

## Review Article

## Online corticomotor modulations in action inhibition: Insights from TMS studies

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## ABSTRACT

Effective response inhibition is crucial for daily functioning. Behavioural inhibition can be assessed using the Stop Signal Task (SST), which requires coordinated activation across a complex network of brain regions, ultimately modulating corticospinal excitability (CSE). Importantly, CSE is not only modulated by excitatory drive but also by intracortical inhibitory processes such as short intracortical inhibition (SICI), which reflects the inhibitory activity of the GABAA receptors within the primary motor cortex. This review examines a series of studies exploring CSE changes, measured through Transcranial Magnetic Stimulation (TMS) applied online, i.e., during SST performance. We mainly focused on the temporal dynamics of CSE and SICI during the SST across healthy and clinical populations, highlighting differences between task-related and unrelated muscles, examining both global and selective modulations in proactive and reactive versions of the SST. Our discussion addresses the methodological and theoretical considerations involved in recording CSE online and questions the SST's effectiveness in accurately capturing inhibitory processes. Additionally, we analyse findings from motor-related disorders in clinical populations to identify specific abnormalities in CSE modulation and their underlying neural mechanisms. By summarizing the existing literature, we aim to offer a comprehensive view of the temporal dynamics of CSE, identifying key factors and methodologies that influence CSE modulation. This review seeks to prompt future directions in cognitive neuroscience research and potential clinical applications.

## 1. Introduction

Response inhibition is a cognitive process crucial for guiding goal-directed behaviour (for reviews, see [Duque et al., 2017](#); [Nikitenko et al., 2020](#)). Behavioural cessation may occur either broadly or specifically ([Bissett and Logan, 2014](#)). Broad cessation results in halting all movement components, whereas specific cessation involves stopping in a manner selective to either the stimulus (i.e., the instruction to stop is related to the perception of a specific stop stimulus) or the response (i.e., the instruction to stop is related to the stop of only one motor component of a complex action) (termed "motor-selective" by [Bissett and Logan, 2014](#)). For instance, imagine running in a park when you suddenly spot a puddle on the path. An efficient strategy may be simply to stop running by broadly suppressing your ongoing motor activity. However, certain stimulus characteristics (stimulus-selective), such as the size of the

puddle, may influence the appropriate motor reaction. Indeed, when facing a large puddle, a complete stop may be the optimal reaction, while facing a small puddle, a response-selective stopping reaction (i.e., simply adjusting the stride to avoid the puddle without stopping) may be preferential. Nonselective response inhibition can also help with stopping specific actions or responses. For example, if something unexpected happens, a person might stop changing their walking pattern and pause several actions until they figure out the best way to respond.

Another important aspect of motor control is that it is enacted through both proactive and reactive mechanisms. Compared to reactive inhibition, which refers to the cessation of a motor response already in progress, proactive inhibition refers to the preparatory processes that result in a response being withheld before it is initiated ([Meyer and Bucci, 2016](#)). Interestingly, foreknowledge, whether implicit from perceived stop signal likelihood or explicit from contextual cues, can be

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used to induce participants to proactively slow their go responses in simple stopping tasks, improving inhibition success (Salomoni et al., 2023). Referring to the previous example, proactive inhibition involves running slower, knowing that the road might be slippery due to the rain.

Response inhibition relies upon a cortico-subcortical network (Aron and Poldrack, 2006; Chambers et al., 2006; Coxon et al., 2009, 2012; Zandbelt et al., 2013) that inhibits corticospinal neurons within the primary motor cortex (M1) to suppress descending motor output (Stinear et al., 2009). A way to directly investigate the corticospinal and the cortico-motor modulations during action control is to use Transcranial Magnetic Stimulation (TMS) to record motor-evoked potential (MEPs) online, i.e., during the SST. In particular, the amplitude of the MEPs indexes the excitability of the corticospinal tract (CSE). However, when TMS is applied to the M1 contralateral to the contracting target muscle, the resulting phenomenon is termed the silent period (SP). Under these conditions, MEP in the target muscle is followed by a disruption in the ongoing voluntary EMG activity for a period of up to several hundred milliseconds (Cantello et al., 1992). Contrary to MEP amplitude, the late part of the SP reflects the involvement of inhibitory neural circuits intrinsic to M1 (Terao and Ugawa, 2002). MEPs elicited by a single-pulse TMS (spTMS) are a compound measure that reflects both cortical and downstream (spinal) processing and, therefore, do not isolate intracortical changes in motor excitability. Conversely, the specific involvement of short-interval intracortical inhibition mechanisms (SICI) at M1 can be assessed by paired-pulse techniques (Borgomaneri et al., 2017; Borgomaneri et al., 2015a; Borgomaneri et al., 2015b; Cardellicchio and Borgomaneri, 2025; Kujirai et al., 1993). Here, a conditioning stimulus (CS) recruits inhibitory interneurons that modulate the MEP amplitude produced by the test stimulus (TS). Paired-pulse TMS (ppTMS) at short interstimulus intervals (1–6 msec) allows the assessment of SICI, mediated by GABAA receptors, whereas longer intervals in the range of 50–200 msec test the involvement of long-interval intracortical inhibition (LICI; see Chen, 2004) mediated by GABAB receptors, which also mediate the duration of the late cortical SP (Werhahn et al., 1999).

An established way to test action suppression is to use the Stop Signal Task (SST; Logan, 1983; Verbruggen and Logan, 2008b; Vince, 1948). Operationally, participants are directed to initiate a response to a go stimulus and withhold their ongoing response when they encounter a stop signal. The model's statistical framework provides a way to estimate the duration of the covert inhibition process, the stop-signal reaction time (SSRT), which serves as an indicator of reactive action inhibition performance, with longer SSRTs suggesting poorer inhibitory performance. According to the horse-race model proposed by Logan et al. (1984), response inhibition in SSTs is based on a race between independent go and stop processes in the brain. In this model, inhibitory control is successful or fails depending on whether the stop process finishes before or after the go process. The model's statistical framework, which involves a competition between the theoretical finishing time distributions, provides a method to estimate the duration of the covert inhibition process (i.e., SSRT). From this perspective, proactive inhibitory control, which slows responses, may increase the likelihood of successful inhibition (Logan et al., 1984). Consistent with this, both behavioural and brain imaging data suggest that a stronger preparatory process enhances the ability to withhold a motor response (Bastin et al., 2014; Castro-Meneses et al., 2015; Chikazoe et al., 2009; Verbruggen and Logan, 2008b). In the SST, a rapid but global mechanism is likely used to counteract the reactive response tendency. The mechanism is global in the sense that it has effects on muscle representations over and above the particular muscle that needs to be stopped (Badry et al., 2009). However, stopping may also be achieved through a response-selective mechanism, asking the participants to selectively withhold one specific motor command. Depending on when the M1 excitability is tested (i.e., during the foreknowledge period, the go or the stop signal presentation) and on the instruction of the SST (i.e., requiring a proactive or a reactive inhibition as well as a muscle-specific or unspecified

