<u>Title</u>:

Stop-signal reaction time correlates with a compensatory balance response.

Type of Article: Full length original article

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Acknowledgements: Jayme Warner, Morgan McJimsey, Mahmoud Mansour, Doug McDannald.

Keywords: Stop Signal Task; Response Inhibition, Balance, Posture, Executive Function

Abstract

<u>Background</u>: Response inhibition involves suppressing automatic, but unwanted action, which allows for behavioral flexibility. This capacity could theoretically contribute to fall prevention, especially in the cluttered environments we face daily. Although much has been learned from cognitive psychology regarding response inhibition, it is unclear if such findings translate to the intensified challenge of coordinating balance recovery reactions.

<u>Research question</u>: Is the ability to stop a prepotent response preserved when comparing performance on a standard test of response inhibition versus a reactive balance test where compensatory steps must be occasionally suppressed?

<u>Methods</u>: Twelve young adults completed a stop signal task and reactive balance test separately. The stop signal task evaluates an individual's ability to quickly suppress a visually-cued button press upon hearing a 'stop' tone, and provides a measure of the speed of response inhibition called the Stop Signal Reaction Time (SSRT). Reactive balance was tested by releasing participants from a supported lean position, in situations where the environment was changed during visual occlusion. Upon receiving vision, participants were required to either step to regain balance following cable release (70% of trials), or suppress a step if an obstacle was present (30% of trials). The early muscle response of the stepping leg was compared between the 'step blocked' and 'step allowed' trials to quantify step suppression.

<u>Results</u>: SSRT was correlated with muscle activation of the stepping leg when sufficient time was provided to view the response environment (400ms). Individuals with faster SSRTs exhibited comparably less leg muscle activity when a step was blocked, signifying a superior ability to inhibit an unwanted step.

Significance: Performance on a standardized test of response inhibition is related to performance on a reactive balance test where automated stepping responses must occasionally be inhibited. This highlights a generalizable neural mechanism for stopping action across different behavioral contexts.

1. Introduction

Response inhibition is an important component of executive function and underlies behavioral flexibility by allowing us to stop highly automated, yet contextually inappropriate action [1]. A classic example of this is the Stroop task where the automatic tendency to read words conflicts with the task of naming the color that the word is written in [2]. Overriding the automaticity of reading words to focus on a much less common task (i.e. color naming) highlights the challenge of inhibitory control. Although traditionally a focus of cognitive psychology, inhibitory control has more recently been speculated to play a role in fall prevention, as it would allow us to suppress prepotent, yet potentially unsafe, postural responses [3]. The value in suppressing an automated response to control postural equilibrium can be appreciated when one considers the cluttered environments we find ourselves in on a daily basis, demanding adaptation of an automatic postural response. However, methods for assessing response inhibition within a postural context pose considerable challenges, making research into this area and clinical application difficult. Given the general nature of stopping ability across tasks [4,5], we wished to investigate if response inhibition in a reactive balance task was related to performance on a cognitive test specifically designed to measure response inhibition.

An established method for assessing response inhibition is the stop-signal task (SST) as it explicitly tests one's ability to suppress an ongoing or already initiated response upon receiving a stop signal [6,7]. This task offers a precise measure of stopping ability known as the Stop-Signal Reaction Time (SSRT). A focus on response inhibition directly (versus 'executive function' more generally) makes the SSRT a valuable tool to evaluate response inhibition across a range of behaviors. Notably, neural markers underlying stopping are preserved across different combinations of stop cues and response modalities [5].

In the SST, the participant is repeatedly exposed to a 'go' stimulus and asked to elicit a specific response, such as quickly pressing a button on a keyboard. Occasionally, a stop signal follows the go cue and the participant is asked to withhold action. The SST is designed to estimate

the stopping process by manipulating specific variables in the performance tracking algorithm. To explain this task, an independent 'horse race model' has been proposed where go and stop processes operate in parallel [6–8]. In this model there is a race between two independent processes - one is a go process in response to a go stimulus, and the other is a stop process in response to a stop stimulus. According to this model, whichever horse finishes the race first will determine if the action is expressed or withheld. This is a stochastic model which provides theoretically justified estimates of the latency of stopping (i.e. SSRT), outlined in detail by Verbruggen & Logan (2009), and depicted visually in **Figure 1**. Such estimation is necessary given the unobservable latency of the stopping process.

