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Selective inhibition of a multicomponent response can be achieved without cost

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Xu J, Westrick Z, Ivry RB. Selective inhibition of a multicomponent response can be achieved without cost. *J Neurophysiol* 113: 455–465, 2015. First published October 22, 2014; doi:10.1152/jn.00101.2014.— Behavioral flexibility frequently requires the ability to modify an on-going action. In some situations, optimal performance requires modifying some components of an on-going action without interrupting other components of that action. This form of control has been studied with the selective stop-signal task, in which participants are instructed to abort only one movement of a multicomponent response. Previous studies have shown a transient disruption of the nonaborted component, suggesting limitations in our ability to use selective inhibition. This cost has been attributed to a structural limitation associated with the recruitment of a cortico-basal ganglia pathway that allows for the rapid inhibition of action but operates in a relatively generic manner. Using a model-based approach, we demonstrate that, with a modest amount of training and highly compatible stimulus-response mappings, people can perform a selective-stop task without any cost on the nonaborted component. Prior reports of behavioral costs in selective-stop tasks reflect, at least in part, a sampling bias in the method commonly used to estimate such costs. These results suggest that inhibition can be selectively controlled and present a challenge for models of inhibitory control that posit the operation of generic processes.

inhibition; selective stop; stop-signal task; plasticity; horse-race model

BEHAVIORAL FLEXIBILITY FREQUENTLY requires the ability to modify an on-going action. In some situations, only part of the planned action must be changed. For example, when walking in the city with a friend, the appearance of a fast-moving car may require that we abort a plan to cross the street but not require that we temporarily halt our conversation. We ask here how people produce selective inhibition.

The *stop-signal* task has been a favorite experimental tool to study inhibitory control (Lappin and Erikson 1966; see a review in Band et al. 2003). In this task, participants prepare to make a speeded response. On some trials, they are cued to abort the planned action. The likelihood of successful stopping has been modeled as a horse race (Logan and Cowan 1984) between signals associated with initiating or aborting the response. At the neural level, this form of inhibition has been linked to interactions between the cortex and basal ganglia (Aron and Poldrack 2006; Aron et al. 2007; Mink 1996; Wessel et al. 2013).

The use of the horse-race model to study inhibitory control was developed for tasks in which a single response was either executed or aborted. Subsequently, researchers extended this work to look at situations in which participants were required to selectively abort one component of a multicomponent action (De Jong et al. 1995; Bedard et al. 2002; van den Wildenberg and van der Molen 2004; Bissett and Logan 2014), asking if similar processes were engaged during such selective-stop tasks. De Jong et al. (1995) proposed that distinct forms of inhibition operate during standard and selective stop-signal tasks. For the former, a peripheral mechanism operates in a generic manner, blocking or aborting the implementation of central motor commands in the face of normal cortical preparatory signals. For the latter, a cortical mechanism is invoked to selectively inhibit a specific action. This two-process hypothesis complemented earlier findings showing that the lateralized readiness potential (LRP), an electrophysiological marker of cortical movement preparation, was only diminished with early stop signals in the standard task; the LRP was of normal magnitude on successful stop trials with a late stop signal, suggestive of a subcortical mechanism for inhibition (De Jong et al. 1990).

An alternative hypothesis, which we refer to as the *restart model*, is that selective stopping entails the operation of two, sequential processes (De Jong et al. 1995; Coxon et al. 2007; Claffey et al. 2009; MacDonald et al 2012). First, a signal is generated to transiently inhibit the motor system in a generic manner and, as such, inhibits all planned actions. Second, the nonaborted response is rapidly reprogrammed. This hypothesis can account for the selective-stop cost, the increase in reaction time (RT) observed for the nonaborted response on Selective-Stop trials compared with Go trials. Physiological support for the initial deployment of a generic stop command comes from studies showing reduced motor-evoked potentials (MEPs) in task-irrelevant muscles on successful Stop trials (Badry et al. 2009; Cai et al. 2012; Greenhouse et al. 2012; Majid et al. 2012), as well as EEG evidence of a similar pattern of activation for successful response inhibition and responses to unexpected events (Wessel and Aron 2013).

While the behavioral and transcranial magnetic stimulation evidence is consistent with the restart model, the data remain inconclusive about whether this process is obligatory. Greenhouse et al. (2012) showed that MEPs elicited from leg muscles were attenuated when participants aborted a manual response. However, Majid et al. (2012) observed a similar attenuation in leg MEPs in a nonselective task but not in a condition requiring selective stopping. Moreover, various lines of evidence suggest that the magnitude of selective-stop costs may vary as a function of various factors such as task preparedness. For example, foreknowledge of the to-be-inhibited

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effector reduces the selective-stopping cost (Aron and Verbruggen 2008; Claffey et al. 2010; Majid et al. 2013). In parallel with this behavioral effect, MEPs in task-irrelevant effectors fail to show inhibition, a result that would argue against the operation of a generic process (Cai et al. 2011). Behavioral evidence of the absence of a selective-stop cost comes from studies in which the selective-stop signal was only associated with one of the potential responses (e.g., Aron et al. 2007; Jahfari et al. 2010) or in conditions involving a precue (e.g., Aron and Verbruggen 2008; Claffey et al. 2010). Restrictive stop tasks may allow people to adopt strategies that entail different preparatory states for the different stimuli (De Jong et al. 1995).

In the present study, we reexamine the restart hypothesis, asking if the initial recruitment of a generic inhibitory process is obligatory in selective-stop tasks. To this end, we used a stop-signal task optimized to favor selective stopping. We show that traditional methods used to analyze the data from the stop-signal task are biased (see MATERIALS AND METHODS). This observation led us to develop a novel statistical method that provides a rigorous test of selective-stop costs. The results challenge the notion of generic inhibition. Rather, they point to a softer constraint that reflects the degree of overlap between representations associated with the selected and nonselected components of a multicomponent action. When this overlap is minimized, either by the task structure or training, we find that the selective-stop cost can be eliminated.

MATERIALS AND METHODS

Participants

A total of 10 right-handed healthy participants (7 women, 3 men; 23.2 ± 5.8 yr old) participated in the training experiment. Handedness was confirmed with a condensed version of the Edinburgh Handedness Inventory (Oldfield 1971). All participants gave written informed consent and were financially compensated for their participation. The protocol was approved by the Institutional Review Board of the University of California, Berkeley.

Experimental Procedure

Participants were tested on a selective stop-signal task to assess the RT cost associated with aborting one response of a multicomponent movement (Fig. 1). Because we were interested in whether a selective cost is inevitable due to the recruitment of a generic stopping process, we designed the experiment to maximize the opportunity for participants to avoid this cost. This was achieved by providing the participants with multiple days of practice and monetary rewards, as well as by assessing the benefit of a highly compatible stop signal.

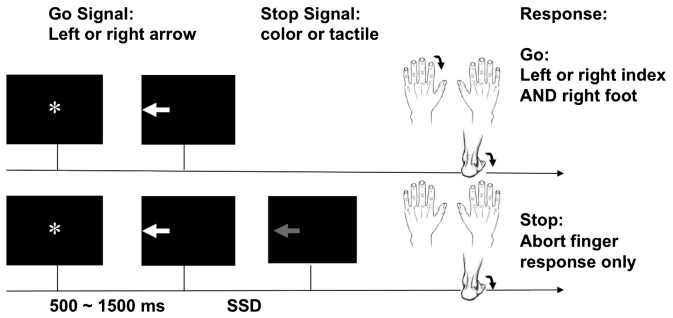

Fig. 1. Selective stop-signal task procedure. The white arrow indicated if a right foot movement should be made simultaneously with a keypress performed with either the right or left index finger. On Stop trials, the arrow turned red in the Color condition or the key under the index finger vibrated in the Tactile condition after an individually adjusted stop-signal delay (SSD). Only the manual response was to be aborted. On all trials, a keypress with the right foot was required.