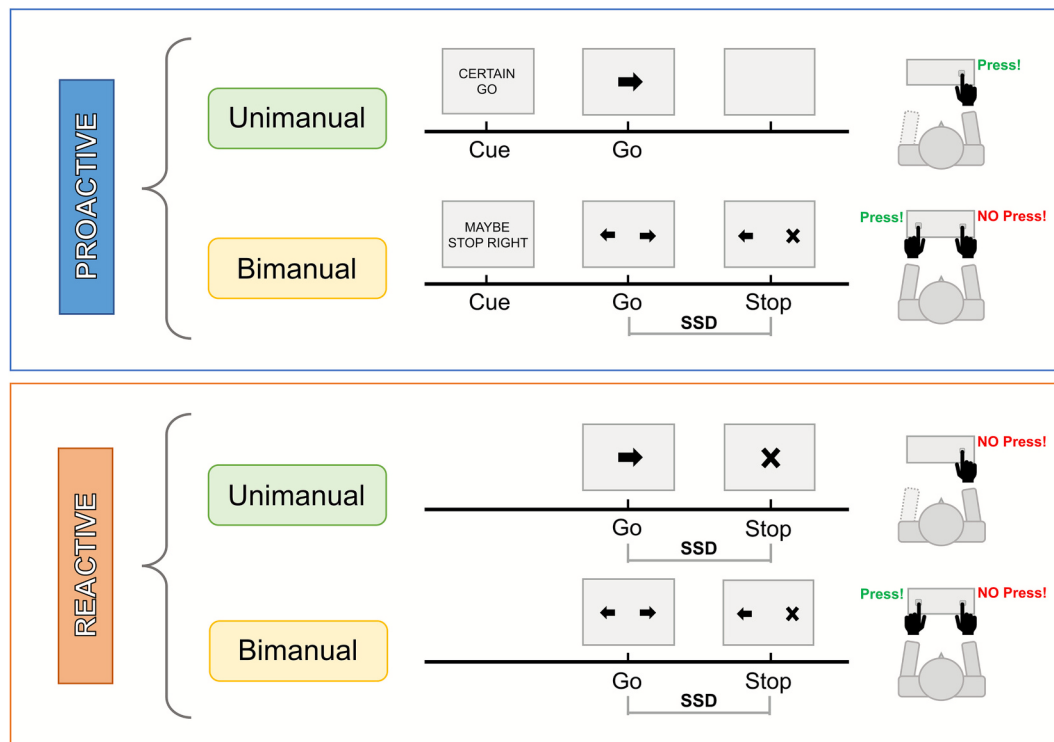
action cancellation), the M1 excitability would be differently modulated to achieve an efficient action control. Fig. 1 illustrates the SST across both its reactive and proactive versions, shown in unimanual and bimanual conditions. In the unimanual condition, participants engage in the task using only one hand—referred to as the task effector. In contrast, the bimanual version requires participants to use both hands, pressing the left and right keys with their respective hands.

Indeed, the vital importance of response inhibition for adaptive behavioural interaction with the ever-changing environment is underscored by a wide range of clinical conditions characterized by inhibitory deficits, such as attention-deficit hyperactivity disorder (ADHD) (Aron and Poldrack, 2005; Nigg et al., 2005; Ridderinkhof et al., 2004), Parkinson's disease (Gauggel et al., 2004; Wylie et al., 2009), and obsessive-compulsive disorder (OCD) (Penadés et al., 2007). Interestingly, clinical studies have found lower levels of SICI in populations who also show slower SSRTs, such as ADHD (Hoegl et al., 2012) and OCD (Greenberg et al., 1998, 2000), meaning that such an index may offer an important biomarker for understanding deficits in action control.

Thus, this review aims to highlight the temporal dynamics of CSE modulation during the SST with the ultimate goal to offer a detailed analysis of how stimulation timing affects CSE, by investigating specific intracortical modulations within M1 (i.e., SICI), exploring the differences in CSE modulation between proactive (i.e., SST using foreknowledge) and reactive contexts and examining the effects of global versus selective inhibition and associated behavioural outcomes in all these conditions and both healthy and clinical populations. Understanding the temporal dynamics of excitability during SST provides insight into how inhibitory control unfolds in real time within the motor system. Indeed, action control is not an instantaneous process, but it evolves dynamically over hundreds of milliseconds. Tracking its temporal evolution reveals when inhibitory control is engaged and how quickly it suppresses motor output. Moreover, by tracking potential differences in CSE modulations, we can infer their relationship with the SSRT, thus combining behaviour and neurophysiology. Additionally, by analysing motor excitability over time, we can disclose how reactive and proactive action inhibition interact. Finally, investigating *when* and *how* excitability fails to modulate in the clinical population can pinpoint at which stage of the inhibition cascade is disrupted, offering potential biomarkers for clinical dysfunction and targets for neuromodulation.

### 1.1. The role of GABAergic modulations in action inhibition

The role of GABAB receptors in the context of the SST was first investigated by Van Den Wildenberg et al. (2010), assessing the duration of the SP. MEPs linked to go trials exhibited an increment in CSE starting approximately at 100 ms after the go signal. Conversely, MEPs linked to successful inhibition showed an initial increase, followed by a decrease only at the last instance, meaning that the instruction to stop responding takes approximately 180 milliseconds after the onset of the stop signal to override go signal processing, replacing it with a pattern of decreasing CSE. Moreover, by asking participants to perform an isometric precontraction force to initiate a trial, the authors were able to measure the SP. Results showed a linear decrease in the SP duration in go trials, while in stop trials it was increased and progressively prolonged, and, interestingly, it was correlated with successful stop probability. The simultaneous reduction in SP duration following go signals suggests that response generation involves the release of intracortical inhibition, increasing CSE. In contrast, the prolonged SP in stop trials appears to cause a subsequent decrease in CSE, highlighting the role of GABAB receptors in action suppression. These results are in line with a subsequent study from Seet et al. (2019), which investigated stimulus-driven activation of SICI during the SST. Furthermore, the authors proposed that these GABAergic interneurons might be automatically activated simply through exposure to the stop-related stimulus, even without a motor task being performed, following SST training. When compared to the control stimulus, exposure to the stop signal led to a decreased MEP



**Fig. 1.** Graphical representation of the Stop Signal Task (SST) in both reactive (bottom) and proactive (top) versions in both unimanual and bimanual conditions. While in the unimanual condition, the participant performs the task with only one hand (i.e., the task effector), in the bimanual version, participants perform the task using both hands and press the right and left keys with the corresponding task effector. The bottom panel represents the reactive unimanual SST, when the participants have no cue of the incoming trial (i.e., if there will be a stop or a go trial), and the reactive bimanual SST condition, where no foreknowledge of the hand that needs to be stopped is provided. The panel on top represents the same SST in the proactive version, divided into both unimanual and bimanual conditions. In the proactive unimanual SST, a cue of the next trial is provided, for instance, if the next trial is a go trial (i.e., “certain go”). In the proactive bimanual SST, foreknowledge of the hand that needs to be stopped is provided (i.e., “maybe stop right”). SSD = Stop Signal Delay.

amplitude 200 ms after the stimulus onset. Thirdly, during passive viewing of the stop signal, there was reduced SICI measured at 200 ms from the stop signal presentation, suggesting the existence of an interaction between the stop signal and GABA-mediated intracortical inhibitory mechanisms elicited in a stimulus-driven manner. This result supports Verbruggen and Logan's (2008a) concept of automatic inhibition, suggesting that a consistent association between a stimulus and stopping can trigger an automatic retrieval of the stop goal. However, an alternative explanation is that the stop signal represents a salient stimulus, which may induce CSE suppression per se, as demonstrated by Wessel and Aron (2017). Such an idea is in line with the Pause-then-Cancel model (Diesburg and Wessel, 2021; Schmidt and Berke, 2017) of action stopping, in which the pause process is triggered even in non-inhibitory tasks following salient, task-relevant stimuli, via the fast-acting hyperdirect pathway involving the subthalamic nucleus (STN) and the basal ganglia (Frank, 2006; Hampshire and Sharp, 2015).

