

Viewpoints

Stopping Interference in Response Inhibition: Behavioral and Neural Signatures of Selective Stopping

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Response inhibition is an essential aspect of cognitive control that is necessary for terminating inappropriate preplanned or ongoing responses. Response-selective stopping represents a complex form of response inhibition where only a subcomponent of a multicomponent action must be terminated. In this context, a substantial response delay emerges on unstopped effectors after the cued effector is successfully stopped. This response delay has been termed the stopping interference effect. Converging lines of evidence indicate that this effect results from a global response inhibition mechanism that is recruited regardless of the stopping context. However, behavioral observations reveal that the stopping interference effect may not always occur during selective stopping. This review summarizes the behavioral and neural signatures of response inhibition during selective stopping. An overview of selective stopping contexts and the stopping interference effect is provided. A “restart” model of selective stopping is expanded on in light of recent neurophysiological evidence of selective and nonselective response inhibition. Factors beyond overt action cancellation that contribute to the stopping interference effect are discussed. Finally, a pause-then-cancel model of action stopping is presented as a candidate framework to understand stopping interference during response-selective stopping. The extant literature indicates that stopping interference may result from both selective and nonselective response inhibition processes, which can be amplified or attenuated by response conflict, task familiarity, and functional coupling.

Introduction

Response inhibition, the process of terminating inappropriate preplanned or ongoing actions to suit environmental demands, is essential for successful goal-directed behavior in dynamic environments (Logan, 1985). Response inhibition manifests in moments of action postponing, withholding, or stopping (Bari and Robbins, 2013). Real-world examples of these moments include a driver waiting to press their foot on the accelerator at a traffic light, a batter resisting the urge to swing at an errant pitch, and a pedestrian abruptly halting at a crossing when a car suddenly appears. In the clinical domain, deficits in response inhibition are evident in conditions associated with poor impulse control, such as attention deficit hyperactivity disorder (Wodka et al., 2007), and in behaviors, such as pathologic gambling (Kertzman et al., 2008).

Response inhibition can be required in selective or nonselective stopping contexts. Nonselective stopping occurs in response inhibition scenarios where all components of a response must be terminated. This may occur in behaviors that require coordination of effectors with a common goal, for example, stopping a reaching action when an unexpected hazard is noticed. Conversely, selective stopping occurs in complex response inhibition scenarios when only a subset of

a response must be terminated (Bissett and Logan, 2014). This may occur in behaviors that require simultaneous coordination of multiple effectors across and within limbs. For example, driving a car requires limb assignments to separate components that are precisely timed to environmental cues, such as steering and shifting gears between the two hands, and acceleration and braking with the foot. One can selectively stop one of these components, such as turning the steering wheel to change lanes, by using an effective and selective response inhibition process. However, this selective stopping may cause a delay in the remaining components, such as shifting gears or controlling pedals. The existence of a stopping interference effect identifies underlying constraints that may prevent purely selective stopping. Converging lines of evidence indicate that selective stopping is achieved through both nonselective and selective response inhibition processes (e.g., Duque et al., 2017) and that the response context can make stopping apparently more or less selective (Xu et al., 2015; Wadsley et al., 2019; Raud et al., 2020).

This review summarizes the current understanding of response inhibition processes in the context of selective stopping. First, it provides an overview of two types of selective stopping (stimulus-selective and response-selective) at the behavioral level. Next, the presence of stopping interference during response-selective stopping is examined and a neuroanatomical basis of response inhibition during selective stopping is considered, along with how this may be modulated by response context. Finally, response-selective stopping in a pause-then-cancel model of action stopping is reviewed and presented as a candidate framework to account for the stopping interference effect.

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Selective stopping

Selective stopping can occur during perceptual or motor stages of cognitive control. Stimulus-selective stopping refers to targeted inhibition at the perceptual stage where response inhibition is only required for a subset of salient stimuli (Bissett and Logan, 2014). Response-selective stopping refers to targeted suppression at the motor stage where inhibition of one of several simultaneously prepared actions is required (Coxon et al., 2007). A selective response inhibition process would provide for optimal behavior for both forms of selective stopping in the example about changing lanes while driving. Stimulus-selective stopping would occur when the decision to change lanes is cancelled by the driver after noticing a car hidden in their blind spot. Response-selective stopping would occur by the driver halting the steering action after such a decision is made. However, stimulus-selective and response-selective stopping can also be supported by nonselective response inhibition. For example, cancelling the decision to change lanes in response to any sudden unexpected event can momentarily pause multiple actions before an appropriate response is then selectively reinstated. Empirical evidence in support of these multiple views is reviewed below.

Proactive versus reactive response inhibition

Selective stopping is enacted through mechanisms that support both proactive and reactive response inhibition. Proactive information may contain foreknowledge about stopping probability (e.g., Zandbelt and Vink, 2010) or cue which response (of two or more) should be terminated if a stop signal is presented (e.g., Aron and Verbruggen, 2008). Proactive response inhibition may occur at different cognitive stages, such as during strategy formation or during anticipation. Whereas proactive response inhibition occurs in anticipation of the need to stop (Verbruggen and Logan, 2009; Jahfari et al., 2010; Zandbelt et al., 2013), reactive response inhibition occurs after the need for stopping has been recognized (Aron, 2011; Braver, 2012). Reactive and proactive response inhibition is enacted through distinct but not mutually exclusive neural mechanisms (Aron, 2011; Pauwels et al., 2019). Numerous studies have shown that the degree to which stopping may be selective is influenced by both proactive and reactive processes.

