J Neurophysiol 101: 580–590, 2009.
First published November 19, 2008; doi:10.1152/jn.90891.2008.

A "Gap Effect" on Stop Signal Reaction Times in a Human Saccadic Countermanding Task

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Submitted 7 August 2008; accepted in final form 12 November 2008

Stevenson SA, Elsley JK, Corneil BD. A "Gap effect" on stop signal reaction times in a human saccadic countermanding task. *J Neurophysiol* 101: 580–590, 2009. First published November 19, 2008; doi:10.1152/jn.90891.2008. The "gap effect" describes a phenomenon whereby saccadic reaction times are expedited by the removal of a visible fixation point prior to target presentation. Here we investigated whether processes controlling saccade cancellation are also subjected to a gap effect. Human subjects performed a countermanding experiment that required them to try to cancel an impending saccade in the presence of an imperative visual stop signal, across different fixation conditions. We found that saccadic cancellation latencies, estimated via derivation of the stop signal reaction time (SSRT), were ~40 ms shorter on trials with a 200-ms gap between fixation point removal and target presentation compared with when the fixation point remained illuminated. Follow-up experiments confirmed that the reduction in SSRTs were primarily due to removal of a foveal fixation point (as opposed to a generalized warning effect) and persisted with an auditory stop signal that controlled for potential differences in stop signal saliency across different fixation conditions. Saccadic RTs exhibited a gap effect in all experiments with reductions in RTs being due to both removal of a foveal fixation point and a generalized warning effect. Overall, our results demonstrate that processes controlling saccade cancellation can be expedited by a 200-ms gap. The simultaneous priming of both saccade cancellation and generation is of particular interest considering the mutually antagonistic relationship between the saccade fixation and generation networks in the oculomotor system.

INTRODUCTION

Foveal vision necessitates a selection process to help determine the relevance of potential saccade locations. Inherent to this selection process is the ability to withhold saccades to stimuli that become irrelevant or inappropriate in a changing behavioral context. The countermanding paradigm, which was initially applied to hand or limb movements (Logan 1994; Logan and Cowan 1984), permits study of such inhibitory control of movement. An oculomotor version of the countermanding task requires the subject try to cancel saccades to a peripheral target in the presence of an imperative stop signal (Hanes and Schall 1995). Performance in a countermanding trial has been conceptualized as a race between a go process dictating saccade generation (initiated on target presentation) and a stop process dictating saccade suppression (initiated on stop signal presentation). The performance on a given trial depends on the outcome of this race, with a saccade being generated or withheld if the go or stop process wins the race, respectively (Fig. 1) (Logan 1994; Logan and Cowan 1984). The countermanding paradigm has become increasingly popular for at least two reasons. First, analysis across multiple trials permits estimation of the duration of the stop process through derivation of a metric called the stop-signal reaction time (SSRT), even though this process cannot be directly observed (Fig. 1*B*) (Logan 1994; Logan and Cowan 1984). Second, it provides a formalized framework in which to interpret neural activity related to the immediate control of movement (Aron and Poldrack 2006; Brown et al. 2008; Curtis et al. 2005; Emeric et al. 2008; Hanes and Schall 1996; Paré and Hanes 2003; Stuphorn et al. 2000).

A number of manipulations influence the distribution of reaction times (RTs) (i.e., the rate of completion of the go process) in simple saccade tasks. The "gap effect" describes the generalized reduction in saccadic RTs observed when a central fixation point is removed prior to the presentation of a peripheral target. A maximal reduction in RTs occurs with a gap of ~200 ms (Dorris and Munoz 1995; Fischer 1987; Munoz et al. 2000; Saslow 1967). Multiple components contribute to the gap effect, including the benefit afforded by warning of impending target presentation (a "warning" component) and by disengaging fixation via removal of a foveal stimulus (a "foveal" component) (Fendrich et al. 1999; Forbes and Klein 1996; Juttner and Wolf 1992; Kingstone and Klein 1993; Paré and Munoz 1996; Pratt et al. 2000; Reuter-Lorenz et al. 1995; Ross and Ross 1980, 1981; Taylor et al. 1998).

Here we investigate whether the introduction of a 200-ms gap prior to target presentation influences the SSRT (i.e., the rate of completion of the stop process). Based on previous results in the literature, two outcomes seem possible. First, because of the assumed independence of the go and stop processes, one could predict that SSRTs will be unaffected by a 200-ms gap. In support of this, simultaneous target presentation and fixation point removal (i.e., a gap duration of 0 ms) expedites the duration of the go process without influencing the duration of the stop process (Morein-Zamir and Kingstone 2006). Second, a manipulation that decreases the duration of the go process may increase the duration of the stop process. This reasoning is based on the mutually antagonistic relationship between the saccade generation and saccade fixation networks throughout the oculomotor system (Findlay and Walker 1999; Meredith and Ramoa 1998; Munoz and Istvan 1998; Scudder et al. 2002; Sparks 2002) and on results that suggest a moderate interaction between the go and stop pro-

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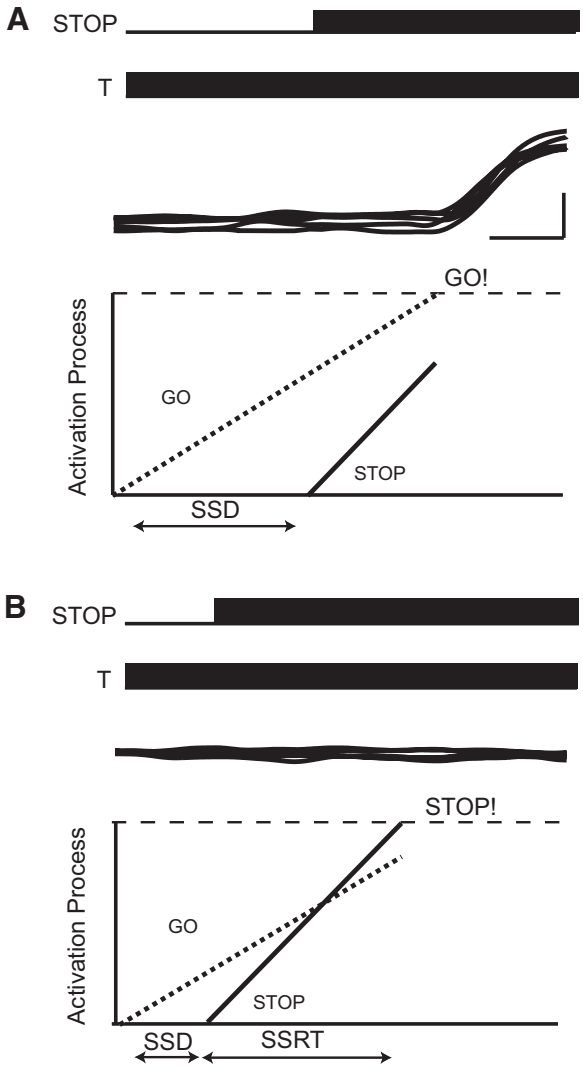

FIG. 1. Schematic drawing of the race model where stochastically independent go and stop processes race toward a common threshold with the outcome of this race determining which response is generated. The go process begins with target onset, whereas the stop process begins with the onset of the stop signal. The time between target and stop signal presentation is the stop signal delay (SSD), which can vary from trial to trial. *A*: the go process starts sufficiently early to beat the stop process to threshold, and hence a saccade is generated. *B*: the go process begins, but the stop process beats the go process to threshold, resulting in the cancellation of a saccade. Electrooculographic (EOG) traces are taken from 1 representative subject to contrast the 2 possible outcomes of the race model (*x* and *y* axes represent 50 ms and 5° saccade amplitude, respectively).

cesses (Boucher et al. 2007a; Ozyurt et al. 2003). In support of this alternative, recent results have reported that SSRTs for arm movements increase with the introduction of a 200-ms gap (Mirabella et al. 2009).

