Contextual factors modulate concurrent planning of sequential saccades

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Natural vision typically involves making multiple eye movements to interpret complex visual scenes. Although previous work has shown that individual saccadic end points are modulated by cognitive context, whether and how contextual factors quantitatively influence the planning of sequential saccades is still unclear. We compared performance of subjects in a modified double-step task under different task instructions (FOLLOW vs. REDIRECT; Ray, Schall, & Murthy, 2004) as well as task structure (40% and 100% FOLLOW). The results support the idea of restricted concurrent preparation when the second saccade was part of the sequence as per task demands as opposed to being inadvertently made following an error. Also, increasing the probability of double-target trials in the task (100% vs. 40% FOLLOW) tended to enhance concurrent planning even when the serial order of saccades continued to remain important. Taken together, these data reveal how the concurrent planning of sequential saccades can be contextually regulated by means of task instruction and trial statistics.

Introduction

Vision is an active process requiring multiple saccadic eye movements to foveate points of interest in a scene (Hayhoe & Ballard, 2005; Land & Hayhoe, 2001). Although the pattern of eye movement fixations have been known to vary under different contexts (Land, 2006; Yarbus, 1967), this modulation has been, so far, mainly studied in terms of the spatial aspects of control, i.e., how the salience of the image together with task-specific goals determine *where* the fovea is directed to (Bisley & Goldberg, 2010; Einhauser, Rutishauser, & Koch, 2008; Fecteau & Munoz, 2006; Itti & Koch, 2001; Kayser, Nielsen, & Logothetis, 2006; Rothkopf, Ballard, & Hayhoe, 2007; Tatler, Hayhoe, Land, & Ballard, 2011; Torralba, Oliva, Castelhano, & Henderson, 2006). Much less is known about the contextual factors that modulate *when* the eyes move (Findlay & Walker, 1999; Gould, 1973; Henderson & Smith, 2009; Hooge, Vlaskamp, & Over, 2007; Nuthmann, Smith, Engbert, & Henderson, 2010; Palmer, Huk, & Shadlen, 2005; Remington, Wu, & Pashler, 2011; Trukenbrod & Engbert, 2012; Wu, Kwon, & Kowler, 2010; Yang & McConkie, 2001), especially in the context of sequential saccades. Although saccades in a sequence have been shown to be strategically regulated under varying contexts (Land & Hayhoe, 2001; Ray, Bhutani, & Murthy, 2012; Wu & Kowler, 2013), how different task parameters regulate the latency and preparation of individual saccades in a sequence is still not clear (Averbeck, Chafee, Crowe, & Georgopoulos, 2002; Inhoff, 1986).

Sequential saccades, separated by an interval that is less than the average latency of a single saccade, have often been taken as examples for concurrent planning (Becker & Jürgens, 1979; Hallett & Lightstone, 1976; McPeek, Skavenski, & Nakayama, 2000; Murthy et al., 2007; Ray, Schall, & Murthy, 2004; Sharika, Ramakrishnan, & Murthy, 2008; Sparks & Mays, 1983). Although concurrent processing of saccades in a sequence facilitates rapid scanning of the image, it comes at a cost of accuracy because the second saccade planned in parallel with an upcoming first saccade is likely to be associated with greater motor noise than those prepared via serial planning. Indeed, the planning of sequential saccades has been shown to take into account speed–accuracy trade-offs depending on the nature of the task demands (Munuera, Morel, Duhamel, & Deneve, 2009; Wu & Kowler, 2013). Motivated by these studies, our goal was to examine whether and how concurrently planned first and second saccades in a sequence are regulated by task context. We used a modified version of the classic double-step task (Ray et al., 2004) wherein two targets are presented one after another 40% of the time ("double-target" trials), while the remaining trials involve the presentation of only

Citation: Sharika, K. M., & Murthy, A. (2015). Contextual factors modulate concurrent planning of sequential saccades. *Journal of Vision*, *15*(2):23, 1–18, http://www.journalofvision.org/content/15/2/23, doi:10.1167/15.2.23.

doi: 10.1167/15.2.23 Received March 26, 2014; published February 20, 2015 ISSN 1534-7362

one target ("single-target" trials). Subjects either make a sequence of saccades to the targets in the order of their presentation (40% FOLLOW task) or are asked to look directly at the second target (40% REDIRECT task) in double-target trials. However, because the double-target and single-target trials are randomly interleaved in both task conditions, often subjects are unable to inhibit the first saccade to the first target in the REDIRECT task and follow the error with a corrective saccade to the second target. The sequence of saccades executed this way in the REDIRECT task is the same as that generated as a correct response in the FOLLOW task. However, because saccades in the FOLLOW task are to be executed in a particular serial order by instruction, we tested how the timing of sequential saccades reflected the concurrent planning of the second saccade in this task when compared to the REDIRECT task. We also tested the role of increased predictability about making a sequence of saccades (100% FOLLOW task vs. 40% FOLLOW) in modulating the degree of concurrent planning.

Methods

Subjects and recording setup

Eye movements of 17 subjects (five males and 12 females, average age = 24 years) with normal or corrected-to-normal vision were recorded with the subjects' heads stabilized by means of a chin rest, a temple rest, and a forehead rest while they performed one or more of the three tasks used in the study. A total of 14, 10, and eight subjects performed the 40% REDIRECT, 40% FOLLOW, and 100% FOLLOW tasks, respectively. Seven subjects performed both the 40% REDIRECT and 40% FOLLOW tasks, and eight subjects were common to the 40% and 100% FOLLOW tasks. The data of the 14 subjects who performed the 40% REDIRECT task has been previously described (Sharika et al., 2008). All subjects gave their informed consent in accordance with the institutional human ethics committee of NBRC and the Declaration of Helsinki. Subjects were monetarily compensated for their participation.

Experiments were computer-controlled using TEMPO/VIDEOSYNC software (Reflective Computing, St. Louis, MO), which displayed visual stimuli and sampled and stored eye position with other behavioral parameters. Eye position was recorded with an infrared pupil tracker running at 240 Hz (ISCAN, Boston, MA) that interfaced with TEMPO software (Reflective Computing) in real time. The spatial resolution of the system was ~0.01°, and the median saccadic accuracy, as estimated by the standard deviation of saccadic end points across three successive trials to single targets presented in the task, was ~0.9° (Sharika et al., 2008). All stimuli were presented on a Sony Trinitron 500 GDM monitor (21-in.; 70 Hz refresh rate) placed 50 cm in front of the subject. Stimuli were calibrated with a Minolta CA-96 colorimeter.

Task and stimuli

The three tasks used in this study to examine the effect of task instruction and task statistics in the planning of sequential saccades were modified versions of the classic double-step task (Ray et al., 2004). In the 40% REDIRECT and 40% FOLLOW tasks, 40% of the trials in a session were *double-target* trials, i.e., trials in which two targets were presented. The remaining 60% of trials in both the tasks were *single-target* trials in which only one target was presented. The 100% FOLLOW task, on the other hand, consisted only of double-target trials.

In a single-target trial (Figure 1A), following fixation on a small white square (0.3° × 0.3°) at the center of the screen for a random duration (300 to 800 ms), a green target (0.5° × 0.5°; 0.9 cd/m^2) was presented. The location of targets was randomized such that they could appear in any one of the four positions specified by a radial distance of 21° and polar angles of 45°, 135°, 225°, or 315° from the fixation point (Figure 2A). Double-target trials in each task were further categorized into two subtypes: *no-shift double-target* and *target-shift double-target* trials. Each of the two trial types occurred with equal probability and was randomized with single-target trials such that subjects could not predict or anticipate the appearance of the targets. In no-shift double-target trials (Figure 1B) as well as target-shift double-target trials (Figure 1C), after fixation and presentation of the initial green target at one of the four positions specified for a single-target trial above, a final red target (0.5° × 0.5°; 0.9 cd/m^2) appeared randomly at any one of the remaining three positions (Figure 2B) following a delay of ~20 to 200 ms called the target step delay (TSD). This range of TSDs correspondingly gave rise to a range of reprocessing times (RPTs), i.e., the time between the presentation of the second target and the onset of the first saccade (Figure 1C). In a target-shift double-target trial, the final, red target was also shifted to a new location during the execution of the first saccade (Figure 1C; Sharika et al., 2008) determined online based on the eye moving out of the electronic window around the fixation point. The "shifted" position of the final target (referred to, hereafter, as the new position of the final target) was at a radial distance of 21° and a polar angle of either 0° or 180° from the fixation point, depending on whether the original position of the final