Assessing response inhibition

The stop-signal task (SST) (Lappin and Eriksen, 1966; Verbruggen et al., 2019) and anticipatory response inhibition (ARI) (Slatter-Hammel, 1960; He et al., 2021) paradigms have been used to investigate response inhibition. Both paradigms involve a participant making a default response, such as pressing a key in response to a go signal, and on occasion, cancelling the default response on presentation of a stop signal. For the SST, responses are equivalent to those in a reaction time task where a speeded action is cued by an explicit go signal. With the ARI paradigm, a response is cued by a predictable indicator reaching a target, thereby reducing response variability (Leunissen et al., 2017). Top-down inhibitory control is required in SST and ARI paradigms as both a go and stop signal are presented on stop trials (Verbruggen and Logan, 2008). The delay between the go signal and the stop signal (termed stop-signal delay) can be adjusted dynamically on a trial-by-trial basis to alter the difficulty of cancelling the prepared response. The stop-signal delay allows the computation of a stop-signal reaction time, which is a proxy for the latency of response inhibition (Band et al., 2003). The underlying assumptions and limitations of SST and ARI paradigms are presented elsewhere (for comparisons, see Leunissen et al.,

2017). For this review, our position is that both SST and ARI paradigms provide a reliable means to assess response inhibition.

Stimulus-selective versus response-selective stopping paradigms

Stimulus-selective stopping can be assessed by introducing task-irrelevant “ignore” or “continue” stimuli to response inhibition paradigms (e.g., Sharp et al., 2010). Like stop signals, task-irrelevant signals are presented on a subset of trials after a delay that is typically based on the most recent stop-signal delay (Bissett and Logan, 2014). Participants are instructed to enact the preplanned go response when a task-irrelevant signal is presented. Thus, participants are required to actively discriminate between nonstopping and stopping stimuli during go performance. A set of strategies have been suggested to describe performance during stimulus-selective paradigms (Bissett and Logan, 2014). A selective “discriminate-then-stop” strategy reflects instances where inhibition occurs only after a stop signal is discriminated, or alternatively, not preparing a response until the correct stimulus is identified. Conversely, a nonselective “stop-then-discriminate” strategy reflects instances where inhibition is automatically initiated on detection of a signal, and then a response is “restarted” once the ignore/continue cue has been discriminated from a stop cue (Sánchez-Carmona et al., 2021).

Response-selective stopping can be assessed with multicomponent variants of SST and ARI paradigms (Coxon et al., 2007; Aron and Verbruggen, 2008). While the objective on go trials is maintained, multicomponent variants use several indicators to cue multieffector responses (Fig. 1A). Effector pairings can be within or between limbs (e.g., left-middle/left-index finger vs hand/hand or hand/foot), with between-limb pairings further distinguishable by homogeneous or heterogeneous pairings (MacDonald et al., 2012). An advantage of the default go response involving two effectors is that both nonselective and selective stopping can be assessed by presenting a stop signal to both (stop-all) or one (partial-stop) indicator, respectively. Success during stop-all trials requires cancellation of the entire preplanned response (Fig. 1B). Conversely, success during partial-stop trials requires cancellation of only the signaled subcomponent, while the remaining subcomponents can proceed as planned (Fig. 1C). The probability of successfully stopping is associated with the stop-signal delay, such that success is proportional to the time available (Coxon et al., 2007). In summary, stop-all trials can be supported by global response inhibition, whereas optimum performance during partial-stop trials requires selective response inhibition (Aron and Verbruggen, 2008). While we acknowledge the potential contribution of both stimulus-selective and response-selective domains of response inhibition (for discussions of stimulus-selective stopping, see Bissett and Logan, 2014; Sebastian et al., 2017; Sánchez-Carmona et al., 2021), the remainder of this review will focus on response-selective stopping (hereby shortened to “selective stopping” for simplicity).

The stopping interference effect

What influence does a stop signal have on effectors that are meant to execute a preplanned response? In their seminal study of selective stopping, Coxon et al. (2007) found that, when the response in the effector cued to stop (the stopped effector) was successfully withheld, the response times for the effector that was not required to stop (the unstopped effector) were systematically delayed relative to go trials. Similar response delays were observed by Aron and Verbruggen (2008), who first coined the term stopping interference effect, because the act of stopping seemingly interfered with

responses in unstopped effectors. The occurrence of stopping interference during partial-stop trials has been replicated consistently across SST (Claffey et al., 2010; Cai et al., 2011, 2012b; Ko and Miller, 2011, 2013; Majid et al., 2012, 2013; Lavalée et al., 2014; Ko et al., 2015; Raud and Huster, 2017; Drummond et al., 2018; Muralidharan et al., 2019; Raud et al., 2020) and ARI paradigms (Coxon et al., 2007, 2009, 2012, 2016; MacDonald et al., 2012, 2014, 2016, 2021; Cowie et al., 2016; Cirillo et al., 2018; Wadsley et al., 2019).

Stopping interference in proactive contexts

Selective stopping can be assessed in proactive response inhibition contexts. Precued selective stopping paradigms involve the presentation of informative (e.g., “Maybe Stop left”) or uninformative (e.g., “Maybe Stop XXX”) warning cues before the start of a trial (Cirillo et al., 2018; Raud et al., 2020). Uninformative partial-stop trials are equivalent to noncued trials as stopping may be required for any given effector in the forthcoming response. As such, proactively suppressing a particular effector is not advantageous to overall performance as the likelihood of stopping, and thus responding, is equally likely for either effector. Informative partial-stop trials cue participants that the response for a particular effector will need to be withheld if a stop signal is presented. Therefore, the contribution of proactive response inhibition for selective stopping can be determined by contrasting informative (proactive) and uninformative (reactive) partial-stop trials.