To study the influence of a 200-ms gap on saccade control, we had human subjects perform a variety of countermanding tasks. In the first experiment, the fixation point either remained illuminated during target presentation (an overlap condition) or disappeared 200 ms prior to target presentation (a gap condition). Contrary to both predictions laid out in the preceding text, SSRTs were *shorter* in the gap condition. A series of two follow-up experiments confirmed the consistency of this effect and identified that this reduction was due more to the removal of a foveal visual stimulus rather than a generalized warning effect and was present for both visual and auditory stop signals.

Portions of this manuscript have been published in abstract form (Stevenson et al. 2007).

METHODS

A total of nine different subjects (ages: 22–35; 2 female) participated in at least one of three variants of the countermanding task after providing their informed written consent. Subjects reported no history of neurological or musculoskeletal disorders, and all had normal or corrected-to-normal vision. Experimental procedures were approved by the University Research Ethics Board for Health Science Research at the University of Western Ontario in accordance with the ethical standards established in the 1964 Declaration of Helsinki. Three subjects (*s1–s3*) were the authors and hence were knowledgeable about the specific goals of the experiment. The remaining subjects were naïve. Subjects were instructed beforehand on the nature of the countermanding task but were not given any feedback during the experiment. All subjects generated qualitatively similar trends in the data. Subjects were seated upright in a straight-back chair in a dark experimental room. The room was compartmentalized by a double layer of thick dark curtains that spanned from floor to ceiling, attenuating the residual illumination given off by the experimental equipment. The visual stimuli consisted of three tri-color light-emitting diodes (LEDs; which could be illuminated red and/or green) embedded within boxes mounted on wooden stands positioned 1.2 m in front of the subject. All LEDs were elevated 1.2 m off the ground to lie on the horizontal meridian from the subject's perspective. One LED was positioned directly in front of the subject to serve as the central fixation point (FP). Two target LEDs were fixed at a radial angle of 10° to the left or right of the FP. Two of the three variants of the countermanding task (see following text) involved an auditory stimulus. The speaker was placed directly behind the subject and consisted of a broadband burst (77 dB) of noise powered by a 5-V TTL pulse.

Countermanding task

Subjects performed three variants of an oculomotor countermanding task. All three variants of the task required subjects to look to visual targets on *control* trials and attempt to maintain fixation on *stop* trials in the presence of a stop signal. Control and stop trials were intermixed, and within the stop trials, we varied the timing of presentation of the stop signal relative to the target [the stop-signal delay (SSD)]. All aspects of the task were controlled by a customized LABVIEW program downloaded onto a PXI box (National Instruments), which controlled the experiment at a rate of 1 kHz. Subjects performed a series of practice trials before the experimental data were collected. Subjects were instructed to look as quickly as possible to the presented target and to try not to move when the stop signal appeared.

Experiment 1

In the first experiment, we investigated the influence of a 200-ms gap on both the go and stop processes. To do this, we introduced two fixation conditions, gap and overlap, and investigated subject performance on both control and stop trials. Within a block of 200 trials, all possible permutations of fixation condition (gap vs. overlap), trial type (control vs. stop), and target direction (left vs. right) were randomly interleaved. Within the stop trials, the possible SSDs were varied equally among six possible values, ranging between 0 to 250 ms in 50-ms steps. Six of the nine total subjects performed a series of six blocks of 200 trials each over two sequential days with 30% of these trials being stop trials.

All trial types started with the illumination of the central FP for an interval selected randomly between values of 1,000, 1,166, 1,333, and

1,500 ms. In the gap condition, the FP was then extinguished for 200 ms, followed by target presentation to the left or right for 1,000 ms. In the overlap condition, the FP remained illuminated during target presentation (overall trial duration remained the same as in the gap condition by adding an additional 200 ms to FP illumination; Fig. 2*A*). On control trials, subjects simply made a saccade to the target. On stop trials in the gap condition, the stop signal consisted of a re-illumination of the green central FP (recall that the central FP is a tri-color LED that can be either red and/or green; Fig. 2*A*). On stop trials in the overlap condition, the stop signal consisted of a color change of the central FP from red to green (Fig. 2*A*). The stop signal remained illuminated for the duration of the trial, and trials were separated by an intertrial interval of 500–1,000 ms.

Experiment 2

In the second experiment, we introduced a third fixation condition to test the influence of a warning cue on subject performance. In this "auditory" condition, an auditory stimulus accompanied FP presentation at the start of the trial but was turned off 200 ms prior to target presentation (the FP remained illuminated for the entire trial; Fig. 2*B*). The overlap and gap conditions were run as in *experiment 1,* and all three fixation conditions were interleaved with the different trial types and target locations. Within stop trials, SSDs were varied over a range of 250 ms in 50-ms steps (6 SSDs total) with SSD ranging from either 0 to 250 or 100 to 350 ms for different subjects. Five of the nine subjects participated in this experiment, performing six blocks of 210 trials each. Within each block, 35% of trials were stop trials.

Experiment 3

In the third experiment, we used an auditory cue as a stop signal to test the influence of a nonfoveal stop signal. All aspects of this experiment were the same as in *experiment 1* (i.e., overlap and gap conditions) excepting the use of an auditory stop signal instead of a visual stop signal (Fig. 2*C*). Five of the nine subjects participated in this experiment, with the SSDs ranging between 0 to 200 ms in 40-ms steps for four subjects, and from 0 to 250 in 50-ms steps for one subject. Within each block, 30% of the 200 trials were stop trials, and subjects performed a total of six blocks over two sequential days.

Calculation of SSRTs

The main goal of this experiment is to compare estimates of the duration of the stop process (SSRT) across fixation conditions. Briefly, the SSRT is a derived parameter that estimates the amount of time required to cancel a planned movement. Here we used two methods of calculating the SSRT: the integration method and the mean method (Hanes and Schall 1995; Logan 1994). Calculating this parameter via the integration method requires both the inhibition function (see Fig. 3 for examples of inhibition functions) from stop trials and the cumulative RT distribution functions (CDF) from control trials. The SSRT is estimated at each SSD by first finding the probability of making a saccade from the inhibition function for that SSD, then running the integral from zero to that probability in the control trial CDF. The SSRT is then estimated by subtracting the SSD from this value (Logan 1994). SSRTs were only calculated at SSDs where the probability of a saccade ranged between 0.1 and 0.9 to capture the linear portion of the inhibition function and cumulative RT distributions.

The mean method for estimating SSRTs assumes that the SSRT for a given subject will be the same regardless of the SSD. While this assumption seems unlikely to be true, violations of this assumption do not significantly affect the validity of the race model (Logan 1994). The mean method for calculating SSRTs simply takes the difference between the mean saccadic RT and the mean of the inhibition function (Hanes and Schall 1995), using a rescaling factor as suggested by Logan (1994) because *P*(saccade) does not always range between 0 and 1.