The trial began with the participants resting their index fingers on two response keys and the right foot on a foot pedal. An asterisk was presented for a random delay (500–1,500 ms) to serve as a fixation and alerting marker. After the delay, the asterisk was replaced by a go signal, an arrow pointing to the left or right. This imperative served as the signal that the participant should initiate two responses, a manual choice response and an invariant foot response. The manual choice was between the left or right index finger, with the selected finger corresponding to the direction of the arrow. For the invariant response, the participants pressed a foot pedal with the right foot. The arrow disappeared when a response was detected, or after 2 s on successful Stop trials, after which the screen went blank for a 1,000-ms intertrial interval.

On 33% of the trials, a stop signal was presented, indicating that the participant should selectively abort the manual response. In separate sessions, we compared two different stop signals. In the Color condition, the color of the arrow turned red. In a Tactile condition, the response key associated with the cued finger vibrated. We reasoned that the high degree of compatibility in the Tactile condition would enable participants to readily identify the response that should be aborted, eliminating any cost associated with mentally assigning a relatively abstract stop signal (e.g., color red) to one of two prepared responses (Rosenbaum et al. 2006). Note that, unlike previous studies, the stop signal is not associated with a single response alternative; across trials, the stop signal occurs on both left- and right-hand trials.

The interval between the onset of the go signal and the stop signal is referred to as the stop-signal delay (SSD). An adaptive, staircase procedure was employed to determine the SSD on a trial-by-trial basis (Osman et al. 1986, 1990; Band et al. 2003). The SSD value was adjusted in steps of 50 ms, increasing after a successful Stop trial and decreasing after a failed Stop trial, with a lower limit of 50 ms. This method converges to an SSD value at which participants succeed in aborting a planned response on ~50% of the trials (Levitt 1971). Two interleaved staircases, one starting at 50 ms and the other at 300 ms, were used to determine the SSD.

Participants were instructed to make the two responses as quickly as possible on a Go trial, responding simultaneously with the finger and foot. On Stop trials, only the manual response was to be aborted; the instructions emphasized that the foot response should be made without hesitation. The participants were informed that it would not be always possible to abort the manual response on Stop trials and that they should avoid adopting a strategy of slowing down to increase the likelihood of successfully stopping.

Participants were trained on 4 different days, with each type of stop signal (Color or Tactile) used on 2 consecutive days. The order of conditions was counterbalanced across participants. During each day, they first performed two pure Go blocks of 32 trials each, containing no stop signals. Following this, they completed 10 Selective-Stop blocks, each composed of 60 trials (40 Go, 20 Selective Stop).

To further optimize the conditions for selective stopping, we provided an incentive for participants to avoid delaying the foot response on subsequent Selective-Stop trials. The mean foot RT from the second of these pure Go blocks was used to establish a benchmark for determining subsequent monetary bonuses. At the end of each block, the mean foot RT was computed and displayed to the participant, along with the amount of money earned on that block based on the following criteria. The participant received $1.00 if the mean foot RT was faster than the benchmark, or $0.75, $0.50, $0.25, or $0.10 if the RT was slower than the benchmark by less than 25, 50, 75, or 100 ms, respectively. To ensure that participants also attended to the stop signals, the reward was only earned if they succeeded in stopping on more than 25% of the Stop trials within the block.

Estimating the Cost Associated with Selective Stopping

Our focus is on the selective-stop cost, the increase in RT observed for the invariant response on Selective-Stop trials compared with Go trials. In previous studies using a selective-stop task, this difference score has been taken to provide an estimate of the cost associated with inhibiting one response of a multicomponent action (Coxon et al. 2007; Aron and Verbruggen 2008; Claffey et al. 2010; Majid et al. 2012; MacDonald et al. 2012). Indeed, the restart model was developed to account for this cost, attributing it to the operation of two, sequential processes, the generation of a generic stop command that is applied to all prepared responses, followed by the reprogramming of the invariant response. By this view, the selective-stop cost provides an estimate of the time required to restart the (transiently) disrupted invariant response. The restart model is inconsistent with the horse-race model, at least on successful Stop trials, because restarting a planned response violates the independence assumption of the go and stop processes in the horse-race model.

However, the comparison of RTs for the nonstopping effector on Selective-Stop and Go trials, the measure used to assess the global restart cost of selective inhibition, is biased. In the standard stop-signal task, where a single response is prepared, RTs on trials in which the participant fails to stop are assumed to reflect the faster half of the RT distribution (Logan and Cowan 1984) (Fig. 2*A*). Indeed, this assumption underlies the computation for estimating the stop-signal reaction time (SSRT). In the selective-stop task, there is an overt response on all Stop trials; in our experiment, this is the invariant foot response. Because the manual and foot responses are coupled (see RESULTS), and fast manual responses occur on some Stop trials (regardless of the existence of a global restart cost), the foot RTs from these failed Stop trials are primarily drawn from the faster half of the overall RT distribution. Correspondingly, foot RTs from successful Stop trials are primarily drawn from the slower half of the distribution. Thus a measure of the cost associated with selective stopping that is based on a comparison of foot RTs for successful Stop trials and Go trials would be biased since the former is typically drawn from the slower half of the full distribution. We refer to this as the *sampling-bias cost* (Fig. 2*B*) since successful Stop trials constitute a biased sample of foot RTs, even in the absence of a global restart cost.