The stopping interference effect is reduced in precued selective stopping paradigms. Aron and Verbruggen (2008) implemented informative partial-stop trials and determined that stopping interference was reduced, whereas stop-signal reaction time was prolonged relative to uninformative partial-stop trials. Based on this finding, the authors suggested that selective stopping within proactive contexts was achieved through a slower, but more selective, response inhibition mechanism. However, the influence of cueing on the speed of selective stopping is less clear because subsequent studies have demonstrated that stop-signal reaction time for informative partial-stop trials can be less (Smittenaar et al., 2013), more (Aron and Verbruggen, 2008; Claffey et al., 2010), or no different (Raud and Huster, 2017; Cirillo et al., 2018) than for uninformative partial-stop trials. Contradictory evidence may be due in part to limitations of stop-signal reaction-time computations (Matzke et al., 2019; Bissett et al., 2021). Regarding the selectivity of stopping, subsequent studies corroborate the existence of a reduced, but not abolished,

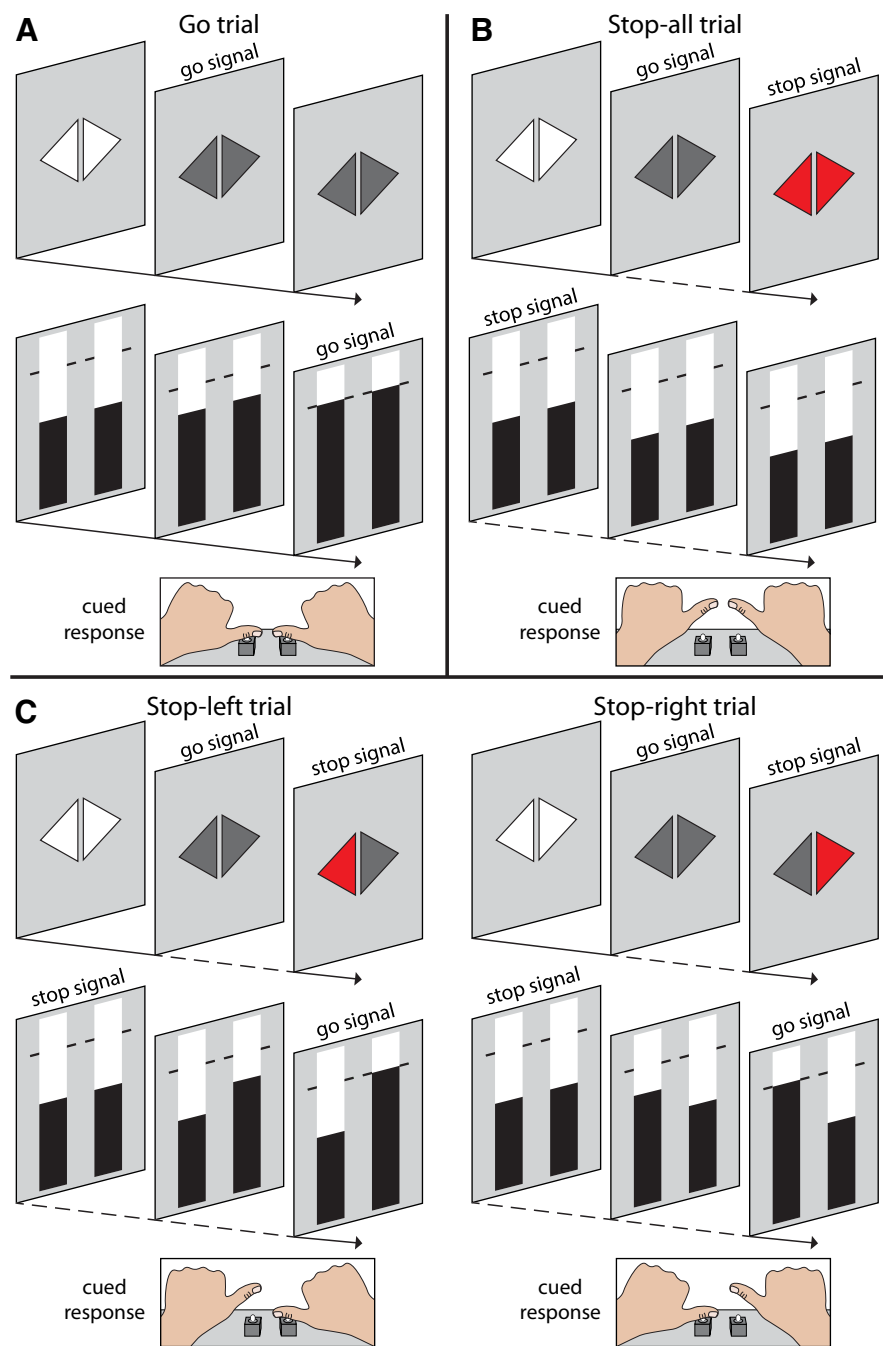


Figure 1. Schematic of primary trial types during multicomponent SST and ARI paradigms. The cued response is demonstrated using an example left and right thumb effector pairing. **A**, A multicomponent response is cued for both subcomponents during go trials by an explicit go signal for SST (top, indicator turning gray) or an implicit go signal for ARI (bottom, indicator reaching target line) paradigms. **B**, Nonselective stopping is assessed during stop-all trials by presenting a stop signal (SST, indicator turning red; ARI, indicator automatically stopping before the target line) based on a variable stop-signal delay (dashed line) for both subcomponents in the response. **C**, Selective stopping is assessed during partial-stop trials by presenting a stop signal across one subcomponent while the other continues as initially cued by the go signal.

stopping interference effect within proactive stopping contexts (Cai et al., 2011; Majid et al., 2012; Smittenaar et al., 2013; Lavalée et al., 2014; Raud and Huster, 2017; Cirillo et al., 2018; Drummond et al., 2018). In summary, stopping can proceed more selectively in proactive contexts.