In the current study we set up a postural recovery task that emphasized the need to suppress a highly automatic compensatory step. On infrequent trials where steps were unexpectedly blocked, participants were instead required to supplant a stepping reaction with a compensatory reach to a supportive handle. Consistent with how automaticity is typically encouraged in tests of response inhibition, we used a scenario where a rapid recovery step was required on most trials (70%) but on occasion this reaction would need to be suppressed (30% of trials). Furthermore, we manipulated the timing of visual access to the response environment to emphasize time pressure for stopping. In the present study we sought to determine if stopping ability as measured by the SSRT is related to performance on a postural recovery task that requires response inhibition.

2. Methods

2.1. Participants

Thirteen, healthy, young adults, (18-30 years) provided written informed consent prior to participation in this study. Procedures were approved by the Utah State University, Institutional Review Board conducted in accordance with the Declaration of Helsinki. One subject's data was not included due to excessive tonic muscle activity throughout testing, leaving twelve participants in the final sample.

2.2. Electromyography

Electromyography (EMG) was recorded using Delsys DE-2.1 differential surface electrodes, and EMG signals were amplified (gain = 1000) using a Delsys Bagnoli-4 amplifier (Delsys Inc., Boston, MA, USA). EMG data was sampled at 5000Hz and bandpass filtered using Signal Software and a Cambridge Electronic device (Power 1401, Cambridge Electronic Design, Cambridge, UK). EMG was collected from the Tibialis Anterior on the right (TA_R) and left (TA_L) legs to measure muscle activity in the stepping leg. Two of the twelve participants stepped with their left legs on all occasions. The remaining ten participants stepped primarily with their right legs. An experimenter made careful note of the stepping leg used on each trial, and the participants were free to step with either leg during testing.

2.3. Procedures

2.3.1. Stop Signal Task (SST)

The SST was custom written in Matlab (Mathworks, MA), and adapted from the version used in Aron & Poldrack (2006) [9]. This was completed while participants sat at a desk facing a computer. The participants were presented with instructions on the monitor and trained with the task prior to testing. Participants were presented with a go signal ("<" or ">") and instructed to respond as quickly as possible by pressing the appropriate button on the keyboard. Specifically, participants were instructed to press ">" if the arrow points to the right, and "<" if the arrow points to the left. They were asked to do this as quickly as possible once the arrow appeared, but to refrain from responding if an auditory stop signal was heard. On 25% of the trials, an auditory stop signal followed the go cue in a randomized fashion.

The delay between the go and stop signals is referred to as the stop-signal delay (SSD). The basic concept is that inhibition of the prepotent response is more difficult when the inhibitory stimulus is presented after a longer time interval than a shorter one. This helps gauge how well the participant is able to inhibit an incipient response. When the stop signal is presented close to the go stimulus onset a response is easier to inhibit, however as the onset of response execution approaches

stopping becomes increasingly difficult. While the go reaction time is included in the tracking algorithm the more relevant factors relate to the SSD and the percentage of successful versus failed stops. Indeed, the SST is designed to assess response inhibition instead of overt reaction speed, as the go reaction time is constrained by task instructions. Because the actual latency of the stopping process cannot be directly measured it must be estimated from a stochastic model and in this way the covert stopping process (SSRT) is estimated.

The SSD was varied to yield a 50% probability of correctly inhibiting a go response (i.e. pressing a "<" or ">" key) after the stop tone was presented. This SSD, where participants were able to inhibit their reaction 50% of the time, was then used to estimate the SSRT. More specifically, the SSRT was determined by subtracting the average SSD from the median correct go reaction time. For our study, the SSD was initially set at 250ms, and adjusted according to participant performance throughout testing, by increasing the delay by 50ms in case of a successful stop-trial, and decreased by 50ms in case of a failed stop-trial. This approach was taken to achieve a probability of successful stopping on about 50% of trials. Participants were instructed that going quickly and stopping successfully were equally important. As the name suggests, the SST measures an individual's capacity for stopping a response after the stop signal has been presented. The data collected from this test provides an SSRT. Participants performed 256 trials divided across 4 blocks with ~1 minute of rest between blocks. Trial duration was 2500ms.