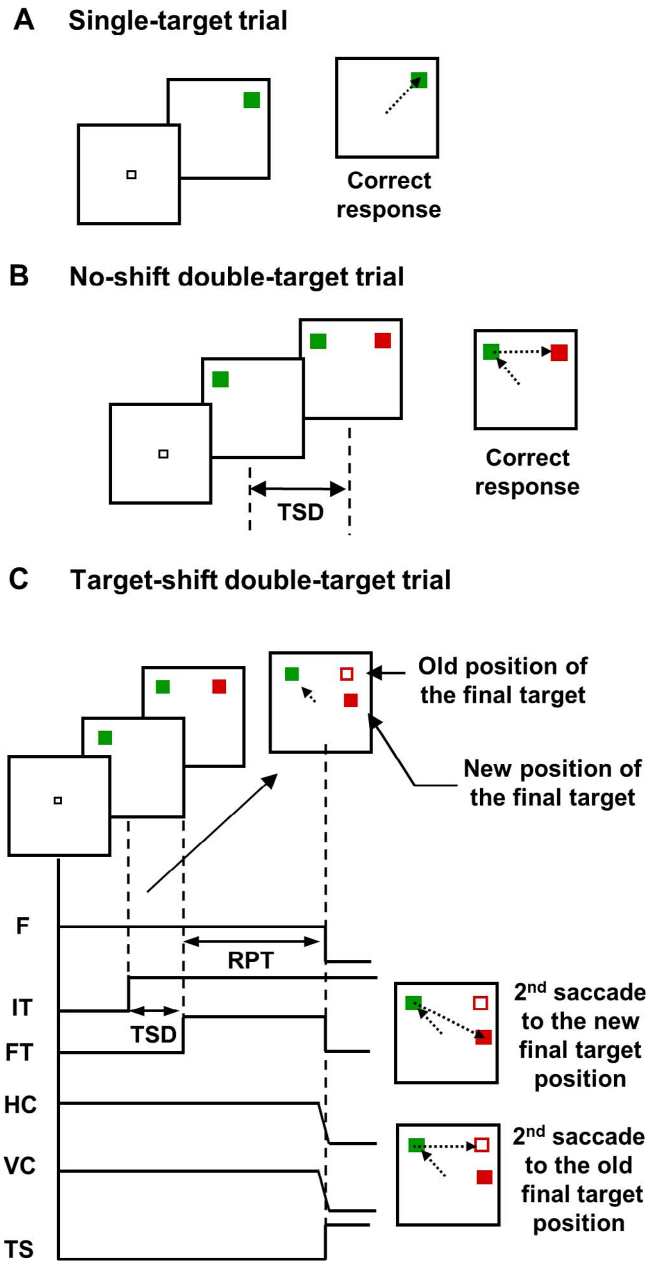

Figure 1. Schematic showing the sequence of events in a single-target trial, a no-shift double-target trial, and a target-shift double-target trial. (A) In a single-target trial, following fixation on a white box at the center of the screen, an initial, green target appears on the screen. Subjects are instructed to make a saccade to it as soon as possible. (B) In a no-shift double-target trial, following fixation and appearance of the green target, a final, red target is presented after a TSD of 20–200 ms. In the 40% and 100% FOLLOW tasks, subjects are instructed to follow the appearance of the targets by a sequence of saccades. However, in the REDIRECT task, subjects are asked to cancel the planned saccade to the initial target and, instead, make a direct saccade to the final target. (C, top) Following fixation, the initial, green and the final, red targets are presented just as in a no-shift double-target trial above. The final target shifts to a new location during the execution of the first saccade. (C, bottom left) Solid vertical line denotes the beginning of the trial. Horizontal lines trace the time of presentation of the fixation box (F), initial target (IT), final target (FT), and the occurrence of horizontal (HC) and vertical (VC) components of the first saccade and the shift of the final target (TS). (C, bottom right) Following the first saccade to the initial target, a second saccade is shown to end at the new (top) or old (bottom) location of the final target. Adapted from Sharika et al. (2008).

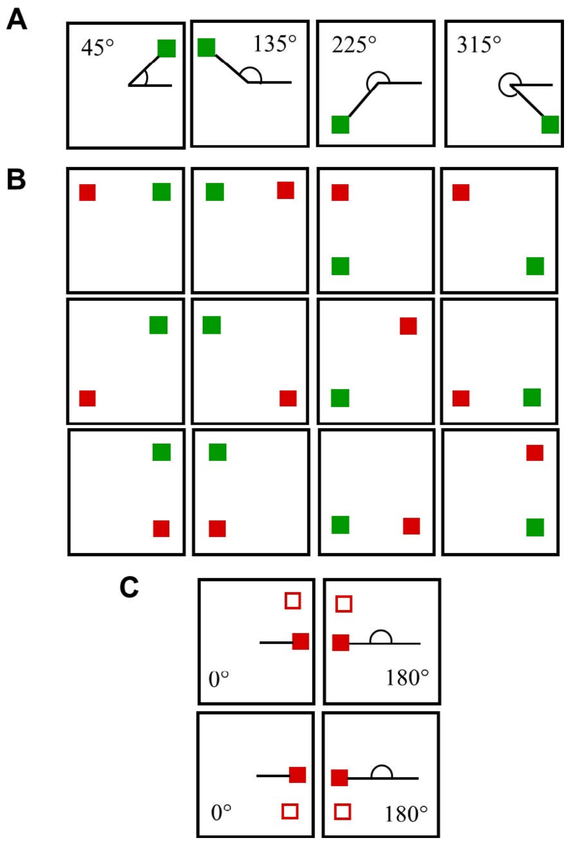

Figure 2. Probable target locations. (A) Probable locations of the green target in single-target and double-target trials at polar angles 45°, 135°, 225°, and 315° from the fixation spot. (B) Probable locations of the red target in double-target trials following the green target presentation at locations shown in A. (C) Probable locations of the red target in a target-shift double-target trial after the shift (filled red square) at a polar angle of 0° or 180° from the fixation point, depending on whether the original position of the final target (empty red square) was on the right or left hemifield, respectively.

target (referred to, hereafter, as the old position of the final target) was on the right or left hemifield, respectively (Figure 2C). In other words, for old positions of the final target specified by polar angles 45° and 315°, the new position was always at a polar angle of 0°, and for old positions of the final target specified by polar angles 135° and 225°, the new position was always at a polar angle of 180°. In all cases, the final target shift amounted to a vertical displacement of 14.5° from its old position. Only those trials in which the target shifted strictly during the execution of the first saccade, i.e., after it began but before it ended, were used for all analysis. The target shifted, on average, 45 ms after the first saccade began (grand average of saccade duration across subjects, 40% REDIRECT = 55 ms, 40% FOLLOW = 64 ms, 100% FOLLOW = 61 ms) but well before it terminated. The luminosity of the target was kept low to minimize any aftershift flash effects. Subjects were given both verbal and written instructions with some practice trials (~50) before data was collected.

In all three tasks, subjects were instructed to make a quick saccade to the initial target as soon as it was presented. In fact, in case subjects took more than 400 ms to make a saccade in single-target trials, they were encouraged to respond quickly by the experimenter via verbal feedback. In both the FOLLOW tasks, the appearance of the final, red target indicated that subjects should look at it following a saccade to the initial, green target, and in the REDIRECT task, the red target was a signal to *cancel* the planned saccade to the green target and, instead, look directly at the red target. Subjects were often unable to inhibit the planned saccade to the green target in the REDIRECT task and frequently followed this with a corrective saccade to the red target. Hence, the sequence of saccades made in both the tasks, although behaviorally similar, was generated under different contexts (Ray et al., 2004), i.e., although the second saccade in the FOLLOW tasks was part of the correct response, the one generated in the REDIRECT task was a correction following an error.

On average, each session lasted for ~45 min in which a subject performed ~550 trials with a 5- to 10-min break in between two halves of the session. Each session was checked for a performance criterion, mentioned in Results, before being combined for further analysis. The total number of sessions depended on the performance of each subject so as to obtain a sufficient number of trials to perform the analyses, although a minimum of at least two sessions (~1,000 trials) per subject was ensured for analysis in any case. The absolute number of trials in which the first saccade reached the green target and the second saccade landed at the red target was not monitored for inclusion; a session was included as long as the performance curve of that session passed the criteria. Trials were scored as successful and conveyed to subjects by auditory feedback, if they fixated the respective targets within an electronic window of ±6.5° centered on the target. A single-target trial was deemed correct in both 40% FOLLOW and 40% REDIRECT tasks if the first saccade was made to the green target. However, the correct response in a double-target trial differed for the two tasks. In the REDIRECT task, the first saccade had to be made to the red target in a no-shift double-target trial and to the new position of the red target in a target-shift double-target trial for the trial to be scored as correct. On the other hand, in the FOLLOW task, following a first saccade to the green target, the second saccade had to be made to the red target in a no-shift double-target trial and to the new position of the red target in a target-shift double-target trial for the trial to be deemed successful. For off-line evaluation of subjects' performance in the REDIRECT task (see Results), trials in which the first saccades went to the old location of the red target were included as well. The second saccades to the old versus new position of the final target were classified off-line based on whether they ended within a spatial window of ±4° from the center of the respective target location. Second saccades that were directed to the remaining 6.5° × 6.5° space between the windows of the old and new final target locations were classified as midway saccades (Sharika et al., 2008).