The restart model

The restart model predicts that the stopping interference effect emerges because of nonselective response inhibition during

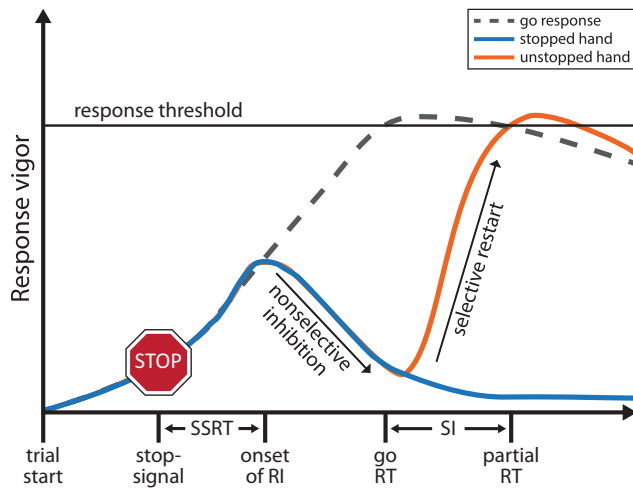


Figure 2. Restart model of the stopping interference effect during selective stopping. Response vigor builds before responding for go trials (assumed identical for both sides). Response inhibition is marked by suppression within the stopped and unstopped effectors after the stop-signal reaction time (SSRT) during partial-stop trials. Response vigor is then restarted at a greater gain (slope of line) than observed during typical responding. The period of nonselective response inhibition and selective restart produces a response delay in the unstopped effector, termed the stopping interference (SI) effect.

selective stopping (De Jong et al., 1995). Nonselective response inhibition manifests not only within the stopped effector, but also within unstopped and task-irrelevant effectors. Nonselective response inhibition must then be countermanded by selectively restarting the response within the unstopped effector (MacDonald et al., 2017). Interestingly, restarting is dependent on the strength of response inhibition. Strong inhibition leads to large stopping interference that requires a complete restart, whereas weak inhibition results in small stopping interference that may only temporarily gate ongoing excitatory processes before its release. Restarting in these cases is likely achieved by some combination of disinhibition and excitation of the unstopped effector (MacDonald et al., 2017). Therefore, the magnitude of stopping interference likely reflects the magnitude of nonselective response inhibition and speed of selective response reinitiation (Fig. 2).

Neurophysiology of response inhibition and selective stopping

Neurophysiological studies of response inhibition indicate that selective stopping is supported by a putative response inhibition neural network (for a detailed review, see Aron et al., 2016). The network comprises a cortico-basal-ganglia hyperdirect and indirect pathway, which are engaged during reactive and proactive response inhibition. The hyperdirect pathway is comprised of white matter pathways projecting between right inferior frontal cortex, the presupplementary motor area, and the subthalamic nuclei. This pathway is engaged during reactive response inhibition for rapid, global suppression of motor output (Fig. 3A) (Nambu et al., 2002; Pauwels et al., 2019). Conversely, the indirect pathway is comprised of projections to the subthalamic nucleus via the striatum and is engaged during proactive response inhibition for slower, targeted suppression of motor output (Fig. 3B) (Leunissen et al., 2016). Functional neuroimaging studies indicate that selective stopping (partial-stop trials) may involve both the hyperdirect and indirect pathway (Coxon et al., 2009, 2012, 2016; Cai et al., 2012b; Majid et al., 2013). In reactive contexts, stopping interference and stop-signal reaction time negatively correlate with the functional integrity along white matter

pathways that correspond to hyperdirect and indirect pathways, respectively (Coxon et al., 2012, 2016). In proactive contexts, contrasts of precued stop-all and partial-stop trials demonstrate greater activation of the striatum, a key region of the indirect pathway, when preparing to stop selectively (Majid et al., 2013). Activation of these same regions during stopping is negatively associated with the stopping interference effect. Therefore, the selectivity of stopping may reside on a continuum of activation between the hyperdirect and indirect pathways, which is shifted by the extent of proactive control.

Neural signatures of the stopping interference effect

Nonselective response inhibition over the sensorimotor cortices has been observed using transcranial magnetic stimulation and motor-evoked potential recordings in surface EMG. Measures of corticomotor excitability (CME) are obtained from motor-evoked potential amplitude and its modulation. For example, there is a period of CME suppression during action preparation (Greenhouse et al., 2015), followed by rapid enhancement during action execution (Coxon et al., 2006). In a unimanual stopping context, response inhibition is marked by suppression of CME within the targeted effector ~140 ms after the stop signal (Jana et al., 2020). Suppression is also observed at an equivalent magnitude within the stopped effector during partial-stop trials (Raud et al., 2020). Intriguingly, examination of the time course of CME modulation during partial-stop trials reveals that the suppression extends simultaneously to the unstopped effector (MacDonald et al., 2014; Cowie et al., 2016). Nonselective response inhibition in this case is marked by a “dip” in CME and followed by a secondary period of facilitation that gives rise to the execution of the delayed response.

Similar CME modulation occurs for task-irrelevant effectors during nonselective response inhibition. For example, suppression of CME of leg muscle representations has been observed after stopping of a unimanual hand response (Badry et al., 2009; Majid et al., 2012), as well as within a hand muscle after stopping of speech (Cai et al., 2012a). The extent of this task-irrelevant muscle suppression is modulated by response strategy, such that less suppression is observed in participants with slow responses in preparation for stopping (Greenhouse et al., 2012). During response preparation in precued selective stopping paradigms, CME directed toward the hand that is cued to stop is suppressed relative to rest (Cai et al., 2011), whereas there is a release of intracortical inhibition for hand representations that are cued to respond (Cirillo et al., 2018). Additionally, CME suppression does not extend to the lower limb during partial-stop trials involving the hands (Majid et al., 2012). Therefore, the extent of nonselective response inhibition observed in CME appears to be reduced in contexts promoting proactive or selective inhibitory control.

Signatures of nonselective response inhibition have also been observed in EMG from primary agonists of the responding effectors. Response inhibition is marked by suppression of agonist EMG bursts within the stopped effector (Coxon et al., 2006). Suppression of EMG follows CME suppression and occurs ~160 ms after a stop signal in healthy young adults (Jana et al., 2020). Similar to CME, suppression of EMG is observed within the unstopped effector during partial-stop trials. The period of EMG suppression is followed by EMG restart at a greater gain than for an equivalent response during go trials (Coxon et al., 2007; Ko and Miller, 2011; MacDonald et al., 2012, 2014; Raud and Huster, 2017; Raud et al., 2020).