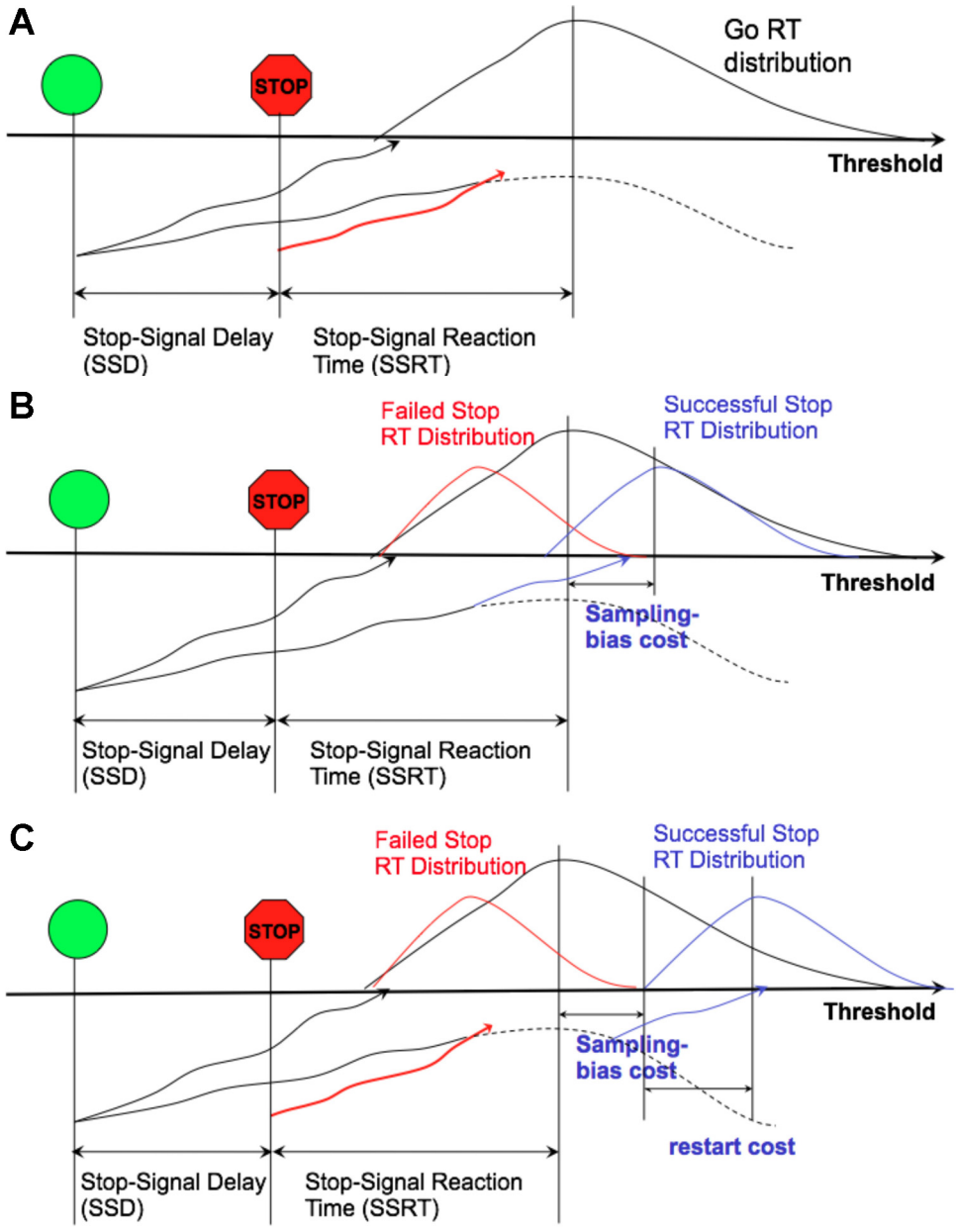

Fig. 2. Horse-race model and the sampling-bias hypothesis for the residual cost. *A*: graphic illustration of the horse-race model for stop-signal paradigm. The Go process (black traces indicate accumulation function for different trials, yielding Go RT distribution) is triggered after a Go cue (green circle) and accumulates over time. An inhibition process (red trace) is triggered after the Stop cue (red stop sign). The outcome is a successful stop when the inhibition process offsets the Go signal (shown here when red trace exceeds black trace, Go traces is dashed), or failed stop if the Go process reaches threshold first. RTs on failed Stop trials are assumed to arise from the faster half of the RT distribution. *B*: graphic illustration of the sampling-bias hypothesis in the selective-stop task. The blue trace indicates the Go trace for the invariant foot response on a successful Stop trial. Sampling-bias cost results from the difference between the medians of Successful Stop and Go RT distributions for the invariant foot responses. *C*: graphic illustration of the restart model of the stopping cost. The Go trace for the foot response is transiently disrupted on successful Stop trials, and then restarted after a short delay (reprogrammed). The difference between the Successful Stop and Go RT distributions would include both the sampling-bias and restart costs.

An unbiased estimate of the cost in selective stopping requires testing whether there is an additional increase in RT on successful Stop trials, above and beyond the sampling-bias cost; this increase would constitute a true *restart cost* (C_r) (Fig. 2*C*). Thus our analysis focused on asking whether the *observed RT cost* (C_{obs}) is significantly greater than the sampling-bias cost (C_{sb}). This method provides an unbiased test of the restart model. This approach is made possible by the fact that the foot and hand RTs are highly correlated, allowing us to directly assess the Successful Stop and Failed Stop RT distributions, even if the manual response is successfully withheld on Stop trials.

Modeling costs in the selective-stop task. Here we give a formal analysis of selective-stop behavior using a generic probabilistic model that can account for both sampling-bias and restart costs.

Let $X = x$ be the SSD, and $T = t_f$ be the foot RT. The trial type is $c = \begin{cases} 0 & \text{if Go} \\ 1 & \text{if Stop} \end{cases}$, and the participant's response is $s = \begin{cases} 0 & \text{if responded} \\ 1 & \text{if no response} \end{cases}$. We define distributions for the *foot RTs* on two different trial types as $P_{GO}(T = t_f)$ (Go trials) and $P_{STOP}(T = t_f)$ (Stop trials), where P_{STOP} can be subdivided to P_{FS} $(T = t_f)$ (Failed Stop trials) and $P_{SS}(T = t_f)$ (Successful Stop trials) as follows:

$$\begin{aligned} P_{GO}(T = t_f) &= P(T = t_f | c = 0, s = 1) \\ P_{STOP}(T = t_f) &= P(T = t_f | c = 1, X = x) \\ P_{FS}(T = t_f) &= P(T = t_f | c = 1, s = 1, X = x) \\ P_{SS}(T = t_f) &= P(T = t_f | c = 1, s = 0, X = x) \end{aligned} \quad (1)$$

Each individual's inhibition function for a given SSD is

$$P_{inhibit} = P(s = 0 | c = 1, X = x, T = t_f) = P.$$

If this inhibition function p is monotonically increasing, which is the case when *1*) the hand and foot RTs are correlated and *2*) failed stops are more likely on trials with faster RTs, it is guaranteed that $C_{sb} > 0$. As shown below, an estimate of the bias is critical for evaluating the restart cost observed in selective stop-signal tasks. The foot RT distribution for Stop trials is then

$$P_{STOP}(T = t_f) = P_{FS} * (1 - p) + P_{SS} * p.$$

As $x \to 0$, $P_{inhibit} \to 1$, $P_{SS}(T = t_f) \to P_{GO}(T = t_f)$. That is, when SSD approaches zero, the participant should be able to successfully inhibit the manual response on all Stop trials, and the foot RT distribution for Stop trials will approach the foot RT distribution for Go trials.

A generic specification for the restart cost, C_r, can be given by

$$\begin{aligned} &P_{STOP}(T = t_f) \\ &= P_{FS} * (1 - p) + P_{SS} * p \\ &= P(T_{NoC_r} | c = 1, s = 1, X = x) * (1 - p) \\ &+ P(T_{NoC_r} - C_r | c = 1, s = 0, X = x) * p \end{aligned} \quad (2)$$

In this formulation, C_r is assumed to be a constant. If $C_r = 0$, then, by the horse-race model, $P_{SS}(T = t_f)$ will be formed by samples from the slower half the Go distribution. Alternatively, if $C_r > 0$, the Successful Stop distribution $P_{SS}(T = t_f)$ is shifted to the right (Fig. 2*C*). We can then ask if the Stop foot RTs reflect samples from the same distribution as the Go foot RTs, allowing us to test if the sampling-bias cost, C_{sb} fully accounts for the observed selective-stop cost (Fig. 2*B*), $P_{STOP}(T = t_f) = P_{GO}(T = t_f)$, or $C_r = 0$. Formally, we can define the null hypotheses that the observed cost is equivalent to sampling cost as:

$$C_{obs} = C_{sb} = \text{median}(P_{SS}) - \text{median}(P_{GO}) \quad (3)$$

Alternatively, if stopping introduces an extra restart cost, the Successful Stop distribution for foot RTs (P_{SS}) would be shifted to larger values than the Go foot RTs (P_{GO}) (Fig. 2*C*). Thus, the Stop and Go foot RT distributions are not the same, $P_{STOP}(T = t_f) \neq P_{GO}(T = t_f)$, or $C_r > 0$. In this case, the observed cost will be a combination of the sampling-bias cost and restart cost:

$$C_{obs} = C_{sb} + C_r = \text{median}(P_{SS}) - \text{median}(P_{GO}) \quad (4)$$

Following *Eq. 2*, we can analytically examine C_r from the means of Go and Stop distributions:

$$\begin{aligned} &E[T_{STOP}] \\ &= E[T_{FS}] * (1 - p) + E[T_{SS}] * p \\ &= E[T_{STOP\_NoC_r} | s = 1, c = 1] * (1 - p) \\ &+ E[T_{STOP\_NoC_r} - C_r | s = 0, c = 1] * p \\ &= E[T_{STOP\_NoC_r}] + C_r * p \end{aligned} \quad (5)$$

For the hypothetical Stop RT distribution without restart cost, we follow horse-race assumptions:

$$E[T_{STOP\_NoC_r}] = E[T_{GO}]$$

yielding

$$C_r = \frac{E[T_{STOP}] - E[T_{STOP\_NoC_r}]}{P} = \frac{E[T_{STOP}] - E[T_{GO}]}{P} \quad (6)$$

This value of C_r can be estimated directly from the observed data.