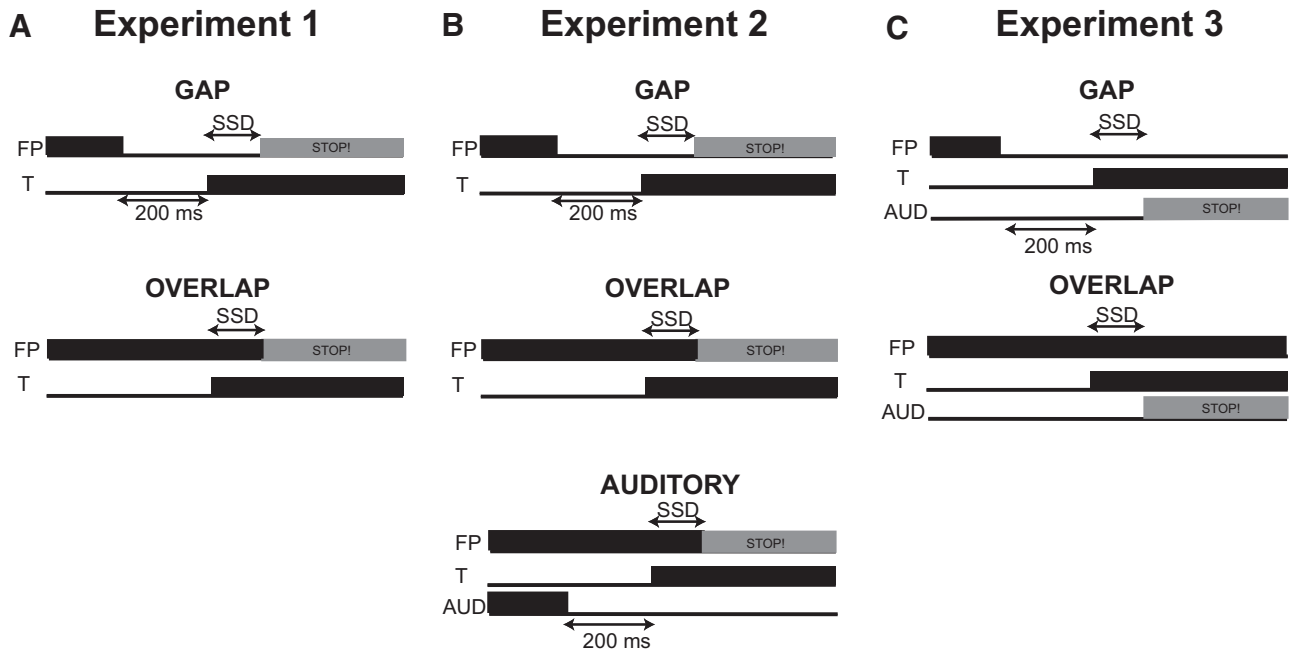

FIG. 2. Schematic drawing of stop trials used in the 3 experiments, which composed 30–35% of all trials. *A*: *experiment 1* used 2 fixation conditions: gap and overlap. The gap condition involves the disappearance of a central fixation point (FP) 200 ms prior to target onset while the FP remains illuminated for the duration of the trial in the overlap condition. On stop trials, after a given SSD, the FP reappears as a green FP (gap) or simply changes color to green (overlap). *B*: in *experiment 2,* we introduced a 3rd condition, the auditory condition, where an auditory cue accompanied FP onset and was extinguished 200 ms prior to target onset while the FP remains illuminated throughout the trial. On stop trials, after a given SSD, the FP changes color, similar to the overlap condition. *C*: in *experiment 3,* gap and overlap conditions were used as in *experiment 1,* but the stop signal consisted of a remote auditory tone.

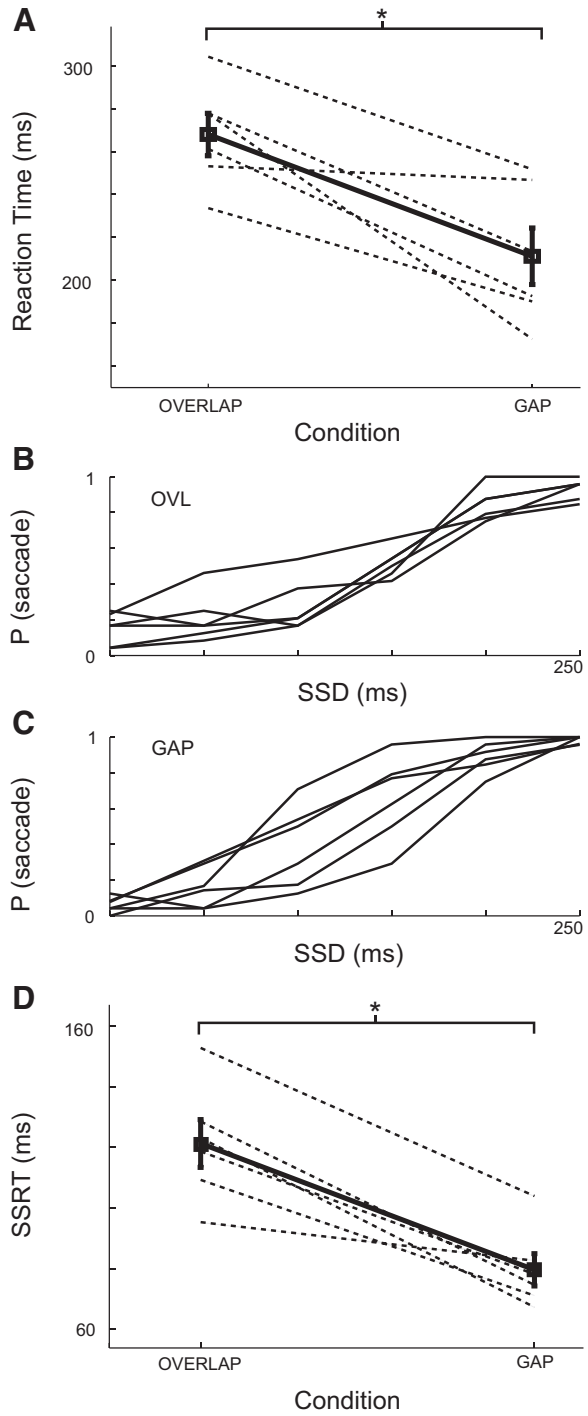

FIG. 3. Results from *experiment 1*. *A*: reaction time (RT) results for control trials for each subject (- - -) and the sample mean (■ and —e) on overlap and gap conditions. A significant gap effect of ~50 ms was seen across the sample with a reduction in RTs observed in all 6 subjects. *B* and *C*: inhibition functions for each subject in overlap (*B*) and gap (*C*) conditions, indicating the probability of making a saccade [*P*(saccade)] at a given SSD. *P*(saccade) increased with increasing SSD. *D*: mean stop signal RTs (SSRTs) from combining the estimates from the integration and mean methods on overlap and gap conditions for each subject (- - -) and the sample mean (■ and —). A consistent gap effect of ~40 ms was seen across the sample, with reductions in SSRT occurring for all 6 subjects. *, $P < 0.05$ using paired *t*-test. Error bars represent SE.

