dimly lit room, in front of a display monitor. The viewing distance to the screen was 650 mm and held constant by a desk-mounted chin rest that also stabilized the head during the task. Eye movements were recorded using the EyeLink 1000 eye tracker (desk-mounted binocular eye tracker, 1000-Hz temporal resolution, 0.2° spatial resolution; SR Research, Mississauga, Ontario, Canada). Stimuli were presented on a 19-in CRT-monitor (screen resolution of 34.2 dva × 26.0 dva) with a refresh rate 120 Hz). Experiment builder software (SR Research) provided stimuli presentation and collected real-time eye movement data. A nine-point gaze calibration was performed at the start of each session, followed by a nine-point validation.

Saccade Classification

Horizontal and vertical movements of both eyes were recorded, but in 18 out of 20 subjects the recordings from the left eye were used for analysis. We used the right eye in the two exceptions because the calibration was significantly more accurate. The resulting data were visualized, filtered, and analyzed offline using MATLAB v. 8.1.0 (Mathworks, Natick, MD). Within the task, eye movements were initially isolated based on the eye position exceeded a small fixation window (3.1 dva × 3.1 dva) boundary within the appropriate time constraints. In the offline analyses, an eye movement was classified as a saccade when the eye velocity exceeded 30 dva/s and the movement was larger than 1 degree visual angle. These thresholds were used to define the saccade onset and offset times; saccade onset time was the first time

point that velocity and amplitude exceeded these values while saccade offset was the first time point that these parameters fell below these values.

Task and Procedure

Experiment 1: Small Target Jumps (20°, 30° and 40°)—The modified paradigm based on a combination of Becker and Jürgens (1979) and Haith et al. (2015) is represented in Figure 1. One group of subjects ($N = 10$) was tested in the laboratory on three separate sessions, each at least 24 hours apart. In the first session, each subject completed a block of 147 practice trials in order to become familiar with the task constraints, and then one block of 480 experimental trials. In each of the remaining two sessions, the subjects completed one block of 480 experimental trials. Each practice trial began with the subject fixating a central cross ($0.7 \text{ dva} \times 0.7 \text{ dva}$). After 750 ms, the first of four tones sounded (660 Hz) and a peripheral target ($0.7 \text{ dva} \times 0.7 \text{ dva}$) concurrently appeared. The target could appear at locations along a hidden arc which was a radial distance of 8 dva from the fixation cross. Subjects were required to maintain central fixation during the sequence of four tones, each separated by 500 ms (again, with the first tone being simultaneous with the peripheral target presentation). The fourth tone was the go-signal for the subjects to move their eyes from the fixation cross to the target in the periphery. Prior to the go-signal, if the subjects moved their eyes outside the hidden fixation boundary ($3.1 \text{ dva} \times 3.1 \text{ dva}$) surrounding the cross, an error message appeared and the trial was cycled back into the remaining trials. After the final fourth tone, the subjects had 150 ms to move their eyes outside the same fixation boundary or the trial was cancelled and recycled. If the saccade was performed correctly, the trial ended 350 ms following the latency window.

The experimental sessions followed the same design as the practice except with a critical manipulation: in 30% of the trials, the target jumped to a new location (Figure 1A) at a variable time around the fourth beep (150 ms before to 50 ms after beep onset). The jump size was uniformly distributed across 20°, 30°, and 40° leftward and rightward displacements (Figure 1B). Note that the starting location was randomly cycled between the 45°, 90°, and 135° positions along the radial arc surrounding the fixation cross.

Experiment 2: Large Target Jumps (60° and 90°)—A second group of subjects ($N = 10$) completed a similar experiment to that described above. This experiment was designed to observe conditions in which intermediate saccades were not predicted to occur due to the large target separations (Van der Stigchel & Nijboer, 2013). The procedure for Experiment 2 was identical to that used in Experiment 1, except that the jump sizes on the experimental trials were 60° or 90° to the left or right of the initial target position. Again, the starting location was randomly cycled between the 45°, 90°, and 135° positions along the radial arc surrounding the fixation cross.

Spatial and Temporal Measurements

The main analysis focused on the spatial and temporal properties of the primary saccades on jump trials. The spatial property of interest for each saccade was the angular deviation between a line through the onset and offset points of the primary saccade and the initial location of the stimulus on any given trial (Figure 1C). Note that the initial target location

was calculated from the mean landing position of saccades on no-jump trials to that location. Relative to the initial location, saccades directed towards the jumped stimulus location were given a positive value, and saccades directed away from the jumped location were given a negative value.

The temporal property of interest was the time available for the oculomotor system to program a saccade to the appropriate jumped target location. This is termed the re-preparation time and was calculated the same way as in the reaching movements investigated by Haith et al. (2015). It is the difference between the time of the saccade onset (the first point at which the eyes pass the velocity and amplitude thresholds detailed above) and the time at which the stimulus jumps to the new location. Note that this is not the latency of the movement, but rather the amount of time available to the subject to change the initial movement plan on the jump trials. In general, earlier target jumps provided more re-preparation time than later jumps, as later jumps occur closer to the onset of the saccade signaled by the fourth beep.

To compare across subjects and jump sizes, we normalized the saccade direction and plotted it as a function of re-preparation time. Within the normalized angle, the initial and jumped stimuli locations, 0 and 100 respectively, are the mean saccade landing locations calculated from the respective no-jump trials. Trials in which the normalized trajectory angle was more than 200% or less than -100% of the jump size were excluded from analysis. This led to an exclusion of less than 5% of the total trials across all subjects.

Psychometric Fit

In order to quantify the changes in the saccade trajectory angle with increasing re-preparation time we fit the behavioral data with a sigmoid function:

$$\theta = F(t) = \frac{A}{1 + e^{-\frac{(t - t_{50})}{(t_{95} - t_5)}}}$$

The model was fit to the experimental data based on the nonlinear least squares solver within MATLAB (*Isqnonlin*). We calculated the sum of squared errors (SSE) as a measure of goodness of fit. Across all participants in all conditions, the average SSE was 4.58 and the range was between 0.78 and 13.27. In the model t represents the re-preparation time. The function contains four free parameters: A , the normalized saccade direction at which the sigmoid function asymptotes, t_{50} the mid-point of the sigmoid function, t_5 and t_{95} the 5% and 95% point of the sigmoid function, respectively. The difference of the last two parameters is essentially the slope of the function. This quantitative spatial-temporal relationship captured the change in trajectory angle as a function of the available time and allowed a comparison of these parameters across the different jump sizes. From this function we examined four temporal properties of the intermediate eye movements with respect to the re-preparation time: when these intermediate movements (1) started to occur (t_5), (2) ceased to occur and went directly to the new target location (t_{95}), and (3) could be directed in between the two locations—the inflection point of the sigmoid function (t_{50}). We also

determined (4) the time range over which intermediate movements could be observed ($t_{95} - t_5$, again equivalent to the sigmoid slope). If movements landed along the slope of the sigmoid, then they were no longer directed towards the initial location, but were not reliably directed towards the jumped location either. Therefore, this time range characterized the re-preparation time over which the oculomotor system could blend movement plans to two competing stimuli locations (i.e., intermediate movements).

Determining the Proportion of Intermediate Saccades

Although the sigmoid function above captures how the saccade direction changed as a function of re-preparation time, two distinct patterns of behavior can be fit by the sigmoid: one where saccade trajectories show a progressive transition from the initial target to the jumped target location, and one where saccade trajectories show an abrupt transition from the initial target to the jumped target location (See Figure 4A and B for a hypothetical representations of these cases and their respective sigmoid function fits). Note that the same function can be fit to very different behavioral data. For the progressive transition, the sigmoid represents the relative contribution of the two stimuli to saccade planning (initial target and jumped location), and on average, saccade trajectories are distributed along the function. For the abrupt transition, the sigmoid represents the relative probability that the eyes will land on either the initial target or jump target location. That is, at the point of inflection, the progressive case predicts that the eyes will uniformly land between the two targets, whereas the abrupt case predicts a bimodal distribution centered around the initial and jumped target locations. The distribution of data along the slope of the sigmoid changes depending on whether there is a progressive or abrupt transition. Within this time window, the progressive case predicts a large proportion of landing points along the slope of the sigmoid (Figure 4A), whereas the abrupt case predicts a sparse collection of data along the sigmoid slope (Figure 4B). Thus, we examined the proportion of saccades within this time window in our behavioral data in order to distinguish how this proportion changed as a function of jump size (Figure 4C).

Classifying Secondary Saccades

We examined the characteristics of the second saccade made on any given trial. Often termed secondary saccades, these saccades were classified as the second movement that satisfied the same velocity and amplitude thresholds as the primary saccade (30 dva/s and 1° visual angle respectively). The distribution of the time between the offset of the primary and the onset of the secondary saccade (the inter-saccade interval, ISI) is displayed in Figure 6.

Statistical Analysis

Due to the fact we used two separate groups of subjects in the small and large jump conditions, statistical significance of the sigmoid parameters in each condition were determined by the following linear mixed-effects model: sigmoid parameter \sim jump size + (1/subject data). Jump size was a fixed effect despite it being dependent on the group in which the subject happens to be. We chose subject data to be our random effect because it would allow us to still examine correlation within our unbalanced design and combine within- and between-subjects data. When determining whether inter-saccade interval (ISI) or secondary saccade amplitude changed across jump sizes, we implemented the same linear

mixed-effects models but used ISI and secondary amplitude were used as the random effect in each analysis. The relationship between inter-saccade intervals and re-preparation times were fit using a robust regression. All statistical analyses were performed within MATLAB. For all tests the significance level was 0.05.