Off-line analyses, including all statistical tests, were done using MATLAB (Mathworks). Normality of data in each condition was checked using the Lilliefors test before nonparametric tests were applied. Analogue eye position data was smoothened and blinks removed. A velocity threshold of 30°/s was used to demarcate the beginning and end of saccades. All blink-perturbed saccades were eliminated from the analysis.

Results

Task performance

A critical variable in all three tasks was the time between the appearance of the initial and the final target, called TSD, which varied across trials and was used to assess performance. Performance was analyzed by plotting the probability of making the first saccade to the green versus the red target in double-target trials as a function of increasing TSDs. Figure 3A shows the performance curve of a representative subject, GA, in all three tasks, quantified by fitting the best-fit cumulative Weibull function:

$$\mathrm{W}(t) = \gamma - (\gamma - \delta) \cdot e^{(-(t/\alpha)\beta)}$$

where t is the TSD, α is the time at which the function reaches 64% of its full growth, β is the slope, γ is the maximum value of the function, and δ is the minimum value of the function. As expected, the inability to cancel the first saccade to the green target and, thus, the probability of making an error in the REDIRECT task increased with TSD. Because the term $(\gamma - \delta)$ describes this increase in the probability of making an error as a

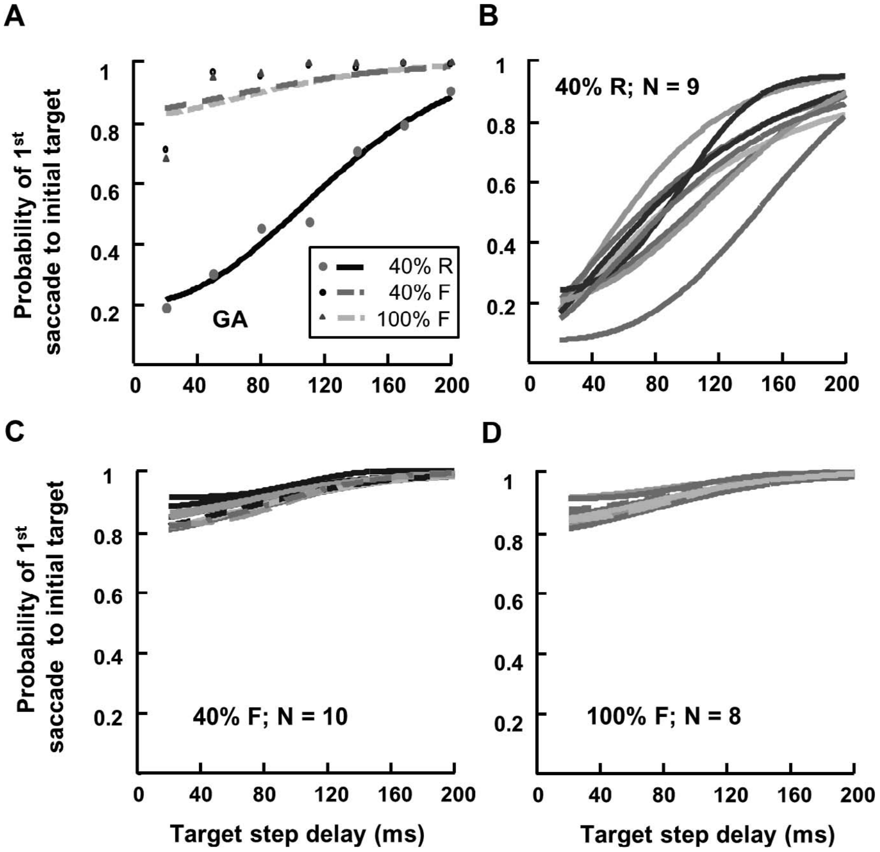

Figure 3. Examination of performance in double-target trials. (A) The probability of making a first saccade to the initial target is plotted as a function of TSD for a representative subject, GA, in all three tasks. Although the saccade to the initial target is an error in the 40% REDIRECT task (40% R), it is part of the correct response in the 40% FOLLOW (40% F) and 100% FOLLOW (100% F) tasks. (B, C, and D) Performance curve for all subjects whose data was included for analysis of concurrent planning following performance check in the 40% REDIRECT, 40% FOLLOW, and 100% FOLLOW tasks, respectively.

function of TSD, it was used to quantify the degree of cancellation and, hence, the level of task performance among subjects in the REDIRECT task. Only those individual sessions of each subject in which the degree of cancellation changed considerably with increasing TSD and had a $(\gamma - \delta)$ value of ≥ 0.5 were pooled for the final analysis of performance. Because the probability of making an error is the lowest at the smallest TSD, for the pooled data, an additional criterion of $\delta < 0.3$ was also applied to include only those subjects who inhibited their saccades efficiently (Sharika et al., 2008). Consequently, nine out of the 14 subjects who had performed sufficiently well (Figure 3B; $n = 9$; mean $[\gamma - \delta] = 0.71 \pm 0.01$; as first described in Sharika et al., 2008) were included for comparison with the 40% FOLLOW task.

Performance was similarly examined for the FOLLOW tasks. Only those individual sessions in which subjects performed sufficiently well ($\delta \geq 0.8$) were included for further analysis. As expected, the probability of making the first saccade to the green target (part of a correct response in this case) did not change much with increasing TSDs for both 40% FOLLOW (Figure 3C; $n = 10$; mean $[\gamma - \delta] = 0.15 \pm 0.01$) and 100% FOLLOW (Figure 3D; $n = 8$; mean $[\gamma - \delta] = 0.13 \pm 0.01$) tasks, suggesting that subjects performed a sequence of saccades in the FOLLOW tasks as per the given instructions. Table 1 shows the total number of sessions recorded for each task condition as well as those pooled together for checking overall performance.

Table 2 lists the number of subjects whose pooled data passed the performance criteria. In all analyses, trials in which the first saccade occurred before the presentation of the second target were eliminated, and only trials with RPTs of $\leq$200 ms were examined because the degree of parallel processing has been shown to reach a plateau at longer RPTs (Becker & Jürgens, 1979; Ray et al., 2004). Table 2 also presents the average first saccade latencies of no-shift double-target trials for subjects in each task condition. We found first saccade latencies (RT1) to be significantly longer in the 40% REDIRECT task compared to the FOLLOW tasks (mean RT1, 40% REDIRECT task: $n = 9$, 221 ± 4.8 ms; 40% FOLLOW task: $n = 10$, 190 ± 3.5 ms; 100% FOLLOW task: $n = 8$, 194 ± 2.3 ms; one-tailed independent samples t test for RT1 (40%

S. no.	Subject	Total sessions recorded	No. of sessions included in the pooled data	No. of total trials in the pooled data	No. of two-saccade trials in the pooled data
40% REDIRECT					
1	GA	10	6	2,874	265
2	JA	6	5	2,705	365
3	RA	6	6	3,270	375
4	TA	7	6	3,228	439
5	JG	6	6	3,145	394
6	MK	12	11	6,207	806
7	KM	5	5	2,655	202
8	MS	7	6	3,327	469
9	UA	4	4	2,083	367
10	CD	6	5	2,907	501
11	VK	4	4	2,149	401
12	SP	5	5	2,888	183
13	NS	9	8	4,524	731
14	DT	10	4	2,201	157
40% FOLLOW					
1	GA	6	3	1,560	248
2	TA	4	4	2,091	461
3	CD	4	3	1,546	419
4	JG	4	4	2,014	311
5	SG	4	4	2,041	397
6	MK	4	3	1,613	334
7	RA	4	2	1,022	213
8	BN	4	3	1,520	381
9	RR	5	3	1,536	284
10	MS	4	3	1,588	389
100% FOLLOW					
1	GA	6	3	1,524	868
2	RA	4	4	2,305	660
3	TA	4	3	1,604	779
4	JG	4	3	1,512	637
5	SG	3	3	1,720	780
6	MK	4	3	1,598	797
7	RR	2	2	1,030	557
8	MS	6	3	1,583	957

Table 1. Total number of sessions recorded for each subject in each task condition and the number of sessions that were pooled to check for performance criteria. *Notes*: Also shown are the total number of trials and the trials in which the first saccade reached the green target and the second saccade reached the old or new location of the red target.

REDIRECT > 40% FOLLOW): $p < 0.0001$; RT1 (40% REDIRECT > 100% FOLLOW): $p < 0.0001$ when corrected for multiple comparisons; alpha for Bonferroni correction = 0.016).