Similar findings were reported by Chowdhury et al. (2019), who conducted two experiments to investigate CSE and SICI during an SST with the specific aim of understanding whether individual differences in the ability to stop are driven by SICI modulations. This study builds upon the recent findings of the same authors, who discovered that 40 % of the variance in SSRT between participants was explained by SICI measured at rest (Chowdhury et al., 2018). Indeed, fast stoppers showed an increased SICI average compared to slow stoppers. Notably, only the fast stoppers group showed an increased SICI on stop trials compared to the go trials. Interestingly, longer SSRTs were correlated with less SICI during stop trials. Moreover, a second experiment revealed that during go trials, MEP amplitudes in the selected hand were significantly higher compared to baseline levels, whereas MEP amplitudes in the non-selected hand were significantly reduced relative to baseline. No

differences were found between selected and non-selected movements during stop trials, exhibiting significant reductions compared to baseline. Regarding the analysis of SICI, no significant differences emerged between selected and non-selected movements across either trial type. These findings consistently demonstrated that individuals who were more efficient at stopping a response exhibited higher SICI, particularly in the context of faster stopping speeds. This association between SICI and stopping efficiency was more pronounced during successful inhibition, emphasizing the role of GABAergic interneurons within M1 in action inhibition, a result in line with our recent study, in which we found that SICI measured at rest can predict action inhibition abilities (Quettier et al., 2024), even though the second experiment did not find differences between selected and non-selected movements. Moreover, these results demonstrated that when no anticipatory information is given before each trial as to which hand may need to be stopped, global suppression of CSE is observed, as well as a global SICI modulation, suggesting that GABAergic mechanisms in M1 may not be involved in the selection of one hand over the other during non-selective response inhibition. Finally, in a more recent study, the same authors (Chowdhury et al., 2020) demonstrated the ability of an SST training to strengthen SICI. Authors found that a single session of SST training increased SICI at rest in the experimental group, while MEP amplitudes remained stable. Individual increases in SICI were correlated with reductions in SSRTs, suggesting that enhanced GABA-mediated inhibition may support more efficient action stopping. Moreover, when SICI and MEPs were collected during the SST execution, a trend toward stronger modulation for both measures has been observed, specifically during stop trials compared to go trials, in the hand that needed to be stopped. This may suggest that inhibitory mechanisms act selectively and action-dependently, although this effect did not reach statistical

significance. The results show that inhibition training may induce GABAA-mediated neuroplasticity within M1 and suggest a temporal link between SICI and stopping efficiency, with changes in SICI correlating with modulation in stopping efficiency (see [Tables 1, 2, and 3](#)).

### 1.2. Proactive action suppression influences CSE and GABA

It is important to note that all of these experiments focused on reactive inhibition. However, in real-life situations, such control is typically proactive, as people often have goals or prior knowledge of what they need to stop, even if they are not actively attempting to inhibit any impulse or action. Using a proactive version of the SST, [Claffey et al. \(2010\)](#) showed that the stopping interference effect (SIE) - where the hand that is supposed to continue responds more slowly than in go trials - was reduced when participants were given advance information. However, SSRT increased with this foreknowledge, compared to when no prior information was provided. This result may be explained by the recruitment of additional cognitive and neural processes, such as those

in the frontal-striatal-pallidal connections of the basal ganglia, which could slow down the overall stopping process. Moreover, participants with better recall accuracy of foreknowledge clues were able to stop more selectively, suggesting a link between goal retention and the recruitment of selectivity-stopping mechanisms. MEPs were significantly smaller in the “Maybe Stop Right” rather than in the “Maybe Stop Left” condition, but no specific effect of the stimulation time was found. These findings suggested that foreknowledge enables a more selective stopping mechanism, with the additional potential involvement of the indirect pathway, which recruited the frontal-striatal-pallidal connections in the basal ganglia. However, Claffey and colleagues did not distinguish whether their results could be explained by the proactive suppression or by the proactive facilitation model (i.e., whether the proactive control is implemented by suppressing the hand to be stopped or facilitating the response representation of the hand that does not need to be stopped). To investigate this issue, [Cai et al. \(2011\)](#) included a “null” condition, in which no action is required. Results supported the proactive suppression model, with smaller MEPs when participants were

**Table 1**

The table summarizes the studies that employed TMS to investigate changes in CSE during the Stop Signal Task, with stimulation delivered at time points following the presentation of the go signal, which serves as a temporal reference for the TMS pulse administration. \* All the studies reported used single-pulse TMS, except for the study by [Puri et al. \(2023\)](#), which employs dual-coil stimulation. r = right, l = left, b = both, \* = Studies that employed multiple choice reaction time.

| Overall data                                     |                       |       | SST data      |              |                 |                         | TMS data                       |                         | Results                                                                                                                                  |                     |
|--------------------------------------------------|-----------------------|-------|---------------|--------------|-----------------|-------------------------|--------------------------------|-------------------------|------------------------------------------------------------------------------------------------------------------------------------------|---------------------|
| Studies                                          | Number of experiments | N     | Foreknowledge | Stop signal  | Task handedness | Effectors               | Stimulation onset (ms)         | Recording muscle (side) | CSE modulation                                                                                                                           | Global or selective |
| <a href="#">Badry et al. (2009)*</a>             | 1                     | 10    | No            | Red Box      | Bimanual        | Thumb                   | 100, 300, 400, 500             | APB (r)                 | > of CSE at every time point during go trials<br>< of CSE at 400 ms during successful stop                                               | G                   |
|                                                  | 2                     | 10    | No            | Red Box      | Bimanual        | Thumb                   | 400                            | APB (l)                 | > of CSE during go trials at 400 ms                                                                                                      | –                   |
|                                                  | 3                     | 10    | No            | Red Box      | Bimanual        | Thumb                   | 400                            | TA (r)                  | < of CSE during successful stop                                                                                                          | G                   |
| <a href="#">Cai et al. (2011)*</a>               | 1                     | 16    | Yes           | Red X        | Bimanual        | Index and little finger | - 800, - 500, - 200            | FDI (r)                 | < of CSE in proactive condition at -500 ms                                                                                               | S                   |
| <a href="#">Cavallo et al. (2014)*</a>           | 3                     | 21    | No            | Red X        | Bimanual        | Index finger            | Go RT - 100                    | TA (r)                  | < of CSE in the Solo condition compared to the Joint condition                                                                           | G                   |
| <a href="#">Claffey et al. (2010)*</a>           | 2                     | 15    | Yes           | Red X        | Bimanual        | Index and little finger | - 800, - 500, - 200            | FDI (r)                 | < of CSE for MSR condition                                                                                                               | S                   |
| <a href="#">Greenhouse et al. (2012)*</a>        | 1                     | 19    | No            | Sound        | Unimanual       | Index and little finger | 120, 200, Go RT - 100          | TA (l)                  | No modulation during the anticipation phase<br>< of CSE during stopping phase                                                            | G                   |
| <a href="#">Jahfari et al. (2010)*</a>           | 1                     | 13    | No            | Sound        | Unimanual       | Index and little finger | 80, 120, 160, 200              | FDI (r)                 | < of CSE during go trials at early time points (80, 120)                                                                                 | G                   |
| <a href="#">Majid et al. (2012)*</a>             | 1                     | 7     | No            | Red Box      | Bimanual        | Index finger            | Go RT - 100                    | TA (l)                  | < of CSE                                                                                                                                 | G                   |
|                                                  | 2                     | 7     | Yes           | Red X        | Bimanual        | Index and little finger | Go RT - 100                    | TA (l)                  | No significant modulation of CSE                                                                                                         | S                   |
| <a href="#">Puri et al. (2023)</a>               | 1                     | 27    | Yes           | Color change | Bimanual        | Index finger            | 0, 150                         | FDI (b)                 | Movement preparation:<br>< of CSE in proactive condition at Go (0 ms) compared to WS and reactive condition, regardless of the cued hand | G                   |
| <a href="#">Raud et al. (2020)</a>               | 1                     | 17–20 | Yes           | Color change | Unimanual       | Thumb                   | -100                           | APB (r)                 | No significant modulation of CSE                                                                                                         | –                   |
|                                                  | 1                     | 17–20 | Yes           | Color change | Bimanual        | Thumb                   | -100                           | APB (r)                 | No significant modulation of CSE                                                                                                         | –                   |
| <a href="#">Rawji et al. (2022)</a>              | 1                     | 16    | No            | Red X        | Unimanual       | Index finger            | 0, 50, 100, 150, 200, 250, 300 | FDI (r)                 | > CSE for only-go trials at 150 ms and 200 ms for SST-go trials                                                                          | –                   |
| <a href="#">Van Den Wildenberg et al. (2010)</a> | 1                     | 8     | No            | Color change | Unimanual       | Index finger            | 35, 69, 104, 139, 174, 208     | APB (r)                 | > CSE during go trials starting from 104 ms                                                                                              | –                   |

**Table 2**

The table summarizes the studies that employed TMS to investigate changes in CSE during the Stop Signal Task, with stimulation delivered at time points following the presentation of the stop signal, which serves as a temporal reference for the TMS pulse administration. r = right, l = left, b = both, \* = Studies that employed multiple choice reaction time.