RESULTS

In this study we sought to examine how limiting the time to readjust an eye movement plan affected the saccade direction for different target location displacements. We trained participants to execute an eye movement to a peripheral target concurrent with the final auditory cue of a four tone sequence. On a minority of trials (30%), the target (located 8° from fixation) could jump 20°, 30°, 40°, 60°, or 90° along a radial arc to the left or right of fixation. The jump occurred within a temporal window (150 ms before to 50 ms after) around the fourth tone of the sequence (see Methods). Target jumps occurred close to the go signal, leaving participants with limited time to re-prepare the eye movement to the new target location. We quantified how the presence of intermediate saccades (movement trajectories falling between the two target locations) was modified by these temporal and spatial manipulations.

Analysis of Saccade Direction with Re-preparation Time

We were interested in the timecourse for updating the saccadic eye movement plan and the extent that the timecourse was modified by the spatial separation of the stimuli locations. Figure 2 shows data from a representative subject for each condition (shown in Figure 2A, B and C, for jump sizes of 20°, 30° and 40°, respectively. A different subject is shown in Figure 2D and E for jump sizes of 60° and 90°). Single trials are represented by the small, dark blue filled circles. At the shortest jump sizes (Figure 2A, B and C) there was a continuous relationship between the angle of the saccade and the available re-preparation time. For each jump size the saccade direction began to deviate away from the initial target location (0% of the Normalized Movement Angle) and towards the jumped location (100% of the Normalized Movement Angle) between approximately 60–80 ms. Between approximately 180–200 ms of re-preparation time the saccades were consistently directed towards the jumped target location. The area between these two points represents the temporal range in which intermediate eye movements were observed (corresponding to the slope parameter of the sigmoid function fit, solid black trace in each panel). Conversely, at the largest jump sizes (60° and 90°, Figure 2D and E), the saccades do not begin to deviate to the jump target location until approximately 100 ms of re-preparation time, but are still consistently directed to the final location between approximately 180–200 ms. Correspondingly, the slope of the sigmoid fits (solid black traces) are steeper for the larger jump sizes.

The psychometric fit of the saccade trajectory as a function of re-preparation time quantified these relationships. Specifically, we estimated t_{50} , the mid-point of the sigmoid function, and t_5 and t_{95} , the 5% and 95% point of the sigmoid function, respectively for each subject. The summary of these parameters is shown in Figure 3 (see Methods). To investigate whether increasing jump size affected these temporal parameters, we ran a linear mixed-effects

model on our data from the two groups for each parameter. Figure 3A displays the re-preparation time at which the intermediate saccade trajectories began for each target jump size; t_5 . We found that as jump size increased, so did the amount of re-preparation time it took for saccades to start being influenced by the target jump location [linear mixed-effects model, $t(48) = 7.19$, $p < 0.001$]. Figure 3B shows the group results for t_{50} , the behavioral inflection point of the sigmoid function fit. Before the inflection point the oculomotor plans are directed closer or more often to the initial location. After this point the plans are directed closer or more often to the final jump location. We found that as jump size increased, so did the behavioral inflection point [linear mixed-effects model, $t(48) = 6.77$, $p < 0.001$]. Figure 3C displays the 95% point of the sigmoid function, t_{95} ; the re-preparation time at which saccades were consistently directed at the jumped target location. We found no significant difference in t_{95} across jump sizes [linear mixed-effects model, $t(48) = 1.87$, $p = 0.06$]. Figure 3D displays the temporal range of re-preparation time over which there were saccades directed to a location between the two targets, $t_{95} - t_5$. We found that as jump size increased, the window in which intermediate movements were observed decreased significantly [linear mixed-effects model, $t(48) = 2.19$, $p = 0.03$].

Proportion of Intermediate Saccades with Jump Size

As mentioned above, we were interested in two possible patterns of behavior in the current eye movement paradigm (see Methods). In the first case, the transition in saccade direction from the initial to the jumped target location could smoothly change with re-preparation time (Figure 4A). In the second case, there could be an abrupt transition in the saccade direction with re-preparation time (Figure 4B). In the former, the progressive transition is characterized by many saccades landing along the slope of the sigmoid fit—the presence of intermediate saccades between the two target locations. In the latter, the abrupt transition is characterized by very few saccades landing between the two locations.

In order to quantify this difference in saccade behavior we defined a region of interest to examine the spatiotemporal relationships established in Figures 2 and 3. We were interested in the proportion of saccades that fell within a spatial range (between 25% and 75% of the normalized saccade direction) and temporal range (between 10 and 90% of the sigmoid slope). Figure 4A and B depict the two simulated cases with this region of interest overlaid (within the red dashed square). Note that the sigmoid function fits in both panels are the same although the saccade behavior is very different, with very few saccades falling within the region for the abrupt case (Figure 4B). Thus, the proportion of saccades falling within this window provides a measure of the type of transition in saccade direction with re-preparation time between the two target locations.

In Figure 4C each filled circle represents the proportion of saccades within our region of interest for each subject as a function of the respective inflection point of the sigmoid fit (t_{50}) for each jump size. The shaded ellipses represent the confidence intervals (2 SEM) for the respective jump sizes. The plot reveals a negative relationship; the proportion of saccades in the region of interest decreases as the inflection point increases (slope = -202.3 , $p = 0.001$, $R^2 = 0.23$). This relationship is also associated with the target jump size. That is, as the jump size increases the inflection point shifts forward (occurs later in time) and the

proportion of saccades in the region of interest decreases. Thus, with the small jump sizes the behavioral data resemble a progressive transition from the initial target to the jumped target, with the presence of numerous intermediate saccades (Figures 3A, 4A). Conversely, when the jump size is large, the transition behavior resembles the abrupt case, where there are few intermediate movements between the two locations (Figures 3E, 4B).

Figure 5 is a summary of the relationships represented in Figure 4C. The blue traces in each panel are the distribution of saccades across all subjects as a function of re-preparation time. Note that across all conditions, there are two distinct peaks representing groups of movements to the initial and final target locations respectively. The first peak is roughly 100 ms of re-preparation time, it is followed by a valley at roughly 150 ms of re-preparation time, and the valley is followed by a second peak at roughly 210 ms. The red traces are the sigmoid fit functions (based on the average of the parameters presented in Figure 3) for each respective jump size. The vertical green lines are the average inflection points, (t_{50} , Figure 3B). As shown in each panel, the point of inflection (when the eye movements go from being directed towards the initial target location and instead directed towards the jumped location) shifts forward in time as the jump size increases; as the jump size increases from 20° (Figure 5A) to 90° (Figure 5E) the vertical green line moves further to the right of the vertical gray dashed line. Interestingly, this is not only a shift along the re-preparation time, but also a shift towards the valley of the saccade distribution. That is, as the target jump size increases the inflection point becomes more aligned with the lowest point of the saccade distribution, signifying a decrease in saccade production—specifically a decrease in the intermediate saccades, as suggested in Figure 4C.

Analysis of Secondary Saccades

Previous research argues that when there is more than one possible saccade goal, the oculomotor system is able to plan multiple saccades in parallel (Mokler & Fischer 1999; McPeck et al. 2000; Hu & Walker 2011; Bhutani et al. 2017). To support this argument, these studies examined the second saccade executed during the trial. This eye movement is often called a secondary saccade because the initial, primary saccade failed to accurately foveate the new target location, and the second eye movement compensates, or “corrects”, for any error in the landing position of the primary saccade. These studies have shown that the interval between the primary and secondary saccade (inter-saccade interval; ISI) is a short duration compared to the normal latency range for reactive saccades to a stimulus (~10–100 ms; McPeck et al. 2000). Figure 6 displays the distribution of inter-saccade intervals across all jump sizes. As shown in the figure, there is a clear peak in the distributions between 100–150 ms regardless of jump size. In fact the mean ISI did not significantly differ across jump sizes [linear mixed-effects model, $t(48) = 0.52$, $p = 0.6$].

Bhutani et al. (2017) examined the properties of the saccade correction to a single target displacement by applying the target jump on a majority of trials. These authors found that the amplitude of secondary saccades increased after prolonged performance in the task, suggesting that the second saccade in a sequence can be guided by prospective motor plans even before the first saccade ended. One important difference between this prior work and the current study is that the current paradigm randomly changed the target location on a

minority of trials (30%). Noting the lack of any consistent trial-by-trial change in initial primary nor secondary saccade amplitude, we conclude that we did not induce similar adaption in the secondary saccade in our study. Although there was no temporal change in the distribution of the timing of the second secondary saccade, we did find that the amplitude of the secondary saccade significantly increased as the jump size increased [linear mixed-effects model, $t(48) = 12.3$, $p < 0.001$]. Figure 7 shows the average secondary saccade amplitude for each jump size and Table 1 reports the mean of the amplitude of the secondary saccade and the ISI, as well as the percentage of trials which elicited a secondary saccade. Consistent with the abrupt transition in the saccade direction for the large target jumps (Figures 2 and 4), there were less trials with a secondary saccade for the 60° and 90° jump conditions. That is, the need to make a correction from an intermediate saccade to the new target location decreased for the large target jumps. To quantitatively determine the increase in secondary saccade amplitude, we fit a linear regression to the data across jump sizes. We found that secondary saccade amplitude significantly increased along with increasing jump size ($R^2 = 0.98$, $F(1,4) = 271.5$, $p < 0.001$).