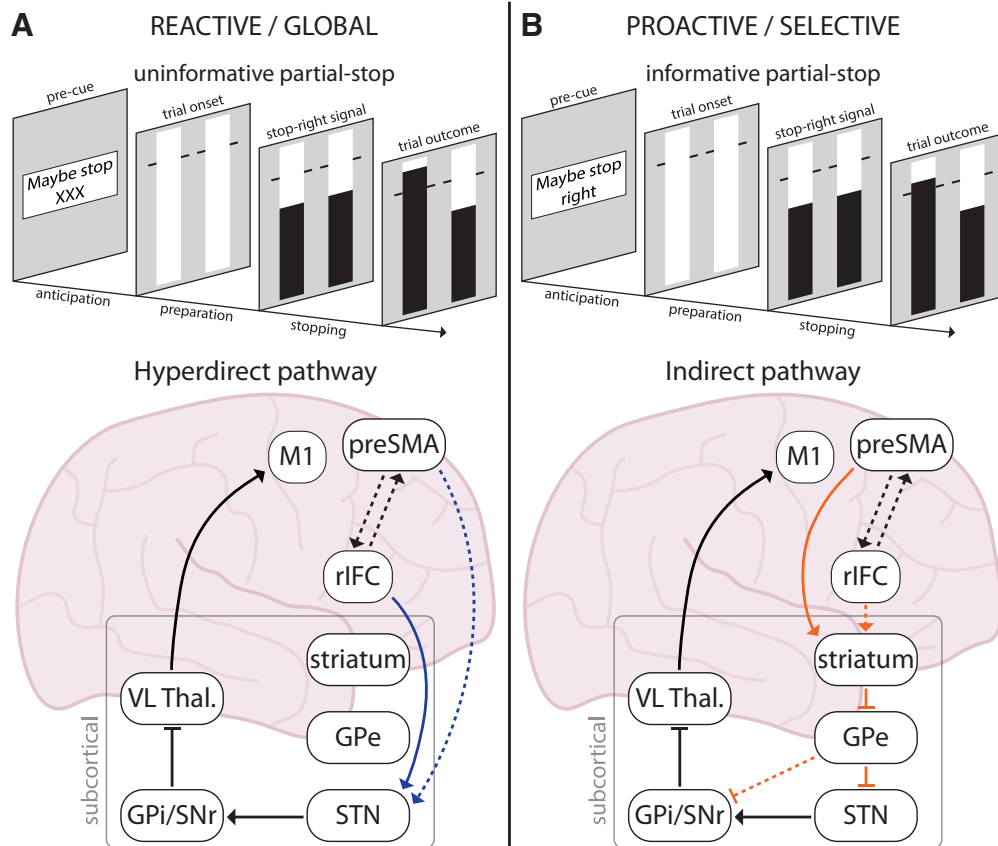


Figure 3. Reactive and proactive inhibition invokes distinct cortico-basal-ganglia pathways within the putative response inhibition neural network. **A**, Global suppression of motor output via the hyperdirect pathway (blue) produces a large stopping interference effect when stopping is ambiguous (uninformative partial-stop). **B**, Targeted suppression of motor output via the indirect pathway (orange) produces less stopping interference when selective stopping can be prepared (informative partial-stop). **A, B**, Stopping interference is indicated by the overshoot of the left indicator relative to target (i.e., late response time). Pointed and flat arrowheads represent excitatory and inhibitory pathways, respectively. Dashed arrows indicate possible interactions. M1, Primary motor cortex; preSMA, presupplementary motor area; rIFC, right inferior frontal cortex; VL Thal, ventrolateral thalamus; GPe, globus pallidus externus; GPi, globus pallidus internus; SNr, substantia nigra; STN, subthalamic nucleus.

The increased gain observable in the EMG of the unstopped effector has been conceptualized within an activation-threshold framework (MacDonald et al., 2017). In this model, the activation threshold for a response to occur is elevated to a level beyond that of the originally planned response by nonselective inhibition after the stop signal. An additional phase of facilitation is then required to overcome the elevated threshold. The secondary phase of facilitation enables rapid response reinitiation and is observable as an increased gain of EMG within the unstopped effector. Further evidence of an elevated activation threshold and increased gain can be observed in the asynchrony between effectors in response times on go trials that occur immediately after a partial trial (Coxon et al., 2007; Cowie et al., 2016).

Nonselective response inhibition observed with EMG is reduced within proactive inhibitory contexts. In their study of selective stopping, Raud and Huster (2017) found that both the magnitude of EMG suppression and restart within the unstopped effector were lower during informative compared with uninformative partial-stop trials. The reduction in the magnitude of nonselective EMG suppression was corroborated by a smaller stopping interference effect in the proactive condition than in the reactive condition. However, the latency of EMG suppression was similar for both proactive and reactive inhibitory contexts. In addition, the latency and magnitude of suppression within the

stopped effector did not differ between unimanual and selective stopping (Raud et al., 2020). Therefore, both selective and nonselective stopping may initially be supported by a global response inhibition mechanism.

The above studies demonstrate a clear pattern of nonselective response inhibition during selective stopping, where suppression of CME and EMG in stopped effectors extends to unstopped effectors during partial-stop trials. Nonselective response inhibition may be the sole consequence of a global inhibitory mechanism being recruited during selective stopping (Fig. 2). However, smaller stopping interference within proactive contexts is accompanied by weaker evidence of nonselective response inhibition (e.g., absence of leg muscle suppression) and greater activation of the indirect basal ganglia pathway. The period of nonselective response inhibition necessitates a subsequent period to restart the response in unstopped effectors. The gain of the restarted response is typically greater than that observed during a go response. The increased gain may be the consequence of an elevated activation threshold driven by the hyperdirect pathway. Alternatively, the brief suppression and then increased gain of the unstopped effector may also be a signature of preparatory suppression that functions to aid rapid reactions during response selection (Greenhouse et al., 2015; Hannah et al., 2018). In summary, neurophysiological signatures of the stopping interference effect reflect a restart process that may be the consequence of both global and selective response inhibition mechanisms.