Effect of task instruction on the planning of sequential saccades

According to the logic of parallel, independent planning of saccades, concurrent motor preparation of the second saccade is dependent on the time available between the appearance of the second target and the beginning of the first saccade, called the RPT (Becker & Jürgens, 1979; McPeek et al., 2000; Ray et al., 2004; Sharika et al., 2008). Consequently, longer RPTs are expected to allow greater concurrent planning and, thus, result in shorter intersaccadic intervals (ISIs; Ray et al., 2004; Sharika et al., 2008). This effect was confirmed by analyzing the no-shift double-target trials in both 40% REDIRECT and 40% FOLLOW tasks. Trials with ISIs > 400 ms were not included in this

S. no.	Subjects	RT1 of no-shift double-target trials
40% REDIRECT		
1	GA	220.42
2	JA	202.59
3	RA	217.79
4	TA	216.58
5	JG	222.8
6	MK	211.14
7	KM	247.65
8	MS	240.77
9	UA	212.19
40% FOLLOW		
1	GA	196.25
2	TA	196.45
3	CD	207.05
4	JG	184.72
5	SG	181.18
6	MK	179.03
7	RA	183.38
8	BN	175.21
9	RR	203.57
10	MS	196.23
100% FOLLOW		
1	GA	185.46
2	RA	189.63
3	TA	197.02
4	JG	205.69
5	SG	198.44
6	MK	187.78
7	RR	192.65
8	MS	191.66

Table 2. The average first saccade latencies of no-shift double-target trials in each of the tasks for all subjects whose pooled data passed the performance criteria.

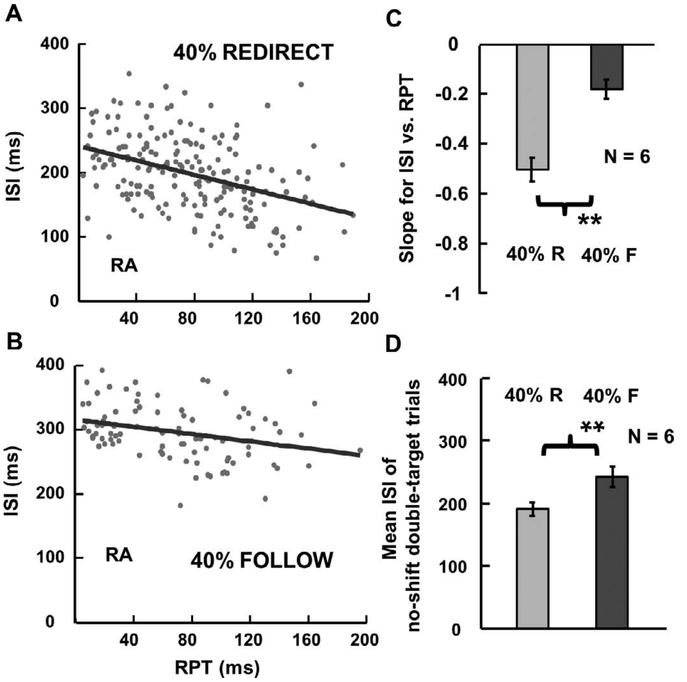

Figure 4. Effect of task instruction on the ISI. Plot between ISI and the RPT for a representative subject, RA, in the 40% REDIRECT task (A) and the 40% FOLLOW task (B). Bar graphs plot the slope of the linear fits between ISI and RPT (C) and the mean ISI of no-shift double-target trials (D) for subjects who performed both the tasks. **Difference significant with $p <$ 0.01. Error bars indicate mean ± *SEM*.

analysis because saccades following such high ISIs were unlikely to have been processed in parallel. Figure 4A and B, respectively, show the change in ISI as a function of reprocessing time for a representative subject, RA, in the 40% REDIRECT and 40% FOLLOW tasks quantified by a linear fit. Consistent with earlier studies (Ray et al., 2004; Sharika et al., 2008), longer RPTs were indeed found to be associated with shorter ISIs (40% REDIRECT: $n = 9$, slope mean $= -0.55$, min. $= -0.92$, max. $= -0.29$, one-tailed, one sample t test [slope < 0]: $p = 0.2 \times 10^{-5}$, individual slopes were significantly different from zero for all nine subjects, R^2 mean $= 0.15$, min. $= 0.04$, max. $= 0.42$; 40% FOLLOW: $n = 10$, slope mean $= -0.16$, min. $= -0.28$, max. $= -0.01$, one-tailed, one sample t test [slope < 0]: $p = 0.3 \times 10^{-3}$, individual slopes were significantly different from zero for seven out of 10 subjects, R^2 mean $= 0.05$, min. $= 0.0001$, max. $= 0.14$). On comparing the relationship between ISI and RPT of six subjects who performed both tasks, the magnitude of the slope was found to be significantly reduced in the 40% FOLLOW task (Figure 4C; $n = 6$, mean [slope] ± *SEM*: 40% REDIRECT $= -0.5 \pm 0.05$, 40% FOLLOW $= -0.2 \pm 0.04$, one-tailed, paired sample t test, slope [40% REDIRECT < 40% FOLLOW]: $p = 0.001$). Although with five out of these six subjects, the slopes were still significantly negative in the 40% FOLLOW condition, with the remaining one subject, the slope was not significantly different from zero, indicating the range of effects the change in task context had on the inverse relationship between ISI and RPT in these six subjects. A comparison of slopes using data from all nine subjects in the 40% REDIRECT task and all 10 subjects in the 40% FOLLOW task was also consistent with this result (mean [slope] ± *SEM*: 40% REDIRECT $= -0.55 \pm 0.07$, 40% FOLLOW $= -0.16 \pm 0.03$, one-tailed, two independent sample t test, slope [40% REDIRECT < 40% FOLLOW]: $p = 1.9 \times 10^{-5}$). Also, the mean ISI for all trials with RPTs ≤ 200 ms was significantly shorter in the 40% REDIRECT task when compared with the 40% FOLLOW task (Figure 4D; $n = 6$, mean ISI [40% REDIRECT] $= 190 \pm 10.3$ ms; mean

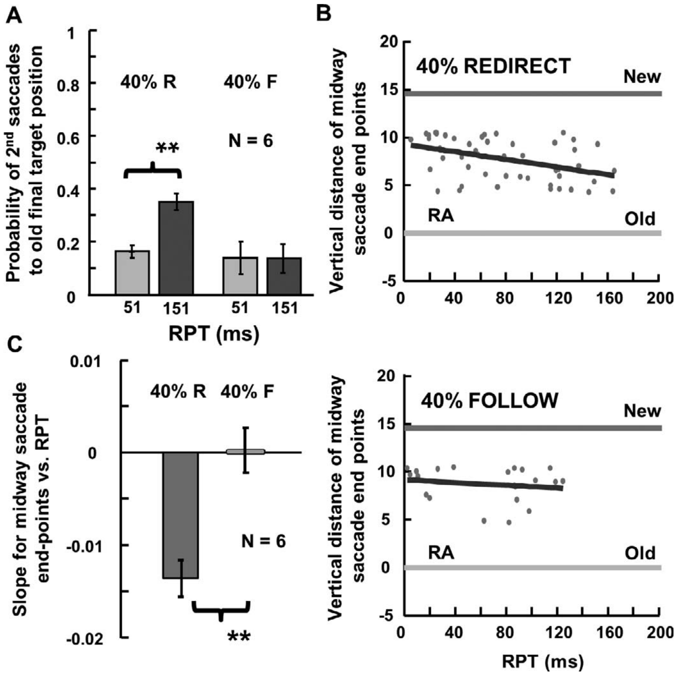

Figure 5. Effect of task instruction on the concurrent motor preparation of the second saccade. (A) Plot between the probability of second saccades to the old location of the final target as a function of RPT for all subjects who performed both the 40% REDIRECT and the 40% FOLLOW tasks. **Difference significant with $p < 0.01$. Error bars indicate mean ± *SEM*. (B) Light and dark gray horizontal lines denote the old and new location of the final target, respectively. Vertical distance of midway saccade end points is plotted against RPT for a representative subject, RA, in the 40% REDIRECT (top) and the 40% FOLLOW (bottom) tasks. (C) Bar graphs plot the slope of the linear fits between the vertical distance of midway saccade end points and RPT for all subjects who performed both the 40% REDIRECT and the 40% FOLLOW tasks. **Difference significant with $p < 0.01$. Error bars indicate mean ± *SEM*.

ISI [40% FOLLOW] = 242 ± 16.9 ms; one-tailed, paired sample *t* test, ISI [40% REDIRECT < 40% FOLLOW]: $p = 0.003$; $n = 9$, mean ISI [40% REDIRECT] = 189 ± 7.2 ms; $n = 10$, mean ISI [40% FOLLOW] = 248 ± 17.5 ms; one-tailed, two independent sample *t* test, ISI [40% REDIRECT < 40% FOLLOW]: $p = 0.004$), consistent with the idea of greater parallel planning in the 40% REDIRECT task versus the 40% FOLLOW task (Ray et al., 2004).