In order to examine the extent to which the amount of time to prepare an initial saccade correlated with interval between primary saccade offset and secondary saccade onset we performed a linear regression analysis between the ISI and re-preparation time. Note that consistent with Figures 6 and 7, we examined this relationship for secondary saccades that occurred after the target had jumped (0 ms re-preparation time) and before the initial saccade was consistently directed to the new target location (< 95% of the sigmoid fit). Figure 8 displays the inter-saccade interval as a function of the re-preparation time. We found a significant negative correlation between ISI and re-preparation time for all target jumps ($p < 0.001$ in all cases). The relationship was determined based on the *fitlm* MATLAB function which calculates a linear regression model of the data that reduces the influence of outliers. The negative correlation between the two timing measures indicate that as the exposure duration (re-preparation time) decreased, the ISI increased. This suggests that subjects transitioned from a reactive movement correction ($ISI > 150$ ms) to a concurrently planned correction ($ISI < 100$ ms) as the re-preparation time increased. To analyze this pattern on an individual subject basis, we performed the regression analysis on each subject with the corresponding ISI and re-preparation time for each trial. The following values list the average correlation value across subjects, the standard error and the respective number of subjects with a negative relationship between ISI and re-preparation time: 20°: $r = -0.22$ (0.05, 10/10); 30°: $r = -0.26$ (0.08, 9/10); 40°: $r = -0.35$ (0.07, 10/10); 60°: $r = -0.31$ (0.07, 9/10); and 90°: $r = -0.48$ (0.10, 9/10).

DISCUSSION

The current study provides insight into how the spatial separation of movement goals and the temporal duration of exposure influence oculomotor control. We examined eye movement behavior for several target separation sizes to determine how saccade direction was modified as a function of re-preparation time (the time between the change in target location and saccade onset). When the spatial separation between the initial and jumped target locations was small (20°, 30° and 40°), intermediate movements began with approximately 80 ms of re-preparation time (equivalent to the 5% point of the sigmoid

function slope). Larger jumps (60° and 90°) required approximately 120 ms of re-preparation time for the initiation of intermediate movements. In addition, the time between the start and end of the sigmoid function slope was used to estimate the temporal range in which intermediate eye movements were observed (between the 95% and 5% points of the sigmoid function). This temporal range was significantly greater for smaller jump sizes (approximately 70–90 ms) compared to the larger jump sizes (< 60 ms). Finally, the transition in saccade direction from the initial to the jumped target location with re-preparation time was a smooth transition for small target jumps, but more abrupt for the larger jumps. This was consistent with a difference in the proportion of intermediate movements, with significantly less intermediate movements and secondary saccades for large target jumps.

Relation to saccadic neural control

Intermediate eye movements have typically been explained in terms of the center of gravity account first suggested by Coren and Hoening (1972). This theory posits that a saccade will land at the point representing the relative salience of elements in the visual display. It is possible that the memory of the initial target location allows its salience to compete with the salience of the jumped target to guide the intermediate movement. In this way the re-preparation time may be related to the diminishing influence of this initial target memory trace. Alternatively, more recent theories on saccadic control such as the competitive integration model (Trappenberg et al., 2001; Meeter et al., 2010) assume that the cortical inputs that determine the saccade trajectory are excitatory and inhibitory, and that saccade trajectories can continue to be influenced mid-movement. Specifically, the competitive integration model states that the brain incorporates information from the occipital cortex, the frontal eye fields (FEF), and the dorsolateral prefrontal cortex (DLPFC) with excitatory or inhibitory signals from the superior colliculus (SC). Signals from the SC can influence saccade trajectories even after they have been initiated through continual processing of information in the accompanying areas mentioned above.

In relation to the current study, competitive integration has three predictions. The first is that with small jump sizes, there is more overlap between competing saccade plans in the retinotopic motor map. Behaviorally, this would lead to fewer intermediate movements (proportion of saccades falling within our defined ROI, Figure 4) as the jump size increases. As in previous studies (Ottes et al. 1985; Van der Stigchel & Nijboer 2013), we observed this exact pattern (Figure 4C). This would also predict that the overlap would cause saccades to be initiated earlier for the short jumps (Figure 3A), which in turn would cause the inflection point to occur earlier (Figure 5), and increase the temporal range of re-preparation (Figure 3D). The second prediction is that due to the progressive buildup of excitatory saccade signals, trials in which the subjects had a longer time to react to the target jump would allow subsequent secondary saccades to be executed quickly. Indeed we observed this pattern in the negative correlations between ISI and re-preparation time, with the longest re-preparation times allowing the shortest ISI's (Figure 8). This suggests that the once the final target location had enough time to accumulate activation on the retinotopic motor map the oculomotor system can use it to quickly adjust for any errors in the primary movement. The third prediction of competitive integration is that for eye movements to be appropriately

directed to the jumped location, the movement plan to the initial location must be inhibited. There is a suggestion of this inhibition in Figure 5; namely, a distinct bimodal pattern in the distribution of saccades across re-preparation times with a decrease in the proportion of saccades between the two peaks. In fact all individual subjects in the current study displayed this bimodal distribution in saccade production to some extent. Although this requires further investigation, we hypothesize that the first peak of the saccade distribution represents the saccade plan to the initial location. To modify the movement angle to the jumped target location this plan must be inhibited, resulting in a subsequent depression in the number of saccades immediately following the first distribution around 150 ms. Interestingly, this point of maximal saccade inhibition differs from Buonocore and McIntosh (2008), who reported that following a transient change in the visual field, saccade inhibition began around 70 ms and maximized at 100 ms. However, participants recruited by Buonocore and McIntosh were never asked to compensate for a change in saccade target location, subjects simply needed to inhibit distractor stimuli. In the current study, our subjects had to recognize a change in target location, inhibit the saccade the old location, and prepare a plan to the jumped location. While both tasks demonstrate saccadic inhibition, we suggest the approximately 50 ms delay in peak inhibition between our results and those reported by Buonocore and McIntosh is due to the additional process the planning of an updated saccade to a new target location.

Recently, a neural recording study by White et al. (2013) reported results largely consistent with the behavioral findings described here. The authors recorded SC activity in monkeys presented with a saccade target and a near or far distractor. There was a two-step process in the response to a competing saccade target (near distractor). There was first a short goal-centered decrease in activation, which was immediately followed by a rapid rebound and rise in activation relative to the target location (occurring approximately 100 ms from target onset). In relation to the current study, a target jump may be analogous to a distractor because it prompts a competing saccade plan to be programmed. As such, the goal-centered decrease in neural activation followed by a rapid rise may manifest itself behaviorally in the temporal distribution of saccades we show in Figure 5. All subjects across all conditions showed a decrease in the proportion of saccades until roughly 150 ms after the go signal, which was then followed by a rapidly ascending proportion of saccades. White et al. found a rapid rise in neural activation at near 100 ms after target onset. Importantly, the rise in neural activity occurs before the behavioral changes within our study (100 ms vs. 150 ms), thus not ruling out a possible causal relationship. If these neural signals in the SC modulate in a similar way in human subjects, the 50 ms difference between changes in neural and movement activity could be the delay that must occur between the motor command signal and the execution of the movement. Although we provide a behavioral timecourse, it would be interesting to investigate the neural activation timecourse within the SC and within related neural regions while exposed to similar task conditions used here. Based on White et al. (2013), starting at the target jump, we would expect to see an increase in activation in cells sensitive to the jumped location. This rapid rise would be accompanied by an active suppression in cells sensitive to the initial location. Comparing the timecourse of this excitation/inhibition pattern in the SC to the saccade trajectory timecourse, as well as any

latencies between the two, might provide insight into how spatial features influence the rate at which oculomotor plans can be updated.

Concurrent Processing of Saccades

There is significant evidence to suggest multiple saccades with different goals can be planned in parallel (McPeck et al. 2000; Hu & Walker 2011; Mokler & Fischer 1999; Bhutani et al. 2017). Results from these studies (McPeck et al. 2000) argue that a second saccade is programmed concurrently with the first based on the finding that the interval between the end of the first saccade and start of the second (inter-saccade interval; ISI) is consistently shorter than the time it takes to react, plan, and execute the initial saccade (reported as latency following the primary saccade, mean ISI between 10–100 ms, compared to the mean primary saccade latency of ~ 200 ms). These studies only examined primary and secondary saccades latencies with one displacement size. Although our primary analysis focused on the timecourse of the change in the initial saccade direction for variable displacements in the movement goal location, temporal properties of the secondary saccade may offer additional insight into sequential saccade planning. Results showed that the average ISI across all jump sizes was 152.6 ms with standard deviation of 42.0 ms, which was slightly lower than the average re-preparation time of the primary saccade (mean of 145.1 ms, standard deviation of 85.1 ms). Note that re-preparation time is not saccade latency, one of the primary measures used in prior studies; due to the structure of the task (the planning of the movement with the beep onset), it is likely that re-preparation time is shorter than traditional measures of saccade latency to the suddenly appearing target. Thus, even though saccade latency and re-preparation time are likely correlated, due to the structure of our paradigm, we cannot use traditional measures of saccade latency to examine the same relationships established in prior work.

