Saccade Reorienting Is Facilitated by Pausing the Oculomotor Program

Antimo Buonocore[1], Simran Purokayastha[2], and Robert D. McIntosh[2]

Abstract

■ As we look around the world, selecting our targets, competing events may occur at other locations. Depending on current goals, the viewer must decide whether to look at new events or to ignore them. Two experimental paradigms formalize these response options: double-step saccades and saccadic inhibition. In the first, the viewer must reorient to a newly appearing target; in the second, they must ignore it. Until now, the relationship between reorienting and inhibition has been unexplored. In three experiments, we found saccadic inhibition ~100 msec after a new target onset, regardless of the task instruction. Moreover, if this automatic inhibition is boosted by an irrelevant flash, reorienting is facilitated, suggesting that saccadic inhibition plays a crucial role in visual behavior, as a bottom–up brake that buys the time needed for decisional processes to act. Saccadic inhibition may be a ubiquitous pause signal that provides the flexibility for voluntary behavior to emerge. ■

INTRODUCTION

As we look around the world, selecting the targets of our eye movements, the scene may change. Our next planned target may move or an event of greater urgency may occur at another location. Depending on current goals, the viewer must decide whether to look at new events or to ignore them. These response options have been formalized within two powerful experimental paradigms: double-step saccades and saccadic inhibition. In the first, the viewer must reorient to a target appearing shortly before a planned saccade; in the second, they must ignore it. Each paradigm has been studied extensively, but the relationship between reorienting and inhibition is hitherto unexplored. This study seeks to bridge that gap, testing the presence and possible functional role of oculomotor distraction in reorienting.

Irrelevant distractors robustly delay saccade execution (e.g., Walker, Kentridge, & Findlay, 1995; Weber & Fischer, 1994). Analysis of latency distributions reveals that distractors cause a specific dip in saccadic activity ~60–120 msec after distractor onset, with the suppressed saccades launching later (Bompas & Sumner, 2011; Edelman & Xu, 2009; Buonocore & McIntosh, 2008). This pause in visual behavior, known as "saccadic inhibition," is a fast, reflexive response of the oculomotor system to any salient visual change, and it occurs regardless of the task instruction (Reingold & Stampe, 1999, 2002, 2003, 2004). We should thus expect that saccadic inhibition will accompany the change in target position in double-step tasks.

The literature on double-step saccadic performance contains hints that this may be the case. In general, saccades launching immediately after a target step do not have time to reflect the step and are directed toward the initial target, whereas saccades launching at longer delays are progressively more likely to go toward the second target (Becker & Jürgens, 1979; Lisberger, Fuchs, King, & Evinger, 1975). At least for large target steps, this "transition function" is discontinuous, with saccades launched less than ~60 msec after the target step going to the initial target, saccades launched more than ~120 msec after the step going to the new target, and few if any saccades in the intervening time window (Aslin & Shea, 1987; Findlay & Harris, 1984). There is thus a pause in behavior in double-step tasks that corresponds roughly with the time course of saccadic inhibition. Speculation that the target step in double-step tasks has a distracting effect can be found quite far back in the literature (Sheliga, Brown, & Miles, 2002; Findlay & Walker, 1999), yet this important possibility has never been formally examined.

The first aim of this study is to assess whether the signature of saccadic inhibition is present in a double-step context, comparing between two tasks, matched for stimulus events, in which a new visual event is to be responded to as a target or ignored as irrelevant. We demonstrate that saccadic inhibition does indeed occur in a double-step context, just as in a distractor context. Experiment 3 is then designed to study the consequences of this reflexive inhibition for reorienting behavior. This is done by boosting the inhibitory signal during double-step reorienting, with a salient generalized flash presented at the same time as the target jump. One might expect that this

[1]Tübingen University, [2]University of Edinburgh

irrelevant event would interfere with the ability to respond to the new target; but a more interesting, counterintuitive possibility is that the flash will interfere mainly with the planned response to the initial target, creating a pause in behavior that would increase the subsequent likelihood of successful reorienting. If so, we would predict that reorienting would be enhanced under conditions of boosted inhibition, indexed by an increased proportion of saccades being successfully redirected. This would provide strong support for a long-standing but little-discussed idea that saccadic inhibition is a feature, not a bug of the oculomotor system, which buys time for the system to evaluate any salient change and to alter the next saccade if necessary (Reingold & Stampe, 2002).

METHODS

Participants

Eighteen volunteers, aged between 18 and 30 years, participated in the three experiments (six in each). This study is concerned with basic design features of the oculomotor system, so we are targeting only very consistent effects that should be near-universal. The number of participants per experiment is therefore small ($n = 6$), with effort directed to maximizing the number of observations per participant to ensure robust individual parameter estimates. Our focus is on a high consistency of behavior across participants, and individual parameters are reported for each participant in each experiment. All were free from neurological and visual impairments. This experiment was conducted in accordance with the 1964 Declaration of Helsinki, with the approval of the University of Edinburgh Psychology research ethics committee.

Apparatus, Stimuli, and Procedure

Stimuli were black on a mid-gray background, presented on a 19-in. CRT monitor (1024 × 768 pixels) at 100 Hz. All the experiments were implemented in Experiment Builder (SR Research, Ottawa, ON, Canada). Participants were seated with their head on a chinrest, their eyes aligned with the center of the screen at a distance of 80 cm. Eye movements were recorded with the EyeLink 1000 system (SR Research; detection algorithm: pupil and corneal reflex; 1,000 Hz sampling; saccade detection based on 30°/s velocity and 8,000°/s^2 acceleration thresholds). Each trial began with drift correction and a tone followed by a 0.5° central fixation cross. In Experiments 1 and 2 (but not Experiment 3), 1° black outline circles were also presented at 6° to left and right of fixation as placeholders for potential targets. In all experiments, a 5-point calibration on the horizontal and vertical axes was run at the beginning of each session and after three consecutive blocks. Additional calibrations were run if the participant's head moved from the chinrest.
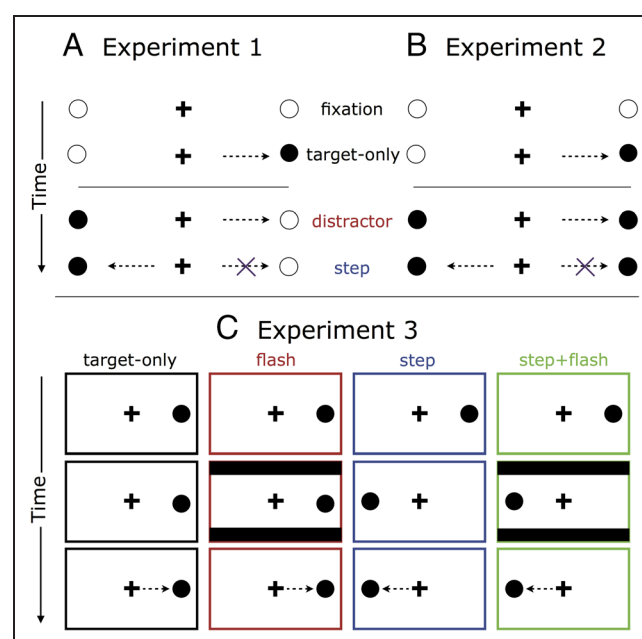
Experiment 1 (Figure 1A)

Each trial began with fixation followed by the onset of Target 1, created by filling in one of the two lateralized outline circles. In half of the trials, Target 1 remained filled until the screen went gray 700 msec later (target-only trials). In the other half of the trials, Target 1 unfilled and the outline on the opposite side filled simultaneously (Target 2), after a delay determined individually for each participant (see Preliminary Block section). In the "distractor" condition, participants were required to ignore Target 2 and to move their eyes to the Target 1 location. In the "step" condition, participants were required to move their eyes to the second target if it appeared.