| Overall data                     |                       |       | SST data      |                            |                 |                         | TMS data                         |                         | Results                                                                                                                                                                         |                     |
|----------------------------------|-----------------------|-------|---------------|----------------------------|-----------------|-------------------------|----------------------------------|-------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------|
| Study                            | Number of experiments | N     | Foreknowledge | Stop signal                | Task handedness | Effectors               | Stimulation onset (ms)           | Recording muscle (side) | CSE modulation                                                                                                                                                                  | Global or selective |
| Chowdhury et al. (2019)*         | 1                     | 30    | No            | Blue Box                   | Bimanual        | Index finger            | 50, 100, 150, 200                | FDI (r)                 | > of CSE up to 100 ms followed by a decline lasting until 200 ms during stop trials                                                                                             | –                   |
|                                  | 2                     | 30    | No            | Blue Box                   | Bimanual        | Index finger            | SSRT - 125, SSRT - 75, SSRT - 25 | FDI (r)                 | > of CSE up to 150 ms followed by a reduction at 200 ms during go trials<br>< of CSE during stop trials<br>> of CSE after the second time point (SSRT - 75 ms) during go trials | –                   |
| Chowdhury et al. (2020)*         | 2                     | 44    | No            | Blue Box                   | Bimanual        | Index finger            | 200                              | FDI (r)                 | > of CSE during go trials particularly for the right hand                                                                                                                       | –                   |
| Greenhouse et al. (2012)*        | 2                     | 20    | No            | Sound                      | Unimanual       | Index and little finger | 200, 220, 240                    | TA (l)                  | < of CSE during successful stop trials                                                                                                                                          | G                   |
| Jana et al. (2020)*              | 3                     | 17    | No            | Color change               | Bimanual        | Index                   | 100, 120, 140, 160, 180          | ECR (r)                 | < of CSE beginning at 140 ms during successful stop trials                                                                                                                      | G                   |
| Majid et al. (2012)*             | 2                     | 11    | Yes           | Red X                      | Bimanual        | Index and little finger | 200, 220, 240                    | TA (l)                  | < of CSE at 200 and 220 ms                                                                                                                                                      | G                   |
| Puri et al. (2023)               | 1                     | 27    | Yes           | Color change               | Bimanual        | Index finger            | 150                              | FDI (b)                 | Movement execution: > Of CSE regardless the cued hand                                                                                                                           | –                   |
| Raud et al. (2020)               | 1                     | 17–20 | Yes           | Color change               | Unimanual       | Thumb                   | 150                              | APB (r)                 | < of CSE for non-cued hand                                                                                                                                                      | G                   |
|                                  | 1                     | 17–20 | Yes           | Color change               | Bimanual        | Thumb                   | 150                              | APB (r)                 | No modulation of CSE                                                                                                                                                            | –                   |
| Seet et al. (2019)               | 1                     | 42    | No            | Color change flanking bars | Unimanual       | Index finger            | 200                              | FDI (d)                 | < of CSE during stop trials                                                                                                                                                     | –                   |
| Tatz et al. (2021)*              | 1                     | 27    | No            | Color change               | Bimanual        | Foot                    | 150, 175, 200                    | FDI (r)                 | < of CSE during stop and ignore trials                                                                                                                                          | G                   |
| Wessel et al. (2013)*            | 1                     | 14    | No            | Color change               | –               | Eyes                    | SSRT - 50                        | FDI (r)                 | < of CSE during successful stop                                                                                                                                                 | G                   |
| Van Den Wildenberg et al. (2010) | 1                     | 8     | No            | Color change               | Unimanual       | Index finger            | 45, 89, 134, 179                 | APB (r)                 | > Of CSE up to 134 ms followed by a sharp decline at 179 ms                                                                                                                     | –                   |

requested to maybe inhibit the right (tested) hand, compared to the null condition. Interestingly, the degree of proactive suppression predicted the subsequent selectivity of stopping at the behavioural level. Rawji et al. (2022) additionally reported that, in go trials, CSE increased at 150 ms after the go cue, while during stop trials, CSE rose 200 ms after the cue presentation. This suggests that proactive inhibition does not cause a slower CSE increment, but rather a delay in its initial rise when the stopping cue is presented. The authors reconciled this finding with the dynamical view of proactive inhibition, which posits that M1 activity before the movement sets the dynamical system state until the trigger to move is initiated. Thus, the delay in the rise of the CSE may be due to the knowledge of the stopping process, which adjusts the dynamic state of the M1 activity until confirmation of the movement decision. These results suggest that the pattern of neural activity within M1 is influenced by the context in which the movement will occur. In line with such findings, a previous study by Jahfari et al. (2010) demonstrated the presence of a Response Delay Effect (RDE) - a form of proactive motor control characterized by slower and more cautious responding when participants anticipate the need to stop - and explored the

neurocognitive mechanisms underlying this phenomenon. The authors employed a conditional SST, in which one finger was designated as critical, while the other was non-critical, instructing participants to ignore the stop signal for the non-critical finger. The findings revealed that MEPs decreased with no differences between critical and non-critical trials. Indeed, at the later time points, MEP amplitudes were notably reduced selectively in the critical condition. Additionally, the rise in CSE was slower when stopping might be required. These findings suggest that the RDE is best explained by the “active braking hypothesis” with the implementation of an early, strategic inhibition of motor activity in preparation for possible stopping (see Tables 1, 2, and 3).

### 1.3. Global versus selective inhibition using both reactive and proactive versions of the SST

Stopping an ongoing action may produce a global and non-selective suppression of CSE in task-irrelevant muscles. In line with this idea, Badry et al. (2009) discovered that successful stop trials correlated with a reduction in CSE observed through a decrease in MEPs. In Experiment

**Table 3**

The table summarizes studies that employed TMS to investigate intracortical inhibition during the Stop Signal Task. Stimulation was delivered at various time points following either the go or stop signal, which served as the temporal reference for TMS administration. The “Stimulation Onset” column specifies both the timing of the stimulation and the reference signal used (go or stop). r = right, l = left, b = both, \* = Studies that employed multiple choice reaction time.

| Overall data             |                       |    | SST data      |               |                 | TMS data     |                  |                                       |                         | Results                                                                                                                                                                              |
|--------------------------|-----------------------|----|---------------|---------------|-----------------|--------------|------------------|---------------------------------------|-------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Study                    | Number of experiments | N  | Foreknowledge | Stop signal   | Task handedness | Effectors    | Stimulation type | Stimulation onset (ms)                | Recording muscle (side) | CSE modulation                                                                                                                                                                       |
| Chowdhury et al. (2019)* | 1                     | 30 | No            | Blue Box      | Bimanual        | Index finger | SICI             | 50, 100, 150, 200 from stop           | FDI (r)                 | > SICI for fast stoppers compared to slow stoppers<br>> SICI during stop trials only in fast stoppers group<br>Negative correlation between SICI and SSRT                            |
|                          | 2                     | 30 | No            | Blue Box      | Bimanual        | Index finger | SICI             | SSRT - 125, SSRT - 75, SSRT - 25      | FDI (r)                 | > SICI for fast stoppers compared to slow stoppers                                                                                                                                   |
| Chowdhury et al. (2020)* | 2                     | 44 | No            | Blue Box      | Bimanual        | Index finger | SICI             | 200 from stop                         | FDI (r)                 | > Resting SICI at session 4 for all subjects<br>Greater SICI modulation during stop trials when the right hand was selected for the response compared to the left                    |
| Puri et al. (2023)       | 1                     | 27 | Yes           | Color change  | Bimanual        | Index finger | LIHI             | 0 (go), 150 from go and 150 from stop | FDI (b)                 | < LIHI reduction during movement preparation (0) in proactive condition regardless the cued hand<br>< LIHI at 150 ms from stop (during movement cancellation) in the continuing hand |
| Seet et al. (2019)       | 42                    |    | No            | Flanking bars | Unimanual       | Index finger | SICI             | 200 ms from stop                      | FDI (d)                 | < SICI during passive observation of the stop signal                                                                                                                                 |

1, the authors observed a selective and muscle-specific increase in CSE at 300 and 400 ms during go and failed stop trials, but not in the other (left) hand. In successful stop trials, MEP amplitude in the selected muscle decreased at 400 ms regardless of the hand used, while a reduction at 300 ms was seen only when the left hand performed the task. In Experiment 2, CSE increased in the selected hand muscle during go and failed stop trials performed with the left hand, with no changes in the control muscle. In Experiment 3, MEP amplitudes in both right and left tibialis anterior (TA) muscles decreased during successful stop trials, regardless of the responding hand.