Average ISI was largely consistent across target jump sizes (range of 148.3 to 158.3 ms). Despite this consistency across jump sizes, there was a difference in the relationship between ISI and the re-preparation time of the initial saccade with the correlation increasing with the increase in jump size (Figure 8). Recently, Bhutani et al. (2017) examined the secondary saccadic eye movements of subjects in a double-step paradigm when a target step was implemented on a majority of trials (60%). Using only one target displacement size, the authors found that the amplitude of the secondary saccade selectively increased to land closer to the final target location, suggesting adaptation of the secondary movement. The authors suggested that this shift in saccade landing position indicated that the oculomotor system was able to take advantage of prospective eye movement plans to guide sequential saccades. In relation to the current study, this would suggest that on jump trials, the oculomotor system was able to prepare a secondary saccade even before the offset of the primary saccade. However, as noted above, the jump sizes in the current study were random in occurrence and size. Thus, subjects likely could not adapt the secondary saccade on a trial-by-trial basis.

Although there are marked differences in the paradigm implemented by Bhutani et al, (2017) and the current study, there are some notable similarities in the secondary saccade behavior. We examined the relationship between the inter-saccade interval and re-preparation time

(Figure 8) by plotting the former as a function of the latter. We found a significant negative correlation between ISI and re-preparation time for all jump sizes. We suggest that when given sufficient time to react (a long re-preparation time), the oculomotor system is able to plan a secondary saccade in parallel with the planning of the primary saccade, indicated by the very short ISI's that followed the longest re-preparation times (Figure 8). However, when the re-preparation time was short, subjects had to rely on visual information when preparing the secondary saccade resulting in a long ISI. This is supported by a recent study (Zimmermann, 2015) that also found a negative correlation between ISI and the latency of the primary saccade in a planned sequence. The author argued that if the second saccade is planned concurrently with the first, then longer first saccade latencies (here the re-preparation time) should be followed by shorter ISIs. Consistent with this earlier report, as described above we found that as this time to plan the movements decreased (a reduced re-preparation time) subjects took longer to produce a secondary saccade to the jumped target (large ISIs). We suggest that this increase in ISI duration is due to the oculomotor system relying on newly updated visual information that is acquired only after the primary saccade has landed.

Saccade Averaging Context

The intermediate movements between the initial and final target locations observed here are similar to experiments that examined saccades directed to an intermediate location between two simultaneously presented targets (averaging saccades: Van der Stigchel et al. 2012; Van der Stigchel & Nijober 2013; Heeman et al. 2014). This finding has been termed the 'global effect' as saccade endpoints are directed to a global average of stimuli locations. As described above, the double-step task has been able to show the timeframe of intermediate saccade (for a limited range of separation sizes) when the planned saccade lands between the initial and jumped target locations. Unlike these experiments, several investigations that specifically examined the properties of averaging saccades directly manipulated the spatial separation between target locations to determine its influence. Note that in these paradigms two possible targets are presented simultaneously (rather than a jump in the double-step paradigm) and the participant is left to decide at which stimulus to execute the saccade. When the target instructions are left ambiguous, and the separation between two competing targets is 35° or less, the landing position of the saccadic eye movements tend to cluster in a unimodal distribution around a central location between two possible targets (Van der Stigchel & Nijober, 2013). Conversely, the same study reported bimodal distributions of saccade landing positions for stimuli separations larger than 45° . Similarly, Aagten-Murphy and Bays (2017) manipulated the task instructions and target-distractor spatial separation (15° to 75°) to parse two concurrent influences on eye movement angle: the automatic capture (due to the presence of a single stimulus, or multiple stimuli) and intentional selection (due to goal directed targeting). The authors found that as separation increased, the probability of average saccades decreased. However, unlike Van der Stigchel and Nijober (2013), average saccades were still present at the separation distance of 75° , suggesting a larger spatial window to observe the global effect. Van der Stigchel et al. (2006) summarized several saccade planning studies that investigated curvature in the saccade trajectories. The analysis of movement trajectory provided interesting insight into the saccade planning process, such as specific conditions which elicit saccade curvature towards and away from

visual targets. The review argues that deviation (curvature) towards an element happens when there is unresolved competition in the saccade plans, and deviation away is observed when top-down influence is afforded. Thus the paradigm used in the current study may provide an ideal experimental structure for several future investigations of the spatiotemporal properties of saccade planning.”

Several previous studies have also shown that saccade averaging is highly dependent on the movement reaction time, with more intermediate movements occurring at the lowest latency times (100–200 ms, Ottes et al. 1985; Chou et al. 1999). Recently, Heeman et al. (2014) examined how the temporal aspects of the eye movement responses affected the production of these intermediate saccades. For example, the authors reported that the top-down influence (in this case the task instructions, i.e., “look at the red target”) on the saccade trajectory begins around 200 ms after the saccade go-signal, a time range previously thought to be dominated by bottom-up sources (Ottes et al. 1985). By 300 ms the majority of the bottom-up influence (in this case distractor onset) can be inhibited. Although clear relationships were found, the above studies examined these properties within a limited temporal range; only saccades that occurred with a latency longer than approximately 160 ms were examined, limiting the ability to understand how temporal manipulations possibly affect the saccade trajectory. In addition, latency from a go-signal may not provide as accurate temporal information with regard to movement planning compared to the defined reprogramming or re-preparation time, utilized in the double-step paradigms. Here our modified paradigm provides a detailed account of the spatiotemporal properties of the saccade trajectory when the motor plan must be updated. Interestingly, we are able to quantify how the intermediate movements, perhaps due to averaging at least two possible movement plans, is concurrently influenced by both the duration of exposure to the new movement goal and the separation between the initial and final saccade target.

Although saccade averaging can explain the pattern of intermediate movements reported here, so can perceptual mislocalization. Recently, Zimmermann et al. (2015) found that during a planned double-step saccade sequence, participants perceived probe stimuli as closer to the first saccade target. Additionally, participants misperceived probe stimuli closer to the second saccade in the sequence, but only when the original target was presented for a long duration. The authors argue that spatial misperception can occur when the target has enough time to be well-coded in visual memory. In the current study, this perceptual bias could manifest itself as a portion of the intermediate movements reported here. Even more so because our paradigm allowed the initial saccade target 1500 ms to be well-coded into visual memory. More research is required to isolate the distinct influences of saccade averaging and perceptual mislocalization on the occurrence of the intermediate movements reported here.

Comparison to reaching movements

There is a natural comparison of the current saccadic eye movement results to the visually guided arm reaching results reported by Haith et al. (2015). In the prior reaching task, subjects had to adjust the movement trajectory in response to jumps of 45°, 90°, and 135° in the initial target location. Instead of examining the entire movement, the authors focused on

biases in the initial movement trajectory (the angle of the tangential velocity 100 ms after movement onset). Unlike saccades, large target jumps elicited intermediate movements in the initial trajectory of reaching arm movements (e.g., 90°). There was also a considerable difference in the timescale of the jumped target influence on the two motor responses. The first time reaching movements were influenced by the target jump occurred at approximately 165 ms of re-preparation time for the 45° jump condition (Haith et al. 2015). This can be compared to saccade results; the movement angle began to deviate away from the initial target location at approximately 78 ms of re-preparation time for the 40° target jump. This deviation occurred even earlier for the smaller jump sizes (20° = 73 ms, 30° = 64 ms). This difference suggests that the changes in the movement goal requires much less processing time to influence saccade movement adjustments compared to reaching. When considering the functional and anatomical differences between the two motor systems (e.g., number of muscles, rotational and translational degrees of freedom, inertial properties), it is logical to expect this disparity in the required modification time.

It is well established that the eyes precede the hand during coordination tasks (Biguer et al., 1982; Johansson et al., 2001; Ariff et al., 2002), with an estimate of a 200 ms lead time (Ariff et al., 2002). It is suggested that this lead time allows the feedback to monitor the current action (Land et al., 1999), as well as provide the information necessary to coordinate the next action (Land 2006). Further comparison of the current results to Haith et al. (2015) provides additional information about the temporal requirements necessary for accurate reaching versus accurate eye movements. Results from Haith et al. (2015) show that arm movements required almost 300 ms of re-preparation time in order to re-directed the movement towards the appropriate location (complete compensation for the target jump), compared to only 155 ms for saccades in response to the smaller jumps. Haith et al. suggest that before this time, the observed intermediate initial movement trajectories reflect an adaptive response of the motor system when confronted with ambiguity about compatible task goals (i.e., two locations close in space). The differences in the time required for complete compensation suggests that the oculomotor system can resolve the ambiguity between two saccade goals more quickly than the resolution between two reaching goals. This difference may be explained by research within motor programming theory. Several studies have shown that the time required to initiate a movement increases as the movement requires more anatomical components (vocalization: Sternberg et al. 1978; reaching: Franks et al. 1998). The larger number of anatomical components to be considered in planning a reaching movement may prolong the time it takes for ambiguity in possible movement plans between task goals to be resolved by the motor system. Additionally, the transmission speed of efferent signals contributes to the delay observed between reaching movements and eye movements. Motor neurons responsible for voluntary movement transmit their signals on the order of 10–50 meters per second (Russell 1980). Goal-directed signals for motor control originate in the cortex (Corbetta & Shulman 2002) and must travel a shorter distance to innervate the eye movement effectors compared to the distance required to reach the arm movement effectors. Collectively, these factors likely account for the differences between our results and those observed by Haith et al. (2015).