Each participant completed two sessions for the distractor and step conditions,[1] following an ABBA sequence, counterbalanced across participants. Within each session, there were 10 blocks of 24 trials; Target 1 appeared equally often on each side and, for each side, was followed by Target 2 in half of the trials. Participants thus completed 240 target-only and 240 distractor trials in the distractor condition and 240 target-only and 240 step trials in the step condition.

Experiment 2 (Figure 1B)

This was identical to Experiment 1, except that Target 1 did not unfill when Target 2 was presented. Instead, for the trials in which Target 2 appeared, both targets remained filled until the end of the trial. Thus, whereas Experiment 1 used stimulus conditions typical of double-step tasks (Target 1 replaced by Target 2), Experiment 2 used conditions more typical of distractor tasks (Target 1 joined by Target 2).

Figure 1. Schematic diagram of trial events. See Methods for details.

Experiment 3 (Figure 1C)

This was similar to Experiments 1 and 2, with some important changes. After the initial fixation period, a 1° black dot appeared on the left or the right (Target 1). After the delay determined individually for each participant (see Preliminary Block section), one or two changes could occur: In flash trials (25% of trials), there was a distracting flash of maximum contrast, lasting 30 msec and covering the top and bottom thirds of the screen; in step trials (25% of trials), Target 1 disappeared and was replaced by an identical target on the opposite side (Target 2); in step-flash trials (25% of trials), both changes happened simultaneously; in target-only trials (25% of trials), neither change happened. In all trials, the participant was required to move their eyes as rapidly as possible to the target, thus to change plan if the target stepped. Note that the flash condition of Experiment 3 is similar to the distractor conditions of Experiments 1 and 2, except that the distracting event is a large generalized flash.

Each participant completed two sessions of 10 blocks each. Within each block, there were 48 trials; Target 1 appeared equally often on the left and the right, and for each target side, there were six trials in each of the stimulus conditions (target-only, flash, step, step-flash). Participants thus completed 240 trials per condition.

Preliminary Block

Before each experiment, participants performed a block of 70 trials of the target-only condition for that experiment. The median saccadic RT of the last 50 trials was calculated, and 100 msec was subtracted from this value to set the timing of transient events for that participant in the subsequent experiment. These participant-specific timings ensure that saccadic inhibition, which is maximal around 90–100 msec after a transient event, will impact upon a dense portion of the expected saccadic distribution. The individual transient onset times relative to initial target onset are listed per participant: Experiment 1: 150, 150, 120, 120, 90, 170; Experiment 2: 120, 90, 140, 130, 150, 140; Experiment 3: 20, 120, 120, 170, 130, 80.

Data Processing

All the data processing and analysis were performed in MATLAB (The MathWorks, Inc., Natick, MA). Only the first eye movement following target onset was analyzed. A total of 9% (Experiment 1), 2.7% (Experiment 2), and 4.3% (Experiment 3) of trials were excluded from the analysis due to blinks, latencies shorter than 70 msec or longer than 500 msec, and saccades smaller than 2° amplitude or with a duration exceeding 100 msec. For the target-only condition, we also excluded saccades made in the wrong direction (Experiment 1: 0.67%, Experiment 2: 1.31%, Experiment 3: 0.21%).

Saccadic Inhibition Analysis

To chart the time course of saccadic activity, we applied a distribution analysis to the saccadic RTs (cf. McIntosh & Buonocore, 2014; Bompas & Sumner, 2011; Reingold & Stampe, 2002). In each experiment, for each participant and condition, we computed the probability density estimate of saccades at each millisecond, with time zero defined by the transient change. The estimate was smoothed using a kernel-smoothing window of 8 msec. For each participant, for each experiment, the target-only condition was taken as the baseline distribution of saccadic activity. We calculated, at each millisecond, the proportional change relative to this baseline in each of the transient change conditions (distractor or step in Experiments 1 and 2; flash, step, or step-flash in Experiment 3) using Equation 1, which expresses reduced saccadic activity as positive:

$$\frac{p^{\text{target}}(t) - p^{\text{change}}(t)}{p^{\text{target}}(t)} \quad (1)$$

where $p(t)$ is the probability for the target-only condition and $p(c)$ is the probability for the transient change condition. To keep the estimate of proportional change reliable, considering the low frequency of saccades in the initial and final part of the distribution, we extracted data only from 45 to 250 msec after the change. From each of these profiles, we extracted inhibition magnitude (maximum inhibition), inhibition latency (time to maximum inhibition), and inhibition start and end times, defined operationally as the times at which inhibition crossed 50% of its maximum level, before and after the maximum, respectively (Reingold & Stampe, 2002).

Double-step Analysis

To characterize reorienting behavior for each condition that had a "step" (i.e., in which the participant was required to reorient to Target 2), we derived a direction transition function. First, we classified each saccade as directed at Target 1 or Target 2, according to the hemifield in which it landed (the distribution of landing positions was bimodal, as is clear in Figures 2, 4, and 6). We then computed the probability of responding to Target 1 as function of time since the step and fitted a logistic function using Equation 2:

$$\frac{1}{1 + e^{(-a \, * \, (t-b))}} \quad (2)$$

where e is the natural logarithm base, a represents the steepness of the curve, b is the inflection point, and the numerator represents the maximum probability.