Data collection and analysis

Bi-temporal DC electrooculography (EOG) was used to measure horizontal eye movements and signals were filtered and amplified with a P122 AC/DC preamplifier (Grass Instruments). Horizontal eye movements were filtered (100 Hz, low-pass), amplified, and digitized at a rate of 1 kHz onto the PXI controller. Digitized data were then transferred to a PC computer and subsequent off-line analyses were performed using customized Matlab (the Mathworks) programs. Movement onsets and offsets were identified by an automarking program, which detected crossings of velocity thresholds (50°/s; velocities were filtered with a low-pass Butterworth filter with fs/fc <17). Eye movements were analyzed via a customized Matlab Graphical User Interface permitting the data analyst to check for errors and ensure consistency. Saccadic RTs, inhibition functions, and SSRTs were calculated off-line and saved for further analyses. Trials where RTs were <80 ms were classified as anticipatory and were excluded from analysis (Corneil and Munoz 1996). Trials with RTs >800 ms were also excluded due to lack of subject alertness. Less than 1% of all trials were excluded with these two criteria. RT and SSRT comparisons for *experiments 1* and *3* utilized paired *t*-tests, whereas *experiment 2* (with three fixation conditions) utilized a one-way repeated-measures ANOVA with a Bonferroni post hoc correction test for multiple comparisons. Differences in RTs and SSRTs across fixation conditions for individual subjects utilized two way *t*-tests.

RESULTS

Within each experiment, we will first present the results from control trials to confirm that subject performance was consistent with previous reports and then describe subject performance on stop trials.

Experiment 1

The six subjects participating in *experiment 1* generated a total of 4,580 control trials, split equally across gap and overlap fixation conditions. We found a robust influence of fixation condition on the RTs with RTs being significantly shorter in the gap condition across all subjects (Fig. 3*A*, Table 1; $P < 0.05$; paired *t*-test). The difference between RTs in the overlap and gap conditions (i.e., the gap effect) has been studied extensively (see Munoz et al. 2000 for review) and in our subjects ranged from 6 to 105 ms [gap effect: 57 ± 32 (SD) ms; the reduction in RTs was significant ($P < 0.05$, 2-way *t*-test) in all 6 subjects].

Logically it should become progressively more difficult to suppress a saccade for more delayed stop signals. Subject performance on stop trials varied in this straightforward fashion depending on the SSD. For each subject, we constructed inhibition functions that describe the probability of generating a saccade as a function of SSD. Separate inhibition functions were constructed for data obtained from gap (Fig. 3*B*) and overlap conditions (Fig. 3*C*) and from these inhibition functions it is apparent that the probability of making saccades (i.e., "noncancelled" trials) increased for progressively longer SSDs.

With the integration method, we observed a gap effect on SSRTs in five of our six subjects in that the SSRTs for these five subjects were shorter in the gap versus overlap condition. In the sixth subject, SSRTs were approximately equal across fixation conditions. Overall the gap effect on SSRTs estimated by the integration method ranged from −3 to 68 ms (45 ± 27 ms; $P < 0.01$; paired *t*-test). Consistent with the integration method, we found a gap effect on SSRTs calculated via the

TABLE 1. *Reaction times from control trials and stop signal reaction times estimated from stop trials for all experiments and all subjects*

	Experiment 1				*Experiment 2*						*Experiment 3*			
	RT_O	RT_G	$SSRT_O$	$SSRT_G$	RT_O	RT_A	RT_G	$SSRT_O$	$SSRT_A$	$SSRT_G$	RT_O	RT_G	$SSRT_O$	$SSRT_G$
S1	261 ± 38	193 ± 43	119	78	289 ± 44	254 ± 43	172 ± 44	140	129	89				
S2	278 ± 59	214 ± 40	123	67	273 ± 46	256 ± 61	197 ± 37	139	144	93	296 ± 59	218 ± 63	180	142
S3					393 ± 46	372 ± 68	324 ± 69	164	129	85	337 ± 71	229 ± 82	220	178
S4	304 ± 50	252 ± 42	153	104	315 ± 51	304 ± 54	270 ± 43	151	141	107	323 ± 57	254 ± 53	176	155
S5	278 ± 51	173 ± 42	129	75	313 ± 61	301 ± 39	213 ± 37	156	151	105				
S6	234 ± 73	190 ± 69	109	71										
S7	253 ± 41	247 ± 50	95	83										
S8											378 ± 85	261 ± 105	216	175
S9											358 ± 64	293 ± 66	188	148
Mean	268 ± 24	212 ± 32	121 ± 20	80 ± 13	317 ± 46	297 ± 48	235 ± 61	150 ± 11	139 ± 10	96 ± 10	338 ± 32	251 ± 29	196 ± 21	159 ± 16

Values are means ± SD. Stop signal reaction times (SSRTs) are the average of the estimates derived from the integration and mean methods. The subscripts *O, G,* and *A* denote overlap, gap, and auditory fixation conditions, respectively. RT, reaction time.

mean method in all six subjects (38 ± 11 ms; range: 27 to 52 ms; $P < 0.01$; paired *t*-test).

The integration and mean methods yield equally valid estimates for SSRTs (Logan and Cowan 1984). Accordingly, we combined these estimates to yield an average SSRT for each subject for each fixation condition (Table 1; Fig. 3*D*). On averaging, a consistent gap effect was observed in all subjects (42 ± 16 ms; range: 12 to 56 ms; paired *t*-test, $P < 0.05$). Together, these data suggest that completion of the stop process can be expedited in the human countermanding task by a 200-ms gap.

Experiment 2

Previous studies have established that the reduction in RTs observed during the gap effect is due to both a warning component (as FP disappearance serves as a cue for impending target presentation) and a foveal component (as FP disappearance removes a visual stimulus from the fovea; see INTRODUCTION). Motivated by the surprising results from *experiment 1, experiment 2* investigates whether the gap effect on SSRTs can be similarly decomposed into a warning and foveal component. Accordingly, we added a third fixation condition, the auditory condition, which provides a warning signal independent of a foveal component (Fig. 2*B*). Any differences in RTs or SSRTs between overlap and auditory conditions would be due to the warning component because neither involves the loss of visual fixation and only the auditory condition has a warning component. Conversely, any differences between auditory and gap conditions would be due to the foveal component since both conditions have warning components, whereas only the gap condition involves the removal of a foveal stimulus.

A total of 5,762 control trials, distributed equally among the overlap, auditory, and gap conditions were analyzed in five subjects. As shown in Fig. 4*A* and Table 1, we again observed a significant gap effect across the sample (comparing RTs in overlap and gap condition; 81 ± 27 ms; range: 45–117 ms; significance assessed by ANOVAs on RTs across all 3 fixation conditions, followed by Bonferroni-corrected post hoc *t*-test; $P < 0.01$) and within all subjects (2-way *t*-test $P < 0.05$). This gap effect was composed of both a warning component (overlap vs. auditory conditions) which ranged from 11 to 35 ms (20 ± 9 ms; $P < 0.05$), and a foveal component (auditory vs. gap conditions) which ranged from 35 to 88 ms (62 ± 22 ms; $P < 0.01$).

As in *experiment 1,* subjects had more noncancelled saccades on stop trials with longer SSDs. Inhibition functions for each subject were constructed for data obtained from gap (Fig. 4*B*), auditory (Fig. 4*C*), and overlap (Fig. 4*D*) conditions. SSRT calculations yielded a significant gap effect (i.e., SSRTs were shorter on gap vs. overlap conditions) for all subjects regardless of which method was used [integration method: 48 ± 5 ms, range: 43–55 ms ($P < 0.01$); mean method: 60 ± 32 ms, range: 36-116ms ($P < 0.05$)]. We also found a significant foveal effect (auditory vs. gap conditions) on SSRTs for all subjects regardless of the method of SSRT calculation [integration method: 43 ± 10 ms, range: 29–54 ms ($P < 0.01$); mean method: 43 ± 9 ms, range: 29–52 ms ($P < 0.01$)]. However, we did not observe a consistent warning effect (overlap vs. auditory) on SSRTs with either method [integration method: 5 ± 18 ms, range: −5–22 ms ($P = 0.35$); mean method: 17 ± 30, range: −5–69 ms ($P = 0.27$)], with auditory SSRTs being shorter in only three of the five subjects for each method.