One of the most complex motor coordination skills is the ability to use visual information to guide hand movements with consistent precision. How the brain is able to transform visual

information into a coordinate system for the limbs has been a critical question for eye-hand coordination. Previous work has shown that during a visually-guided reaching task, areas in the posterior parietal cortex (PPC) are capable of representing target position and current hand position. However, of critical importance, both target and current hand position is represented relative to eye position (Buneo & Andersen 2006). Leveraging relative position allows the coordination between the eye and hand movement systems to reduce multiple sources of estimation error in comparison to an interaction that relies on absolute spatial position (Pesaran et al. 2006). Combined with the Haith et al. (2015) study, our results demonstrate that the updating a motor plan for different effectors (the eye versus the arm) operate on quantitatively different timecourses. Although the current study does not directly address how accurate eye-hand coordination can account for this temporal discrepancy, it provides novel insight into how the faster process for saccades could subsequently aid limb movement.

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REFERENCES

- Aagten-Murphy D, & Bays PM (2017). Automatic and intentional influences on saccade landing. *Journal of Neurophysiology*, 118(2), 1105–1122. [PubMed: 28539394]
- Ariff G, Donchin O, Nanayakkara T, and Shadmehr R (2002). A Real-Time State Predictor in Motor Control: Study of Saccadic Eye Movements during Unseen Reaching Movements. *The Journal of Neuroscience*, 22(17), 7721–7729. [PubMed: 12196595]
- Aslin RN, & Shea SL (1987). The amplitude and angle of saccades to double-step target displacements. *Vision research*, 27(11), 1925–1942. [PubMed: 3447347]
- Becker W, & Jürgens R (1979). An analysis of the saccadic system by means of double step stimuli. *Vision research*, 19(9), 967–983. [PubMed: 532123]
- Bhutani N, Ray S, & Murthy A (2012). Is saccade averaging determined by visual processing or movement planning?. *Journal of neurophysiology*, 108(12), 3161–3171. [PubMed: 23018999]
- Bhutani N, Sengupta S, Basu D, Prabhu NG, & Murthy A (2017). Parallel activation of prospective motor plans during visually-guided sequential saccades. *European Journal of Neuroscience*, 45(5), 631–642. [PubMed: 27977051]
- Biguer B, Jeannerod M, and Prablanc C (1982). The coordination of eye, head, and arm movements during reaching at a single visual target. *Experimental Brain Research*, 46(2), 301–304. [PubMed: 7095037]
- Buneo CA, & Andersen RA (2006). The posterior parietal cortex: sensorimotor interface for the planning and online control of visually guided movements. *Neuropsychologia*, 44(13), 2594–2606. [PubMed: 16300804]
- Buonocore A, & McIntosh RD (2008). Saccadic inhibition underlies the remote distractor effect. *Experimental Brain Research*, 191(1), 117–122. [PubMed: 18784920]
- Camalier CR, Gotler A, Murthy A, Thompson KG, Logan GD, Palmeri TJ, & Schall JD (2007). Dynamics of saccade target selection: Race model analysis of double step and search step saccade production in human and macaque. *Vision research*, 47(16), 2187–2211. [PubMed: 17604806]
- Chou IH, Sommer MA, and Schiller PH (1999). Express averaging saccades in monkeys. *Vision research*, 39(25), 4200–4216. [PubMed: 10755158]
- Corbetta M, & Shulman GL (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature reviews neuroscience*, 3(3), 201–215. [PubMed: 11994752]

- Coren S, and Hoenig P (1972). Effect of non-target stimuli upon length of voluntary saccades. *Perceptual and motor skills*, 34(2), 499–508. [PubMed: 5063190]
- Deubel H, Wolf W, and Hauske G (1984). The evaluation of the oculomotor error signal. *Advances in Psychology*, 22, 55–62.
- Findlay JM (1982). Global visual processing for saccadic eye movements. *Vision research*, 22(8), 1033–1045. [PubMed: 7135840]
- Gallivan JP, Barton KS, Chapman CS, Wolpert DM, and Flanagan JR (2015). Action plan co-optimization reveals the parallel encoding of competing reach movements. *Nature communications*, 6.
- Gallivan JP, Bowman NA, Chapman CS, Wolpert DM, and Flanagan JR (2016). The sequential encoding of competing action goals involves dynamic restructuring of motor plans in working memory. *Journal of neurophysiology*, 115(6), 3113–3122. [PubMed: 27030738]
- Haith AM, Huberdeau DM, and Krakauer JW (2015). Hedging your bets: intermediate movements as optimal behavior in the context of an incomplete decision. *PLoS Comput Biol*, 11(3), e1004171. [PubMed: 25821964]
- Heeman J, Theeuwes J, and Van der Stigchel S (2014). The time course of top-down control on saccade averaging. *Vision research*, 100, 29–37. [PubMed: 24732567]
- Hu Y, & Walker R (2011). The neural basis of parallel saccade programming: an fMRI study. *Journal of cognitive neuroscience*, 23(11), 3669–3680. [PubMed: 21563883]
- Johansson RS, Westling G, Backstrom A, and Flanagan JR (2001). Eye-hand coordination in object manipulation. *the Journal of Neuroscience*, 21(17), 6917–6932. [PubMed: 11517279]
- Kastner S, DeSimone K, Konen CS, Szczepanski SM, Weiner KS, & Schneider KA (2007). Topographic maps in human frontal cortex revealed in memory-guided saccade and spatial working-memory tasks. *Journal of neurophysiology*, 97(5), 3494–3507. [PubMed: 17360822]
- Krappmann P (1998). Accuracy of visually and memory-guided antisaccades in man. *Vision research*, 38(19), 2979–2985. [PubMed: 9797993]
- Land MF (2006). Eye movements and the control of actions in everyday life. *Progress in retinal and eye research*, 25(3), 296–324. [PubMed: 16516530]
- Land M, Mennie N, and Rusted J (1999). The roles of vision and eye movements in the control of activities of daily living. *Perception*, 28(11), 1311–1328. [PubMed: 10755142]
- McPeck RM, Skavenski AA, & Nakayama K (2000). Concurrent processing of saccades in visual search. *Vision research*, 40(18), 2499–2516. [PubMed: 10915889]
- Meeter M, Van der Stigchel S, and Theeuwes J (2010). A competitive integration model of exogenous and endogenous eye movements. *Biological cybernetics*, 102(4), 271–291. [PubMed: 20162429]
- Mokler A, & Fischer B (1999). The recognition and correction of involuntary prosaccades in an antisaccade task. *Experimental Brain Research*, 125(4), 511–516. [PubMed: 10323298]
- Murthy A, Ray S, Shorter SM, Schall JD, & Thompson KG (2009). Neural control of visual search by frontal eye field: effects of unexpected target displacement on visual selection and saccade preparation. *Journal of Neurophysiology*, 101(5), 2485–2506. [PubMed: 19261711]
- Ottes FP, Van Gisbergen JA, and Eggermont JJ (1985). Latency dependence of colour-based target vs nontarget discrimination by the saccadic system. *Vision research*, 25(6), 849–862. [PubMed: 4024483]
- Pesaran B, Nelson MJ, & Andersen RA (2006). Dorsal premotor neurons encode the relative position of the hand, eye, and goal during reach planning. *Neuron*, 51(1), 125–134. [PubMed: 16815337]
- Ray S, Schall JD, & Murthy A (2004). Programming of double-step saccade sequences: modulation by cognitive control. *Vision research*, 44(23), 2707–2718. [PubMed: 15358065]
- Russell NJ (1980). Axonal conduction velocity changes following muscle tenotomy or deafferentation during development in the rat. *The Journal of physiology*, 298(1), 347–360. [PubMed: 7359413]
- Trappenberg TP, Dorris MC, Munoz DP, & Klein RM (2001). A model of saccade initiation based on the competitive integration of exogenous and endogenous signals in the superior colliculus. *Journal of cognitive neuroscience*, 13(2), 256–271. [PubMed: 11244550]

- Van der Stigchel S, Heeman J, and Nijboer TCW (2012). Averaging is not everything: The saccade global effect weakens with increasing stimulus size. *Vision Research*, 62, 108–115. [PubMed: 22521658]
- Van der Stigchel S, Meeter M, & Theeuwes J (2006). Eye movement trajectories and what they tell us. *Neuroscience & biobehavioral reviews*, 30(5), 666–679. [PubMed: 16497377]
- Van der Stigchel S, & Nijboer TCW (2013). How global is the global effect? The spatial characteristics of saccade averaging. *Vision research*, 84, 6–15. [PubMed: 23523571]
- White BJ, Marino RA, Boehnke SE, Itti L, Theeuwes J, and Munoz DP (2013). Competitive integration of visual and goal-related signals on neuronal accumulation rate: A correlate of oculomotor capture in the superior colliculus. *Journal of Cognitive Neuroscience*, 25(10), 1754–1765. [PubMed: 23691982]
- Zimmermann E (2015). Visual mislocalization during double-step saccades. *Frontiers in systems neuroscience*, 9, 132. [PubMed: 26539085]
- Zimmermann E, Morrone MC, & Burr D (2015). Visual mislocalization during saccade sequences. *Experimental brain research*, 233(2), 577–585. [PubMed: 25370348]