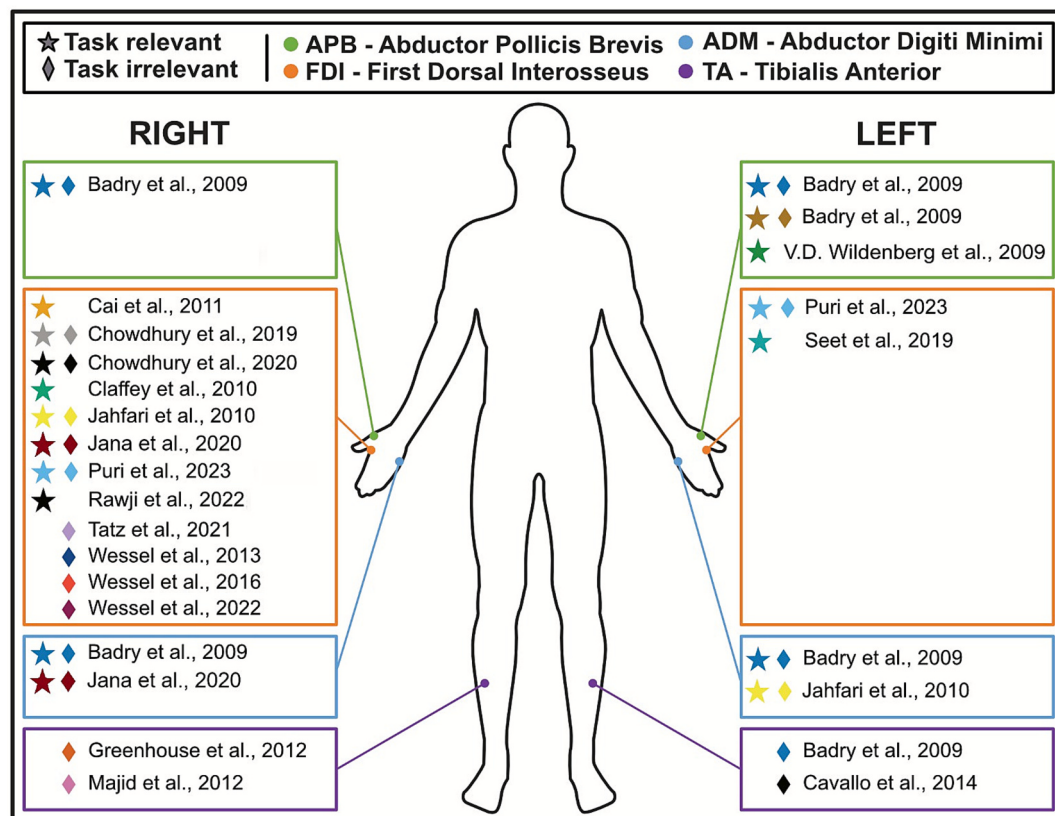
Thus, these results can be interpreted as an emergency brake triggered by the stop signal, causing a global suppression of the motor system. These results corroborate the hypothesis that non-specific inhibition generates a global suppression of CSE (Band and Van Boxtel, 1999; Wessel and Aron, 2013). Another study that supports the global action suppression hypothesis is the one conducted by Tatz et al. (2021). Participants were involved in two different experiments. The first experiment tested whether salient or infrequent events, even without requiring action cancellation, trigger early CSE suppression similar to that observed with stop signals. Results support previous findings of non-selective CSE suppression in task-irrelevant muscles following both stop (Badry et al., 2009) and ignore signals (Iacullo et al., 2020). MEP suppression appeared around 175 ms, with stronger CSE reduction in successful stop trials than in ignore trials. These distinct CSE patterns suggest a two-stage inhibitory process: an initial automatic response to stimulus salience (common to both signals), followed by a second, action-specific stage unique to stopping. However, during everyday tasks, we also need a form of muscle-selective suppression, which may help to suppress undesired actions while continuing to perform others. To investigate the existence of selective motor suppression, Majid et al.

(2012) performed different experiments in which they aimed to test the CSE of the bilateral leg muscles. In their first experiment, the authors replicated previous findings from Badry et al. (2009), revealing the existence of suppression of the task-irrelevant leg muscles during non-selective stopping. However, the second experiment revealed no significant inhibition of the leg muscles during the selective stopping of one hand while continuing with the other, thus demonstrating that selective stopping mechanisms may also be involved. Finally, the third experiment found significantly greater CSE suppression selectively in the behaviourally nonselective condition. A temporal specificity of CSE suppression was observed, occurring at 200 and 220 ms after the stop signal, but not after 240 ms. Arguably, the lack of CSE suppression after 240 ms may be due to the coincidence of this time with the end of the inhibitory process (i.e., the SSRT). These results argue for the existence of distinct mechanisms for global and selective stopping, potentially involving different fronto-basal-ganglia pathways (Aron, 2007; Duque et al., 2017; Wessel and Aron, 2017), which aligns with previous findings (Cai et al., 2011; Claffey et al., 2010). According to these results, the observed global suppression during nonselective stopping could be attributed to the activation of a fast hyperdirect stopping mechanism (Jahfari et al., 2011), resulting in a widespread motor suppression affecting the irrelevant leg, while selective stopping can be additionally implemented via an indirect fronto-striatal-pallidal pathway. In a similar study, Greenhouse et al. (2012) used a proactive SST. No global suppression of MEP amplitude was observed during the anticipation phase. However, during the actual stopping phase, a reduction in leg muscle excitability was observed, suggesting CSE suppression at the time of response inhibition, a result in line with Badry et al. (2009)'s and Majid et al. (2012)'s findings. A deeper data inspection revealed that individuals who demonstrated greater behavioural slowing for critical

versus noncritical trials had less leg suppression when they stopped. A second experiment replicated these findings, demonstrating that if participants do not prepare to stop (manifest in minimal RT slowing), then, if they are required to stop, they resort to using an emergency global stopping mechanism. A few years later, Cavallo et al. (2014) tested whether the introduction of the social component (i.e., a joint action) may influence global and selective action suppression. Longer SSRT was selectively observed for the joint conditions, suggesting the existence of selective stop mechanisms in a social context. Moreover, a significant reduction in the MEP suppression was found in the task-irrelevant muscle in the joint condition compared to the solo condition, suggesting that when participants acted alone, stopping the hand had global suppressive effects across effectors not related to the task.

To compare the global inhibition model with the dual-inhibition model (which defines global and selective inhibition as distinct mechanisms), Raud et al. (2020) conducted a study in which participants performed two versions (unimanual and bimanual) of the SST with proactive cues. MEPs were suppressed in the unimanual task and in the unselected stopped hand, while there were no differences between the unimanual and bimanual tasks in MEPs amplitude in the stopped hand, nor between the stopped hand and the responding hand in the bimanual version. On a behavioural level, reaction times in the bimanual version were longer. This finding may be explained by the SIE, which refers to a consistent delay in reaction times for the hand that is not required to stop, resulting from interference caused by the selective inhibition of the other hand (Aron and Verbruggen, 2008). Lastly, in the bimanual task MEPs were suppressed in the hand cued to stop compared to the certain go condition. Interestingly, there were no differences in the unimanual version. Taken together, these findings reveal that proactive control prepares the motor system on a cortical and corticospinal level in anticipation of stopping, especially in the bimanual task, and points in