2.3.2. Lean and Release Task

A custom-made 'lean and release' cable system was used to impose unpredictable forward perturbations. Although some aspects of the perturbation were predictable, such as the direction and amplitude of perturbation, the exact onset of the cable release was unpredictable to the participant. **Figure 2** depicts the lean and release apparatus, and the various conditions encountered during testing. Participants were placed in a harness connected by cables to the wall behind them. The experimenter instructed participants to lean as far forward as the cable allowed while keeping both feet in contact with the floor. This position required anterior rotation about the ankle, as the rest of

the body remained aligned. The exact forward lean position for each participant was determined as the minimal lean angle where a change-of-support reaction (i.e. forward step) was necessary to recover balance upon cable release.

In the less frequent response condition, the participants had an obstacle placed in front of their legs so that when the harness was released from the wall they were prevented from taking a forward step and forced to grab a wall-mounted handrail (**Figure 2A**, upper left). In the more frequent response condition, no blocks were present, therefore allowing a forward step to recover balance after cable release (**Figure 2A**, upper right). Notably, when the leg block was present, the nearby safety handle was uncovered to allow a compensatory reaching response. To control vision, the participant wore liquid crystal goggles (Translucent Technologies Inc. Toronto, ON, Canada) to occlude vision prior to the start of each trial. These goggles were then opened a few seconds later to reveal the specific response condition. This ensured that participants did not know what environment they were exposed to until the goggles open. A secondary failsafe cable was attached from the ceiling to the harness to catch the participant in the event of a fall. Throughout testing, participants were told to remain relaxed and to look at a fixation point on the ground ~1.5 metres in front of them. This fixation point was adjusted slightly to ensure that the top of the leg block and the safety handle were visible in peripheral vision when the goggles were opened.

The participant was released shortly after the goggles open, either 200 milliseconds or 400 milliseconds later. On a small portion of trials (~14%) no perturbation was delivered to act as a 'catch' trial, in an effort to encourage participants to only act in response to the perturbation. Following a familiarization period, testing began using 4 blocks of 28 trials each, with a brief rest between each block. On 70% of the trials the handle was covered and a stepping response was required. For 30% of the trials, a leg block was present and the handle was uncovered, therefore a compensatory reach-to-grasp was required without taking a forward step. This ratio of 70:30 was intended to heavily bias an automated stepping response, in turn forcing them to suppress that prepotent stepping response when the step was blocked. The basic protocol is visually depicted in **Figure 2B.** The present study investigated the link between compensatory stepping reactions and

stopping ability, thus it was important to bias a step reaction, in the same way that a rapid button pressing reaction is promoted in the stop signal task. A Cambridge Electronic device with expansion box and Signal software (Power 1401-3A, Cambridge Electronic Design, Cambridge, UK) was used to control timing for cable release, to open/close the occlusion goggles, and to drive the servo motors in order to move the handle cover and leg block into position.

2.4 Analysis

EMG signals from the TA_R and TA_L muscles were band-pass filtered (10-500 Hz) and fullwave rectified. The magnitude of the EMG response was assessed as the integrated EMG for a period of 200ms (iEMG_{200ms}), between 100ms to 300ms following perturbation onset. This time frame was selected to capture the early muscle response of the *stepping* leg. This specific window was based upon previous results by Thelan et al. (2000) where the authors measured muscle responses and contact forces associated with compensatory forward steps following sudden release from a support cable [10]. In their study, the average onset for the stepping leg TA was ~100ms, thus selected as our start point. For an end point, 300ms was selected given that unloading of the step leg in the Thelan study occurred between 255ms - 322ms in young adults depending on how much body weight was supported by the cable during the forward lean (i.e. 15-25%). Moreover, visual inspection of their group average TA waveforms in the step leg of young adults revealed that the bulk of the TA activity was captured within this timeframe. Our rationale for focusing on the earliest stepping EMG activity in the stepping leg was to capture the early motor activity that would be most susceptible to errors in response inhibition under time pressure. The point here was to emulate the type of rapid response errors captured by the SST using a button press on a keyboard.

Any trials where an anticipatory muscle response occurred prior to postural perturbation were identified and eliminated from further analysis. For this purpose, two discrete time windows of EMG activity were measured, one immediately before the goggles opened and another after the goggles opened, but immediately before perturbation. Both windows took the average rectified EMG for a period of 100ms. If EMG activity in the second time window exceeded the mean of

EMG activity in the first time window by more than one standard deviation, that trial was removed from analysis. This allowed exclusion of trials where participants may have prematurely responded before the actual magnet release.