The derivation described above is conditioned on a fixed SSD and thus, this parameter is not included in the equations. The horse-race model also has a strong assumption that the mean SSD will produce a stop rate of 50%. While the staircase algorithm for updating SSD is designed to produce this value, the observed values often deviate from 50%. We use two simulation approaches to address this issue and directly model the sampling-bias and restart costs.

Modeling sampling-bias cost. We directly sampled from the observed Go foot RT distribution for each participant and assigned them to FS and SS samples using each individual's inhibition function, p. We then estimated C_{sb} following *Eq. 3*. We recognize that there are various ways in which we could model the inhibition function. We chose to use logistic regression, such that $P_{inhibit} = p^* = \text{logit}^{-1}(\beta T)$ is the probability of successfully stopping for a given RT on a Stop trial. The calculations here were done on the observed individual data sets, with separate functions computed for each of the four test sessions (300 observations/data set). To generate a sample of foot RTs (T_{GO}), we fit the foot RT data from the Go trials with an ex-Gaussian distribution (Ratcliff 1979; Ratcliff and Murdock 1976) and resampled 1,000 times from this distribution (see Lacouture and Cousineau 2008). Using the function p^* obtained from logistic regression on the behavior data, each sample was classified as Successful Stop RT (T_{SS}) or a Failed Stop RT (T_{FS}). From the distributions formed by these samples, we estimated the sampling-bias cost following *Eq. 3*.

Figure 3 illustrates simulations of the null (no restart cost) and alternative (with restart cost) hypotheses under consideration. In each case, we simulated one data set and ran the modeling procedure 1,000 times to establish a confidence interval (CI) for the modeled sampling-bias cost, C_{sb}. In Fig. 3, *A–D*, the T_{SS} and T_{GO} trials are sampled from the same distribution, given the null hypothesis that there is no restart process. In this scenario, the modeled sampling-bias cost should fully account for the behavioral cost. In Fig. 3, *E–H*, the T_{SS} trials come from a different distribution due to the restart process. Here the sampling-bias cost will not fully account for the observed cost.

Modeling restart costs. We modeled the restart cost by sampling 1,000 trials with replacement from the observed Go and Stop distributions for each individual. This procedure was performed separately for each day and condition. We then computed the restart cost, C_r, using Eq. 6 for the sampled data set, where the stop rate, p, was taken directly from the observed data. As with the procedure to estimate the sampling-bias cost, this procedure was repeated 1,000 times to obtain 95% CIs for the simulated restart cost (see below).

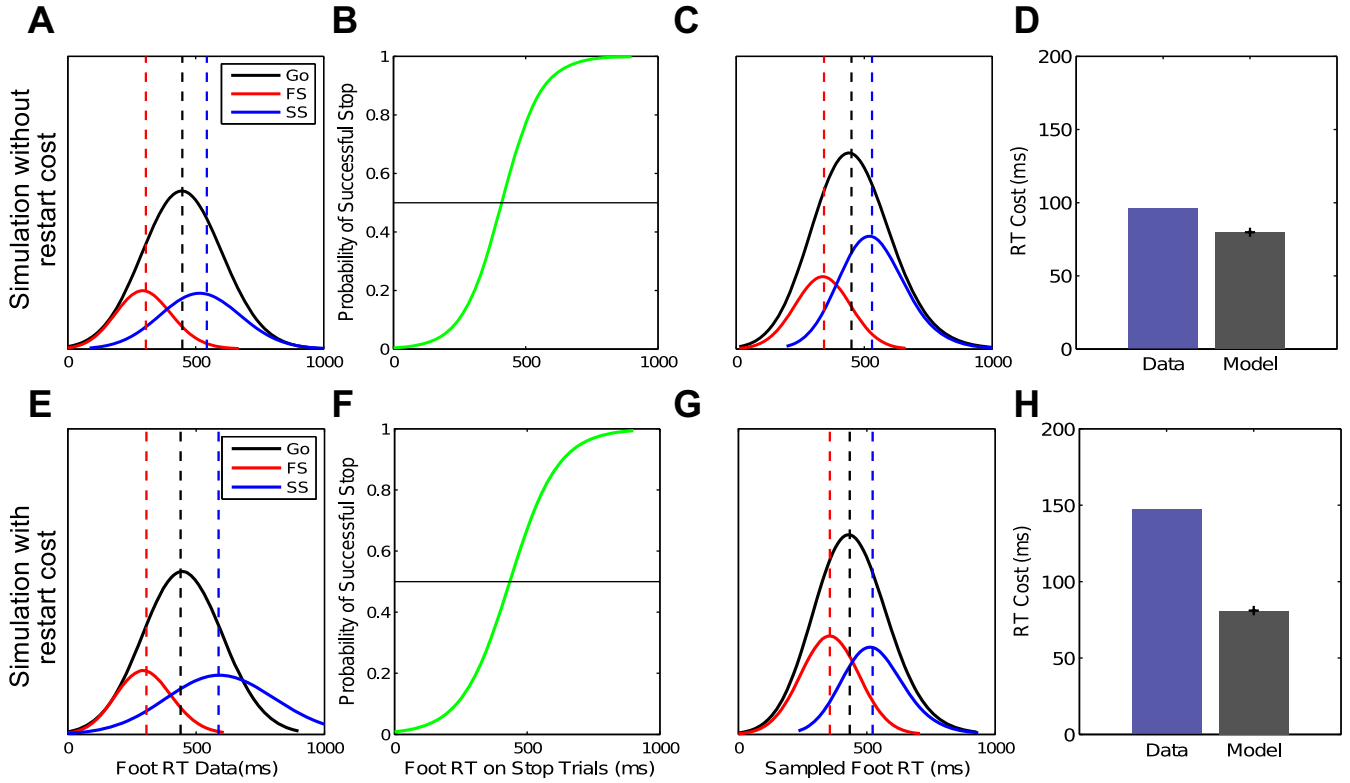

Fig. 3. Simulations to illustrate how increase in reaction times (RTs) on Selective-Stop trials could arise solely from sampling bias (*A–D*) or due to the operation of a restart process invoked following the transient disruption of the response by the stop signal (*E–H*). *A* and *E*: Simulated Go, Failed Stop (FS), and Successful Stop (SS) Foot RT data using ex-Gaussian distributions. *B* and *F*: inhibition function $P_{\text{inhibit}} = p^* = \text{logit}^{-1}(\beta T)$ using logistic regression (see MATERIALS AND METHODS) to fit the FS and SS data sets shown in (*A* and *E*). *C* and *G*: ex-Gaussian fits of a new set of Bisset samples drawn from the Go distribution in *A* and *E*, and FS and SS distributions classified using the stopping function in *C* and *F*. *D* and *H*: cost in the simulated data (*A* and *E*) compared with the modeled Sampling-Bias cost.