Probability of Responses to Target 1

In each experiment, for each condition, we estimated the proportion of responses to Target 1, with Target 1 responses coded as 1 and Target 2 responses coded as 0.
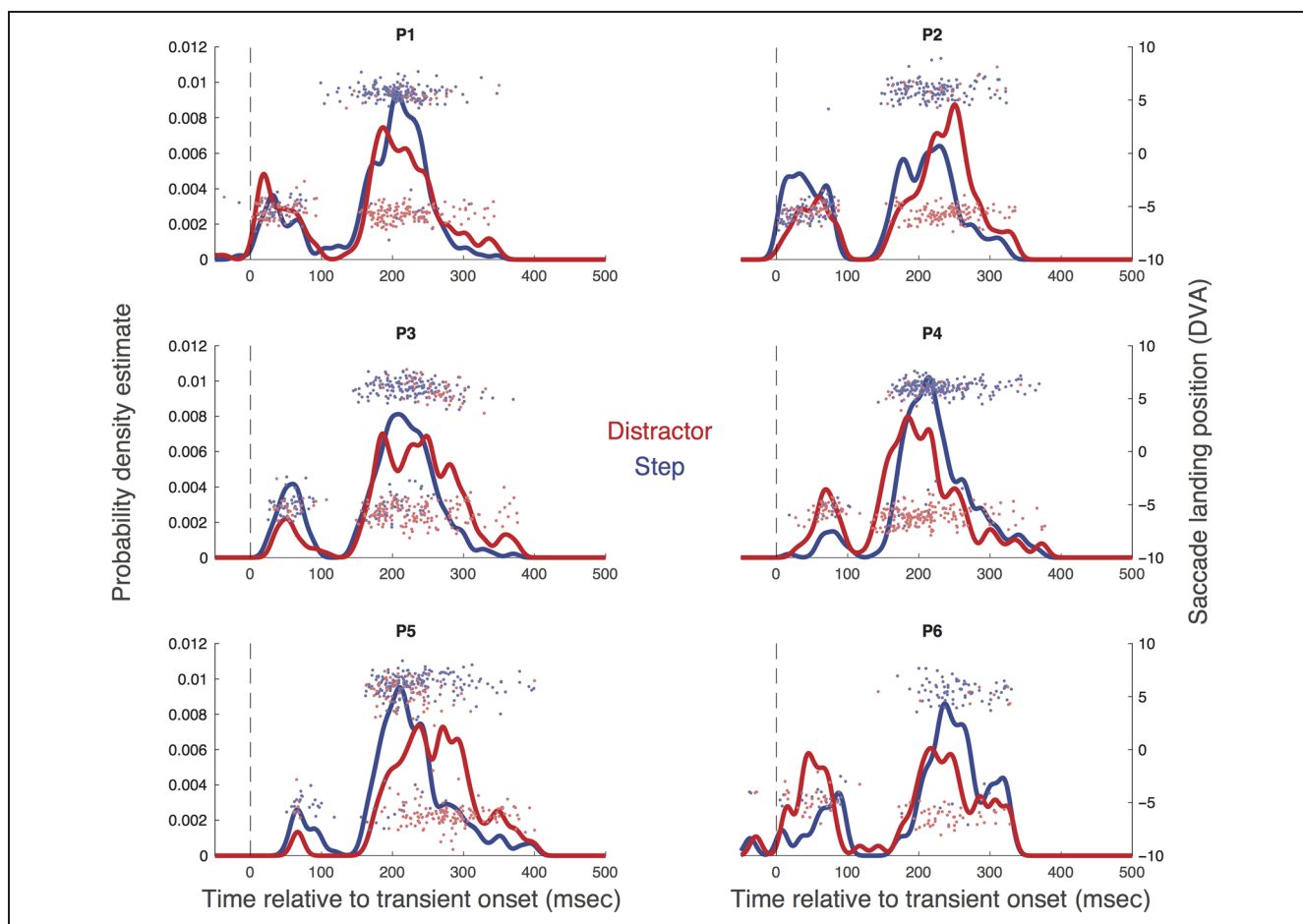
Figure 2. Each panel shows the probability density estimate derived from the raw data of each participant (P1–P6) in the distractor (red) and step (blue) conditions of Experiment 1. The horizontal components of the saccade landing positions are overlaid (negative values indicate Target 1 location, and positive values indicate Target 2 location). Time on the *x* axis is coded relative to transient onset (i.e., positive numbers indicate saccades launched after distractor onset), rather than initial target onset to reveal the time course of responses to the transient change.

In distractor and flash conditions, participants were required to respond to Target 1, so the expected probability is very high. Conversely, in step and step-flash conditions, participants had to reorient to Target 2, making the expected probability to Target 1 lower, to the extent that the participant was able to reorient. We were most interested in these proportions for step and step-flash conditions in Experiment 3, in which lower numbers indicate more reliable reorienting (i.e., lower error rate).

Reorienting Latency

For conditions involving a step, we also estimated the average latency of successful reorienting responses, as the median saccadic RT for saccades to Target 2, coded relative to the target step.

Statistical Analysis

Experiments 1 and 2 were designed as exploratory studies to assess whether the signature of saccadic inhibition

was present in a double-step context. There were no critical hypotheses for these two experiments, so formal statistical tests were not used. Experiment 3 was then designed to test whether saccadic inhibition facilitated reorienting. For this experiment, we ran a series of pairwise *t*-test comparisons to test differences among parameters of interest. Given the low number of participants ($N = 6$), which makes parametric assumptions hard to verify, we also ran nonparametric statistics. We report the parametric analysis in the Results section, but all nonparametric comparisons had similar outcomes and do not modify our findings.

RESULTS

Experiments 1 and 2 were designed to provide a descriptive comparison of saccadic activity in distraction and double-step tasks. We expected to observe the classic reduction in saccade frequency around 100 msec after the transient event. Experiment 3 was designed to test the influence of saccadic inhibition upon measures of reorienting and the influence of the reorienting instruction

upon measures of inhibition. Formal statistical tests are reported for Experiment 3 only.

Experiment 1

Figure 2 shows the saccadic RT profiles for each participant, showing the probability of saccade launching by time after transient onset. Saccadic inhibition is indicated by the bimodality of these distributions; its consistency across participants is striking, with a depression of saccadic activity centered around 100 msec after the transient change (Buonocore, McIntosh, & Melcher, 2016; Buonocore & McIntosh 2008, 2012, 2013; Bompas & Sumner, 2011; Edelman & Xu 2009; Reingold & Stampe, 1999, 2000, 2002, 2004). Even more striking is that this bimodal pattern emerged regardless of whether the participant was required to ignore or to reorient to a target step. The data show, for the first time, that the discontinuity of saccadic behavior in double-step reorienting (Ludwig, Mildinhall, & Gilchrist, 2007; Findlay & Harris, 1984; Becker & Jürgens, 1979) closely matches the characteristic time course of saccadic inhibition.

The horizontal components of the saccade landing positions are overlaid in each panel of Figure 2. For the step condition, these clouds of points cluster to Target 1 or Target 2 along the time dimension, reflecting the double-step transition. Virtually no eye movements toward Target 2 were launched before the start of the inhibition. In all participants bar one (P02), reorienting was permeated by erroneous saccades to Target 1 (mean

probability of Target 1 = 0.26, SD = 0.1), even after the maximum of inhibition.

The group average time course of inhibition derived from the saccadic inhibition analysis for each condition is shown in Figure 3, and the individual parameters are shown in Table 1. Inhibition starts around 81 msec, with saccadic activity driven almost to zero by 119 msec, returning to normal levels by 165 msec. The overlaid group average direction transition function for the step condition implies that the transition is parallel to the time course of saccadic inhibition, with its inflection point on average ~16 msec after the peak of inhibition (see Table 2 for individual parameters).

Experiment 1 thus demonstrates saccadic inhibition in a double-step context and further shows a temporal overlap of saccadic inhibition and reorienting. Experiment 2 asks whether the pattern holds under stimulus conditions more similar to a classic distractor paradigm, in which Target 1 does not disappear with the appearance of Target 2 but persists (Buonocore & McIntosh, 2008; Walker et al., 1995).

Experiment 2

Figure 4 shows the distributions for each participant, with horizontal landing positions overlaid. As in Experiment 1, there is clear impression of bimodality consistent with saccadic inhibition in distractor and step conditions; this is, if anything, more pronounced in the step condition. The landing positions show that erroneous saccades

Figure 3. Group average time course of proportional inhibition derived from the saccadic inhibition analysis for distractor (red) and step (blue) conditions of Experiment 1. For the step condition, the black line represents the group average direction transition function coded as the proportion of saccades directed to Target 1 (right *y* axis). Time on the *x* axis is coded relative to transient onset (i.e., positive numbers indicate saccades launched after distractor onset), rather than initial target onset to reveal the time course of responses to the transient change.