On averaging SSRT estimates, a gap effect was observed for all five subjects [54 ± 14 ms; range: 44–79 ms ($P < 0.01$); Fig. 4*E,* Table 1]. A foveal component was also observed in all subjects [43 ± 9 ms; range: 30–51 ms ($P < 0.01$); Fig. 4*E,* Table 1]. However, we did not observe a significant warning component, even though modest reductions in SSRTs were observed in four of five subjects [11 ± 14 ms; range: −5–35 ms ($P = 0.17$); Fig. 4*E,* Table 1].

In summary, we found that the foveal and warning components each contribute significantly to the gap effect on RTs (Fig. 4*A,* Table 1), whereas only the foveal component contributes significantly to the gap effect on SSRTs (Fig. 4*E,* Table 1).

Experiment 3

Experiments 1 and *2* provide strong evidence for the priming of the stop process in the gap condition versus the overlap condition. However, the reappearance of the FP as a stop signal in the gap condition in both experiments could be perceived as a more salient stop signal than the color change in the overlap condition. A potential difference in stop signal saliency could confound our results because SSRTs have been shown to be shorter for more intense stop signals (Hanes and Carpenter 1999). To avoid this potential confound, in *experiment 3,* we presented a remote auditory stop signal in both gap and overlap

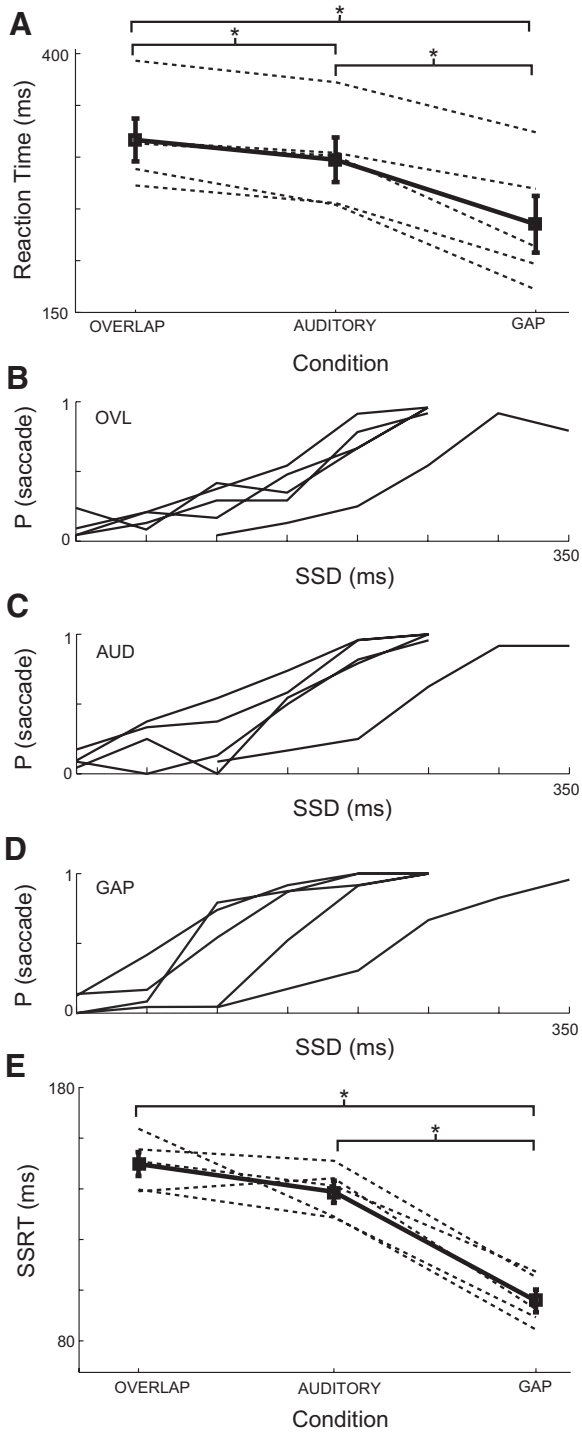

FIG. 4. Results from *experiment 2*. Same format as Fig. 3. *A*: a significant gap effect of ~82 ms was seen across the sample with RT reductions occurring in all 5 subjects. Significant warning (~20 ms) and foveal (~62 ms) effects were also observed for all 5 subjects. *B–D*: inhibition functions for each subject in the various fixation conditions. *E*: SSRTs for the 3 fixation conditions. A significant gap effect of ~50 ms was observed. No significant warning effect is observed, but a significant foveal effect (~40 ms) was observed for all 5 subjects. *, $P < 0.05$ using repeated-measures ANOVA followed by Bonferroni post hoc correction test for multiple comparisons.

conditions. Remote auditory stop signals have been used extensively in saccadic countermanding (Aron and Poldrack 2006; Cabel et al. 2000; Colonius et al. 2001; Curtis et al. 2005) and provide the advantage of being spatially displaced from the fovea, where the fixation point manipulation is taking place. Although we could have used a remote visual stop signal (e.g., illumination of a background light), we felt that an auditory stop signal removed potential concerns regarding the use of a single modality. Accordingly, we believe that the saliency of the auditory stop signal was equal in the gap and overlap conditions.

We analyzed a total of 5,257 control trials over the entire sample. Consistent with previous findings, including *experiments 1* and *2,* we found a significant gap effect on RTs both across our sample [87 ± 24 ms, range: 65–117 ms ($P < 0.005$); Fig. 5*A,* Table 1] and in all five subjects (all $P < 0.05$, 2-way *t*-test). As in *experiments 1* and *2,* subjects had more noncancelled saccades on stop trials with longer SSDs, regardless of fixation condition (Fig. 5, *B* and *C*). Consistent with the findings from *experiment 1,* we found a robust gap effect on SSRTs with this reduction occurring in at least four of the five subjects using each method [integration method: 22 ± 15 ms, range: −2–40 ms ($P < 0.05$); mean method: 51 ± 23 ms, range: 24–86 ms ($P < 0.01$)].

On averaging SSRT estimates, a significant gap effect remained and this reduction occurred for all subjects [37 ± 9 ms; range: 21–42 ms ($P < 0.001$); Fig. 5*D,* Table 1]. Overall, these data provide strong evidence that the stop process can be primed by a 200-ms gap regardless of stop signal saliency and modality.