However, because saccade planning involves both visual processing of the target and preparation of the motor command (Thompson, Hanes, Bichot, & Schall, 1996), we examined the extent of concurrent planning affected by task instruction. We used target-shift double-target trials to assess this because concurrent motor preparation of the second saccade has been previously shown to result in second saccades directed to the old location of the final target (Sharika et al., 2008). Because concurrent planning is expected to increase with longer reprocessing times, the tendency to execute second saccades to the old position of the final target was examined as a function of reprocessing time (RPT) in the two tasks. Trials were divided based on their RPTs into two bins of 100 ms each (with RPTs ranging from 1 to 100 ms and 101 to 200 ms, respectively). The frequency of second saccades to the old versus the new location of the final target was then estimated for trials in each bin. The data from all six subjects who performed both the 40% REDIRECT and 40% FOLLOW tasks was also used to perform a two-way repeated-measures ANOVA with RPT and Task Condition as the two factors. Although RPT had a significant effect on the frequency of second saccades to the old final target location, $F(1, 5) = 15.12$, $p = 0.01$, there was a significant interaction between RPT and Task Condition as well, $F(1, 5) = 23.64$; $p = 0.005$. Although the probability of second saccades to the old final target location significantly increased at high RPTs (mean ± *SEM*: 0.35 ± 0.03) compared to low RPTs (0.16 ± 0.02) in the 40% REDIRECT task (Figure 5A; two-tailed, paired sample *t* test, probability of old [high RPT, low RPT]: $n = 6$; $p = 0.006$), it was not statistically different between the two RPT bins in the 40% FOLLOW task (0.14 ± 0.06 for both RPT groups; two-tailed, paired sample *t* test, probability of old [high RPT, low RPT]: $n = 6$; $p = 0.89$). These results are consistent with the idea of concurrent motor preparation of the second saccade not proceeding as effectively as possible in the time available for parallel planning in the 40% FOLLOW task as compared with the 40% REDIRECT task. We also compared the average frequency of second saccades to the old location of the second target using data from all nine subjects in the 40% REDIRECT task and all 10 subjects in the 40% FOLLOW task and found consistent results (mean [% old] ± *SEM*: 40% REDIRECT = 32.6 ± 5%, 40% FOLLOW = 13.6 ± 5%, two-tailed, Wilcoxon rank sum test, old % [40% REDIRECT, 40% FOLLOW]: $p = 0.03$).

As a further verification of the above result, we examined the end points of second saccades in target-shift trials as a function of RPTs. This function has been previously shown to indicate the extent of concurrent motor preparation such that the greater the degree of concurrent planning, the closer the second saccade end points are expected to be to the old location of the final target (Sharika et al., 2013; Sharika et al., 2008). The vertical distances of midway saccade end points from the corresponding old final target locations were plotted as a function of their RPT. The spread of these vertical distances quantified by a linear fit represented the gradual shift of the midway saccade end points from the new to the old position of the final target with increasing reprocessing time. Figure 5B, top and bottom, shows such a plot for a representative subject, RA, in the 40% REDIRECT (slope = –0.02, $R^2 = 0.2$, $n = 49$, one-tailed, one sample t test [slope < 0]: $p = 0$) and 40% FOLLOW (slope $= -0.007$, $R^2 = 0.03$, $n = 21$, one-tailed, one sample t test [slope < 0]: $p = 0.47$) tasks. The individual slopes were significantly less than zero for six out of nine subjects in the 40% REDIRECT task but for none in the 40% FOLLOW task, indicating how a change in task context affected the preparation of second saccades. For all six subjects who performed both tasks, slope of the fits were significantly different from zero in the 40% REDIRECT task ($n = 6$, slope mean $= -0.01 \pm 0.002$, min. $= -0.02$, max. $= -0.006$, R^2 mean $= 0.09$, R^2 min. $= 0.02$, R^2 max. $= 0.2$, one-tailed, one sample t test [slope $<$ 0]: $p = 0.0005$), but it was not the case for any of them in the 40% FOLLOW task (slope mean $= 0.0002 \pm 0.002$, min. $= -0.007$, max. $= 0.008$, R^2 mean $= 0.01$, R^2 min. $= 0.0001$, R^2 max. $= 0.03$, one-tailed, one sample t test [slope < 0]: $n = 6$; $p = 0.53$), and the overall difference in slope was significant between the two groups (Figure 5C; $n = 6$, two-tailed, paired sample t test, slope [40% REDIRECT, 40% FOLLOW]: $p = 0.003$; $n = 9$, mean slope [40% REDIRECT] $= -0.01 \pm 0.002$; $n = 10$, mean slope [40% FOLLOW] $= -0.0002 \pm 0.002$; two-tailed, two independent sample t test, slope [40% REDIRECT, 40% FOLLOW]: $p = 1.5 \times 10^{-4}$). Thus, taken together, the data indicate that task instruction has a significant effect on the extent of concurrent planning of sequential saccades, namely, concurrent motor preparation of the second saccade was compromised in the 40% FOLLOW task compared to the 40% REDIRECT task.

Effect of task instruction on the time course of concurrent planning

We have previously used a linear rise to threshold model (LATER: Linear Approach to Threshold with Ergodic Rate; Carpenter & Williams, 1995; Hanes & Carpenter, 1999; Hanes & Schall, 1996; Reddi, Asrress, & Carpenter, 2003) to examine and estimate the time at which the concurrent planning of the second saccade begins in the REDIRECT task (Sharika et al., 2008; Sharika, Ray, & Murthy, 2009). Here, we used the same model to estimate and contrast the time course of concurrent planning across the two task contexts: the 40% FOLLOW and the 40% REDIRECT tasks. The LATER model proposes the latency of a given saccade to be a result of the time taken by a decision variable to linearly accumulate information until it reaches a criterion level of activation at which time the saccade is executed. We assumed the rate of the decision variable accumulating information for second saccades in the target-shift trial ($GO2_{Old}$) to vary with the same distribution as the rate of a decision variable responsible for generating a single saccade in the single-target trial (GO1) and both to, thus, give rise to the same latency profiles (Figure 6A). Based on this assumption, we predicted the reaction time of second saccades to the old location of the final target if the concurrent planning of the second saccade were to begin as soon as the final target was presented (Figure 6Ba, vertically striped latency distribution). However, in all cases, the predicted reaction times of the second saccades to the old final target position failed to match the longer reaction times observed for each subject (Figure 6Ab, light gray latency distribution). Because the LATER model assumes the rate of accumulation to be invariant during the latency of one trial (and instead vary in a Gaussian fashion across trials), the observed longer reaction times of second saccades to the old final target location was hypothesized to be a result of a delay in the onset of the $GO2_{Old}$ process from the time of final target presentation. By shifting the onset of the $GO2_{Old}$ process iteratively, the minimum delay (denoted by d in Figure 6Cb) required to match the predicted and observed predicted reaction times was calculated. The reaction times of second saccades to the new location of the final target (Figure 6Ba, horizontally striped latency distribution) were predicted to result from saccade planning that begins at the end of the first saccade ($GO2_{New}$). Hence, an overlap of the $GO2_{Old}$ and $GO2_{New}$ distributions (grid region in Figure 6Ca) was assumed to correspond to second saccades landing midway between the old and new positions of the final target and excluded from estimating the predicted reaction times of second saccades to the old final target position during the iteration. Trials were separated on the basis of their RPTs, which were divided into bins of 40 ms each. Only bins with at least three trials were selected. By subtracting the onset delay from the mean RPT of trials in the corresponding bin, the onset of second saccade preparation was obtained relative to the start of the first saccade (denoted by o in Figure 6Cb). Data from all nine subjects in the 40% REDIRECT task (Figure 6D, left) and from all 10 subjects in the 40% FOLLOW task (Figure 6D, right) was then pooled separately to plot the frequency histogram of the onset of second saccade preparation with respect to the start of the first saccade in each condition. Figure 6D (left) is similar to figure 8 in Sharika et al. (2008), which was generated following a more stringent criteria for end point–based saccadic classification. Not only were the two distributions significantly different (two sample Kolmogorov-Smirnov test: $p < 0.0001$, KS test statistic $= 0.8$), the average onset of second saccade planning was found to occur significantly earlier with respect to the beginning of the first saccade in case of the 40% REDIRECT task (-5 ± 7.7 ms) compared to the 40% FOLLOW task (56 ± 2.8 ms; one-tailed, two sample t test [REDIRECT $<$ FOLLOW]: $p < 0.0001$), consistent with the idea of concurrent preparation of the second saccade proceeding to a greater extent in the 40% REDIRECT task compared to the 40% FOLLOW task.