For the reactive balance test, the iEMG_{200ms} was assessed for each trial, and grouped according to (a) delay (400ms or 200ms), and (b) condition (step or reach). The purpose was to use whichever action was afforded (step forward or reach for the handle) to group the EMG activity of the stepping leg, not necessarily the response that actually transpired. This means that on those trials where a participant accidently failed to suppress a step (i.e. leg block was present) such trials were still classified as 'reach' trials. In this way, the muscle response from the step leg could be compared between trials where the participant should reach versus trials where they should step. To accomplish this, a ratio was calculated by dividing iEMG_{200ms} of the reach condition, by the iEMG_{200ms} of the step condition. The assumption in using this ratio is that the closer the value is to one, the more difficult suppressing the normal step response is. Alternatively, as the ratio becomes smaller this would indicate a greater ability to refrain from stepping, while the participant grasps the handrail instead. By using the magnitude of muscle activation the intention was to provide a sensitive measure of a tendency to respond with the leg either appropriately or inappropriately given the context.

Primary outcome measures were (a) muscle response ratio (i.e. iEMG_{200ms} Reach/Step trials), and (b) the SSRT. The SSRT was first used to classify participants as having either 'fast' or 'slow' stopping ability by ranking relative to the group as an upper and lower half (six per group). The muscle response ratio was then compared between groups to determine if suppression was greatest (i.e. lower ratio) in those with a faster SSRT. A mixed design ANOVA was used, where the within-subjects factor was defined as 'Delay' of magnet release relative to opening of the goggles (200ms, 400ms), while 'group' (fast, slow) was defined as a between-subjects factor. As a followup to any significant group differences, a bivariate correlation determined if SSRT was correlated with muscle response ratio during conditions where a compensatory forward step should be inhibited. A standard 5% significance level was used throughout.

3. Results

3.1 Stop signal task

Median Go reaction time was 424ms (SEM: 14) with participants stopping on 49 % of cued stop trials. All twelve participants successfully stopped in 46 and 58% of trials, which indicates that the SSD staircase algorithm was effective. The average SSRT was 175ms (SEM: 8) with a range of 141ms to 230ms. The average SSD was 249ms (SEM: 18) with a range of 171ms to 347ms. Participants responded to almost all Go cues (99.8%) and made discrimination errors on less than 1% of the Go trials. The final sample consisted of 5 males and 7 female participants, with no significant gender differences in SST performance. Median Go reaction time for females was 430ms (SEM: 21) and 416ms (SEM: 18) for males, $t_{10} = 0.44$, p = 0.667, while SSRT was 171ms (SEM: 6) for females and 181ms (SEM: 17) for males, $t_{10} = 0.65$, p = 0.533.

3.2 Lean and release compared with stop signal reaction time

Figure 3 shows average waveforms from two separate participants, with step trials and reach-to-grasp trials on separate, overlapping waveforms, both aligned to perturbation onset. The upper panel provides exemplar data from averaged postural responses in the stepping leg muscles for a participant with a relatively fast SSRT, while the lower panel shows a participant with a comparatively slower SSRT. Mixed design ANOVA revealed a significant interaction between the factors 'Group' and 'Delay', $F_{1,10} = 6.138$, p = 0.033 and a main effect for 'Delay', $F_{1,10} = 8.208$, p = 0.017. Dividing into groups (fast vs. slow) was an initial exploratory step to make the data suitable for the ANOVA model, so when this revealed a significant interaction we then followed with the correlation taking advantage of SSRT as a continuous variable. Visual inspection of group averaged data in **Figure 4** suggests that the ability to suppress a highly automatic, yet unwanted step is better if more time is available to view the leg block (400ms delay vs. 200ms delay). This is supported by a main effect for 'Delay'. A closer look at the between-group data indicates that the faster SSRT group was driving this effect, confirmed by the interaction above. Post-hoc analysis on the