Table 1. Individual Parameters, Means, and Standard Deviations Extracted from the Saccadic Inhibition Profiles for Each Experiment and Condition

Experiment	Participant	Inhibition Magnitude			Inhibition Latency			Inhibition Start			Inhibition End		
		Distractor	Step	Step-flash	Distractor	Step	Step-flash	Distractor	Step	Step-flash	Distractor	Step	Step-flash
1	P1	1.00	0.92	—	115	92	—	76	77	—	157	157	—
	P2	1.00	1.00	—	120	115	—	80	84	—	168	158	—
	P3	1.00	1.00	—	127	117	—	63	78	—	157	152	—
	P4	0.97	1.00	—	112	124	—	79	76	—	145	164	—
	P5	1.00	1.00	—	103	136	—	78	75	—	174	166	—
	P6	0.97	1.00	—	101	130	—	80	98	—	163	194	—
	Mean	0.99	0.98	—	113	119	—	76	81	—	161	165	—
	SD	0.01	0.03	—	9.94	15.39	—	6.54	8.76	—	10.09	15.00	—
2	P1	0.47	0.85	—	135	134	—	111	71	—	148	153	—
	P2	0.81	0.85	—	105	111	—	76	81	—	133	144	—
	P3	0.69	0.94	—	85	92	—	66	73	—	126	106	—
	P4	0.59	0.81	—	78	132	—	56	59	—	103	150	—
	P5	0.69	0.90	—	115	113	—	71	89	—	130	134	—
	P6	0.85	1.00	—	106	106	—	74	74	—	123	168	—
	Mean	0.69	0.89	—	104	115	—	76	75	—	127	143	—
	SD	0.14	0.07	—	20.61	16.00	—	18.73	10.07	—	14.69	21.09	—
3	P1	1.00	0.97	1.00	98	126	109	50[a]	77	50[a]	136	153	155
	P2	1.00	0.97	1.00	99	133	99	69	73	69	145	182	168
	P3	0.78	0.87	0.86	67	113	72	54	85	52	106	134	108
	P4	1.00	0.97	1.00	106	117	114	53	68	62	137	153	165
	P5	1.00	0.87	1.00	86	119	88	56	69	56	118	140	124
	P6	0.96	1.00	1.00	82	127	104	50[a]	89	53	124	153	147
	Mean	0.96	0.94	0.98	90	123	98	55	77	57	128	153	145
	SD	0.09	0.06	0.06	14.21	7.43	15.42	7.09	8.59	7.21	14.38	16.55	23.84

The distractor condition of Experiment 3 corresponds to the flash condition.

[a]For P6 in Experiment 3, saccadic inhibition was strong from the earliest part of the saccade distribution in the conditions with a flash, and the algorithm computed an inhibition start time below 50 msec (i.e., 41 msec); we coerced this to a value of 50 msec for a more plausible neurophysiological estimate. Although the precise estimate of onset time is uncertain for P1 in these conditions, there is no doubt that it is earlier than the onset of inhibition in the step condition.

Table 2. Individual Parameters, Means, and Standard Deviations for Direction Transition Function (DTF) and Other Measures of Reorienting Behavior for Each Experiment and Condition

Experiment	Participant	DTF Slope		DTF Inflection		Probability T1			Reorienting Latency	
		Step	Step-flash	Step	Step-flash	Distractor	Step	Step-flash	Step	Step-flash
1	P1	−0.90	–	88	–	0.89	0.26	–	208	–
	P2	−0.09	–	108	–	0.91	0.36	–	217	–
	P3	−0.02	–	152	–	0.80	0.37	–	222	–
	P4	−0.06	–	149	–	0.94	0.12	–	220	–
	P5	−0.06	–	152	–	0.69	0.18	–	223	–
	P6	−0.06	–	162	–	0.90	0.28	–	251	–
	Mean	*−0.20*	*–*	*135*	*–*	*0.86*	*0.26*	*–*	*223*	*–*
	SD	*0.35*	*–*	*29.69*	*–*	*0.10*	*0.10*	*–*	*14.34*	*–*
2	P1	−0.05	–	165	–	0.94	0.38	–	205	–
	P2	−0.05	–	152	–	0.92	0.33	–	199	–
	P3	−3.30	–	109	–	0.92	0.23	–	162	–
	P4	−0.07	–	145	–	0.99	0.37	–	188	–
	P5	−0.05	–	138	–	0.98	0.37	–	199	–
	P6	−0.06	–	185	–	0.99	0.29	–	243	–
	Mean	*−0.60*	*–*	*149*	*–*	*0.96*	*0.33*	*–*	*199*	*–*
	SD	*1.32*	*–*	*25.71*	*–*	*0.03*	*0.06*	*–*	*26.30*	*–*
3	P1	−0.11	−1.34	116	108	1.00	0.10	0.01	220	219
	P2	−0.86	−3.10	135	154	1.00	0.44	0.34	256	278
	P3	−0.26	−0.14	126	124	1.00	0.65	0.51	188	211
	P4	−1.74	−0.34	136	115	1.00	0.51	0.44	239	250
	P5	−1.51	−1.01	121	152	0.99	0.61	0.47	203	242
	P6	−1.49	−0.29	127	146	1.00	0.14	0.08	202	198
	Mean	*−1.00*	*−1.04*	*127*	*133*	*1.00*	*0.41*	*0.31*	*218*	*233*
	SD	*0.69*	*1.11*	*7.80*	*19.91*	*0.01*	*0.24*	*0.21*	*25.62*	*29.31*

to Target 1 (failures of reorienting) were relatively common in the step condition (mean probability of Target 1 = 0.33, $SD = 0.06$). Once again, virtually no reorienting saccades to Target 2 were launched before the start of inhibition.

In Figure 5, the group average transition function for the step condition is overlaid on the average profile from the saccadic inhibition analysis and alongside the inhibition profile for the distractor condition. There is a broad superimposition of the temporal profiles of inhibition and reorienting, and the point of inflection in the transition function lags the peak of inhibition (by ~34 msec). However, visual inspection suggests that the transition function now extends further beyond the end of the inhibition profile than in Experiment 1. This is not due to a change in the direction transition function, which is closely similar between Experiments 1 and 2, but

instead to alterations in the inhibition profile. Descriptively, the magnitude of the inhibition is reduced in Experiment 2 (due to the persistence of Target 1), and this is associated with a weaker and contracted inhibitory profile, a lower maximum inhibition being reached relatively sooner, and an inhibition ending earlier (the numerical differences between these parameters can be appreciated in Table 1).