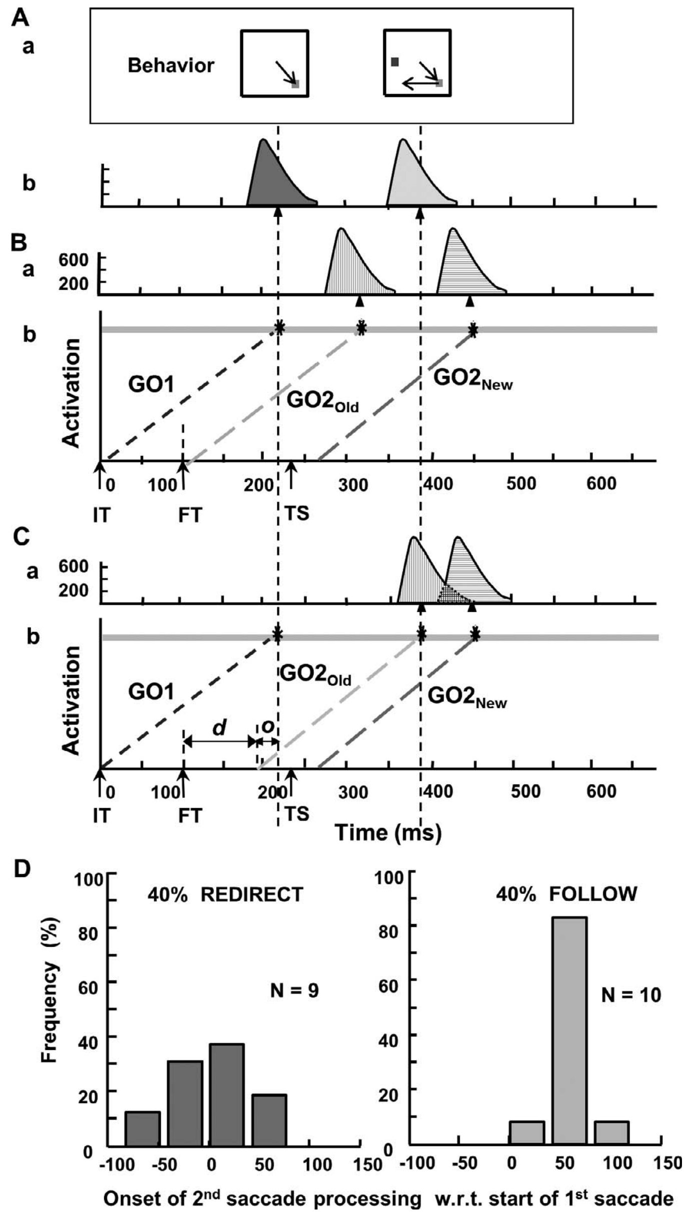

Figure 6. LATER model-based estimation of when concurrent planning starts. (A) Schematic of a saccade in a single-target trial and the second saccade to the old target location in a target-shift double-target trial (a), aligned to their average reaction time (b, broken vertical line passing through the respective latency profiles, which are assumed to be the same). (B) Latency profiles of second saccades to the old (vertically striped) and new (horizontally striped) target locations arising as a result of decision processes, $GO2_{Old}$ and $GO2_{New}$, rising toward a threshold (gray horizontal band) soon after final target (FT) presentation and end of first saccade, respectively. (C) Onset of $GO2_{Old}$ is shifted iteratively by a delay *d* with respect to FT until the predicted reaction times of second saccades to the old final target location match their observed value. At this time, onset of concurrent planning, or *o*, is computed with respect to the start of the first saccade. Note: Predicted reaction times are estimated after excluding the region common to both $GO2_{Old}$ and $GO2_{New}$ distributions (grid region) corresponding to midway saccades. IT: initial target presentation, TS: target-shift. (D) Histogram showing the onset of concurrent planning for subjects who performed the 40% REDIRECT task (left) and the 40% FOLLOW task (right). Zero on the x-axis represents the start of the first saccade. Adapted from Sharika et al. (2008).

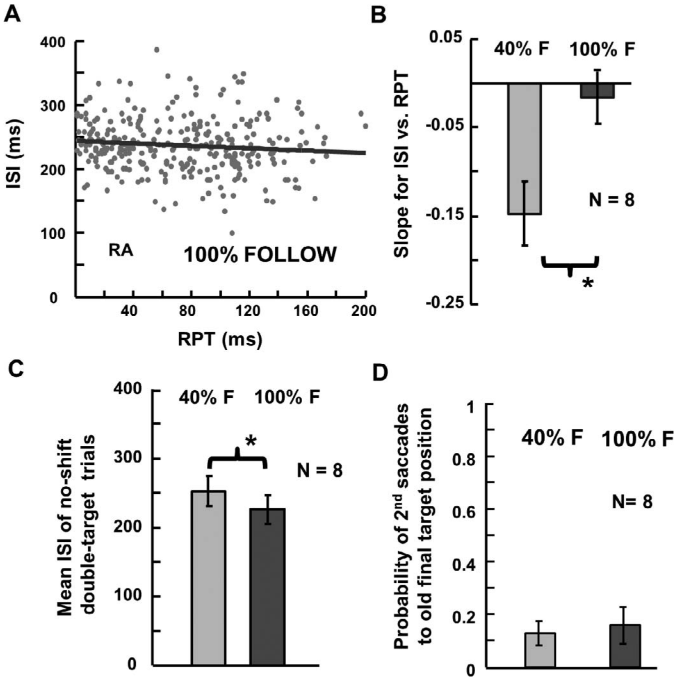

Figure 7. Effect of task statistics on concurrent planning. (A) Plot between ISI and RPT for a representative subject, RA, in the 100% FOLLOW task. Bar graphs plot the slope of the linear fits between ISI and RPT (B), the mean ISI of no-shift double-target trials (C), and the average probability of second saccades to the old final target location (D) for the eight subjects who performed both the 40% and 100% FOLLOW tasks. *Difference significant with $p < 0.05$. Error bars indicate mean ± *SEM*.

Effect of task statistics on the concurrent planning of saccades

We examined if predictability about having to make a sequence of saccades in a given trial modulated concurrent planning in the 100% FOLLOW task relative to the 40% FOLLOW task. Using the same procedure as described for testing the effect of task instruction on the planning of sequential saccades (i.e., using trials with ISIs $\leq$ 400 ms and RPTs $\leq$ 200 ms), we plotted the change in ISI of no-shift double-target trials as a function of reprocessing time for the 100% FOLLOW task. Figure 7A shows data from a representative subject, RA, quantified by a linear fit. As noted earlier, although the individual slopes were significantly different from zero for seven out of 10 subjects in the 40% FOLLOW task, the same was true for five out of eight subjects in the 100% FOLLOW task. Comparing data between the eight subjects who performed both tasks, although the average slope was found to be significantly negative in the 40% FOLLOW task ($n = 8$; slope mean $= -0.15 \pm -0.04$, min. $= -0.28$, max. $= -0.01$, R^2 mean $= 0.05$, min. $= 0.0001$, max. $=$ 0.14, two-tailed, one sample t test [slope, 0]: $p = 0.004$), the same was not found to be significantly different from zero in the 100% FOLLOW task ($n = 8$, slope mean $= -0.02 \pm 0.03$, min. $= -0.1$, max. $= 0.13$, R^2 mean $= 0.009$, min. $= 0.0004$, max. $= 0.02$, two-tailed, one sample t test (slope, 0): $p = 0.6$), and the overall difference between task conditions was statistically significant (Figure 7B; $n = 8$, two-tailed, paired sample t test, slope [40% FOLLOW, 100% FOLLOW]: $p = 0.03$; $n = 10$, mean slope [40% FOLLOW] $= -0.16 \pm 0.03$; $n = 8$, mean slope [100% FOLLOW] $= -0.02 \pm 0.03$; two-tailed, two independent sample t test, slope [40% FOLLOW, 100% FOLLOW]: $p = 0.004$). The mean ISI across subjects was also significantly shorter in the 100% FOLLOW task (226 ± 21 ms) when compared with the 40% FOLLOW task (253 ± 22 ms) on performing the statistically more powerful paired sampled comparison ($n = 8$; two-tailed, paired sample t test [40% FOLLOW, 100% FOLLOW]: $p = 0.01$; Figure 7C), although pooling data for all subjects who performed the two tasks in an independent sample analysis made this difference nonsignificant ($n = 10$, mean ISI [40% FOLLOW] $= 248 \pm 18$; $n = 8$, mean ISI [100% FOLLOW] $= 226 \pm 21$; two-tailed, two independent sample t test, ISI [40% FOLLOW, 100% FOLLOW]: $p = 0.43$).