Bootstrapping to construct CIs of the model's predictions. To access the accuracy and robustness of the model, we generated 1,000 hypothetical data sets, each composed of data from 10 hypothetical participants by nonparametric case sampling with replacement from our observed 10 participants. We then performed the model simulations for each simulated participant to generate a distribution of the group mean cost values at the population level. We compared the simulated sampling-bias and restart costs from these 1,000 hypothetical participants with the observed costs.

RESULTS

Behavioral Data

Trials in which the RTs for the finger and foot responses were >100 ms apart were considered desynchronization errors. Most of these occurred during the first few blocks of training and were rare in later blocks (~1% in both Color and Tactile conditions). To further verify that the participants followed instructions to synchronize their response on Go trials, we calculated the correlation between the RTs for the two responses. In the Tactile condition, the mean correlations were 0.77 (SD = 0.13) and 0.78 (SD = 0.14) for the left hand/foot and right hand/foot trials. In the Color condition, the comparable values were 0.76 (SD = 0.15) and 0.76 (SD = 0.19). Participants maintained a high level of accuracy on the choice reaction time task, with Go trial accuracy at 96% across the entire experiment (SE = 0.003).

A summary of the RT data and measures of stop-signal performance is presented in Table 1. RTs were generally faster than

Table 1. *Behavioral results for the training experiment*

	Color		Tactile	
	Day 1	Day 2	Day 1	Day 2
Go RT hand, ms	319 (15.23)	296 (11.51)	309 (21.59)	276 (11.91)
Foot, ms	344 (19.62)	315 (15.04)	332 (20.12)	302 (12.64)
Failed Stop RT hand, ms	290 (10.64)	272 (10.41)	279 (13.79)	256 (8.54)
Foot, ms	327 (14.03)	303 (13.47)	309 (12.83)	288 (10.46)
SSD, ms	106 (13.30)	88 (6.49)	106 (11.42)	92 (6.32)
SSRT, ms	213 (8.77)	208 (9.70)	204 (12.70)	184 (8.79)
Percent successful stop	0.38 (0.03)	0.38 (0.02)	0.39 (0.02)	0.38 (0.02)

Mean (SE) hand and foot reaction time (RT) for go and failed stop trials, stop-signal delay (SSD), stop-signal reaction time (SSRT), and percentage successful stop; $n = 10$.

the values reported in previous stop-signal studies (e.g., Logan et al. 1984; Badry et al. 2009; Cai et al. 2011, 2012; Greenhouse et al. 2012; Majid et al. 2012). We analyzed the RT data with a repeated-measures ANOVA that included the factors Signal Type (Color/Tactile), Effector (hand/foot), RT Type (Go/Failed Stop), and Day. Foot RTs were slower than manual RTs, [$F(1,9) = 17.31$, $P < 0.005$, effect size $\eta_p^2 = 0.66$], but the mean difference was only 28 ms (SE = 6.6), consistent with the fact that the two responses were initiated in a synchronized manner. Mean RTs were relatively fast and improved over the 2 days of training [$F(1,9) = 10.30$, $P < 0.05$, effect size $\eta_p^2 = 0.53$; foot data shown in Fig. 4*A*]. RTs were also faster on Failed Stop trials compared with Go trials [$F(1,9) = 32.15$, $P < 0.001$, effect size $\eta_p^2 = 0.78$]. The effect of Signal Type was not reliable [$F(1,9) = 1.03$, $P = 0.34$, effect size $\eta_p^2 = 0.10$].

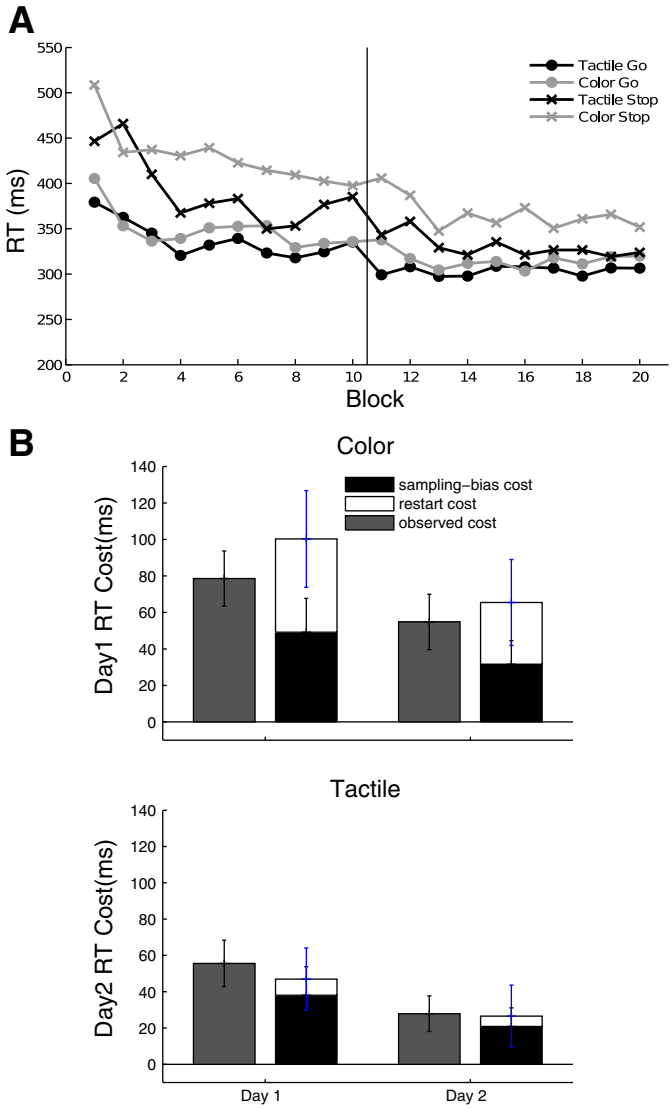

Fig. 4. RTs for the invariant foot response and selective-stopping costs. *A*: foot RTs by block. *B*: solid gray bars indicate stopping cost when calculated as foot RT difference between Successful Stop and Go trials (error bars are SE). Solid black and open bars indicate model estimate of sampling-bias cost and restart cost, respectively, with the open bars stacked on top of the solid black bars. The error bars here indicate 95% confidence intervals estimated from the bootstrapping distributions.

The percentage of successful stops averaged 38%, a value less than the target rate of 50%. We assume the lower rate was due, in part, to the difficulty associated with selectively stopping one movement within a compound response, especially given our monetary incentive system. Nonetheless, the fact that successful stop rates were consistent across days and conditions, whereas RTs were reduced over training, indicates that participants were clearly attentive to the stop signals for the manual responses.

We estimated SSRT according to the assumptions of the horse-race model, defined as the difference between the median of the Go RT distribution and the mean of the SSD (Logan and Cowan 1984; Band et al. 2003). The SSD averaged 98 ms (SE = 7), and a repeated-measures ANOVA of Signal Type vs. Day showed that SSD did not differ between the Color and Tactile conditions [$F(1,9) = 0.04$, $P = 0.84$, effect size $\eta_p^2 = 0.005$] nor vary across days [$F(1,9) = 3.88$, $P = 0.08$, effect size $\eta_p^2 = 0.30$]. Similarly, the SSRT tended to be faster after the tactile stop signal and showed a reduction across days, but only the effect of Day was significant [Signal Type: $F(1,9) = 2.35$, $P = 0.16$, effect size $\eta_p^2 = 0.21$; Day: $F(1,9) = 4.76$, $P = 0.06$, effect size $\eta_p^2 = 0.35$].