interaction was performed using separate t-tests to address our question if the faster SSRT group produced a smaller muscle response ratio. No significant differences were noted between groups at the 200ms delay, $t_{10} = 0.75$, p = 0.471, however the faster SSRT group showed a lower ratio at the 400ms delay, $t_{10} = 1.84$, p = 0.048. Since the general difference between groups could only be resolved at the later (400ms) delay, our decision was to focus the correlation on this time point as more promising to expose a preserved capacity for response inhibition across tasks. Follow-up analysis on this 400ms delay revealed a significant correlation between the SSRT and muscle response ratio, r = 0.561; p = 0.029, shown in **Figure 5**. We conducted a follow-up comparison on median Go reaction time between Fast SSRT 434.1ms (SEM: 45.8) and Slow SSRT 414.2ms (SEM: 54.4) groups to determine if overall response speed differed between groups. This comparison revealed no differences, $t_{10} = 0.68$, p = 0.51.

4. Discussion

Individuals with a faster SSRT also revealed reduced activation in a stepping leg when an obstacle was present versus trials where a recovery step was allowed. This suggests that stopping ability measured in the SST is related to an individual's capacity for response inhibition during compensatory stepping. Of particular interest is the fact that a measure derived from seated participants reacting with focal finger movements generalizes to performance on a whole-body, balance recovery task.

An important question to address is whether a failure to reduce muscle activation in a stepping leg is related to a broad-spectrum delay in reaction speed versus stopping speed. No significant differences were found in median Go reaction times between Fast and Slow SSRT groups, suggesting that response speed is unlikely to account for present results. It is important to recognize that the SST is designed to measure stopping ability specifically. Conversely, the median Go reaction time in this task does not truly reflect a 'fast-as-possible' reaction time, but instead measures how quickly participants respond within the context of a task that occasionally requires

stopping. This is a meaningful distinction as the need to occasionally stop (due to task instruction) would constrain Go reaction speed.

Given the generic nature of stopping, it seems logical that neural networks contributing to behavioural suppression [4,5,11,12], may also contribute to maintenance of postural equilibrium. However, it's not obvious that stopping ability necessarily generalizes to reactive balance control which imposes an intensified challenge. For example, unlike voluntary reactions, righting responses can originate entirely from spinal and brainstem circuits [13–15], which means that descending commands must often revise subcortical-evoked responses already in progress. Further challenges exist when one considers that a decision to step requires one leg to support body weight, while the other leg (already preoccupied with body support) must establish a new support base. Such compulsory coordination across limbs emphasizes a unique challenge with reactive balance, which is compounded by the time pressure to avoid a fall. Indeed, even without a balance context, the fact that the stepping response must accelerate a much larger body mass, and coordinate many more muscles in the process, makes the step response a greater challenge compared with the SST's simple finger response in seated participants.

An assumption that went into our study design was that a stepping command must be primed once the goggles open since rapid cable release may ensue. The setting must be quickly perceived and translated into a suitable leg or arm reaction depending on the presence of a leg block or access to a handle. While many of the righting mechanisms for balance recovery reside within the brainstem and spinal cord [16,17], using vision to shape the motor response and the need for response inhibition require the cerebral cortex [1]. (Note: Specific networks have been identified as part of the brain's stopping network, including the pre-supplementary motor area and the right inferior frontal cortex in addition to the subthalamic nucleus of the basal ganglia [12]). This cortical contribution to the postural response becomes increasingly probable as more time is allowed to appraise the scene following the perturbation [18]. The fact that the distinction between those with Slow versus Fast SSRTs only manifests in the muscle response ratio at the later (400ms)

delay, but not the earlier (200ms) delay suggests that a set amount of time may be necessary to inhibit the recovery step upon viewing the leg block.

4.1 Methodological considerations

The primary objective of the present study was to determine if response inhibition expressed in a seated 'cognitive' task correlated with performance on a standing reactive balance task that required occasional suppression of a highly automatic recovery step. Such a relationship would support a shared cognitive mechanism underlying both behaviors. To accomplish this, there were notable differences in the way response inhibition was assessed to best capture how it was manifest in each task. For example, in the SST, a Go cue was first presented (arrow on screen) followed by a stop tone, but in our reactive balance task the stop cue (leg block) was presented before the Go cue (cable release). The question could be raised why different approaches were used since it would be more consistent with the SST to open the goggles and then reveal a leg block *after* cable release. However, online inhibition of a rapid recovery step poses an extreme challenge given that corrective balance reactions are so much faster than voluntary reactions [19]. As a further point of distinction, our response inhibition SST outcome measure is a reaction time, whereas balance performance is measured as *response magnitude*. Here, it is important to recognize that the SST holds participants in a set response time zone which requires fast go reactions (but not fast as possible), while also adjusting the difficulty of stopping based on individual performance. By contrast, our Lean & Release test was unable to titrate inhibitory performance (step or no-step) in the same way, not least of which is due to the large number of trials that would be required to achieve this aim (i.e. numerous repetitions would be impractical considering the energy demands with rapid, whole-body balance reactions). Instead we selected two early time points that could in theory offer a sufficient challenge to expose response inhibition errors, but still provide a realistic opportunity to suppress a step when required. A consequence of clamping time in this way was that it required an alternate means to assess response inhibition in the reactive balance task – in this case, magnitude.