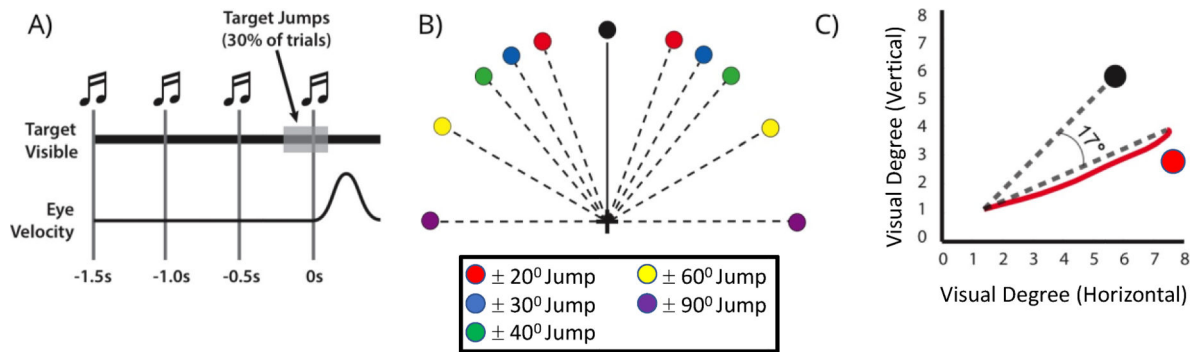


Figure 1. Experimental paradigm and saccade direction estimation

(A): Subjects heard four beeps 500 ms apart and were instructed to initiate their eye movement (saccade) to the target on the fourth beep. The peripheral target appeared with the onset of the first beep. On a minority of trials (30%) the target in the periphery jumped location to the left or right of its initial location at a random time (-150 ms to $+50$ ms) around the onset of the fourth beep. **(B)** Possible jump sizes. Experiment 1 used three small jump sizes (20° , 30° and 40°). Experiment 2 used two large jump sizes (60° and 90°). **(C)** Example saccade trajectory taken from a trial in which the target jumped 20° to the right (red filled circle) of its initial 45° position (black filled circle). The primary saccade in this trial (red trace) was made at an angle of 17° . This angle was determined between the vector connecting the initial fixation location and the initial stimulus location, and the vector between the onset and offset point of the saccade. Relative to the initial target location, saccades directed toward the jumped location were characterized by a positive value; saccades in the opposite direction were characterized by a negative value. The saccade directions were normalized by the target jump size.

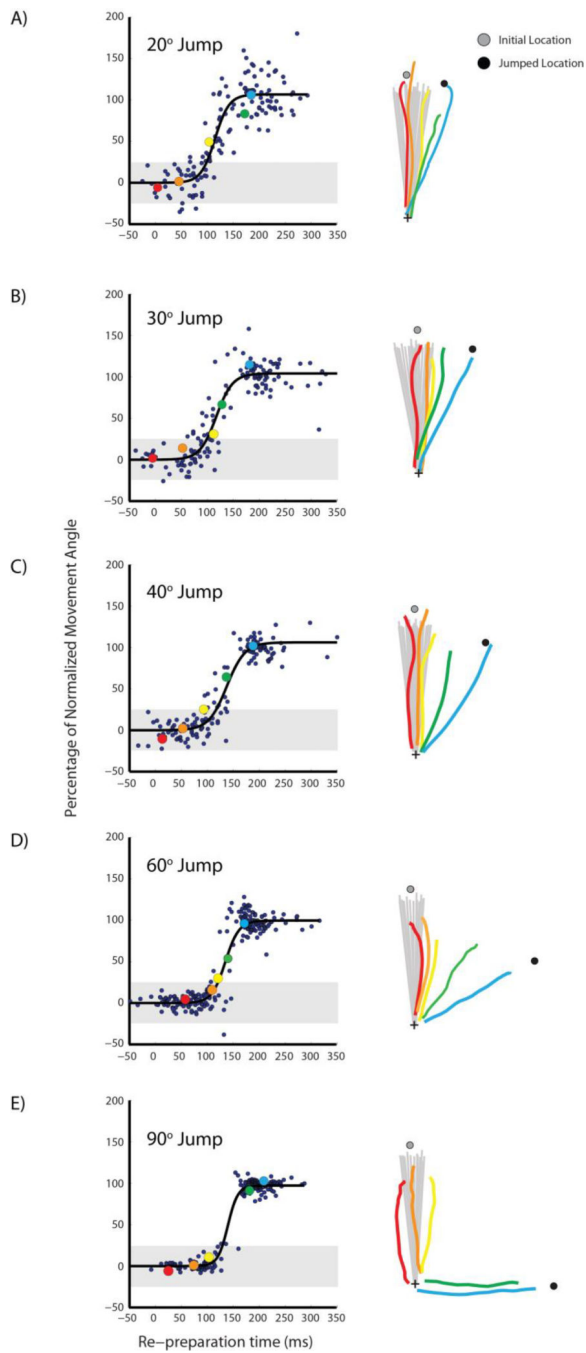


Figure 2. Saccade direction and trajectories for representative subjects in each experiment. In the left column are data from a representative subject of (A-C) Experiment 1 and (D and E) Experiment 2. Each small dark blue filled circle represents the normalized saccade direction on a single trial. The saccade direction was normalized by the jump size (0 and 100 percent represent the initial and jumped target locations respectively). The black trace is the psychometric fit to the normalized saccade direction. The grey shading represents the range of the mean ± 2 SD of the saccade direction on non-jump trials to the initial target location. The right column displays the corresponding saccade trajectories from the representative

subjects on the jump (colored traces) and non-jump (gray traces) trials. The gray filled circle is the initial target location and the black circle is the jumped location. There are selected saccade trajectories that correspond to the colored filled circles in the left column plots. The gray traces on the non-jump trials are a sample of 50 trajectories to the initial target location.

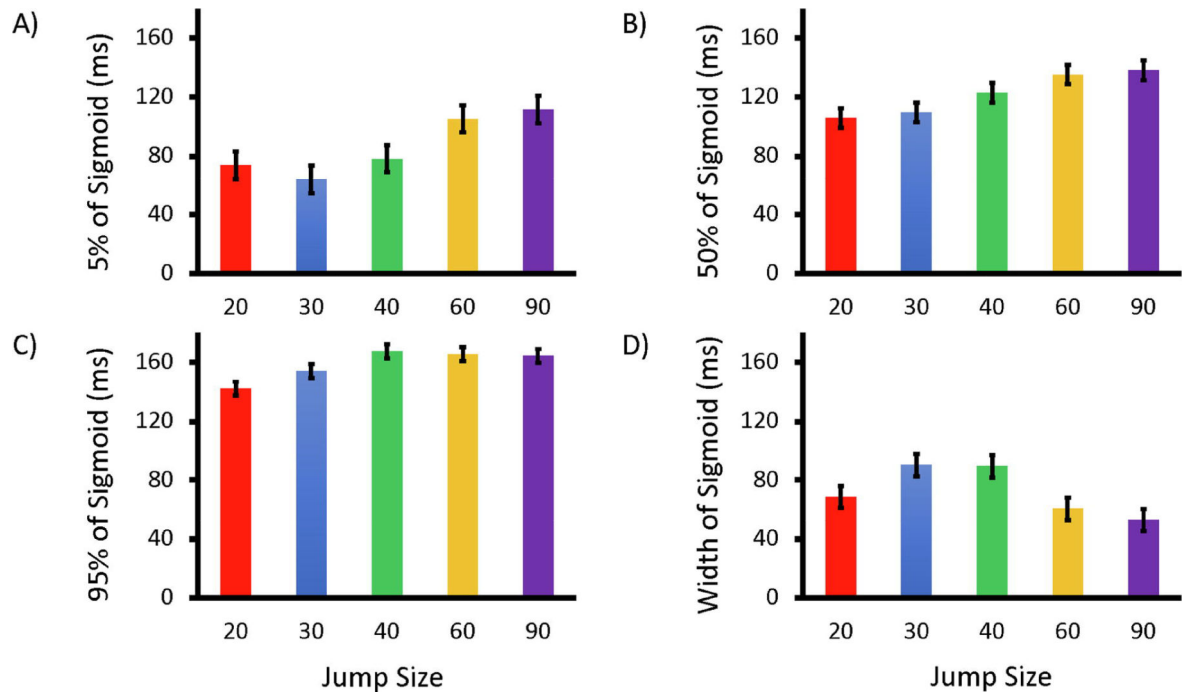


Figure 3. Group results from the fitted psychometric functions.

Each bar graph represents the parameters of psychometric fits across jump sizes: **(A)** Start of the sigmoid rise (t_5). **(B)** Inflection point of the sigmoid (t_{50}). **(C)** End of the sigmoid rise (t_{95}). **(D)** Width (slope) of the sigmoid ($t_{95}-t_5$). The colors represent the different jump angle: 20°, 30°, 40°, 60° and 90° (red, blue green, yellow and purple, respectively). Black vertical lines represent standard error of the mean.