The main data of interest were the RTs for the invariant foot response (foot RT), comparing when this response was produced in combination with a manual response (Go trials) to when this response was produced alone because the manual response was aborted (Successful Stop trials). These data were analyzed with a repeated-measures ANOVA with the factors Signal Type (Color/Tactile), RT Type (Go/Successful Stop), and Day (1/2). The effect of Signal Type was not significant [$F(1,9) = 1.02$, $P = 0.34$, effect size $\eta_p^2 = 0.10$]. As can be seen in Fig. 4*A*, the foot RTs decreased over the 20 blocks for both the Color and Tactile conditions, a pattern that is reflected by the significant effect of Day [$F(1,9) = 19.29$, $P < 0.005$, effect size $\eta_p^2 = 0.68$]. Moreover, in both conditions, the foot RTs were slower on successful Selective-Stop trials compared with Go trials [$F(1,9) = 28.61$, $P < 0.001$, effect size $\eta_p^2 = 0.76$], the standard signature of a selective-stopping cost (Coxon et al. 2007; Majid et al. 2012; Aron and Verbruggen 2008). There was also a significant interaction between RT Type and Day [$F(1,9) = 12.72$, $P < 0.01$, effect size $\eta_p^2 = 0.59$], indicating that the selective-stopping cost was reduced with training (see below).

The difference between the foot RTs on Successful-Stop and Go trials is used to estimate the observed selective-stop cost. To evaluate how this cost was influenced by the manner in which the stop signal was cued as well as by practice, we performed a two-way repeated-measures ANOVA with the factors Signal Type and Day on the difference scores (RT cost). The cost was numerically larger for the Color stop signal (67 ms, SE = 15 ms) compared with the Tactile-stop signal (42 ms, SE =10 ms), but the effect was not reliable [$F(1,9) = 2.73$, $P = 0.13$, effect size $\eta_p^2 = 0.23$]. The selective-stop cost was reduced with practice in the 2 days [$F(1,9) = 12.72$, $P < 0.01$, effect size $\eta_p^2 = 0.59$], dropping from 67 ms (SE = 12) on Day 1 to 41 ms (SE = 9) on Day 2. The interaction of these two factors was not reliable [$F(1,9) = 0.14$, $P = 0.71$, effect size $\eta_p^2 = 0.02$] Because only the right foot was used in the task, we separated the left and right hand trials to examine if there was any difference between trials involving same-side responses and trials involving different-side responses. We

analyzed the cost data using a three-way repeated-measures ANOVA with the factors Side, Signal Type, and Day. There was no significant effect of Side [$F(1,9) = 0.009$, $P = 0.93$, effect size $\eta_p^2 = 0.001$], nor did it interact with any of the other factors.

Importantly, the size of the cost is significantly greater than zero for both signal types, even during the second day {collapsed over signal types: $t(19) = 4.438$, $P < 0.001$, 95% CI [22, 61]}. Based on this analysis, one would conclude that selectively stopping one movement within a compound response imposes a cost on the invariant response no matter what, a central assumption of the restart model. However, we show in the following section that this is not the case.

Modeling Results

As described in MATERIALS AND METHODS, a comparison between foot RTs on successful Stop and Go trials is biased since the former is composed mostly of the slower half of the full RT distribution. Given this, we used the stop probability functions and foot Go RT (T_{GO}) distributions for each participant to estimate both the magnitude of this bias and the restart cost. We compared these estimates to the observed costs.

Using a bootstrapping procedure, we modeled the sampling-bias and restart costs predicted by the selective-stop model for the two types of stop signals for each day (Fig. 4*B*). A two-way repeated-measures ANOVA of Signal Type × Day on the restart cost data yielded a main effect of Signal Type [$F(1) = 8.55$, $P < 0.05$]. Although there was a trend for the restart cost to be reduced across the two sessions, this effect as not reliable [$F(1) = 1.58$, $P = 0.24$].

For the Color condition, the difference between the observed costs and modeled sampling-bias costs was significantly different on both days [Day 1: $t(9) = 4.44$, $P < 0.005$; Day 2: $t(9) = 2.27$, $P < 0.05$]. A two-way repeated-measures ANOVA of Data Type (sampling-bias vs. observed cost) × Day showed a significant main effect of Day [$F(1) = 9.35$, $P < 0.05$]. Thus, while although training reduced the restart cost, the sampling bias does not fully account for the observed cost even on Day 2, consistent with the idea that there is a restart process on successful Stop trials in this variant of a selective-stop task. This conclusion was also supported by the observation that the restart costs fall greater than zero when 95% CIs are constructed by bootstrapping (C_r intervals: Day 1 95% CI [25, 78]; Day 2 95% CI [10, 57]).

For the Tactile condition, the difference between the observed and modeled sampling-bias costs was marginally significant on Day 1 [$t(9) = 2.22$, $P = 0.053$] but not on Day 2 [$t(9) = 0.92$, $P = 0.38$]. Moreover, the ANOVA here revealed a significant effect of Day [$F(1) = 7.40$, $p < 0.05$] and the 95% CIs for the restart costs span zero on both days (C_r intervals: Day 1 95% CI [−8, 26]; Day 2 95% CI [−11, 23]). Thus, if we were to repeat the same experiment in the population, participants should be able to successfully abort one component of a planned action in the Tactile condition by the second day without a corresponding cost in a second component of that action.

To examine how the observed costs may arise from the sampling bias, we examined the modeled results for each individual (Fig. 5). On Day 2, the observed cost fell within the upper bound of the 95% CIs of the modeled sampling-bias costs for three participants when the stop signal was visually cued and for six participants when the tactile cue was used as the stop signal. Thus, with just 2 days of training, a considerable number of participants were able to produce the foot response independent of whether they were simultaneously initiating or aborting a planned manual response.

DISCUSSION

The difficulty people have in selectively stopping one movement within a multicomponent action has been taken to imply that this form of inhibitory control operates in a relatively generic manner, one that targets all potentiated actions (De

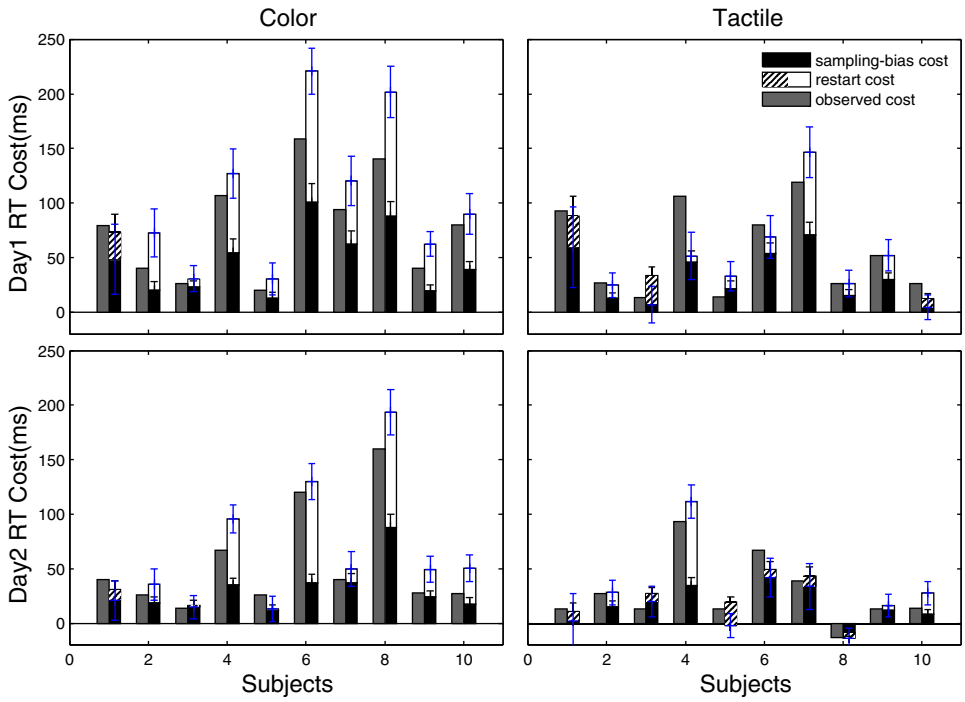

Fig. 5. Selective-stopping costs for individual subjects. Solid black are estimated sampling-bias costs. Open bars are restart costs, stacked on top of the solid black bars. Negative values for the restart costs are indicated with striped bars. The gray bars indicate the value for the observed cost for each subject.