Tests of the race model

One assumption of the race model is that the go and stop processes are stochastically independent. Therefore the growth of the go process should not affect the growth of the stop process and vice versa. One test of such independence is to see how well RTs of noncancelled saccades can be predicted using control trial RTs (Logan 1994). To do this, we compared noncancelled stop trials from a given SSD (≥15 noncancelled saccades for a given subject) with their corresponding control trials, the RTs of which were less than the sum of the subject's SSRT plus the given SSD (Fig. 6*A*). Over all three experiments, and all fixation conditions, we found that the representative noncancelled portion of the control RT distribution predicted the actual RTs of noncancelled saccades well (for simplicity, we present here the prediction based on the SSRT from the integration method, although the mean method produced equivalent results). In *experiment 1,* the mean predicted RTs for the gap and overlap conditions exceeded the observed noncancelled RTs by 2.9 and 0.7 ms, respectively, with the differences on a per-SSD basis reaching significance in only 1/17 (gap) and 2/13 (overlap) comparisons. In *experiment 2,* the mean predicted RTs for the gap, auditory, and overlap conditions exceeded the observed noncancelled RTs by 2.8, 0.3, and 1.5 ms, respectively, with the differences on a per-SSD basis reaching significance in only 4/20 (gap), 1/12 (auditory), and 1/15 (overlap) comparisons. In *experiment 3,* the mean predicted RTs for the gap and overlap conditions exceeded the observed noncancelled RTs by 3.2 and 7.8 ms, respectively, with the differences on a per-SSD basis reaching significance in only 6/25 (gap) and 2/13 (overlap) comparisons. Overall, these data are consistent with the assumption of independence of the go and stop processes.

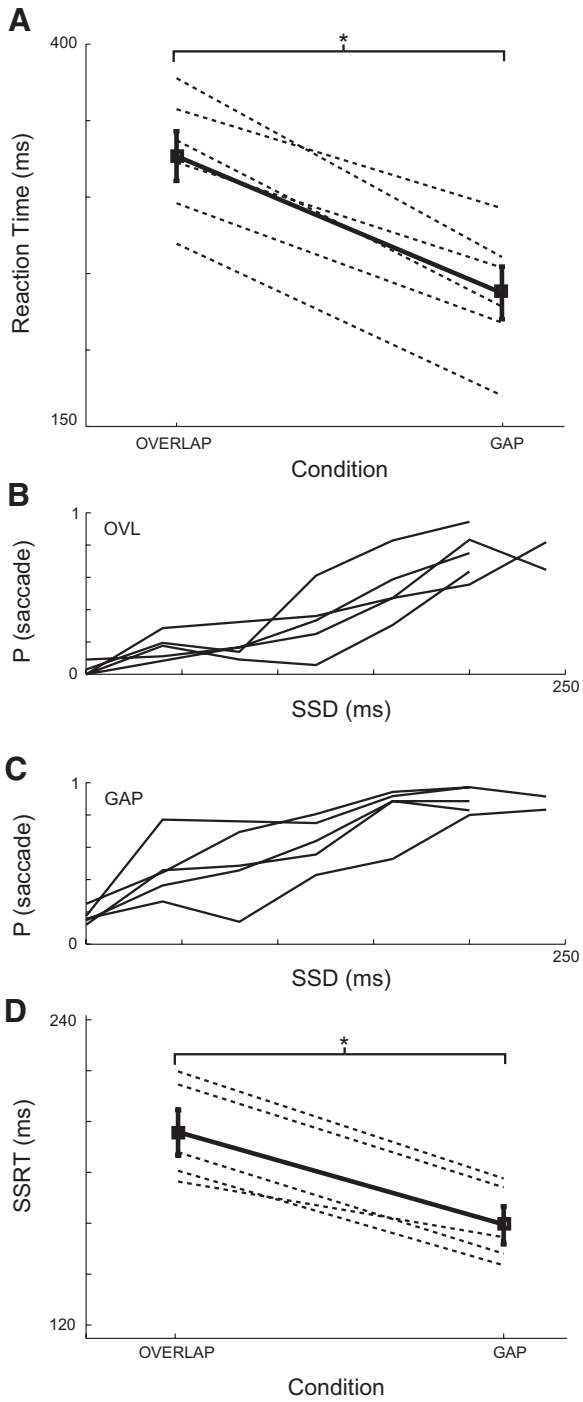

FIG. 5. Results from *experiment 3,* using same format at Fig. 3. *A*: A significant gap effect of ~90 ms was observed across the sample: *B* and *C*. Inhibition functions for the overlap (*B*) and gap (*C*) conditions. *D*: a significant gap effect on SSRTs of ~35 ms was observed.

Another test of the independence assumption in the race model is that the RTs for noncancelled saccades should increase progressively for longer SSDs as the delayed stop process should eliminate less of the upper tail of the control RT distribution at longer SSDs (e.g., imagine how Fig. 6*A* would look for longer SSDs). Our observations validated this prediction for all three experiments as the observed RT for noncancelled saccades increased for longer SSDs for all fixation conditions in all three experiments (Fig. 6, *B–D*). The change in RTs reached significance for the overlap condition in *experiments 2* and *3* ($P < 0.05$; 2-way *t*-test; for inclusion, ≥3 subjects had to have ≥10 noncancelled saccades at a given SSD). The change in RT approached significance for the other fixation conditions ($P = 0.07$ for overlap and $P = 0.08$ for gap conditions in *experiment 1,* Fig. 6*B; P* = 0.06 for auditory and $P = 0.13$ for gap conditions in *experiment 2,* Fig. 6*C; P* = 0.08 for gap in *experiment 3;* a 1-way ANOVA was used when the inclusion criteria were met at >2 SSDs). These patterns are also generally consistent with the independence assumption of the go and stop processes.

DISCUSSION

We investigated the effect of introducing a 200-ms gap between the offset of a foveal fixation point and target presentation on subject performance in an oculomotor countermanding task. Previous work has established that such a manipulation expedites RTs to the target on a simple saccade task. This phenomenon has been termed the "gap effect" and neural correlates have been observed in both the superior colliculus and frontal eye fields (Dorris and Munoz 1995; Hanes and Schall 1995; Hanes et al. 1998; Opris et al. 2001; Paré and Hanes 2003; Schall 1991). Here we report a surprising finding that parallels the gap effect on RTs: the introduction of a 200-ms gap also expedites the time required to cancel an impending saccade. Follow-up experiments confirmed the robustness of this effect and also demonstrated that this effect is due primarily to the removal of a foveal visual stimulus and is present for both visual and auditory stop signals. In this discussion, we first contextualize our results in comparison to others in the literature and then briefly speculate on possible underlying neural mechanisms.

Comparison to previous results

There is a rich literature in psychophysics regarding the gap effect on simple RT tasks. The effect was first reported by Saslow (1967), and subsequent experiments over the past 40 yr have confirmed the consistency of this effect, and its presence in both human and animal studies (see Munoz et al. 2000 for review). In general, our results from control trials are consistent with this literature in that we found a consistent gap effect in all three experiments, which averaged ~75 ms. The overall magnitude of this gap effect is somewhat larger than most other human studies (Munoz and Corneil 1995; Pratt et al. 2000; Reuter-Lorenz et al. 1995), which reported gap effects ranging from 30 to 60 ms. These differences could be subject related (note from Table 1 that the gap effect varied considerably in different subjects) or perhaps related to the nature of the countermanding task. For example, it is known that RTs on control trials in the countermanding task are longer than in simple RT tasks (Lappin and Eriksen 1966). Therefore if both overlap and gap RTs were lengthened by a similar percentage, due to the presence of infrequent stop trials, it could lead to the larger gap effect seen in this study. Further, the SSRTs in the gap condition, while shorter than in the overlap condition, are consistent with previous results from our lab (Corneil and Elsley 2005). The SSRTs we observed in the overlap conditions are generally consistent with those reported elsewhere (Morein-Zamir and Kingstone 2006).