We examined if the degree of motor preparation occurring in a trial as indicated by the frequency of second saccades to the old position of the final target was any different between the 40% and 100% FOLLOW conditions. The overall probability of second saccades to the old final target location was similar for the two tasks ($n = 8$, mean ± *SEM*, 40% FOLLOW $=$ 12.6 ± 5%; 100% FOLLOW $= 15.2 \pm 7\%$; Wilcoxon signed rank test on probability of old [40% vs. 100% FOLLOW]: $p = 0.2$; Figure 7D). Also, as in the case of the 40% FOLLOW task before, the probability of second saccades to the old final target location in the 100% FOLLOW task did not differ significantly with an increase in the RPT of the corresponding trials (mean [probability of old] ± *SEM*, trials with RPT 1–100 ms $= 0.14 \pm 0.06$, trials with RPT 101–200 ms $=$ 0.18 ± 0.09; Wilcoxon signed rank test on probability of old [RPT 1–100 ms vs. RPT 101–200 ms]: $n = 8$, $p =$ 0.55). The individual slopes between end points of midway saccades and RPT were also found to be not significantly different from zero in both 40% and 100% FOLLOW task conditions and, hence, were not examined further. On the whole, other than the relationship between ISI and RPT as well as the mean value of ISI itself, there were no significant differences in the behavior produced in the two FOLLOW tasks. Although the ISI versus RPT slopes were flatter in the 100% FOLLOW task compared to the 40% FOLLOW task, shorter ISIs observed in the 100% FOLLOW task were suggestive of enhanced concurrent planning of second saccades just as in the 40% REDIRECT task. We examined this further by studying the second saccades to the old final target location in the 40% REDIRECT and 100% FOLLOW tasks and testing the nature of concurrent planning in the two cases.

Although the efference copy of the first saccade has been chiefly implicated in the predictive planning of the second saccade (Murthy et al., 2007; Phillips & Segraves et al., 2010; Sommer & Wurtz, 2004b), in a stable task environment, the exocentric representation of the second target has also been proposed to facilitate concurrent planning of sequential saccades (Sharika, Ramakrishnan, & Murthy, 2014). In that study, we showed how the two mechanisms differ in the way the errors in reaching the first target are propagated by the second saccade. These saccadic end point errors will be referred to as localization errors here although we are agnostic of their origin as being visual, motor, or both. Although the localization errors in the first saccades are compensated in the efference copy–based planning of sequential saccades even in the absence of continued visual feedback (Bock, Goltz, Belanger, & Steinbach, 1995; Collins, 2010; Ditterich, Eggert, & Straube, 1998; Joiner, Fitzgibbon, & Wurtz, 2010; Sommer & Wurtz, 2004b), they are expected to propagate in second saccades planned without this information (Ditterich et al., 1998; Dore-Mazars, Vergilino-Perez, Collins, Bohacova, & Beauvillain, 2006; Sharika et al., 2014). We computed an index for the magnitude of first saccade errors that was propagated (or not compensated) by the second saccade. If the localization error in the first saccade with respect to the center of the first target is denoted by vector A and the localization error in the second saccade with respect to the center of the second target is represented by vector B, the magnitude of the first saccade error that was propagated in the second saccade was estimated by computing the second saccade error in the direction of the first saccade's error or B$\cos\theta$ (θ being the angle between vectors A and B) (Figure 8A; Collins, 2010). Using second saccades to the old final target location, the average magnitude of propagated error (B$\cos\theta$) during predictive planning of sequential saccades was computed for all subjects with more than one such trial and then contrasted against their individual tendencies for concurrent planning as indexed by their frequency of second saccades to the old final target location.

Because the efference copy–based planning of the second saccade predicts a decrease in error propagation

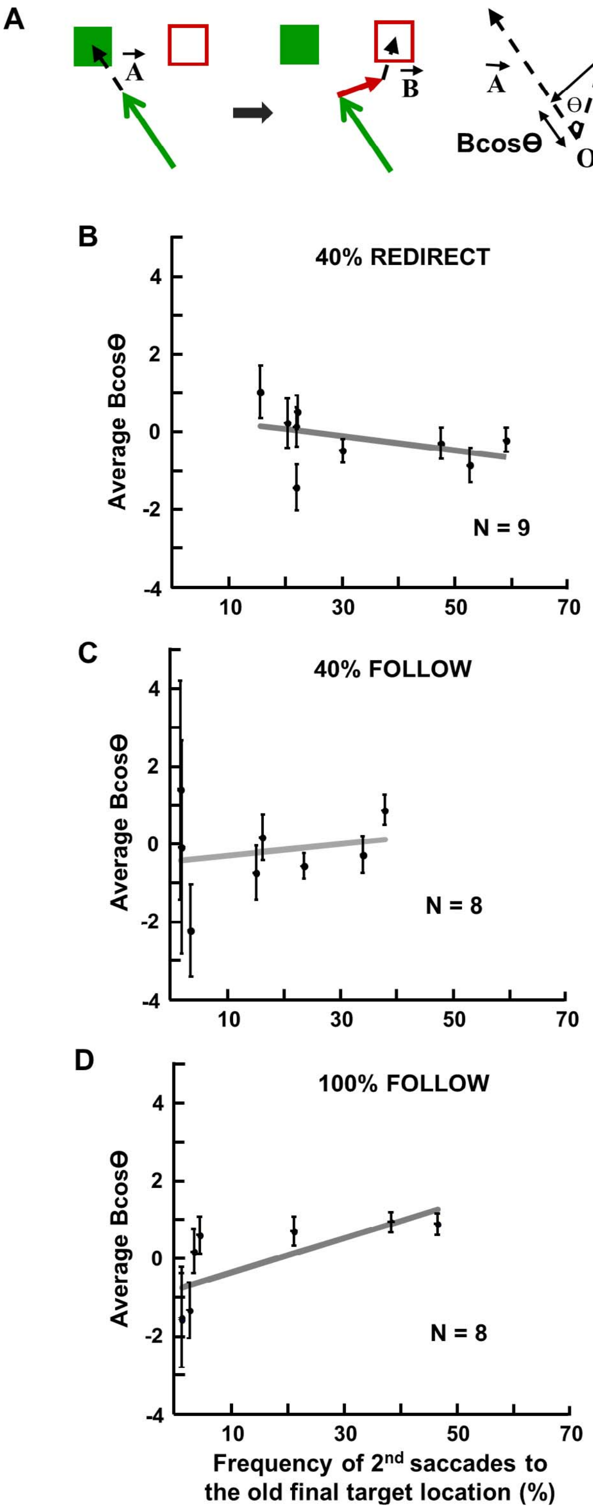

Figure 8. Effect of task context on the propagation of localization errors. (A) Green arrow denotes the first saccade to the green target, and red arrow denotes the second saccade to the old final target location in a target-shift double-target trial. Vectors A and B (black arrows) represent the localization errors in the first and second saccades, respectively, joined together at O such that angle AOB = θ. The projection of B on A (Bcosθ) gives the magnitude of second saccade error that is in the

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direction of the first saccade's error. Mean Bcosθ of second saccades to the old final target location is plotted against the frequency of such saccades in the 40% REDIRECT (B), 40% FOLLOW (C), and 100% FOLLOW (D) tasks. Error bars indicate mean ± *SEM*.

with an increase in the tendency for concurrent planning, we expect mean Bcosθ across subjects to be negatively correlated with the frequency of second saccades to the old final target location. However, concurrent planning based on the exocentric encoding of the second target (with respect to the first target in this case) predicts an increase in Bcosθ or propagation of localization errors with an increase in the tendency for concurrent planning or the frequency of second saccades to the old position of the second target. Although the average propagation of error varied inversely with the tendency for concurrent planning across subjects in the 40% REDIRECT task (Figure 8B; $n = 9$; slope = –0.02; Spearman's correlation $R = -0.51$; two-tailed, one sample t test [slope, 0]: $p = 0.16$) as well as the 40% FOLLOW task (Figure 8C; $n = 8$; slope = 0.01; Pearson's correlation $R = 0.19$; two-tailed, one sample t test [slope, 0]: $p = 0.65$), the correlation was not statistically significant. On the other hand, there was a significant positive correlation between the two variables across subjects in the 100% FOLLOW task (Figure 8D; $n = 8$; slope = 0.04; Spearman's nonparametric correlation $R = 0.98$; two-tailed, one sample t test [slope, 0]: $p = 0$), suggesting the possible role of exocentric representations in the concurrent planning of second saccades in the 100% FOLLOW task.

Discussion

Using a modified version of the classic double-step task, we have shown evidence for the role of task instruction and statistics in modulating the planning of sequential saccades. Specifically, concurrent motor preparation of the second saccade was significantly attenuated in the 40% FOLLOW task relative to the 40% REDIRECT task. In addition, greater predictability about the need to plan a sequence of saccades in the 100% FOLLOW task versus the 40% FOLLOW task was found to facilitate concurrent planning in the former task, probably via a mechanism independent of the efference copy of the first saccade.