Comparing inhibition profiles between the step and distractor condition of Experiment 2 (Figure 5 and Table 1), the onset times are similar, but the maximum inhibition is stronger (in every participant) and often ends later (in five of six participants) in the step than in the distractor condition of Experiment 2. This may suggest that the bottom–up inhibition associated with the target step accounts for only a proportion of its inhibitory effect in the step condition, having its main influence in
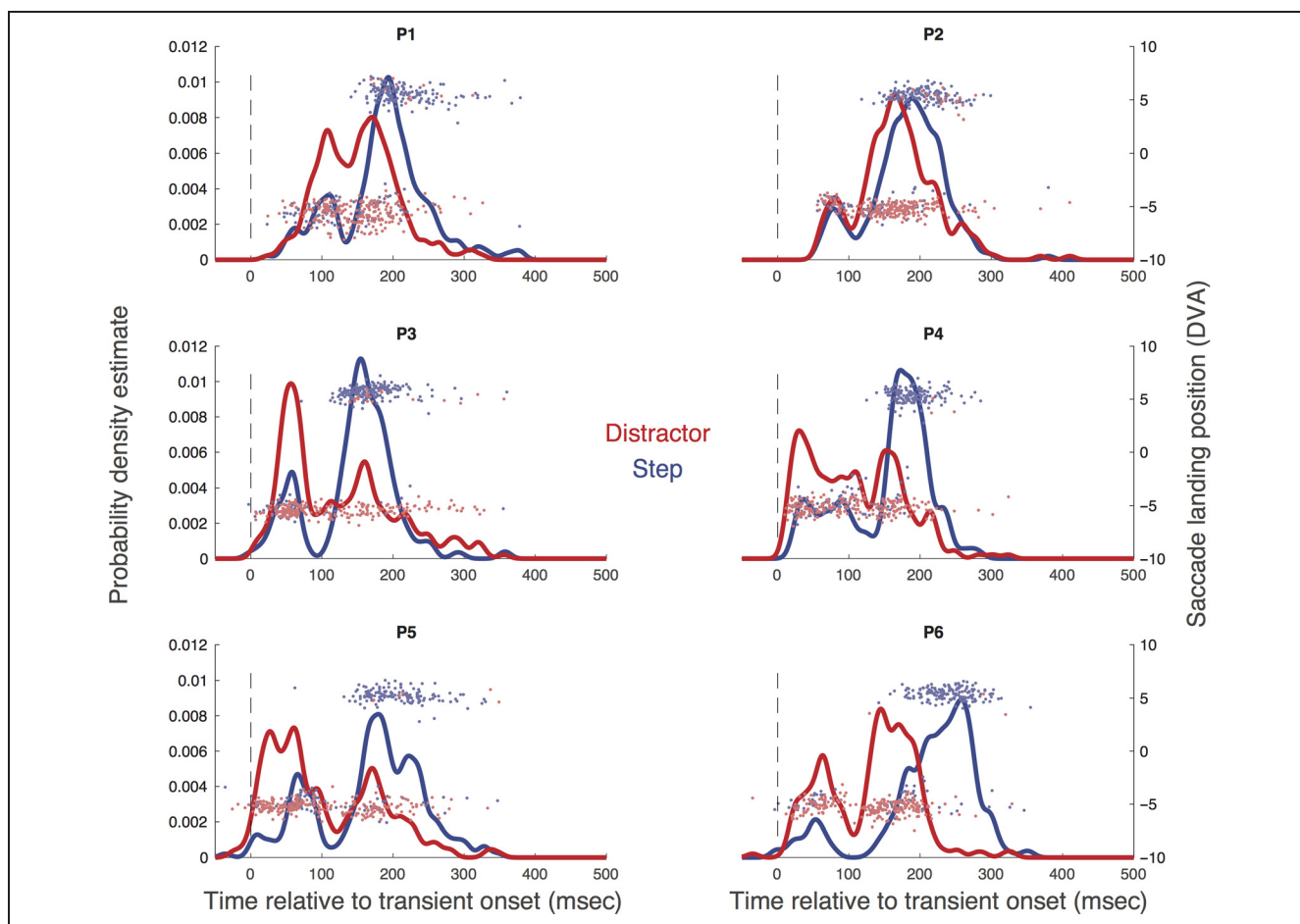
Figure 4. Each panel shows the probability density estimate derived from the raw data of each participant (P1–P6) in the distractor (red) and step (blue) conditions of Experiment 2. The horizontal components of the saccade landing positions are overlaid. Time on the *x* axis is coded relative to transient onset, rather than initial target onset, to reveal the time course of responses to the transient change.

the early part of the profile, and that the latter part of the profile is additionally shaped by reorienting behavior. Experiment 2 thus replicates the finding of saccadic inhibition in a double-step context, but additionally suggests some possible dissociability from the time course of reorienting.

Having demonstrated that saccadic inhibition occurs in double-step tasks, Experiment 3 is designed to ask whether inhibition plays a functional role in reorienting behavior by testing the counterintuitive idea that reorienting behavior might actually benefit from additional bottom–up interference, in the form a salient irrelevant flash. Moreover, because Experiment 3 manipulates reflexive inhibition (the occurrence of flash) and voluntary reorienting (the occurrence of a target step) without any differences in task instruction, it provides a firmer basis for assessing possible dissociations between the time courses of inhibition and reorienting.

Experiment 3

Figure 6 shows the distributions for each participant, with horizontal landing positions overlaid. There is a clear reduction in saccadic activity for all the conditions, within a common temporal window. Yet we can also observe consistent differences between conditions, which are clear from the inhibition profiles in Figure 7 and the individual parameters in Table 1. The latency of inhibition was lower in the flash and step-flash conditions than in the step condition, $t(5) = 6.27, p = .002; t(5) = 4.47, p = .007$, and inhibition began earlier in these conditions, $t(5) = 4.05, p < .01; t(5) = 3.48, p = .02$. By contrast, inhibition ended later in the step and step-flash conditions compared with the flash condition, $t(5) = 7.57, p = .001; t(5) = 3.96, p = .01$. These patterns strongly support the idea that the total inhibitory period during reorienting is a combination of an early bottom–up effect (driven by the salient visual change) and a sustained effect (driven by goal-related reorienting). The addition of the flash to the step manipulation boosts the early component, and the intention to reorient influences the later component.

Because the addition of the flash shifts the start of inhibition to an earlier moment, we can examine how this impacts upon reorienting behavior. The first thing to note is that there is no corresponding shift in the

Buonocore, Purokayastha, and McIntosh   2075
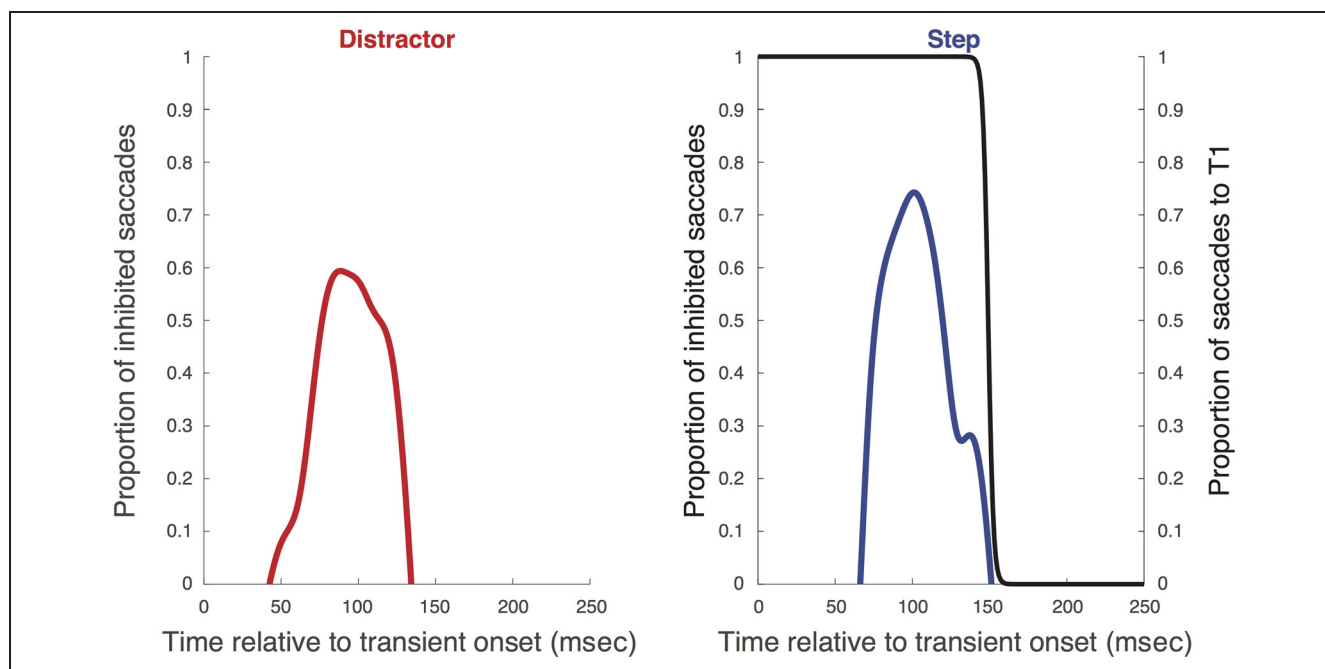
Figure 5. Group average time course of proportional inhibition derived from the saccadic inhibition analysis for distractor (red) and step (blue) conditions of Experiment 2. For the step condition, the black line represents the group average direction transition function (right y axis). Time on the x axis is coded relative to transient onset (i.e., positive numbers indicate saccades launched after distractor onset), rather than initial target onset, to reveal the time course of responses to the transient change.

direction transition function (average function in Figure 7; individual parameters in Table 2): The time course of reorienting is invariant across the shift in inhibition onset. Table 2 similarly shows that the median latency of reorienting to Target 2 was not reduced by the flash (if anything, there was a tendency toward an increase). This implies that saccadic inhibition does not facilitate faster reorienting to Target 2, but this does not mean that it has no functional benefit for reorienting behavior.