Contributing factors of the stopping interference effect

The stopping interference effect is likely the product of factors that extend beyond overt response inhibition. As noted above, the selectivity of stopping and signatures of nonselective motor suppression can vary across response contexts. For example, Raud et al. (2020) examined the selectivity of stopping on a trial-by-trial basis by comparing EMG peak onsets of the unstopped and stopped effector during partial-stop trials. Despite the average difference indicating a stopping interference effect, response delays varied from none to exceedingly large at the single-trial level, as was also observed in the stopping interference measures of earlier studies (e.g., Coxon et al., 2007). Furthermore, the stopping interference effect can be eliminated or reduced by manipulating response context. Factors, such as response conflict generated by opposing goals, a lack of familiarity with selective stopping, as well as functional coupling during movement preparation, may all result in nonselective response inhibition (Xu et al., 2015; Wadsley et al., 2019). Therefore, rather than being the consequence of an invariant global inhibitory mechanism, the stopping interference effect may be a consequence of factors that result in nonselective response inhibition, or vice-versa, the absence of factors that allow individuals to engage in selective response inhibition. Identifying these factors will provide for a more nuanced understanding of the stopping interference effect and alternative explanations for evidence of nonselective response inhibition.

Response conflict

Competing stimuli or response options produce conflict (Botvinick et al., 2001) that may generate broad motor suppression through mechanisms associated with response inhibition (Wessel and Aron, 2017; Wessel et al., 2019; Sebastian et al., 2021). For example, CME suppression of task-irrelevant effectors has been observed in response to an unexpected and unrelated signal within the task environment (Wessel and Aron, 2013; Dutra et al., 2018). This suppression has been postulated to serve a functional role, such as momentarily braking motor output while the meaning of unexpected signals is extracted (for detailed review, see Wessel and Aron, 2017). Response conflict is naturally generated during response inhibition paradigms as the fundamental manipulation is the presentation of an additional, infrequent stop signal in direct opposition to the go signal. Therefore, response conflict may contribute to nonselective response inhibition during selective stopping (Fig. 4A).

Response conflict can be disentangled from overt response inhibition by using stimulus-selective response inhibition paradigms. Ko and Miller (2013) used an ignore signal during a force-variant of a multicomponent SST to examine signal-related contributions to the stopping interference effect. Ignore signals required no change to the preplanned response and were presented in an equivalent manner to stop signals during partial-stop trials. At the behavioral level, ignore signals produced a small, insignificant response delay that was considerably less than the stopping interference effect observed during partial-stop trials. In addition, peak force of the unstopped effector was greater during partial-stop trials compared with ignore trials. Greater gain during restart indicates stronger nonselective response inhibition within the activation threshold framework (MacDonald et al., 2017). Therefore, the magnitude of the stopping interference effect cannot be exclusively accounted for by response conflict.

Although the magnitude of the stopping interference effect is reduced in contexts that facilitate proactive control, presentation of infrequent but expected stimuli can still produce broad motor

suppression (Iacullo et al., 2020). Thus, observations of equivalent inhibitory signatures during nonselective and selective stopping (e.g., Raud et al., 2020) may reflect automatic recruitment of the hyperdirect pathway during attentional capture (Wessel et al., 2019). In summary, the selectivity of response inhibition, and thereby magnitude of stopping interference, likely depends on additional modulating factors after an initial period of global motor suppression caused by response conflict.

Task familiarity

Nonselective response inhibition may be recruited when one is unfamiliar with selective stopping (Fig. 4B). Using a multicomponent SST paradigm, Xu et al. (2015) trained participants over four sessions. Monetary rewards were given to each participant based on the speed of responses made on partial-stop trials relative to go trials. In addition, stop signals were presented across conventional (visual stimulus) or high-congruence (key vibrating) conditions. The stopping interference effect within the high-congruence condition was absent after training when the delays were modeled as part of the entire response time distribution. The authors suggested that stopping interference likely emerged as a result of improper assignment of the inhibitory process. However, the reward scheme prioritized fast over accurate responding as participants only required a 25% stopping success rate. Therefore, the abolishment of the stopping interference effect likely reflected a shift in response strategy, rather than a shift to a selective response-inhibition mechanism. This interpretation is further supported by empirical evidence showing that stopping interference is not reduced when stopping success increases (Cowie et al., 2016). These findings indicate that the stopping interference effect can be mitigated by training in response contexts that facilitate fast responding.

Task familiarity may produce a gradual shift from reactive to proactive response inhibition processes. Participants are likely to proactively adjust response strategies as they become more experienced with stop trials (Verbruggen and Logan, 2008). Indeed, a behavioral marker of proactive response inhibition is the slowing of responses to improve stopping success (e.g., Vink et al., 2015). Proactive adjustments to response strategies can also occur in reactive stopping contexts as participants develop an implicit expectation of a stop signal occurring (Verbruggen et al., 2013). A shift toward proactive response control is likely exacerbated by rewarding accurate performance during partial-stop trials (Xu et al., 2015). Thus, response inhibition during selective stopping in reactive contexts may become closer to that engaged in proactive contexts as experience increases. This may also account for the somewhat blurred distinction between reactive and proactive selective stopping that has been observed in previous studies. In summary, the stopping interference effect is likely naturally attenuated by proactive adjustments to response strategies as task familiarity increases.