the direction of a unified inhibitory process. This interpretation has been corroborated by Puri et al. (2023), who showed that, during movement preparation, CSE decreased in the proactive condition at the imperative signal (IS) relative to the warning signal (WS) regardless of the hand cued to stop. In the proactive condition, CSE in both hands was lower than in the reactive condition at IS. The authors aimed to test inter-hemispheric inhibition (IHI), which can be measured by applying a conditioning stimulus to M1, which inhibits the size of the MEP produced by the test stimulus of the opposite motor cortex (Ferbert et al., 1992; Hanajima et al., 2001). IHI can be observed at ISIs between 6 and 50 ms (Ferbert et al., 1992; Gerloff et al., 1998). In the present study, long-interval interhemispheric inhibition (LIHI) was evaluated using an ISI of 40 ms, and it is thought to be mediated by GABAB receptors. Results on LIHI manifested a reduced inhibition at IS in the proactive condition in the hand that was cued to go. Both CSE and LIHI were reduced at IS presentation, regardless of whether foreknowledge indicated the hand that needed to be stopped. During movement execution, the stopping hand showed higher CSE 150 ms after the stop signal and IS. They also observed reduced LIHI in the continuing hand, indicating a general increase in CSE in both hands, while a hand-specific reduction in LIHI was observed in the continuing hand after the stop signal. Taken together, these findings further explain the global versus selective inhibitory mechanisms and how CSE is modulated when contextual information increases the specificity of behavioural inhibition. Finally, the global motor system suppression's effects seem to be present in broader stopping modalities. To address this issue, Cai et al. (2012) investigated whether global suppression also applies to stopping speech. MEPs were significantly smaller on successful stop trials than on go trials, failed stop trials, and baseline trials. When participants successfully stopped their speech, there was a reduced CSE of the task-irrelevant hand. This result extends previous findings (Badry et al., 2009; Greenhouse et al., 2012;



**Fig. 2.** Summary of the muscles selected for EMG recording in the reviewed studies. The star indicates a task-relevant muscle while the diamond represents a task-irrelevant one. Both right and left sides are depicted. FDI = first dorsal interosseus, APB = abductor pollicis brevis, ADM = abductor digiti minimi, TA = tibialis anterior.

Majid et al., 2012) and confirms the idea of a global suppressive effect across response modalities (see Fig. 2). Fig. 2 provides an overview of all the muscles examined in the reviewed studies, distinguishing between task-relevant muscles (those instructed to stop, marked with a star) and task-irrelevant muscles (those instructed not to stop, marked with a diamond).

#### 1.4. Action inhibition in motor-related disorders

Wessel et al. (2016) investigated CSE during SST in a sample of nine Parkinson's disease (PD) patients undergoing STN electrode implantation for deep brain stimulation (DBS). In line with the non-clinical population (Chowdhury et al., 2019, 2020), successful stop trials were associated with a reduction in CSE across muscles, even if the hand from which the CSE was recorded was irrelevant to the task performance. This suggests that the global suppression associated with general response inhibition remains intact in PD patients. Moreover, a heightened beta-band activity in the STN correlated with a reduction in CSE in unrelated muscles further corroborates the hypothesis of STN involvement in global motor suppression (Wessel et al., 2016; Wessel and Aron, 2017). This hypothesis was supported by a follow-up study by Wessel et al. (2022). Patients performed the task both with the DBS activated (ON-DBS) and deactivated (OFF-DBS), with the former case allowing to causally hamper STN's functioning, thus interfering with its inhibitory influence on the motor system. Comparing the two conditions, the study found significant differences in CSE during successful stop trials between PD patients with STN-DBS ON and OFF. A significant decrease in CSE was seen in both patients and healthy controls starting at 170 ms after the stop signal compared to go trials in the OFF-DBS condition, indicating effective inhibitory control processes. However, in the ON-DBS condition, patients did not show significant CSE suppression during successful stop trials, suggesting that STN-DBS disrupted the typical pattern of CSE modulation observed during response inhibition. A direct comparison between the stop trials of patients with DBS ON and OFF showed that CSE was lower in the OFF-DBS condition compared to when ON-DBS was at 230 ms after the stop signal and marginally at 200 ms

after the stop signal. These results support the STN involvement in a broad and non-selective motor inhibition through the hyperdirect pathway. The authors demonstrated that disrupting STN activity affects CSE during action inhibition. Several other disorders might be related to deficits in motor inhibition. For instance, primary tic disorder is characterized by the fact that tics can be transiently suppressed by volitional effort or will, so it is possible to suppose that tics result from a failure of inhibition. To investigate this issue, Rawji et al. (2020) tested volitional reactive and proactive inhibition, as well as automatic inhibition in primary tic disorder patients. Results show that volitional inhibition, measured by proactive and reactive inhibition in a conditional SST, shows no significant difference between tic disorder patients and healthy controls. Initially, patients with tic disorders exhibited longer SSRT relative to healthy control subjects, suggesting deficits in reactive inhibition. However, further analysis revealed that this delay in reactive inhibition was specifically observed in patients with tic disorders who also had comorbid obsessive-compulsive disorder (OCD). It is worth noting that comorbidity of psychiatric conditions is common in primary tic disorders (Specht et al., 2011). Moreover, CSE showed initial differences between patients with tic disorders and healthy controls. However, when data were aligned with response onset to account for reaction time differences, there were no significant differences between groups in CSE before movement. This suggests that the difference between the clinical population with OCD and healthy individuals may not lie in the CSE modulation itself, but rather in the timing of its manifestation (see Table 4 and Fig. 3). Fig. 3 provides a summary of studies. CSE effects are represented graphically using triangles at specific time points: upward-pointing triangles indicate increased CSE, while downward-pointing triangles reflect decreased CSE. Additionally, empty triangles denote findings from patient populations, distinguishing them from studies on healthy participants.

## 2. Discussion

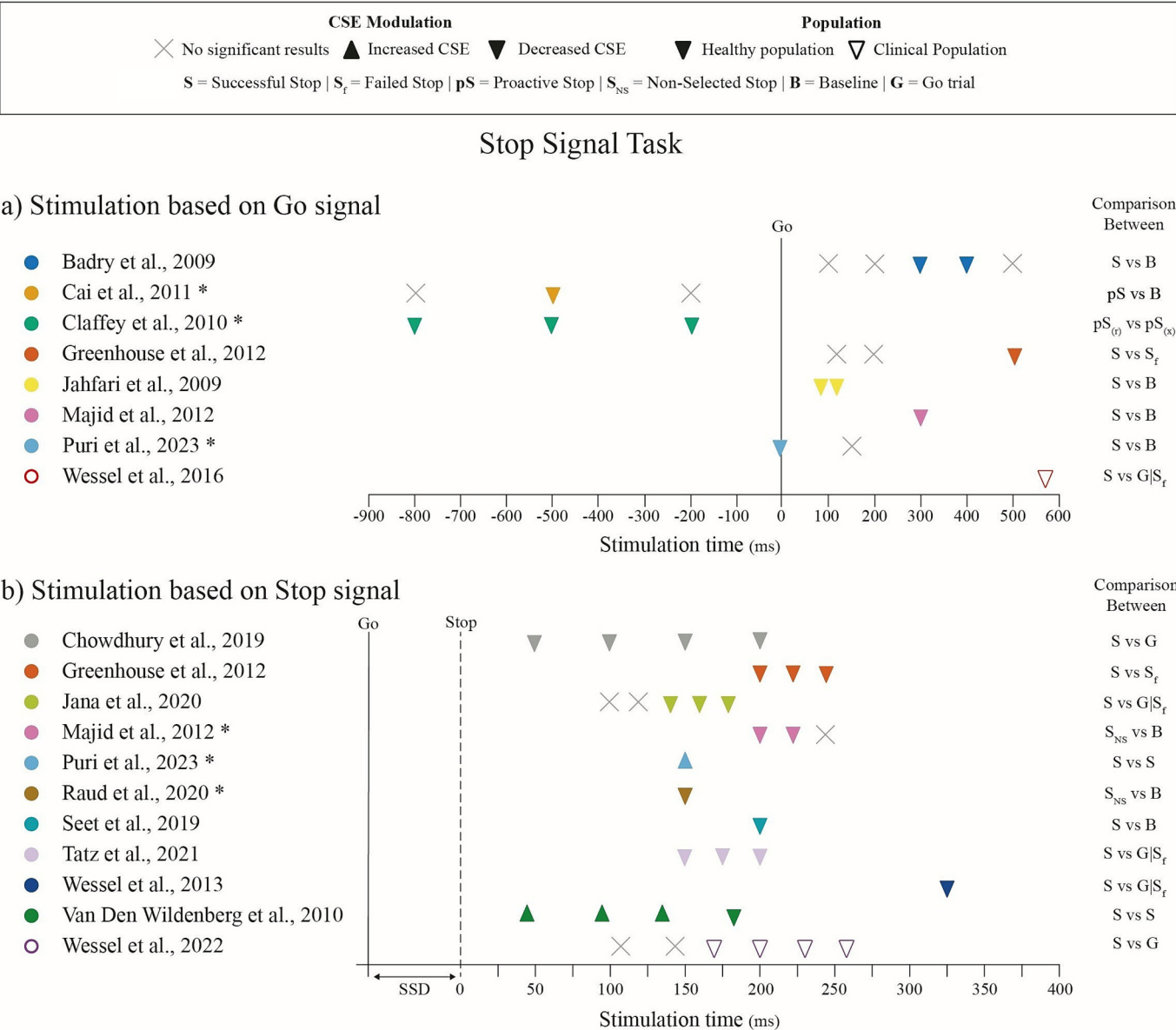
Action inhibition is a crucial and complex process for goal-directed behaviour, requiring the suppression of dominant responses (Duque