The most crucial data are the probabilities of Target 1 responses in step and step-flash conditions (i.e., the error rate), reflecting the overall proportion of saccades in which reorienting was unsuccessful. The probability of Target 1 responses is relatively high in the step condition (mean = 0.41, SD = 0.24), but significantly reduced in the step-flash condition (mean probability of Target 1 = 0.31, SD = 0.21), a difference that was seen in every participant, $t(5)$ = 6.78, p = .001. Reorienting thus becomes more reliable when inhibition is boosted by the flash. We infer that reflexive inhibition rapidly interrupts ongoing activity, allowing a higher proportion of saccades to be reprogrammed for the new target, yet without speeding their redirection.

DISCUSSION

Our experiments show that saccadic inhibition occurs in typical double-step tasks and that it promotes successful reorienting. In our critical third experiment, double-step

reorienting was improved by a distracting flash, coincident with the change in target position, even though the flash carried no spatial information about the target. However, although reoriented saccades were more likely after a flash, we did not find that they took any less time to emerge. Thus, oculomotor inhibition improves reorienting, but the benefit is quite specific: Inhibition helps to countermand the planned response at short latency, making an alternative response possible, but it does not speed the generation of that alternative response.

The short-latency inhibitory effect of a visual change is apparent across all conditions of our three experiments. The onset of inhibition is insensitive to the task relevance of a visual change but is modulated by its salience. In Experiment 3, the onset of inhibition was thus earlier in conditions with a salient flash (flash and step-flash conditions) than in the simple target step condition, consistent with a low-level reflexive response to the flash impacting on a time scale close to the minimum neural delays for the visual information to reach the superior colliculus (Rizzolatti, Buchtel, Camarda, & Scandolara, 1980). By contrast, the late, recovery portion of the inhibition profile was affected by the task context, with the offset of inhibition relatively later in conditions requiring reorienting, presumably because it takes longer to program a new saccade than to restore a prior plan. So, reflexive inhibition facilitates reorienting by automatically suppressing a planned saccade, but the generation of a replacement response depends on participant intentions and unfolds over a longer time scale.
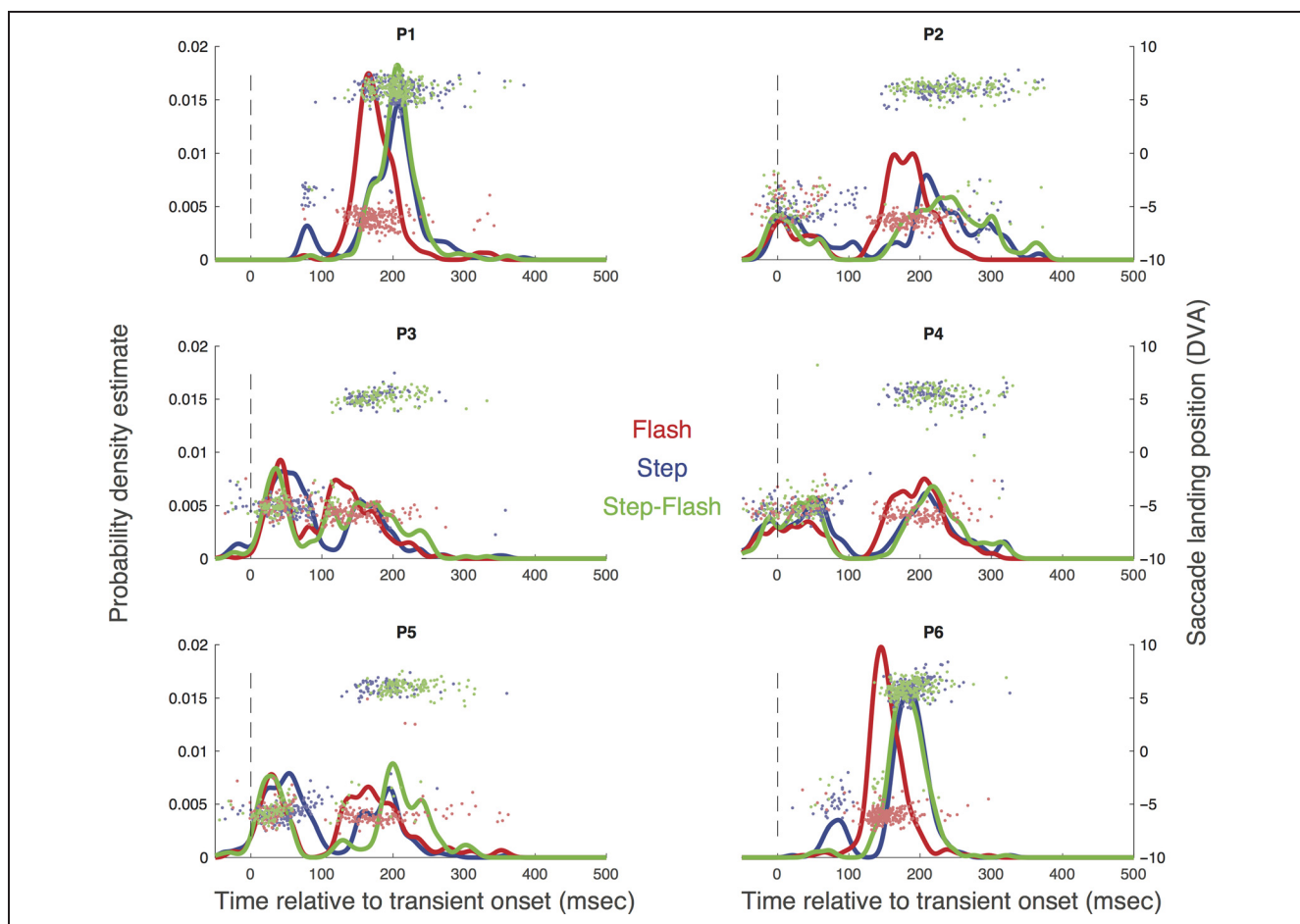
Figure 6. Each panel shows the probability density estimate derived from the raw data of each participant (P1–P6) in the flash (red), step (blue), and step-flash (green) conditions of Experiment 3. The horizontal components of the saccade landing positions are overlaid. Time on the *x* axis is coded relative to transient onset, rather than initial target onset, to reveal the time course of responses to the transient change.

These findings are consistent with a contemporary model of double-step behavior, which suggests that reorienting cannot succeed simply by activation of a replacement response but also requires a STOP process to countermand the initial planned response (Camalier et al., 2007; see also Bissett & Logan, 2013). This "independent horse race" model involves three processes: a GO process (GO1) accumulating activation to respond to the first target; a STOP process, triggered by the target step, accumulating activation to countermand the GO1 response; and a second GO process (GO2), also triggered by the target step, accumulating activation to respond to the new target. Within this model, each process develops independently of the others, except that the STOP process inhibits the GO1 process if it reaches threshold first. Note that this mutual independence implies that a GO2 response will not be speeded by a successful STOP process; it will just be more likely to occur because GO1 has been withdrawn from the race.