Jong et al. 1995; Coxon et al. 2007; MacDonald et al. 2012; Majid et al. 2012; Aron and Verbruggen 2008; Greenhouse et al. 2012; Cai et al. 2012). A restart process would be required to offset this generic inhibition, resulting in delays on Selective-Stop trials (Coxon et al. 2007; MacDonald et al. 2012). The notion of a structural constraint that results in relatively generic response inhibition is consonant with neurobiological models that emphasize cortico-basal ganglia networks and in particular the hyperdirect projection to the subthalamic nucleus (STN) (Aron and Poldrack 2006; Aron et al. 2007). While there is evidence of some degree of functional specialization and somatotopy within the STN (Greenhouse et al. 2011; Nambu et al. 1996), the relatively small size and divergent projections from the STN to the output nuclei of the basal ganglia (Parent and Hazrati 1995) would suggest that this network is unlikely to be recruited to abort selective components of ongoing actions.

The results of the present experiment and modeling are at odds with the hypothesis that the termination of a planned response always involves the generation of generic inhibitory signals. With a modest degree of training, financial motivation, and a salient cue (tactile), people were able to selectively inhibit one movement within a multicomponent action without any cost on an invariant response. This indicates a degree of flexibility in the inhibitory control of movement. Our modeling work here suggests that the "restart cost" observed in many previous studies of selective stopping (e.g., Coxon et al. 2007) may be the result of a statistical artifact inherent in the standard way of assessing this cost.

Reliability of the Selective-Stop Model

As with any modeling approach, it is important to consider how the predictions of the model are sensitive to different parameters. To model the sampling-bias cost, three parameters are relevant, the means, variances, and skewness of the RT distributions for the foot on Go (P_{GO}) and Successful Stop (P_{SS}) trials. The restart hypothesis assumes that these two distributions are statistically independent. If the P_{SS} and P_{GO} samples are not from the same distribution, the horse-race model must be violated (as illustrated in the simulation in Fig. 3*E*).

It is important to also consider how assumptions of our model of selective stopping might influence the estimates of the restart cost. We note that if we fix the parameters of the P_{GO} distribution, the observed sampling cost will correlate with the mean of the P_{SS} distribution. This is a potential bias in estimating the sampling-bias cost since the modeled cost could be inflated if the mean of the P_{SS} is contaminated by restart values in the real data. However, this potential should not affect the utility of the model for assessing restart costs. The P_{SS} samples are taken solely from the P_{GO} distribution and this distribution would not contain trials with a restart cost. Thus, even if the Stop trials might be contaminated by restart costs, and, as a result, p^* would be affected by restart process, our procedure nevertheless partitions an unbiased distribution. In fact, in the event of this occurring, the modeled cost is guaranteed to have an upper bound that is less than the observed cost (Fig. 3*G*), allowing us to use the model to test the restart hypothesis.

The variances (σ) and skewedness (τ) in the P_{GO} and P_{SS} distributions also affect the modeled cost. When the P_{GO} distribution is held constant, increased σ in the P_{SS} and/or P_{FS} distributions will result in an underestimate of the modeled sampling-bias cost: as σ increases, the inhibition function becomes shallower, with greater intermixing of samples from the P_{FS} and P_{SS} distributions, resulting in a smaller difference between the medians of the P_{GO} and P_{SS} means. However, this scenario is rare in real data since the variances of the P_{SS} and P_{FS} distributions are larger than the P_{GO} distribution. As such, variances of P_{FS} and P_{SS} in the model are less likely to be inflated.

The more interesting case concerns skewedness (τ) in the P_{SS} distribution. When other parameters are held constant, increased τ results in a larger observed cost but a relatively stable and small estimate of the sampling-bias cost. This is what might be expected if there is a mixture of global and local inhibitory processes, where the P_{SS} distribution has a long tail due to a restart delay in a (small) percentage of the trials. Our modeling approach accurately captures this phenomenon.

In the current implementation, we chose to use individualized inhibition functions. The advantage of this approach is that it bypasses the assumption of a fixed 50% stopping rate. While the staircase algorithm is set to achieve a 50% stopping rate, the observed data may not match this value (e.g., Cai et al. 2011; Majid et al. 2012), an outcome present in the current data set. Because of the potentially existing restart cost in the real data, this approach might result in the higher mean value for P_{SS} and, therefore, a larger estimate of the SSRT in the simulated results. As such, the model's prediction of the sampling-bias cost would be biased towards a larger value. This scenario arises because the inhibition function used for classifying the RTs may be shallower if there is a "restart cost" in the real data. This would polarize the means of the sampled P_{SS} and P_{FS} distributions and introduce longer tails to these two distributions (also resulting in a smaller SSD or larger SSRT, see Band et al. 2003). Note that, here again, the horse-race model is violated with some restart cost contaminating the RT distribution. More trials will be labeled Failed Stop rather than Successful Stop, and the Successful Stop samples will be shifted toward the right tail of the P_{GO} distribution (Fig. 3*G*). The net result is that the sampling-bias cost is slightly overestimated. However, as noted above, this issue does not affect the utility of the model for discriminating between the restart hypothesis and the sampling-bias hypothesis given that the samples are taken solely from the P_{GO} distribution. Moreover, this guarantees an upper bound of the modeled sample-bias cost based on the variance of the original full P_{GO} distribution.

To fully explore the "contamination" issue, we conducted two additional analyses in which we used the stopping rate for each individual and their mean SSD + SSRT to define the cut-off values for the P_{GO} distribution. These values were used to classify the sampled data as failed or successful stops. The results from these approaches were similar to those obtained from the initial model. For example, the observed cost was not reliably different than the modeled sampling-bias cost on either day in the Tactile condition, although the difference was marginal on Day 1 [SSD + SSRT model: $t(9) = 1.94$, $P = 0.08$ for Day 1, and $t(9) = 0.63$, $P = 0.54$ for Day 2; stop-rate model: $t(9) = 1.76$, $P = 0.11$ for Day 1, and $t(9) = 0.09$, $P = 0.93$ for Day 2]. For the Color condition, this difference was

only reliable on Day 1 [SSD + SSRT model: $t(9) = 3.24$, $P < 0.05$ for Day 1, and $t(9) = 1.58$, $P = 0.15$ for Day 2; stop-rate model: $t(9) = 4.23$, $p < 0.005$ for Day 1, and $t(9) = 2.32$, $P < 0.05$ for Day 2].