Functional coupling

Selective stopping is typically assessed in response contexts that necessitate bimanual coordination. Limitations of bimanual coordination have been demonstrated across a variety of tasks. For example, the hands tend to adopt similar spatial trajectories during asymmetric circle and line drawing (Franz et al., 1991). Temporally, there is a tendency to synchronize reaching movements when task difficulty differs between the hands (Kelso et al., 1979). This innate tendency for functional coupling between the hands is likely a consequence of both perceptual and action constraints (for review, see Shea et al., 2016). It is important to

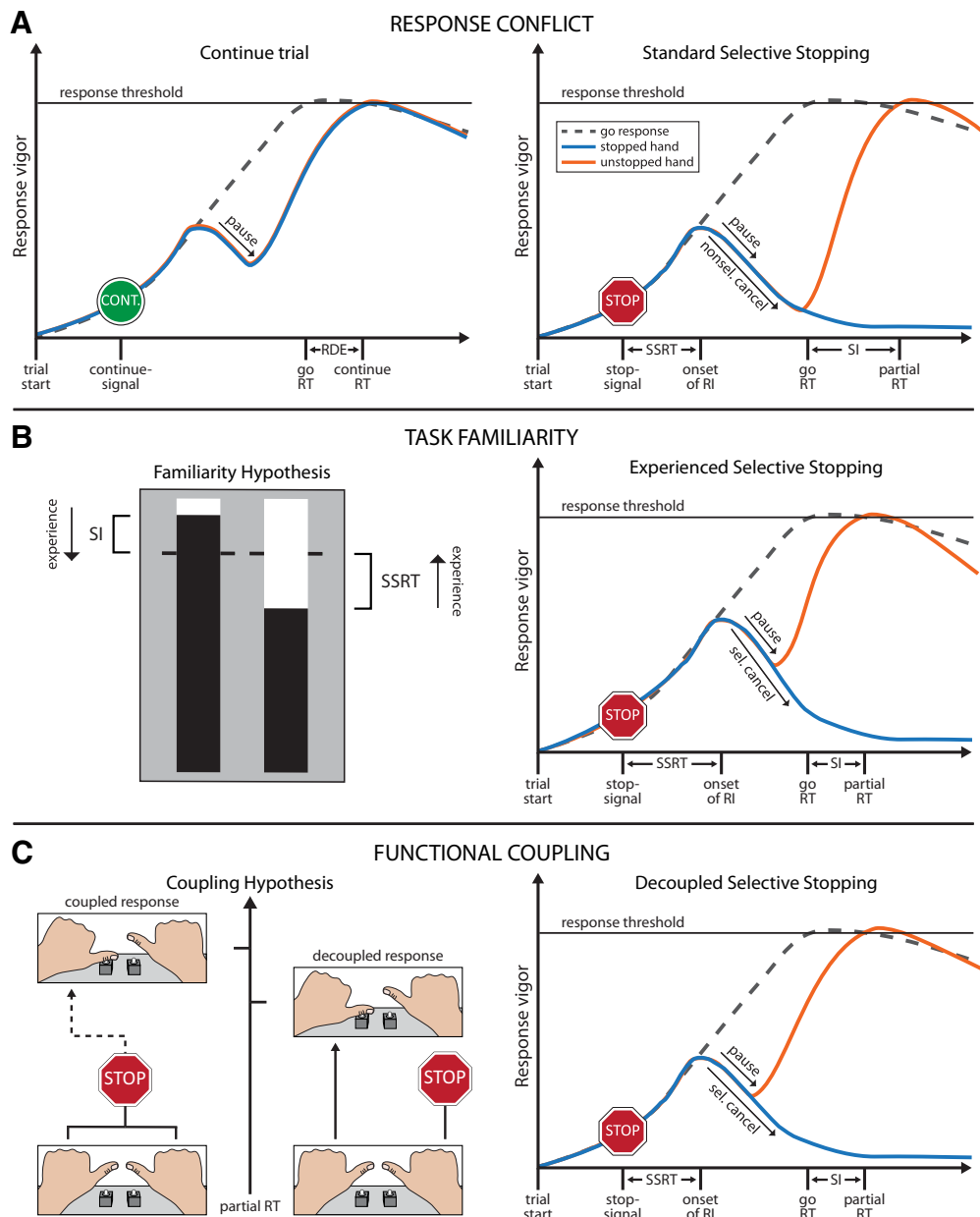


Figure 4. The stopping interference (SI) effect during selective stopping is modulated by response context. **A**, Response conflict initiates a pause process. The pause process produces global motor suppression, evidenced by a response delay effect (RDE) following task-irrelevant stimuli (e.g., ignore trial). Response conflict caused by the stop signal represents part of the nonselective response inhibition (RI) and may inflate SI during partial-stop trials. **B**, The task familiarity hypothesis proposes that stopping interference emerges because of improper assignment of the inhibitory process during selective stopping. Stopping interference is gradually reduced through a slower (increased stop-signal reaction time [SSRT]) and more selective cancellation process as experience with selective stopping is increased. **C**, The coupling hypothesis proposes that nonselective response inhibition arises because of functional coupling during response preparation. During coupled preparation, the cancel process is assigned to a conceptually bound response. Conversely, there is reduced stopping interference during decoupled preparation, owing to selective cancellation of the cued hand.

consider the effect that functional coupling during movement preparation has on the selectivity of response inhibition.

The coupling hypothesis proposes that the innate tendency to conceptually bind effectors produces nonselective response inhibition during selective stopping (MacDonald et al., 2012). Go trials during multicomponent response inhibition paradigms typically involve presentation of two go signals that cue a synchronous bimanual response. Effectors may be functionally coupled at some point along the neuroaxis to reduce processing costs associated with bimanual movements (Wenderoth et al., 2009). Although functional coupling would benefit the planned go response, it would simultaneously impair selective stopping.

Presentation of a stop signal would entail the cancellation of the integrated response regardless of the cued subcomponent, resulting in a nonselective pattern of response inhibition. The stopping interference pattern has been observed across a variety of effector pairings, both within and across limbs, suggesting that functional coupling is not restricted to bimanual coordination only but, instead, may be driven by a common go process (e.g., Jana et al., 2017). By manipulating effector pairings during partial-stop trials, MacDonald et al. (2012) showed that both the stopping interference effect and the gain of the EMG burst at restart were smaller during selective stopping of heterogeneous than homogeneous effector pairings. Furthermore, the stopping interference

effect was more profound on response times of the nondominant hand, supporting the idea that the nondominant hand is more stringently coupled to the dominant hand than vice versa (Byblow et al., 2000). Therefore, stopping interference may be in part modulated by functional coupling during preparation of the go response (Fig. 4C).