**Table 4**

The table summarizes the studies conducted on patient populations that employed TMS to investigate changes in corticospinal excitability (CSE) during the Stop Signal Task. Stimulation was delivered at various time points following either the go or stop signal, which served as the temporal reference for TMS administration. The "Stimulation Onset" column indicates both the timing of the stimulation and the reference signal used (go or stop). r = right, l = left, b = both, \* = Studies that employed multiple choice reaction time.

| Study                | Overall data        |                       | N  | SST data                             |                 | Stop signal  | Effectors | TMS data                                                                |                         | Results                                                                                                                                                                                                                         |
|----------------------|---------------------|-----------------------|----|--------------------------------------|-----------------|--------------|-----------|-------------------------------------------------------------------------|-------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                      | Clinical population | Number of experiments |    | Population characteristics           | Characteristics |              |           | Stimulation onset (ms)                                                  | Recording muscle (side) |                                                                                                                                                                                                                                 |
| Rawji et al. (2020)  | TIC disorder        | 1                     | 19 |                                      | Conditional SST | Red X        | Hand      | 200, 250, 300, 350, 400 from Go                                         | FDI (r)                 | Slower build-up after go signal (no sig.) in TIC patients > of CSE for non-critical compared to critical between 200 and 350 ms                                                                                                 |
| Wessel et al. (2016) | Parkinson's disease | 1                     | 9  | DBS with electrodes in STN           | Vocal SST       | Color change | Voice     | −100 ms from Go                                                         | FDI (r)                 | < of CSE (global inhibition)                                                                                                                                                                                                    |
| Wessel et al. (2022) | Parkinson's disease | 1                     | 20 | Bilateral DBS with electrodes in STN | Vocal SST       | Color change | Voice     | 110, 140, 170, 200, 230, 260 from Stop Signal (with DBS on and DBS off) | FDI (r)                 | < of CSE in patients with DBS off and controls from 170 ms during stop trials. No modulation for DBS on patients during successful stop trials < CSE in off patients compared to on patients at 230 ms and marginally at 200 ms |

# Corticospinal Excitability Modulation during SST



**Fig. 3.** Summary of studies employing stimulation during the Stop Signal Task. Data presented are exclusively from stop trials, except for the study by [Jahfari et al. \(2010\)](#), where stimulation was applied during the go trials. Panel (a) presents timings expressed concerning the go signal, defined as the reference point at 0 ms, while Panel (b) shows timings concerning the stop signal, also defined as 0 ms. Only studies that indicated the trend in corticospinal excitability (CSE) have been represented, specifically at time points where some form of modulation (positive or negative) was observed. Overall data regarding stimulation timings can be found in the summary tables. Temporal points are represented by triangles, with their orientation indicating the direction of modulation of CSE: triangles pointing upwards indicate an increase in CSE, while those pointing downwards signify a decrease. Crosses indicate a non-significant finding reported, and empty triangles correspond to studies conducted on patients rather than healthy subjects. Lastly, on the right of each graph, we reported the comparison conducted in each study. Studies marked with an asterisk indicate that a proactive condition was present. SSD = Stop Signal Delay.

[et al., 2017](#)). In real-world settings, it involves flexible modulation of actions based on external cues. Rapid action-stopping can produce either global or selective motor effects, as shown by changes in CSE in both task-relevant and irrelevant muscles. CSE modulation depends on prior information about which muscle to inhibit and when. In contrast, unexpected stopping often triggers broad, non-selective motor suppression (see [Bundt and Huster, 2024](#); [Derosiere and Duque, 2020](#)). The importance of flexible and accurate behavioural control is evident in several clinical conditions in which such ability is compromised, including schizophrenia ([Tsujii et al., 2018](#); [Yu et al., 2019](#)), bipolar disorder ([Farahmand et al., 2015](#); [Hidiroğlu et al., 2015](#)), ADHD ([Janssen et al.,](#)

[2015](#); [Senderecka et al., 2012](#)), Parkinson's disease ([Di Caprio et al., 2020](#); [Mirabella et al., 2017](#)), substance use disorders ([Smith and Matlick, 2013](#)) and obsessive-compulsive disorder ([De Wit et al., 2012](#); [Lipszyc and Schachar, 2010](#); [McLaughlin et al., 2016](#); [Sohn et al., 2014](#)). Thus, understanding the neural dynamics of action suppression can provide important biomarkers for the diagnosis and treatment of such clinical conditions.

### 2.1. Overall findings in the healthy and clinical samples

Stopping an action can involve a global suppression of CSE, affecting

both task-relevant and task-irrelevant muscles. This “emergency brake” is fast and non-selective, as shown by decreased MEPs in distant or unrelated muscles during successful stop trials (Badry et al., 2009). However, under certain situations (e.g., proactive cues, social tasks), selective inhibition is recruited, allowing precise suppression of specific effectors (Badry et al., 2009; Cavallo et al., 2014; Majid et al., 2012; Puri et al., 2023; Raud et al., 2020). Proactive control shapes motor readiness, often reducing CSE before movement onset (Cai et al., 2011; Claffey et al., 2010; Puri et al., 2023). Together, these findings suggest that context, task demands, foreknowledge, and social context determine whether inhibition is global or selective, engaging different neural circuits and temporal dynamics. Specifically, global suppression during nonselective stopping may result from the rapid engagement of the hyper-direct pathway, leading to broad motor inhibition, including task-irrelevant muscles. In contrast, selective stopping appears to involve the slower, more targeted indirect fronto-striatal-pallidal pathway, allowing for precise inhibition of specific responses. Similarly, action suppression was found to impact GABAA- and GABAB-mediated inhibitory mechanisms, which can also be dynamically and differentially modulated in response to go signals, stop signals, or even passive viewing of stop cues, supporting the idea of stimulus-driven inhibition. Notably, these intracortical inhibitory processes appear to be linked to behavioural performance, which can be enhanced through training. Finally, the few studies carried out on clinical samples suggested that clinical conditions do not reflect an absence of CSE modulation, but rather a disruption in the temporal dynamics of its engagement.