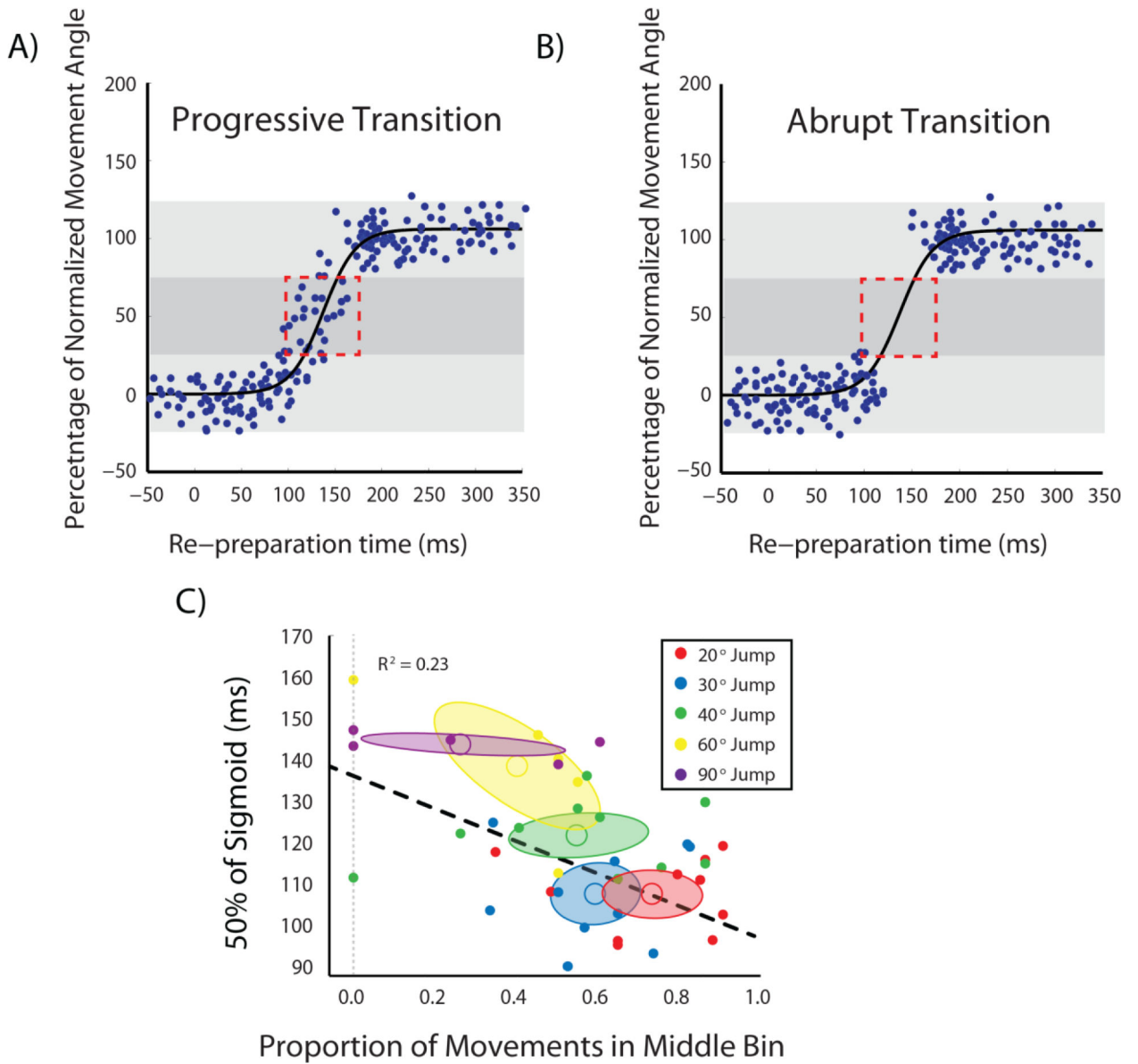


Figure 4. Saccade distribution as a function of inflection point and jump size. Simulated representations of two distinct transition patterns of saccade direction from the initial target location to the jumped location. **(A)** A smooth transition in saccade direction with re-preparation time with many intermediate saccades between the two target locations. **(B)** An abrupt transition in the saccade direction with re-preparation time with very few saccades landing between the two locations. For our analysis we examined the proportion of eye movements that fell within the middle region of interest (ROI: red dashed box). **(C)** The abscissa represents the proportion of observed data found within the ROI for all subjects for each jump size. The ordinate represents the re-preparation time corresponding to the 50% inflection point of the psychometric fits shown in Figures 2 and 3B. The small circles represent individual subject data. The large ellipses represent 2 SEM across subjects for the respective jump size. The large circles within the ellipses represent the mean proportion of

observed data within the ROI and the mean re-preparation time at the 50% inflection point across subjects for each jump size.

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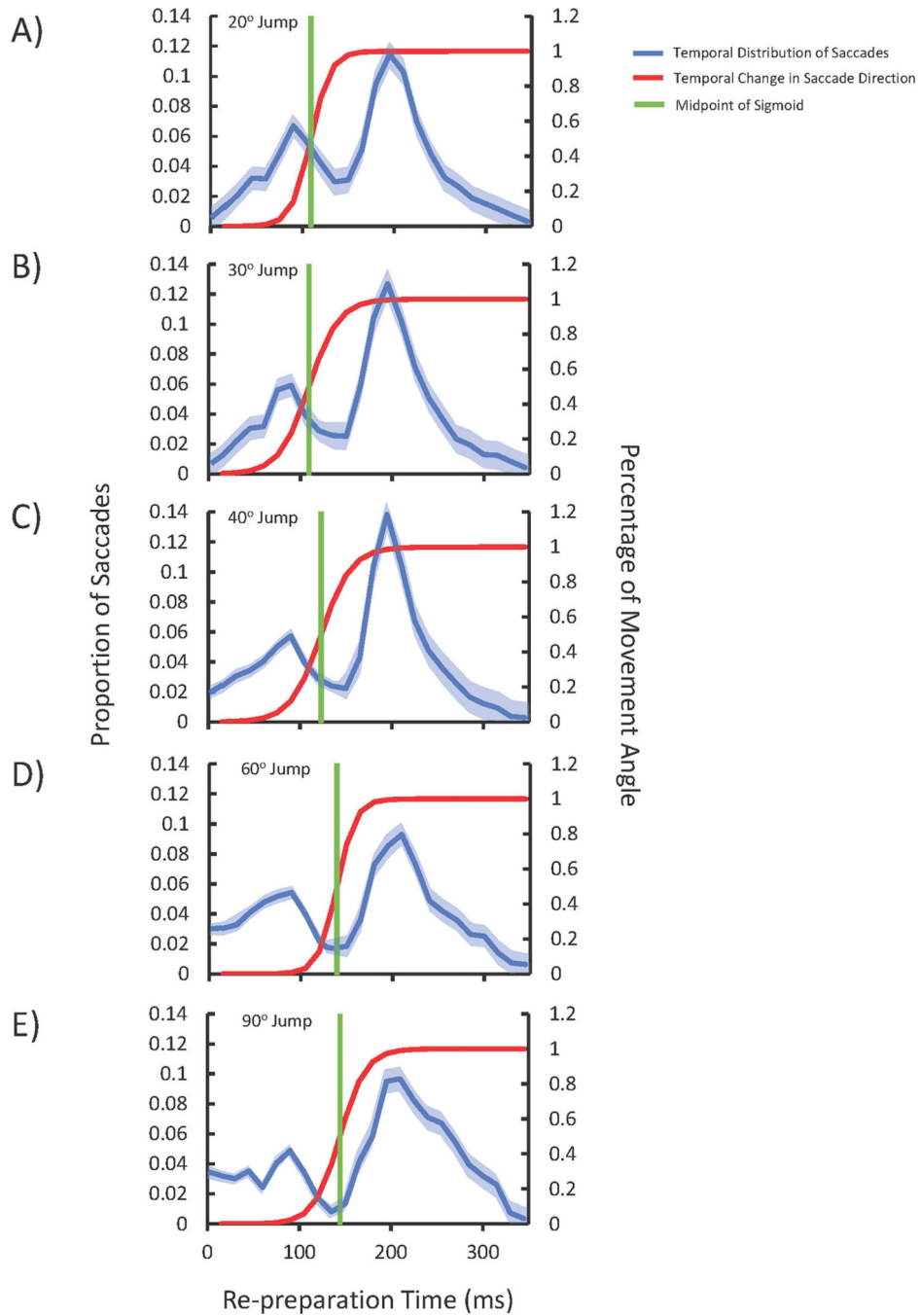


Figure 5. Changes in the saccade spatial distributions with re-preparation time

(A-E): **Abscissa:** The left ordinate represents the proportion of saccades across subjects. The right ordinate represents the normalized saccade direction as in Figure 2. Both of these measures are plotted as a function of the re-preparation time along the abscissa. Each plot displays the results for the respective target jump size. In each plot the blue traces show the distribution of the saccades as a function of the re-preparation time (bin width of 10 ms, SEM is represented by blue shaded area). The red traces display the average psychometric fits based on the average parameter results reported in Figure 3. The green traces represent

the re-preparation time at the average inflection point of the sigmoid fits, again based on Figure 3B.