Role of task instruction in the planning of sequential saccades

Although the double-step paradigm has been often used to study oculomotor control, explicit instructions were almost never given to subjects, and mostly, the pattern of responses corresponded to that observed in the REDIRECT task (Becker & Jürgens, 1979; Hallett & Lightstone, 1976; Sparks & Mays, 1983). Ray et al. (2004), for the first time, examined the role of explicit instruction on the planning of sequential saccades in a modified double-step task. The authors used the inverse relationship between the ISI and RPT to suggest that the rate of planning the second saccade in parallel is higher in the 40% REDIRECT task compared to the 40% FOLLOW task. The findings of the current study confirm and extend these results by introducing target-shift double-target trials (Sharika et al., 2013; Sharika et al., 2008). Frequency of second saccades to the old final target location increased significantly at higher RPTs in the 40% REDIRECT task (Figure 5A) but not in the 40% FOLLOW task, suggesting that concurrent motor preparation was restricted in the 40% FOLLOW task. This is consistent with the predictions of the model recently proposed by Ray et al. (2012) based on the idea of capacity sharing in dual-task paradigms (Kahneman, 1973; McLeod, 1977; Navon & Gopher, 1979; Pashler, 1994; Tombu & Jolicoeur, 2002). According to the model, mutual inhibition between two concurrently active saccade plans, acting in proportion to the capacity allocated to each plan, is critical in maintaining the serial order of saccades in a sequence. Such an inhibition is proposed to attenuate the planning of the second saccade while allowing the first one to proceed up to a stage at which the two plans are no longer interfering with each other. Consistent with this idea, concurrent planning of the second saccade was suppressed in the 40% FOLLOW task, in which preserving the serial order of saccades was essential for successful task performance. The role of such mutual inhibition in capacity allocation and queuing of saccade plans has also been demonstrated in Parkinson's disease patients and in inactivation studies of basal ganglia in monkeys in which reduced inhibition resulted in greater frequency of midway saccades as well as serial order errors (Bhutani et al., 2013). On the other hand, the REDIRECT task demands dynamic allocation of priorities to saccade plans such that although the correct behavior involves making the first saccade plan to the initial target irrelevant and allocating priority/capacity to a new saccade plan directed to the final target, corrective behavior requires the allocation of priority/capacity to the second saccade plan when an error is expected. If mutual inhibition, presumably mediated by structures such as basal ganglia mediates such dynamic allocation of capacity/priority, concurrent planning of the second saccade is expected to proceed at a higher rate, generating corrective saccades with shorter reaction times and ISIs relative to the second saccades in the FOLLOW task (Ray et al., 2004) as well as a higher frequency of second saccades to the old final target location as observed in this study (Figure 5A).

By fitting the reaction times of second saccades to the old position of the final target in the LATER model, based on an assumption that the rates of accumulation remain unchanged within a trial (Sharika et al., 2008), we estimated and compared the effective delay in the onset of second saccade preparation in the 40% FOLLOW task versus the 40% REDIRECT task (Figure 6D). Because the visual processing of respective targets is postulated to occur in parallel for the two saccade plans (Bhutani et al., 2013; Ray et al., 2012), the estimated delays are likely to account for the time the second saccade plan was "waiting" for access to processing resources before proceeding to response preparation. Results suggesting that the second saccade preparation in the two tasks can start before the visual feedback at the end of the first saccade can influence the process (Figure 6D), are consistent with the electrophysiological recordings from the frontal eye fields (FEF) when monkeys perform a similar double-step task (Murthy et al., 2007). In the study by Murthy et al. (2007), although the movement-related activity corresponding to that of the second saccade was reported to begin for some neurons before the first saccade was initiated, significant modulation was observed for 41% of neurons before the first saccade was completed and for 39% of neurons after the error but before the earliest visual feedback could reach FEF. The onset of second saccade preparation before the visual reafference can influence the oculomotor system is also consistent with the finding that efference copy signals pertaining to the first saccade have been reported to reach the oculomotor cortex before the end of the first saccade (Duhamel, Colby, & Goldberg, 1992; Li & Andersen, 2001; Merriam, Genovese, & Colby, 2003, 2007; Nakamura & Colby, 2002; Parks & Corballis, 2010; Sommer & Wurtz, 2004a) and have been implicated in concurrent planning of sequential saccades (Becker & Jürgens, 1979; Collins, 2010; Hallett & Lightstone, 1976; Honda, 1989, 1993; Joiner et al., 2010; McPeek et al., 2000; Melcher, 2007; Melcher & Colby, 2008; Murthy et al., 2007; Ray et al., 2004; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011; Ross, Morrone, Goldberg, & Burr, 2001; Sharika et al., 2008; Sparks & Mays, 1983). Taken together, the results of the current study suggest that concurrent planning of sequential saccades, presumably dictated by the amount of mutual inhibition between saccade plans, can be contextually regulated by means of task instruction.

Role of task structure in the planning of sequential saccades

If mutual inhibition between saccade plans limits concurrent planning in the 40% FOLLOW task in order to maintain the sequential rank of saccades, one would expect that increasing the probability of making a sequence of saccades in every trial, as in the case of the 100% FOLLOW task, would further suppress concurrent planning. Contrary to this expectation, the findings of the current study show that concurrent planning of sequential saccades is enhanced in the 100% FOLLOW task when compared with the 40% FOLLOW task observed in terms of significantly shorter ISIs in the 100% FOLLOW task as compared to the 40% FOLLOW task (Figure 7C). Despite this effect, a decrease in ISI of no-shift double-target trials with increasing RPT—a classic pattern indicative of concurrent planning—was not observed; instead, the ISI was found to be invariant to RPT in the 100% FOLLOW task (Figure 7B). This deviation from the expected relationship between ISI and RPT in the 100% FOLLOW task is indicative of concurrent planning in this task being mechanistically different from that occurring in the 40% REDIRECT task. We believe that this difference could arise from the differential use of exocentric versus efference copy–based mechanisms of concurrent planning in the two tasks. Although concurrent planning has been, so far, chiefly proposed to occur via the efference copy of the first saccade, available to the oculomotor system around the time of the saccade (Sommer & Wurtz, 2004a), in a relatively predictable environment, representations of target location in either allocentric (relative to a fixed location) or exocentric (relative to another object) frames of reference (Byrne & Crawford, 2010; Zimmermann, Morrone, Fink, & Burr, 2013) have been suggested to provide an alternate, more efficient mechanism to plan a sequence of saccades in parallel (Sharika et al., 2014). This possibility was tested in the current study by examining the localization errors of second saccades to the old final target location in all three tasks. A significant positive correlation between the average propagation of localization errors in the second saccade and the tendency for concurrent planning across subjects was observed in the 100% FOLLOW task (Figure 8D) but not in the 40% REDIRECT task (Figure 8B) or the 40% FOLLOW task (Figure 8C). Although the difference in the relationship between error propagation and concurrent planning in the 100% FOLLOW task relative to the other two tasks is weak, we have recently shown a more robust propagation of error across saccades when subjects perform the same FOLLOW task with a longer fixation hold time period that further facilitates the use of the first target as a stable, exocentric reference for concurrent planning (Byrne & Crawford, 2010; Schutz, Henriques, & Fiehler, 2013; Sharika et al., 2014; Thompson, Glover, & Henriques, 2012), because such representations have been thought to take longer to develop when compared to those based on egocentric mechanisms (Hu & Goodale, 2000; Westwood, Heath, & Roy, 2000; Zimmermann et al., 2013). Taken together, our results raise the possibility that compared to the other two tasks, the predictability of the task environment in the 100% FOLLOW task may allow greater use of exocentric cues for planning concurrent saccades, independent of the efference copy information about the preceding saccade (Becker & Fuchs, 1969; Ditterich et al., 1998; M. M. Hayhoe, Shrivastava, Mruczek, & Pelz, 2003; Inhoff, 1986; Vergilino-Perez & Beauvillain, 2004; Vergilino-Perez & Findlay, 2006; Zingale & Kowler, 1987).

Conclusion

In this study, we show, using three versions of the modified double-step task, how task instruction and trial statistics can quantitatively modulate the concurrent planning of sequential saccades. While monitoring of errors was shown to facilitate motor preparation of corrective responses relative to a task that pressed on the maintenance of the saccadic sequence, a highly predictable task design also tended to enhance concurrent planning even when the serial order of saccade execution continued to remain important.

Keywords: task predictability, efference copy, parallel programming, error correction, LATER model

Acknowledgments

This work was supported by the Department of Biotechnology, Government of India. We thank all the reviewers for their comments and suggestions.

Commercial relationships: none.

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