Applying this model to the present context, saccadic inhibition would be a rapidly rising STOP process, triggered by the target step, which countermands the initially planned (GO1) response whenever it reaches threshold first; on these occasions, the GO2 response will subsequently complete, and a reorienting saccade will follow. In our Experiment 3, the addition of a large flash, simultaneous with the target step, would selectively boost the STOP signal. This would raise the likelihood that the STOP process achieves threshold before GO1, reducing the frequency of Target 1 saccades and thereby increasing the frequency of Target 2 saccades, yet without speeding them (just as we observed). We can similarly apply the model to the differences between Experiments 1 and 2, in which all stimulus events were matched, except that the initial target persisted after the step in Experiment 2. This selective boosting of the GO1 process in Experiment 2 would make it less likely to be countermanded by STOP and thereby less likely to be superseded by GO2, so that inhibition would be reduced and reorienting less successful (again as we observed). Saccadic inhibition seems like a phenomenon ready-made for the role of STOP process in this independent race model.

But, although functional independence of STOP and GO processes may work within computational models of double-step behavior, mutual independence seems less plausible at the neurophysiological level. Reingold and
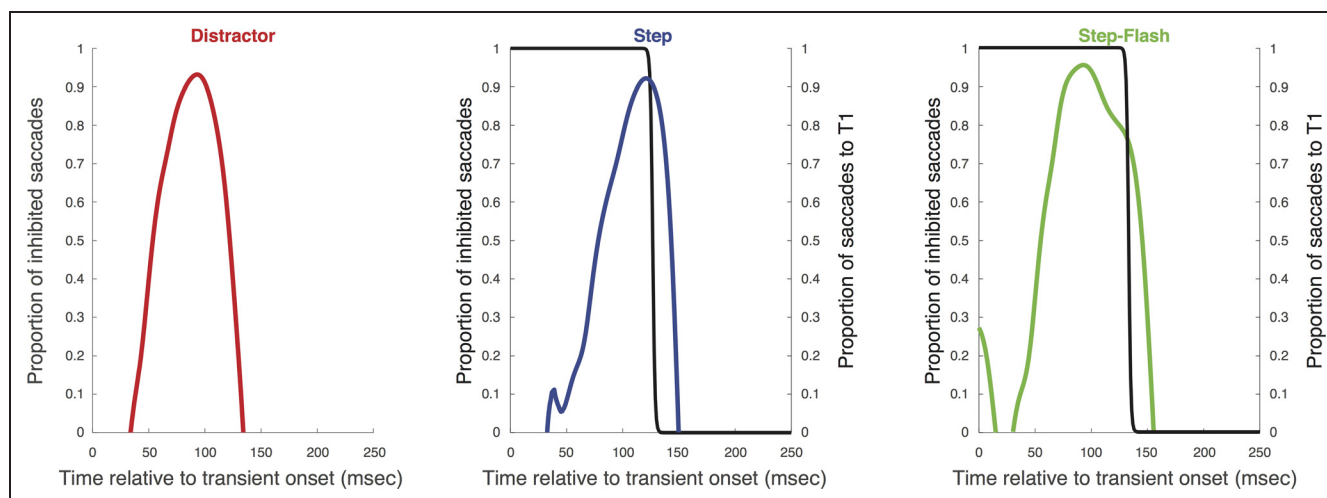
Figure 7. Group average time course of proportional inhibition derived from the saccadic inhibition analysis for flash (red), step (blue), and step-flash (green) conditions of Experiment 3. In the step and step-flash conditions, the black lines represent the group average direction transition function (right *y* axis). Time on the *x* axis is coded relative to transient onset, rather than initial target onset, to reveal the time course of responses to the transient change.

Stampe (2002) originally speculated that saccadic inhibition might arise from competitive interactions between populations of neurons, within the motor maps of the intermediate superior colliculus, building up activity for saccades to target and distractor locations (Olivier, Dorris, & Munoz, 1999). Dorris, Olivier, and Munoz (2007) subsequently confirmed that preparatory activity for an expected saccade target is decreased transiently by the onset of a distractor elsewhere in the visual field (nearby distractors can conversely facilitate build-up activity). Recently, a physiologically inspired model, incorporating long-range inhibition and local facilitation, has been found to simulate empirical patterns of saccadic inhibition with impressive accuracy (Bompas & Sumner, 2011, 2015).

Superior colliculus neurons thus show competitive interactions sufficient for causal involvement in saccade generation and countermanding (see also Paré & Hanes, 2003), though extrinsic connections may also be involved, particularly with FEF (Brown, Hanes, Schall, & Stuphorn, 2008; Hanes et al., 1998) and BG (Schmidt, Leventhal, Mallet, Chen, & Berke, 2013; Hikosaka, Takikawa, & Kawagoe, 2000). In addition, a more direct inhibitory effect may involve omnipause neurons in the brainstem, which gate the activity of saccade burst neurons and show spikes of activity time-locked to sudden visual changes (Missal & Keller, 2002; Everling, Paré, Dorris, & Munoz, 1998). This signal might delay the execution of a planned saccade, creating a pause in behavior, during which competitive interactions between target and distractor activity would have time to play out. The saccadic inhibition phenomenon might then result from a combination of competitive integration within the superior colliculus and saccade gating in the brainstem followed by top–down signals from cortical areas such as the FEF (Peel, Hafed, Dash, Lomber, & Corneil, 2016), promoting either reorienting or a reinstatement of the original plan.

How can we reconcile evidence for neural interactions among oculomotor STOP and GO signals, with an independent race model of double-step behavior? This "neural paradox" has been noted already within the response inhibition literature, and to address it, an interactive race model was proposed, which allows interactions between STOP and GO processes (Boucher, Palmeri, Logan, & Schall, 2007; Boucher, Stuphorn, Logan, Schall, & Palmeri, 2007). This interactive model produces behavior equivalent to that of the independent version, provided that the influence of the STOP process is brief and potent (Boucher, Palmeri, et al., 2007; see also Salinas & Stanford, 2013). This would be consistent with the character of saccadic inhibition, most of the latency of which is accounted for by afferent delays, implying a brief and potent inhibitory interaction. Frameworks thus exist for modeling response inhibition and response selection that allow underlying neural interactions while giving the appearance of independent processes at the behavioral level.

Conclusions

Saccadic inhibition is a reflexive phenomenon that follows whenever a visual change occurs while a saccade is planned, even if the change is known to be irrelevant (e.g., Buonocore & McIntosh, 2008; Reingold & Stampe, 2002). We suggest that it plays a crucial role in behavior, acting as a bottom–up brake that buys the time needed for voluntary processes to act. Reflexive inhibition follows a visual change at latencies too brief for voluntary control; the voluntary part is whether to subsequently recover the original plan (distractor context) or to switch to an alternative (double-step context). In a rapid behavioral system like the oculomotor one, saccadic inhibition may be a ubiquitous pause signal that provides the flexibility for voluntary behavior to emerge.

Acknowledgments

Note

1. Participant 6 in Experiment 1 completed only one session per condition.

REFERENCES

Aslin, R. N., & Shea, S. L. (1987). The amplitude and angle of saccades to double-step target displacements. *Vision Research, 27,* 1925–1942.

Becker, W., & Jürgens, R. (1979). An analysis of the saccadic system by means of double step stimuli. *Vision Research, 19,* 967–983.