The presence of an observable and consistent gap effect on SSRTs in all three experiments suggests that both the go and stop processes are primed by the introduction of a 200-ms gap. These results are consistent with a recent report using a double-step task, which demonstrated that both inhibitory and saccade preparatory processes could be primed in delayed- or memory-guided fixation conditions (Kapoor and Murthy 2008). Although the magnitude of the gap effect on SSRTs was roughly comparable across all three variants of the task (~40 ms, see Table 1), the gap effect was proportionally smallest in *experiment 3* (e.g., overlap vs. gap SSRTs were reduced by 34, 36, and 19% in *experiments 1–3,* respectively). This comparative result may attest in part to a perceptually more salient stop signal in the gap condition in *experiments 1* and *2* (due to re-illumination of the fixation point; recall that the stop signal in the overlap condition consisted of a change in the color of the fixation point). However, the results from *experiment 3* demonstrate a persistent gap effect on SSRTs even when the presumed saliency of the stop signal is equated.

Experiment 2 confirmed that the gap effect on RTs can be decomposed into two components, one warning of impending target presentation and the other due to the loss of a foveal stimulus (Reuter-Lorenz et al. 1995; Ross and Ross 1980, 1981). However, only the foveal component seems to be involved in the reduction of SSRTs with no discernible contribution from the warning component. This finding emphasizes distinctions between the processes dictating saccade generation and cancellation.

To our knowledge, there are only two other reports that have examined the influences of manipulating the fixation point in countermanding paradigms. The most pertinent comparison of our work is to that of Morein-Zamir and Kingstone (2006), who examined human performance in an oculomotor countermanding task. The authors reported a negligible influence of the offset of a fixation point on SSRTs despite a modest decrease in saccadic RTs on control trials (which averaged ~18 ms). However, it is important to emphasize that Morein-Zamir and Kingstone studied the influence of simultaneous fixation point offset and target presentation (i.e., a gap of 0 ms), whereas we employed a gap of 200 ms. We suggest that the longer gap interval employed in our experiment is in a more optimal range to study the influences of fixation point manipulations on processes related to saccade cancellation as reductions in saccadic RTs are greatest for gaps ranging between 200 and 400 ms (Dorris and Munoz 1995; Juttner and Wolf 1992; Munoz et al. 2000).

A similar mechanism cannot reconcile results reported for the countermanding of arm movements (Mirabella et al. 2009). This study reports that SSRTs for arm movements increase when a gap interval is increased from 0 to 212 ms despite decreases in the RTs of arm movements on control trials. Our results attest to possible effector-related differences between the control of oculomotor versus limb-movement responses, consistent with previous reports that have suggested an independence between stop processes for eye and hand movements (Boucher et al. 2007b; Logan and Irwin 2000). In light of these results and those reported by Mirabella and colleagues (2009),

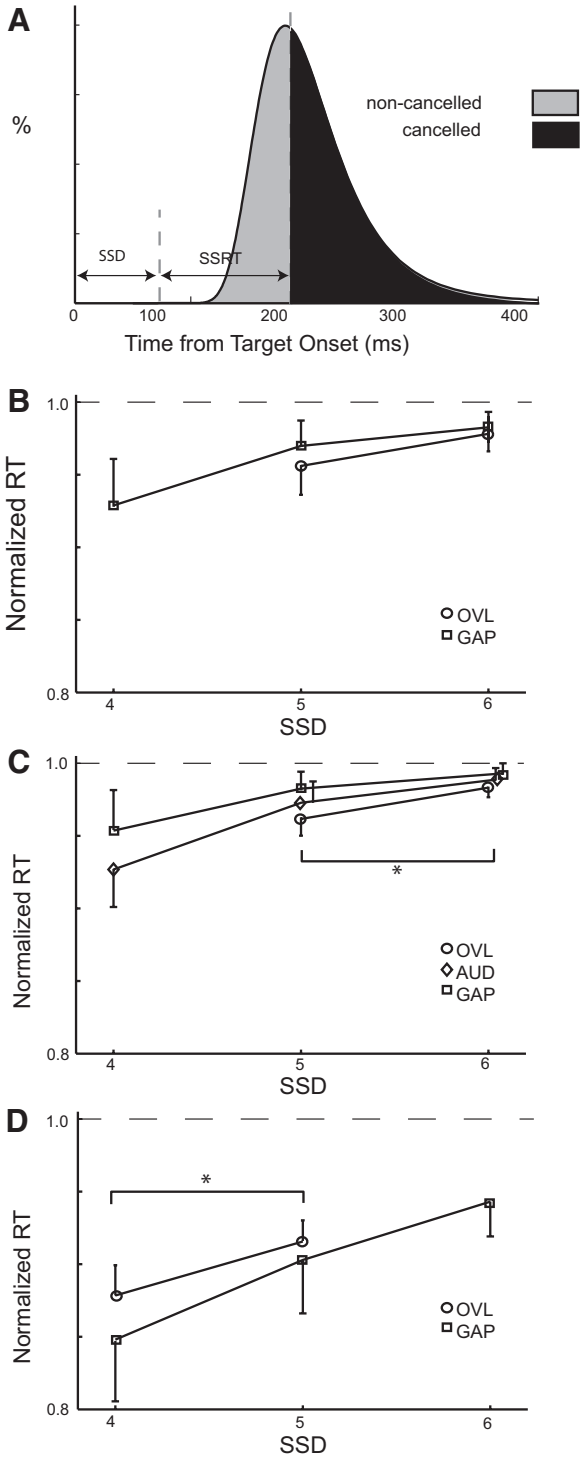

FIG. 6. Tests of the race model. *A*: depiction of how the race model can be used to predict RTs of noncancelled saccades at a given SSD. The RT distribution from control trials can be subdivided into a portion that would or would not have been cancelled, had the stop signal been presented, by the sum of the predetermined SSRT and the given SSD. Those movements falling into the noncancelled portion predict the RTs of noncancelled movements at that SSD. *B–D*: normalized RTs of noncancelled saccades as a function of SSD in *experiments 1* (*B*), *2* (*C*), and *3* (*D*). Within each plot in *B–D*, mean RTs from all noncancelled trials are normalized to the mean RT from control trials for that subject, and data were then pooled across all subjects. Consistent with the race model, RTs of noncancelled movements increased for longer SSDs in all experiments. *, significant observations using 2-way *t*-test, $P < 0.05$. The SSDs in *B–D* are denoted in rank order because not all subjects had the same series of SSDs (e.g., see Fig. 4). To compare observations across subjects, SSDs were ordered from shortest to longest. Therefore SSDs 4–6 refer to the longest 3 SSDs for each subject.

it would be particularly interesting to examine the magnitude and direction of gap effects on eye and hand SSRTs for combined eye-hand movements.

Underlying neural substrates

Based on the comparison of our results to those of Mirabella and colleagues (2009), we speculate that the implementation of the gap effect on SSRTs occurs downstream of general sensory or attentional processes, otherwise one would expect similar results for both eye and hand SSRTs. We therefore speculate that the priming of the stop process we have observed is unique to the oculomotor system.