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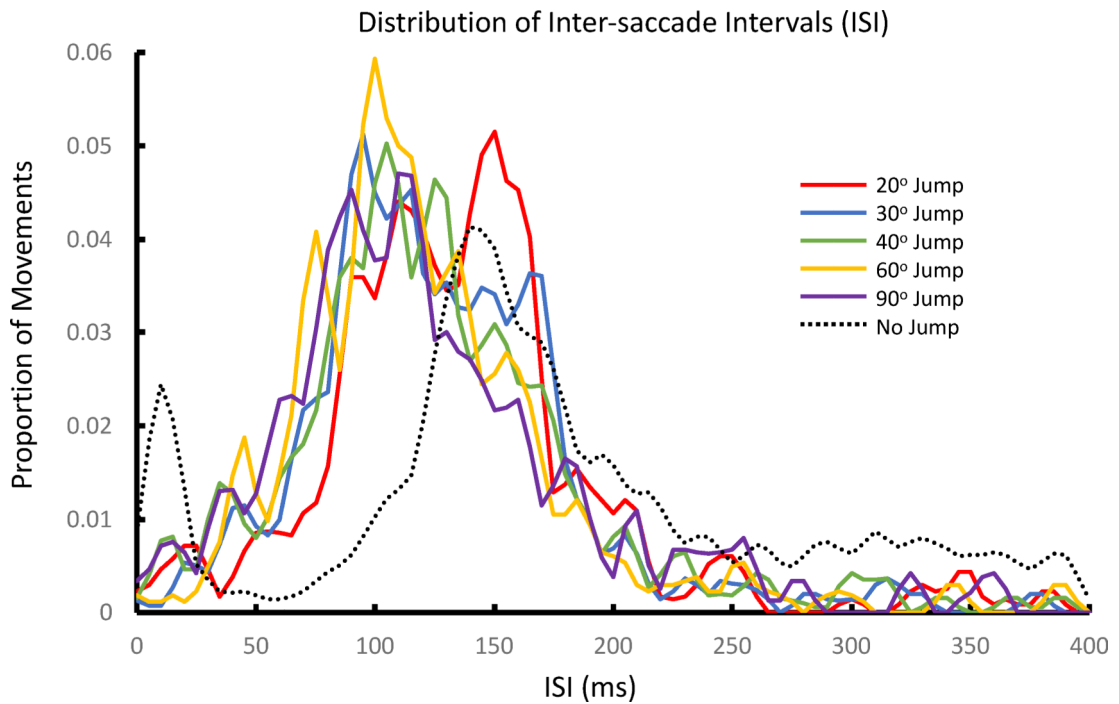


Figure 6. Distribution of Inter-saccade Intervals across all conditions.

The distributions represent the time between the offset of the initial saccade and the onset of any secondary saccade (the inter-saccade interval, ISI) for each target displacement size.

Displayed are the timing values for secondary saccades that occurred after the target had jumped, but only for the temporal range that we observed secondary saccades. Thus, within this defined range, the earliest the secondary saccade could occur was 0 ms re-preparation time. The latest the secondary saccade could occur was set by the 95% point of the sigmoid fit; primary saccades after this time point were consistently directed to the new target location resulting in a decrease in the occurrence of secondary movements.

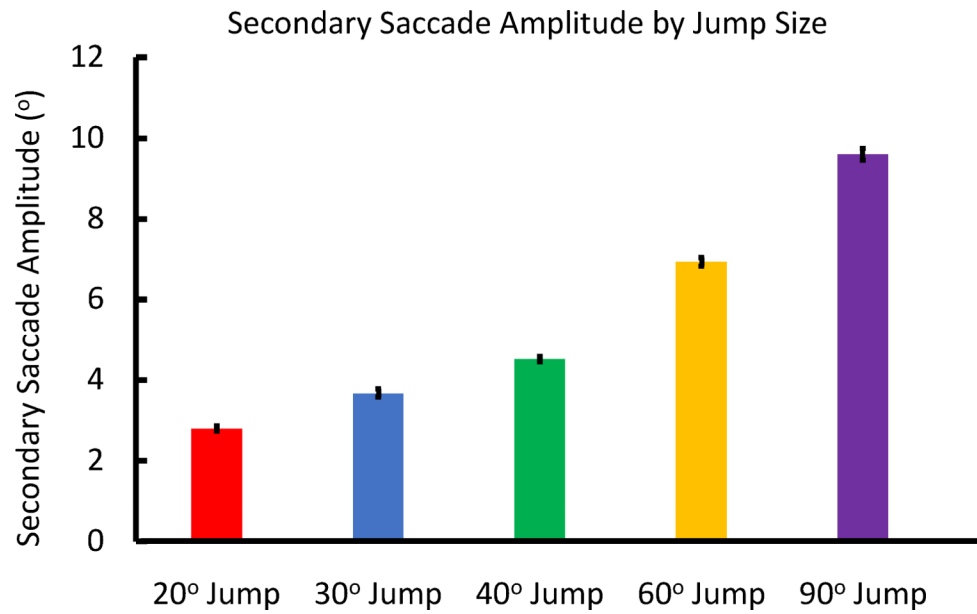


Figure 7. Average amplitude of the secondary saccade across jump sizes. Similar to Figure 6, displayed are the amplitude values for secondary saccades that occurred after the target had jumped, but only for the temporal range that we consistently observed secondary saccades. Thus the temporal range began at 0 ms re-preparation time and ended at the 95% point of the sigmoid fit. Black vertical lines represent the standard error of the mean.

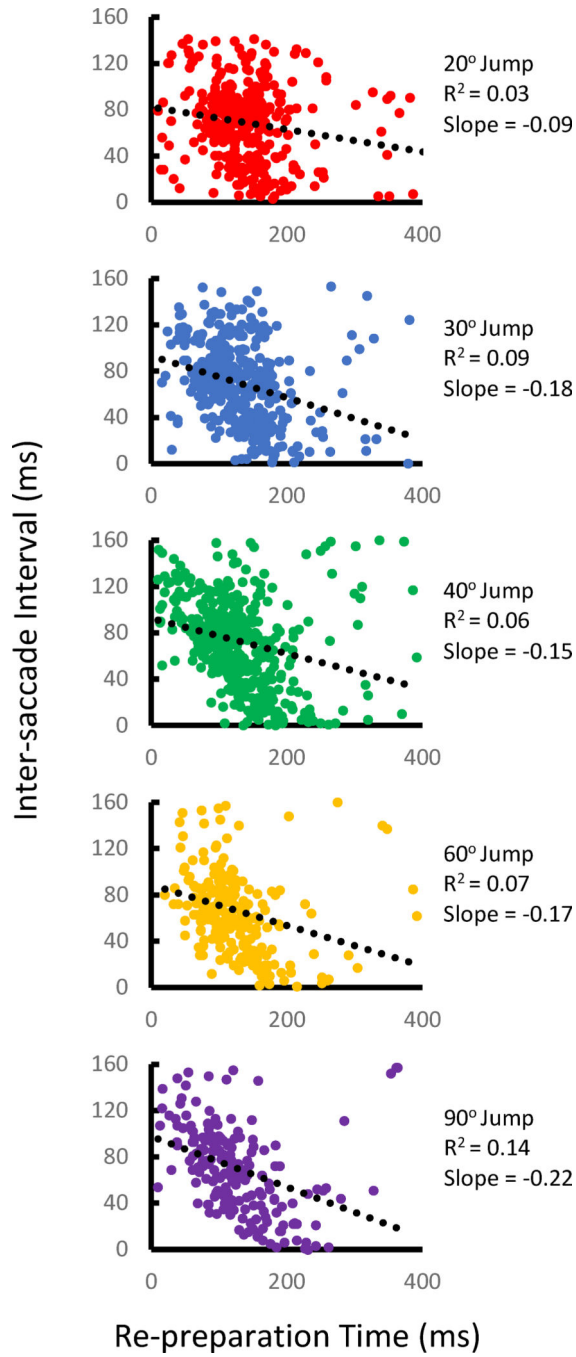


Figure 8: Inter-saccade interval (ISI) as a function of re-preparation time across all jump sizes. The abscissa shows the re-preparation time and the ordinate displays the ISI in for each trial. Dotted black lines are the linear regression line (based on the *fitlm* MATLAB function) and the R^2 and slope values are displayed to the right of each graph.

Table 1.**Secondary Saccade Metrics:**

The average (and SEM) saccade amplitude and inter-saccade interval (ISI) of the secondary saccades are shown. In addition, the percentage of trials in which a secondary saccade was observed is displayed for all jump sizes.

	Amplitude (°)	ISI (ms)	% of trials
20° Jumps	3.04 (± 0.27)	151.18 (± 10.5)	36.4
30° Jumps	3.81 (± 0.30)	158.29 (± 11.0)	39.7
40° Jumps	4.39 (± 0.22)	151.94 (± 8.97)	45.6
60° Jumps	6.14 (± 0.37)	153.21 (± 13.7)	14.7
90° Jumps	7.95 (± 0.59)	148.34 (± 12.5)	16.1