Bissett, P. G., & Logan, G. D. (2013). Stop before you leap: Changing eye and hand movements requires stopping. *Journal of Experimental Psychology. Human Perception and Performance, 39,* 941–946.

Bompas, A., & Sumner, P. (2011). Saccadic inhibition reveals the timing of automatic and voluntary signals in the human brain. *Journal of Neuroscience, 31,* 12501–12512.

Bompas, A., & Sumner, P. (2015). Saccadic inhibition and the remote distractor effect: One mechanism or two? *Journal of Vision, 15,* 15.

Boucher, L., Palmeri, T. J., Logan, G. D., & Schall, J. D. (2007). Inhibitory control in mind and brain: An interactive race model of countermanding saccades. *Psychological Review, 114,* 376–397.

Boucher, L., Stuphorn, V., Logan, G. D., Schall, J. D., & Palmeri, T. J. (2007). Stopping eye and hand movements: Are the processes independent? *Perception and Psychophysics, 69,* 785–801.

Brown, J. W., Hanes, D. P., Schall, J. D., & Stuphorn, V. (2008). Relation of frontal eye field activity to saccade initiation during a countermanding task. *Experimental Brain Research, 190,* 135–151.

Buonocore, A., & McIntosh, R. D. (2008). Saccadic inhibition underlies the remote distractor effect. *Experimental Brain Research, 191,* 117–122.

Buonocore, A., & McIntosh, R. D. (2012). Modulation of saccadic inhibition by distractor size and location. *Vision Research, 69,* 32–41.

Buonocore, A., & McIntosh, R. D. (2013). Attention modulates saccadic inhibition magnitude. *Quarterly Journal of Experimental Psychology, 66,* 1051–1059.

Buonocore, A., McIntosh, R. D., & Melcher, D. (2016). Beyond the point of no return: Effects of visual distractors on saccade amplitude and velocity. *Journal of Neurophysiology, 115,* 752–762.

Camalier, C. R., Gotler, A., Murthy, A., Thompson, K. G., Logan, G. D., Palmeri, T. J., et al. (2007). Dynamics of saccade target selection: Race model analysis of double step and search

step saccade production in human and macaque. *Vision Research, 47,* 2187–2211.

Dorris, M. C., Olivier, E., & Munoz, D. P. (2007). Competitive integration of visual and preparatory signals in the superior colliculus during saccadic programming. *Journal of Neuroscience, 27,* 5053–5062.

Edelman, J. A., & Xu, K. Z. (2009). Inhibition of voluntary saccadic eye movement commands by abrupt visual onsets. *Journal of Neurophysiology, 101,* 1222–1234.

Everling, S., Paré, M., Dorris, M. C., & Munoz, D. P. (1998). Comparison of the discharge characteristics of brain stem omnipause neurons and superior colliculus fixation neurons in monkey: Implications for control of fixation and saccade behavior. *Journal of Neurophysiology, 79,* 511–528.

Findlay, J. M., & Harris, L. R. (1984). Small saccades to double-stepped targets moving in two dimensions. *Advances in Psychology, 22,* 71–78.

Findlay, J. M., & Walker, R. (1999). A model of saccade generation based on parallel processing and competitive inhibition. *Behavioral and Brain Sciences, 22,* 661–721.

Hanes, D. P., Ii, W. F. P., Schall, J. D., Doug, W. F., Patterson, W. F., & Schall, J. D. (1998). Role of frontal eye fields in countermanding saccades: Visual, movement, and fixation activity. *Journal of Neurophysiology, 79,* 817–834.

Hikosaka, O., Takikawa, Y., & Kawagoe, R. (2000). Role of the basal ganglia in the control of purposive saccadic eye movements. *Physiological Reviews, 80,* 953–978.

Lisberger, S. G., Fuchs, A. F., King, W. M., & Evinger, L. C. (1975). Effect of mean reaction time on saccadic responses to two-step stimuli with horizontal and vertical components. *Vision Research, 15,* 1021–1025.

Ludwig, C. J. H., Mildinhall, J. W., & Gilchrist, I. D. (2007). A population coding account for systematic variation in saccadic dead time. *Journal of Neurophysiology, 97,* 795–805.

McIntosh, R. D., & Buonocore, A. (2014). Saccadic inhibition can cause the remote distractor effect, but the remote distractor effect may not be a useful concept. *Journal of Vision, 14,* 15.

Missal, M., & Keller, E. L. (2002). Common inhibitory mechanism for saccades and smooth-pursuit eye movements. *Journal of Neurophysiology, 88,* 1880–1892.

Olivier, E., Dorris, M. C., & Munoz, D. P. (1999). Lateral interactions in the superior colliculus, not an extended fixation zone, can account for the remote distractor effect. *Behavioral and Brain Sciences, 22,* 694–695.

Paré, M., & Hanes, D. P. (2003). Controlled movement processing: Superior colliculus activity associated with countermanded saccades. *Journal of Neuroscience, 23,* 6480–6489.

Peel, T. R., Hafed, Z. M., Dash, S., Lomber, S. G., & Corneil, B. D. (2016). A causal role for the cortical frontal eye fields in microsaccade deployment. *PLoS Biology, 14,* e1002531.

Reingold, E. M., & Stampe, D. M. (1999). Saccadic inhibition in complex visual tasks. In W. Becker, H. Deubel, & T. Mergner (Eds.), *Current oculomotor research* (pp. 249–255). Boston: Springer US.

Reingold, E. M., & Stampe, D. M. (2000). Saccadic inhibition and Gaze Contingent Research Paradigms. In A. Kennedy, R. Radach, D. Heller, & J. Pynte (Eds.), *Reading as a Perceptual Process* (pp. 119–145). Oxford: Elsevier.

Reingold, E. M., & Stampe, D. M. (2002). Saccadic inhibition in voluntary and reflexive saccades. *Journal of Cognitive Neuroscience, 14,* 371–388.

Reingold, E. M., & Stampe, D. M. (2003). Using the saccadic inhibition paradigm to investigate saccadic control in reading.

In J. Hyönä, R. Radach & H. Duebel (Eds.), *The Mind's Eye* (pp. 347–360). Amsterdam: Elsevier.

Reingold, E. M., & Stampe, D. M. (2004). Saccadic inhibition in reading. *Journal of Experimental Psychology: Human Perception and Performance, 30,* 194–211.

Rizzolatti, G., Buchtel, H. A., Camarda, R., & Scandolara, C. (1980). Neurons with complex visual properties in the superior colliculus of the macaque monkey. *Experimental Brain Research, 38,* 37–42.

Salinas, E., & Stanford, T. R. (2013). The countermanding task revisited: Fast stimulus detection is a key determinant of psychophysical performance. *Journal of Neuroscience, 33,* 5668–5685.

Schmidt, R., Leventhal, D. K., Mallet, N., Chen, F., & Berke, J. D. (2013). Canceling actions involves a race between basal ganglia pathways. *Nature Neuroscience, 16,* 1118–1124.

Sheliga, B. M., Brown, V. J., & Miles, F. A. (2002). Voluntary saccadic eye movements in humans studied with a double-cue paradigm. *Vision Research, 42,* 1897–1915.

Walker, R., Kentridge, R. W., & Findlay, J. M. (1995). Independent contributions of the orienting of attention, fixation offset and bilateral stimulation on human saccadic latencies. *Experimental Brain Research, 103,* 294–310.

Weber, H., & Fischer, B. (1994). Differential effects of non-target stimuli on the occurrence of express saccades in man. *Vision Research, 34,* 1883–1891.