On the surface, the simultaneous priming of both the go and stop processes in the gap condition would seem to support the assumption of independence common to many race model architectures. However, this assumption of independence runs counter to the mutually antagonistic relationship between saccade generation and saccade fixation mechanisms thought to exist in the oculomotor system. Within the superior colliculus (SC) and frontal eye field (FEF), neural correlates of the gap effect (Dorris and Munoz 1995; Opris et al. 2001), and go and stop processes (Brown et al. 2008; Hanes et al. 1998; Paré and Hanes 2003) have been observed. At least within the SC, there is neurophysiological evidence for short-latency, mutually antagonistic projections between saccade- and fixation-related neurons (Meredith and Ramoa 1998; Munoz and Istvan 1998). Given that the introduction of a 200-ms gap increases saccade-related activity and decreases fixation-related activity, one would have expected that priming the go process in the gap condition should have slowed the stop process, prolonging SSRTs. How can we reconcile our behavioral evidence for simultaneous priming of go and stop processes with known patterns of oculomotor activity?

A recent model of saccadic countermanding potentially resolves the paradox between the computational assumption of independence and neurophysiological activity within the oculomotor system (Boucher et al. 2007a). The crux of this model is that the go and stop processes remain independent for most of the processing but then interact in a latter stage such that the stop process potently inhibits the go process. Unlike independent race model architectures, which remain agnostic about underlying patterns of neural activity, this interactive race model is consistent with both behavior and profiles of oculomotor activity in a saccadic countermanding task.

We believe that our results can be explained within the context of this interactive race model. To illustrate this, consider first the idealized profiles of fixation-related activity recorded on cancelled and noncancelled saccades in the overlap condition [top part of Fig. 7*A*; activity profiles are based on those recorded from the SC by Paré and Hanes (2003; see their Fig. 7)]. Note how fixation-related activity remains fairly constant through the time of target and stop signal presentation but then diverges sharply depending on ensuing behavior with activity increasing or decreasing depending on whether the saccade is cancelled or not, respectively. The timing of this divergence becomes particularly clear by taking the difference between these two profiles (Fig. 7*A, bottom*). The key observation made by Paré and Hanes (2003) was that this divergence in activity, which they term the "neural estimate of SSRT" preceded behavioral estimates of SSRTs. This is a logical

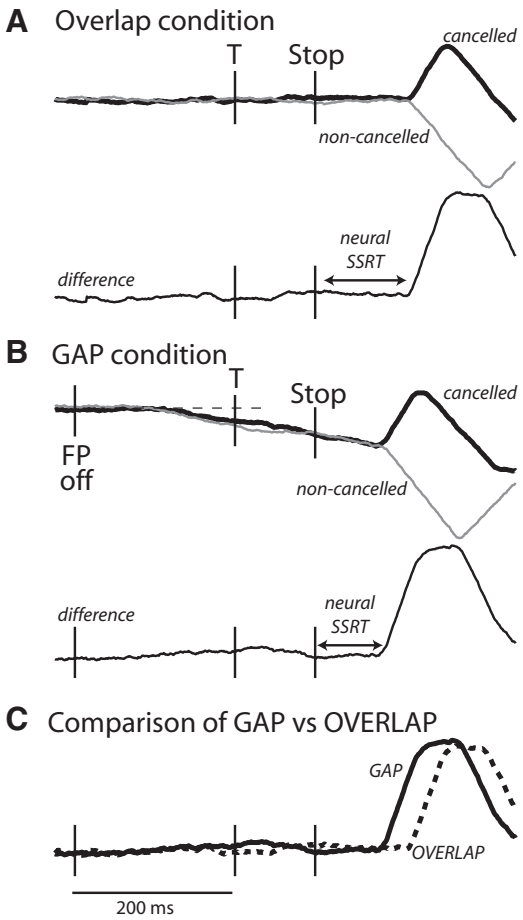

FIG. 7. Sketch of predicted profiles of the activity of superior colliculus (SC) fixation-related neurons. The activity profiles are based on those recorded during a saccadic countermanding task (Paré and Hanes 2003) and during a saccade task with a 200-ms gap (Dorris and Munoz 1995). *A* (for the overlap condition) and *B* (for the gap condition), *top,* show fixation-related activity on stop trials, segregated based on whether the saccade was successfully cancelled (thick line) or not (thin line). Note how neural activity begins to decrease before target (*T*) presentation in *B,* consistent with Dorris and Munoz (1995). *A* and *B, bottom*: the difference between these 2 curves, emphasizing that a neural estimate of SSRT runs from stop signal presentation until the divergence in neural activity. These difference curves are contrasted directly in *C,* emphasizing our prediction that the divergence in activity depending on performance occurs early in the gap vs. overlap condition.

prerequisite if fixation-related neurons are to play a causal role in saccade control.

We speculate similar profiles of fixation-related activity will be observed in the gap condition but with a few important differences. First, fixation-related activity would begin to decrease during the 200-ms gap [idealized profiles in Fig. 7*B, top,* are based on those recorded by Dorris and colleagues (1995)], with this decrease continuing through target and stop-signal presentation. Because the subjects cannot anticipate trial type or the SSD, the decrease in fixation-related activity would be the same for both cancelled and noncancelled trials. Second, we believe that the divergence in fixation-related activity on cancelled versus noncancelled trials would be occurring *earlier* in the gap condition compared with the overlap condition (Fig. 7, *B* and *C, bottom;* as discussed in the following text, we believe the signal dictating such divergence does not originate in the SC). This earlier divergence of fixation-related activity in the gap versus overlap condition (Fig. 7*C*) would then

explain our behavioral observations of priming of the stop process in the gap condition.

Although we have only depicted fixation-related activity in Fig. 7, we speculate that reciprocal profiles of activity would be observed on movement-related neurons (e.g., neural activity would increase during the gap period and increase further only on noncancelled trials). In this regard, the asymmetric inhibition predicted by Boucher and colleagues (2007a) (that fixation-related neurons inhibit saccade-related neurons more than vice versa) is particularly important; otherwise the increase in movement-related activity during the gap period would prevent the subsequent increase in fixation-related activity for cancelled trials.

Within the context of our predicted profiles of activity, the pertinent question then becomes why the fixation-related neurons diverge in activity earlier in the gap versus overlap condition. Although recordings of activity during saccadic countermanding have been made from a number of areas, to date only neurons within the FEF and SC have the appropriately timed divergence in activity to be involved in saccade control [i.e., whereby neural SSRTs precede behavioral SSRTs; (Brown et al. 2008; Hanes et al. 1998; Paré and Hanes 2003)]. A number of groups have speculated on the role of fronto-striatal networks in saccade cancellation (Aron and Poldrack 2006; Paré and Hanes 2003), but it remains to be determined whether these networks directly implement saccade control. However, recording studies throughout the basal ganglia have demonstrated changes in activity during a gap period preceding target presentation (Hikosaka and Wurtz 1983; Kobayashi et al. 2002). Thus circuits through the basal ganglia could provide the means by which priming of the stop process is implemented.

In conclusion, the stop process can be primed in a human saccadic countermanding task by the introduction of a 200-ms gap. This robust priming is mainly driven by a foveal component and occurs regardless of stop signal saliency or modality. Further investigation is required to understand how, on a neural level, oculomotor areas manifest simultaneous priming of the go and stop processes.

ACKNOWLEDGMENTS

We thank Dr. S. Goonetilleke and B. Chapman and M. Pace for comments on earlier versions of the manuscript.

GRANTS

This work was supported by an operating grant from the Natural Sciences and Engineering Research Council (NSERC RGPIN-311680). S. A. Stevenson was supported by an Ontario Graduate Scholarship. J. K. Elsley was supported by a NSERC PGS-M. B. D. Corneil is a Canadian Institute of Health Research New Investigator.

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