As a final point, the present balance test used a choice-reaction task versus a pure stopping task. Namely, our stop cue (leg block) demands not only suppression of one action (forward step), but also selection of a replacement action (grasp a support handle). Our approach aimed to impose heightened postural threat to force a change-of-support reaction. Therefore, the lean angle was set for each participant to ensure that a step was required and to promote step automaticity. For trials where a step was blocked, a forward fall was prevented by participant's resorting to grasping the available handrail. Despite this departure from traditional stopping tasks, there is evidence that the selection of appropriate behaviour (i.e. engaging appropriate motor responses while withholding inappropriate motor responses) engages similar neural processes [20].

5. Conclusions

The relationship between SSRT and compensatory stepping, suggests that an individual's capacity to inhibit an incipient finger response is linked to their ability to make a corrective balance response in a choice-demanding environment. One potential implication is that assessment of response inhibition via the stop signal task could identify a specific risk factor leading to falls. This standardized cognitive test could be accomplished safely and in a manner that is clinically feasible to expose response inhibition deficits.

References

- [1] J.M. Fuster, The Prefrontal Cortex, Academic Press, 2008.
 - [2] J.R. Stroop, Studies of interference in serial verbal reactions, J. Exp. Psychol. 18 (1935) 643–662. doi:10.1037/h0054651.
 - [3] T. Liu-Ambrose, L.S. Nagamatsu, C.L. Hsu, N. Bolandzadeh, Emerging concept: "central benefit model" of exercise in falls prevention, Br. J. Sports Med. 47 (2013) 115–117. doi:10.1136/bjsports-2011-090725.
- [4] J.R. Wessel, A.R. Aron, On the Globality of Motor Suppression: Unexpected Events and Their Influence on Behavior and Cognition, Neuron. 93 (2017) 259–280. doi:10.1016/j.neuron.2016.12.013.
- [5] J.R. Wessel, A.R. Aron, It's not too late: The onset of the frontocentral P3 indexes successful response inhibition in the stop-signal paradigm, Psychophysiology. 52 (2015) 472–480. doi:10.1111/psyp.12374.
 - [6] F. Verbruggen, G.D. Logan, Response inhibition in the stop-signal paradigm, Trends Cogn. Sci. 12 (2008) 418–424. doi:10.1016/j.tics.2008.07.005;
 - [7] G.D. Logan, W.B. Cowan, K.A. Davis, On the ability to inhibit simple and choice reaction time responses: a model and a method, J. Exp. Psychol. Hum. Percept. Perform. 10 (1984) 276–291.
 - [8] F. Verbruggen, G.D. Logan, Models of response inhibition in the stop-signal and stop-change paradigms, Neurosci. Biobehav. Rev. 33 (2009) 647–661. doi:10.1016/j.neubiorev.2008.08.014.
- [9] A.R. Aron, Cortical and Subcortical Contributions to Stop Signal Response Inhibition: Role of the Subthalamic Nucleus, J. Neurosci. 26 (2006) 2424–2433. doi:10.1523/JNEUROSCI.4682-05.2006.
 - [10] D.G. Thelen, M. Muriuki, J. James, A.B. Schultz, J.A. Ashton-Miller, N.B. Alexander, Muscle activities used by young and old adults when stepping to regain balance during a forward fall, J. Electromyogr. Kinesiol. 10 (2000) 93–101. doi:10.1016/S1050-6411(99)00028-0.
 - [11] A. Jha, P. Nachev, G. Barnes, M. Husain, P. Brown, V. Litvak, The Frontal Control of Stopping, Cereb. Cortex. 25 (2015) 4392–4406. doi:10.1093/cercor/bhv027.
 - [12] A.R. Aron, S. Durston, D.M. Eagle, G.D. Logan, C.M. Stinear, V. Stuphorn, Converging evidence for a fronto-basal-ganglia network for inhibitory control of action and cognition, J. Neurosci. Off. J. Soc. Neurosci. 27 (2007) 11860–11864. doi:10.1523/JNEUROSCI.3644-07.2007.
- [13] S. Mori, Integration of posture and locomotion in acute decerebrate cats and in awake, freely moving cats, Prog. Neurobiol. 28 (1987) 161–195. doi:0301-0082(87)90010-4 [pii].
- [14] C.F. Honeycutt, T.R. Nichols, The decerebrate cat generates the essential features of the force constraint strategy, J. Neurophysiol. 103 (2010) 3266–3273. doi:10.1152/jn.00764.2009.
- [15] J.M. Macpherson, J. Fung, Weight support and balance during perturbed stance in the chronic spinal cat, J. Neurophysiol. 82 (1999) 3066–3081.
 - [16] J.V. Jacobs, F.B. Horak, Cortical control of postural responses, J. Neural Transm. Vienna Austria 1996. 114 (2007) 1339–1348. doi:10.1007/s00702-007-0657-0.
- [17] J.M. Macpherson, F.B. Horak, Chapter 41: Posture, in: E.R. Kandel, J.H. Schwartz, T.M. Jessell, S.A. Siegelbaum, A.J. Hudspeth (Eds.), Princ. Neural Sci., McGraw-Hill, New York, 2013: pp. 935–959.
- [18] D.A. Bolton, The role of the cerebral cortex in postural responses to externally induced perturbations, Neurosci. Biobehav. Rev. 57 (2015) 142–155. doi:S0149-7634(15)00232-8 [pii].
- [19] W.H. Gage, K.F. Zabjek, S.W. Hill, W.E. McIlroy, Parallels in control of voluntary and perturbationevoked reach-to-grasp movements: EMG and kinematics, Exp. Brain Res. Hirnforsch. Cerebrale. 181 (2007) 627–637. doi:10.1007/s00221-007-0959-3.
 - [20] S.H. Mostofsky, D.J. Simmonds, Response Inhibition and Response Selection: Two Sides of the Same Coin, J. Cogn. Neurosci. 20 (2008) 751–761. doi:10.1162/jocn.2008.20500.