Models of Selective Stopping

Our task entailed a simultaneous selective-stop method in which one component of a complex response is aborted on Stop trials (e.g., Coxon et al. 2007; Aron and Verbruggen 2008; Claffey et al. 2010; MacDonald et al. 2012). Selective stopping has been examined in other tasks in which the stop signal is only relevant for a subset of the stimuli. In the conditional selective-stop task, one member of the stimulus-response set is designated as the critical stimulus for the entire block of trials, with participants instructed to respond to stop signals only on trials with this stimulus (De Jong et al. 1995; Aron et al. 2007; Swann et al. 2009; Jahfari et al. 2010; Greenhouse et al. 2012). In the precued selective-stop task, the critical stimulus is cued before the onset of the go signal and may vary across trials (Aron and Verbruggen 2008; Claffey et al. 2010; Cai et al. 2011; Swann et al. 2012, 2013; Majid et al. 2012, 2013). When comparisons are made (in most cases, across studies), the restart costs tend to be the largest in the simultaneous selective task compared with the other two (e.g., Aron and Veruggen 2008).

These differences likely reflect the fact that these three selective-stop tasks impose different demands on cognitive control operations and online processing. In simultaneous selective stopping, the participant presumably adopts a similar set for all stimuli since the stop signal is treated similarly on all trials. Moreover, the recruitment of inhibitory processes is likely delayed until the onset of the stop signal, especially in a version such as ours where monetary bonuses depend on the RT of the nonstopped response (e.g., the foot). In contrast, in the conditional stopping task, the critical stimulus is fixed throughout the experiment and in the precued selective-stopping task, the critical stimulus is identified prior to the onset of the trial. Thus, in these two tasks, the participant can adopt a differential set towards the stimulus alternatives; for example, the criterion for responding to the critical stimulus may be different than that applied to the noncritical stimulus. Indeed, RTs on Go trials in which a stop signal might occur (e.g., critical stimulus) are slower than on Go trials in which a stop signal will not occur (e.g., noncritical stimulus) (De Jong et al. 1995; Aron et al. 2007; Jahfari et al. 2010; Greenhouse et al. 2012; Swann et al. 2012, 2013). We expect that the restart cost could also be eliminated in these other conditions with training and/or the use of a salient stop signal, although this prediction remains to be tested.

Bissett and Logan (2014) recently proposed that stop-signal tasks should be viewed in terms of whether inhibition can be directed at perceptual or motor stages of processing. In their view, with cueing tasks (either by block or trial-by-trial), the cue specifies whether a stop signal is relevant (i.e., requires attempting to abort a planned response) or irrelevant (i.e., can be ignored). Selection here, and perhaps inhibition of selected items, can be perceptually based: If the stimulus is not the critical one, then there will be no need to attend to stop signals. In contrast, with simultaneous selective-stopping tasks, selection for inhibition is shifted towards motor stages since the stop signal likely comes after selection of the response. While we recognize that the perception vs. motor distinction is surely blurred, simultaneous selective tasks such as that used here seem most appropriate for testing the restart hypothesis. A key assumption of the hypothesis is that a selected response is transiently disrupted by the stop signal.

Psychological Sources of Selective-stop Costs

Several models for aborting a planned response have been proposed. At a taxonomic level, there are three main types of models: *1*) single-process models that entail global inhibition, *2*) dual-process models in which inhibition can either be global or selective, and *3*) single-process models that entail selective inhibition.

The single-process, global inhibition model postulates that control signals deployed to abort an initiated action are relatively generic. The advantage of this form of control is that it can be implemented in a rapid manner (e.g., along the hyperdirect pathway of the STN, see Coxon et al. 2007). The cost, however, is that there is a transient, generic disruption of all on-going responses.

The dual-process model is similar to that proposed by De Jong et al. (1995), with the core idea that the form of the control signal will be context dependent. Global mechanisms are recruited when the situation benefits from the utilization of generic commands; selective mechanisms are recruited when inhibitory commands must be targeted to specific components of an action. Based on EEG data, De Jong et al. suggested that global signals arise along a cortico-subcortical pathway that operates quickly, albeit at a cost of specificity, whereas selective signals are slower and depend on interactions that are purely cortical. The results of the current study underscore that stop signals can be selective. It remains to be seen if selectively aborting one component of a planned action is inherently slower than aborting the entire action and whether the two processes rely on different neural pathways. Our results indicate that with training and appropriate task segregation, people may prove to be equally facile in both conditions.

The third class of models is based on the idea that there are no global control signals; by this view, all control signals have some degree of specificity, and the fidelity of these signals can be modified by training and task conditions. Within the framework of the stop signal task, the argument would be that the control processes are capable of directing their output in a selective manner. This hypothesis is consistent with the successful elimination of restart costs with training in the current experiment, a result that was only evident when the data were analyzed to account for the sampling-bias cost. By this class of models, signatures of global inhibition such as selective-stopping costs result from a failure to segregate the different components of a complex action, rather than some structural constraint of the control signals. Evidence of generic inhibition, either from transcranial magnetic stimulation studies (e.g., Badry et al. 2009; Cai et al. 2012; Greenhouse et al. 2012) or neuroimaging studies (e.g., Majid et al. 2013), may reflect the simplicity of experimental tasks that favor aborting the entire action rather than invoke targeted inhibition.

Our results lead us to reject the hardwired restart model as an obligatory manner in which people respond in selective-stop tasks. This raises the question of why selective-stop costs are

generally observed and why training and stop-signal saliency might reduce these costs. We propose that stop-signal tasks can be viewed as a type of dual task, one in which the second stimulus/task requires that the action associated with the first stimulus/task be counteracted. In the selective-stop task, the stop command has an additional task demand in which one response must be sustained while the other is inhibited. The selective-stopping cost may reflect an assignment problem (Duncan 1977; Ivry et al. 1998). The participant must detect the stop signal and then rapidly assign the stopping operation to one of two activated responses. By this view, the stronger compatibility of the tactile stimulus and the to-be-aborted response could account for the fact that participants showed lower residual costs for tactile stop signals. Further support for this idea comes from studies showing the performance on stop-signal tasks is influenced by the degree of congruency between the stop signal and the targeted response for inhibition (Claffey et al. 2010; Kramer et al. 1994; Verbruggen et al. 2004).

In the current study, training not only reduced RTs on Go trials but also reduced the SSRT and residual stopping cost. We assume that training increases the separation between the manual response that may be aborted and the invariant foot response, an effect likely enhanced by our monetary incentives. This effect is similar to that observed in studies where practice effects can abolish all dual-task costs, at least when there is some degree of congruency between the stimulus and response sets (e.g., Schumacher et al. 2001; Hazeltine et al. 2002). These effects further argue against the idea that the constraints associated with selective stopping are structural in nature. We expect that, given enough training, the restart-cost in the Color condition would also reduce to zero as participants develop automaticity in not only isolating the invariant foot response but also in assigning the visual stop signal to the targeted response.

Conclusion

The experiment and modeling results presented here demonstrate that people can selectively inhibit a specific component of an on-going action. These findings argue against models in which aborting a planned action under speeded constraints is dependent on the operation of a structural control process, one that produces a generic inhibitory signal. Rather, the results point to a softer set of constraints, ones that reflect more general properties of our cognitive architecture.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: J.X. and R.B.I. conception and design of research; J.X. and Z.W. analyzed data; J.X., Z.W., and R.B.I. interpreted results of experiments; J.X. prepared figures; J.X. drafted manuscript; J.X., Z.W., and R.B.I. edited and revised manuscript; J.X., Z.W., and R.B.I. approved final version of manuscript; Z.W. performed experiments.

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