A possible interpretation of the reviewed findings is that motor inhibition is instantiated in two stages, according to the Pause-then-Cancel model (Diesburg and Wessel, 2021; Schmidt and Berke, 2017), which proposes the existence of an initial, rapid, and non-selective suppression of motor activity (i.e., Pause process), which rapidly freezes the motor system, followed by a more strategic and selective cancellation of the movement (i.e., Cancel process). On the other hand, while the Pause-then-Cancel framework interprets motor inhibition as a two-stage process, recent evidence suggests that action stopping may involve only a global motor system suppression (Chaudhuri et al., 2025). In this framework, suppression of motor activity reflects a unitary, rapidly deployed inhibitory process that transiently suppresses CSE. The apparent temporal progression from “pause” to “cancel” may arise from the evolving dynamics of the same inhibitory event rather than from two mechanistically separate stages. Such an idea is in line with recent studies showing that motor inhibition relies on a single functional network involving interconnected frontal and subcortical regions, characterized by a temporal progression rather than a dual anatomical architecture (Aron et al., 2014; Hampshire and Sharp, 2015; Jana et al., 2020; Wessel, 2020). Although the global motor suppression system proposed by Chaudhuri et al. (2025) is an interesting model, we suggest that caution should be exercised when attempting to generalize it to the highly complex situations encountered in real-world behaviour. Indeed, Chaudhuri et al. (2025) demonstrated that a single process is engaged during a relatively simple whole-arm reaching SST, in which participants acted without foreknowledge or changes in goal states. Therefore, it is reasonable to hypothesize that the “pause-alone” process described by the authors may operate primarily under conditions where action suppression demands are relatively simple. Moreover, in line with TMS evidence showing that unexpected visual flashes can reduce CSE within 55–70 ms after stimulus onset (Cantello et al., 2000), and the sudden appearance of an object rapidly approaching the body suppresses CSE with a latency of 70–80 ms (Makin et al., 2009), it is reasonable to assume that the “pause process” operates at a very fast timescale. However, since CSE suppression has been found to persist until around 350 ms after the stop signal (see Wessel et al., 2013), it is also plausible to envision a more complex mechanism capable of supporting multiple phases of action control.

## 2.2. Methodological considerations and future directions

The literature reviewed often provides contrasting findings, which can be explained by different methodological approaches used across experiments. A first methodological concern relies on the fact that, while some studies compare MEP amplitude recorded during the SST with those recorded at rest, other studies compare MEP between different active conditions (i.e., MEP recorded in stop vs go trials) and even between different groups of participants. This heterogeneity of comparisons may result in a difficult interpretation and integration of the results across different studies. A decrease in CSE compared to baseline may suggest a reduced muscle activation relative to rest, while differences in CSE between go and stop trials may indicate facilitation during the go trials rather than an active inhibition following stop instructions. To differentiate the effect of the stop trials on CSE, certain studies included passive or catch trials, where stimuli similar to stop and go signals are presented without requiring an active motor response. These trials exclude that the observed CSE modulations are driven by stimuli’s inherent characteristics or specific responses to the stop and go trials.

Another important issue regards the comparison between studies that investigated global vs selective inhibition, recording MEPs from task-irrelevant and task-unrelated muscles. For instance, some authors collected MEPs from the leg TA muscle even if the SST requires the hand to be stopped (Badry et al., 2009; Cavallo et al., 2014; Greenhouse et al., 2012; Majid et al., 2012; Tatz et al., 2021). In addition, certain studies recorded and compared MEPs from both hands (Puri et al., 2023), while other studies recorded MEPs only from one hand, even when both were task-relevant (e.g., participants had to move the right hand and inhibit the left (Badry et al., 2009; Chowdhury et al., 2019, 2020). Refining this methodological aspect may also lead to a more effective analysis of the inhibitory processes.

Another important aspect for future studies is measuring the baseline levels of GABAergic activity at rest, as well as how this activity is modulated during the task, which could potentially help distinguish between trigger failures and a successfully canceled action, as described by Wadley and Greenhouse (2024). Indeed, before movement initiation, M1 inhibition is released to prepare for action (Dupont-Hadwen et al., 2019; Kolasinski et al., 2019). In trigger failures, this release (e.g., decreased SICI) is reduced or absent, as the go process never starts. In contrast, successful cancellation involves transient GABAergic release after the go signal, followed by rapid suppression. In stop-trigger failures, SICI may remain near baseline, indicating no stopping process. Thus, by analysing GABAergic inhibition relative to baseline, it may be possible to distinguish between go trigger failure and successful action cancellation. Moreover, few studies have examined the link between intracortical inhibition (SICI and LICI) and SST performance. However, SICI at rest has been shown to predict motor inhibition in healthy individuals (Chowdhury et al., 2020; Loomes et al., 2023; Quettier et al., 2024). Given that deficits in these mechanisms are common across various clinical conditions, including chronic pain, Parkinson’s disease, Alzheimer’s, schizophrenia, Tourette’s, and post-COVID complications, further research using paired-pulse TMS, both online and at rest, is needed to explore SICI and LICI as potential biomarkers of impaired behavioural inhibition.

An additional important methodological issue is the increasing difficulty of the SST employed in studies aimed at investigating selective vs global inhibition. Bissett and Logan (2014) investigated how selective inhibition tasks differ from traditional SST, revealing that, contrary to assumptions, selectivity introduces variability in participant strategies. Rather than simply adding a discrimination layer, selective stopping prompts different behavioural approaches. For example, participants may first discriminate the signal before initiating inhibition, a process that lengthens SSRTs compared to simpler tasks, assuming independence between the go and stop processes. Alternatively, participants may initiate stopping upon any signal and then decide whether to respond, a strategy that preserves traditional SSRTs but results in slower

response times when signals should be ignored. In other cases, the discrimination process and the go process interact, creating a dependency that compromises SSRT validity and violates the independent race model. Such variability in behavioural strategies complicates SST interpretation and raises important questions about the reliability of measurements based on the classic independent race model (Logan and Cowan, 1984). Moreover, recent evidence showed that classic measures of behavioural inhibition (i.e., the SSRTs) overestimate the true timing of motor inhibition (Jana et al., 2020). To address both these complications, studies may consider incorporating neurophysiological measures collected during the task, such as the partial-response EMG (Raud et al., 2022) or electrophysiological correlates (Raud and Huster, 2017).

Further, it is worth noting that these CSE modulation patterns were extrapolated from standard SST, that is, the go and stop-signals were neutrally characterized. An important aspect that future studies need to address is the impact of emotion on action inhibition, considering the intricate link between actions and emotions (Frijda, 2012; Pessoa et al., 2012) as well as interindividual differences and personality traits like trait anxiety (Avila and Parcet, 2001; Hsieh et al., 2022; Neo et al., 2011) and impulsivity (Bari and Robbins, 2013; Logan et al., 1997; Pawliczek et al., 2013), which may impact the SSRT. Indeed, several studies demonstrated that emotions influence CSE (Borgomaneri et al., 2020, 2021, 2024) as well as our ability to withhold motor responses (Battaglia et al., 2024; Quettier et al., 2024), especially in the clinical population (Battaglia et al., 2021). However, it remains unclear whether and how the presence of an emotional stop signal, as opposed to a neutral one, might differently influence CSE during the SST. It is possible to predict emotional stimuli used as stop signals to induce even higher or faster CSE suppression relative to neutral stops.

Finally, very few studies have investigated online changes in CSE in the clinical population, and the existing studies (Rawji et al., 2020; Wessel et al., 2016, 2022) have focused solely on clinical conditions characterized by evident motor deficits (i.e., PD and tics). However, even in pathologies not primarily characterized by motor dysfunction, action suppression is often compromised (for a review, see Battaglia et al., 2021). This highlights the urgent need to investigate how CSE is affected in other clinical domains to gain a deeper understanding of the underlying mechanisms. These findings may offer valuable guidance for designing innovative non-invasive stimulation protocols, such as cortico-cortical paired associative stimulation (ccPAS, as previously used in Borgomaneri et al., 2023; Chiappini et al., 2024; Di Luzio et al., 2024), aiming at strengthening already existing connections within the cortical areas involved in action control, such as the presupplementary motor area and right inferior frontal gyrus (Duann et al., 2009; Neubert et al., 2010), potentially improving their behavioural performances.

#### CRedit authorship contribution statement

**Nicolò Arlati:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Lorenzo Peró:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Laura Lenzi:** Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Data curation. **Thomas Quettier:** Writing – review & editing. **Giuseppe Ippolito:** Writing – review & editing, Visualization, Data curation. **Simone Battaglia:** Writing – review & editing, Visualization. **Sara Borgomaneri:** Writing – review & editing, Writing – original draft, Project administration, Methodology, Conceptualization.

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#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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