Figures and Legends

Figure 1: (A) Graphic representation of the horse-race model. The length of the bars represents the duration of the internal mental process (SSD = stop-signal delay; SSRT = stop-signal reaction time). (B) Graphic representation of the assumptions of the independent horse-race model of Logan and Cowan (1984), indicating how the probability of responding [p(respond|signal)] and the probability of inhibiting [p(inhibit|signal)] depend on the distribution of go reaction times, stop-signal delay (SSD) and stop-signal reaction time (SSRT). RTir = the point at which the internal response to the stop signal occurs. Adapted from Fig. 2. (Verbruggen & Logan 2009).

Figure 2: *Lean and release*. A) Participants were suspended in a leaning position with a wallmounted safety handle positioned within graspable range of the right arm. Visual access was controlled by liquid crystal goggles and the response environment was unpredictably altered while goggles were closed. Upon opening, participants could see either an available handrail with leg block present to afford a reach-to-grasp reaction, or a covered handrail with no leg block to allow a stepping reaction. The latter condition was presented more frequently (70% of trials) to bias a step reaction. B) Timeline for visual access relative to perturbation onset and muscle response.

Figure 3: Average step leg response. Average waveforms are shown for the Tibialis Anterior in the stepping leg - step trials in red and reach trials in black. Exemplar muscle response data shown for two participants with either a fast SSRT (top) or slow SSRT (bottom). The early muscle response (integrated EMG) was measured from 100 – 300ms (light shaded region).

Figure 4: Muscle response relative to SSRT. Average muscle response ratio (Reach iEMG200ms / Step iEMG200ms) at 200ms and 400ms visual delay. The slow SSRT group is in blue, while the fast SSRT group is in yellow.

Figure 5: Scatterplot showing the correlation between the muscle response ratio and SSRT at the 400ms visual delay.











Conflict of interest statement: None to declare