The stopping interference effect is reduced during selective stopping of a decoupled response. Wadsley et al. (2019) investigated the influence of between-hand coupling during partial-stop trials by introducing asynchronous go trials during a multicomponent ARI paradigm. While functional coupling benefits synchronous go trials, this strategy would be detrimental for asynchronous go trials that require a temporally dissimilar response. As predicted by the coupling hypothesis, the stopping interference effect was essentially abolished during asynchronous partial-stop trials. Similarly, Xu et al. (2015) showed that enhanced decoupling (by increasing the salience of the stop signal) also facilitates selective stopping. Importantly, selective stopping at the behavioral level does not necessarily imply that the underlying inhibitory mechanism was also selective (Duque et al., 2017). In summary, selective stopping may be facilitated in contexts that either prevent coupling or enhance decoupling, but the absence of neurophysiological evidence currently precludes firm conclusions about the selectivity of the underlying response inhibition mechanism.

Stopping interference in a pause-then-cancel model of action-stopping

The pause-then-cancel model of action stopping posits that action stopping is supported by two complementary inhibitory stages (Schmidt and Berke, 2017; Diesburg and Wessel, 2021). The pause process reflects broad motor suppression generated during attentional orienting (i.e., response conflict) to a salient stimulus via the fast acting hyperdirect cortico-basal-ganglia pathway (Frank, 2006; Hampshire, 2015). The cancel process reflects deliberate response inhibition via the slower but more selective indirect cortico-basal-ganglia pathway after retrieval of a stop signal (Aron, 2011). Importantly, the model predicts that successful stopping is not contingent on a pause process, such that successful stopping can be achieved solely through the cancel process if there is enough time available for stopping.

The pause-then-cancel model can be extended to selective stopping contexts. The presence of both a pause and cancel process would account for the coactivation of the hyperdirect and indirect cortico-basal-ganglia pathways observed during partial-stop trials (Coxon et al., 2009, 2012). During selective stopping, the pause process would produce inappropriate suppression of the stopped and unstopped effector, whereas the cancel process should only produce selective inhibition of the stopped effector. We propose that the cancel process may also be less selective because of modulating factors, such as task familiarity and functional coupling. For example, nonselective cancellation of both effectors may be a default strategy when there is a lack of task experience (Xu et al., 2015), or when functional coupling is driven by a common go process (Jana et al., 2017; Wadsley et al., 2019). A nonselective cancel process is unique from the invariant pause process as it represents deliberate response inhibition influenced by higher-order processes, such as functional coupling. Therefore, nonselective response inhibition during selective stopping may be the consequence of both the pause and cancel process.

Stopping interference would be variable within a pause-then-cancel model of selective stopping (Fig. 4). Nonselective response

inhibition generated by the pause or a nonselective cancel process would reduce response vigor of the unstopped effector. Inappropriate suppression of the unstopped effector would necessitate a period of selective response reinitiation (i.e., restart) and produce a response delay. Importantly, between-trial variability in the stopping interference effect (e.g., Raud et al., 2020) can be accounted for if nonselective response inhibition is viewed as an interplay between the pause and cancel process. Stopping interference would be longer when initiating both pause and nonselective cancel processes, for example, in an individual that was unfamiliar with selective stopping or had a strong tendency to couple effectors. The extent of stopping interference may be decreased in the same individual during a later trial where a more selective cancellation process was engaged because of greater experience with selective stopping. This perspective provides for a theoretical account of why the stopping interference effect tends to be reduced but not abolished during precued selective stopping (Cirillo et al., 2018) and ignore trials (Ko and Miller, 2013). Instances of no observable stopping interference would represent selective stopping scenarios in which only a selective cancel process was engaged, such as the occurrence of a highly predictable and timely stop signal. Therefore, the magnitude of nonselective response inhibition, and thus stopping interference, may fluctuate based on the presence of the nonselective pause process and selectivity of the cancel process.

Conclusions and future directions

Selective stopping is a complex form of response inhibition. The presence of a response delay in the unstopped effector (stopping interference effect) indicates that there is an underlying constraint on selective stopping. Studies to date demonstrate how the stopping interference effect can be conceptualized with a restart model, where response delays reflect nonselective response inhibition and selective response reinitiation. Nonselective response inhibition is typically attributed to a context-independent, global inhibitory process. However, current research findings show the variability of stopping interference, where behaviorally selective stopping can occur by manipulating the response context (Xu et al., 2015; Wadsley et al., 2019; Raud et al., 2020). The balance of evidence favors an interpretation that nonselective response inhibition is a consequence of factors not directly related to overt action stopping. Within a pause-then-cancel model of action stopping, a global inhibitory mechanism may be recruited regardless of the stopping context (nonselective pause process) because of response conflict, whereas the selectivity of the deliberate response inhibition (cancel process) may be modulated by the degree of proactive control, task familiarity, and functional coupling.

Further research is required to determine the behavioral and neural constraints underlying selective stopping. Recently developed “ β burst” analyses from EEG are providing new insight into response inhibition processes (Hannah et al., 2020; Wessel, 2020). Neurophysiological investigations of motor excitability and inhibitory processes with transcranial magnetic stimulation may further elucidate the selectivity of the underlying response inhibition process. Neurophysiological signatures of nonselective and selective response inhibition should be conceptualized within the pause-then-cancel framework to determine the interplay between automatic and deliberate response inhibition (Diesburg and Wessel, 2021). Selective stopping paradigms have already provided new insights into healthy aging (Coxon et al., 2012, 2016) and may lead to a better understanding of neurologic conditions associated with impaired impulse control. As argued in this review, studies should consider manipulating not only the stopping context, but also the

response context to formally investigate the conflict, task familiarity, and functional coupling components of the stopping interference effect.

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