Title: Motor Output Matters: Evidence of a Continuous Relationship Between Stop/No-go P300 Amplitude and Peak Force on Failed Inhibitions at the Trial-Level.

Running Head: Motor Output and Inhibitory-Control

Authors and Affiliations

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Abstract

Motor actions can be suppressed with varying degrees of success, but this variability is not often captured as responses are typically represented as binary (response vs. no-response). Although the Stop/No-go P300 has been implicated as an index of inhibitory-control, it is unclear how the range of motor outputs relates to the P300. We examined the nature of this association in two experiments using an Anticipatory Timing and a Go/No-go Task, while measuring peak force, movement onset time, and P300. In both experiments, our results showed that trial-by-trial P300 amplitude on Failed Inhibitions were continuously related to peak force, where higher force (reflecting a greater degree of error) was associated with smaller P300 amplitude. Compared to Successful Inhibitions, P300 amplitude and onset latency on Failed Inhibitions were significantly reduced and delayed. Although the binary categorisation of inhibition-success (Successful vs. Failed) accounts for significant variance in the P300, it misses a reliable linear relationship that can be captured by continuous measures of motor output. Overall, the results provide evidence that P300 may reflect the continuously varying engagement of inhibitory-control. We present an activation model to visualise the P300-force association and to illustrate how motor output might be modelled in the context of inhibitory-control. Our results highlight the relevance of P300 amplitude and the importance of studying the spectrum of motor output and the need for future models to account for motor output.

1. Introduction

Elite athletes in sports such as tennis and baseball, have little time to prepare and execute successful actions (e.g. hitting a fast pitch). To deal with these high temporal demands, humans rely on advanced motor planning (de Rugy, Marinovic, & Wallis, 2012; Gray, 2002; Lacquaniti & Maioli, 1989; Marinovic, Tresilian, Chapple, Riek, & Carroll, 2017; Reuter, Marinovic, Welsh, & Carroll, 2019; Senot, Zago, Lacquaniti, & McIntyre, 2005). Although this strategy increases the chances of success when our predictions are correct, it becomes challenging to change or inhibit these highly prepared actions when they become undesirable (e.g. not hitting a ball that is going 'out', checked swings in baseball). Current psychophysiological models conceptualise inhibitory-control as a race or competition between excitatory and inhibitory processes, resulting in a binary event where responses are either suppressed or not, often marked by the registration of a key-press (Boucher, Palmeri, Logan, & Schall, 2007; Logan & Cowan, 1984; Logan, Van Zandt, Verbruggen, & Wagenmakers, 2014; Verbruggen et al., 2019). Motor actions, however, can be suppressed with varying degrees of success (de Jong, Coles, Logan, & Gratton, 1990; Marinovic, Plooy, & Tresilian, 2009; Marinovic, Reid, Plooy, Riek, & Tresilian, 2010; Marinovic, Reid, Plooy, Tresilian, & Riek, 2010; McGarry & Franks, 1997, 2003; McGarry, Inglis, & Franks, 2000; Nguyen, Moyle, & Fox, 2016; Scheffers, Coles, Bernstein, Gehring, & Donchin, 1996), ranging from no output on Successful Inhibitions, to slight twitches and larger movements on Partial and Failed Inhibitions, respectively. In this study, we examined how the range of motor outputs relates to electrophysiological measures of inhibitory-control.

A common approach to studying inhibitory-control is to assign responses to discrete categories (e.g. Correct or Incorrect Response, Successful or Failed Inhibition) with little

regard to the fact that these responses are likely to be distributed on a continuum. This assumes that all responses within a category are equivalent, which is not necessarily the case. Behavioural experiments have shown that the timing of the response on the correct limb is interfered by the additional presence of a sub-threshold electromyographic (EMG) response on the incorrect limb, indicating that not all correct trials are alike (Coles, Gratton, Bashore, Eriksen, & Donchin, 1985; Eriksen, Coles, Morris, & O'hara, 1985). Similarly, electrophysiological studies have shown that partial errors elicit reduced error-monitoring signals compared to complete errors, highlighting that not all errors are comparable and suggesting that differences in the brain's responses may be related to motor output and vice-versa (Meckler, Carbonnell, Ramdani, Hasbroucq, & Vidal, 2017; Vidal, Hasbroucq, Grapperon, & Bonnet, 2000). In the context of inhibitory-control, it has been demonstrated that inhibition failures varied in their force and EMG profile, showing variation in the movement distance, peak acceleration, rate of change in EMG activity, and EMG peak latency (Atsma, Maij, Gu, Medendorp, & Corneil, 2018; de Jong et al., 1990; Marinovic et al., 2009; McGarry & Franks, 1997, 2003; McGarry et al., 2000). While it is known that actions can be inhibited to varying degrees, the relationship between classic electrophysiological indices of inhibitory-control and the varying motor outputs is not well understood.

In inhibitory-control tasks, the Stop/No-go P300 event-related potential (ERP) component – a frontocentrally distributed positivity in the electroencephalogram (EEG) peaking around 300 ms after the onset of a Stop-signal or No-go stimulus - has been associated with the inhibitory-control process (Kenemans, 2015; Pires, Leitão, Guerrini, & Simões, 2014). It is typically enhanced on Successful Inhibition compared to Go trials (de Jong et al., 1990; Dimoska, Johnstone, & Barry, 2006; Randall & Smith, 2011; Smith, Johnstone, & Barry, 2008). It has also been shown to be earlier and/or larger on Successful

compared to Failed Inhibitions (Carrillo-de-la-Peña, Bonilla, & González-Villar, 2019; de Jong et al., 1990; Dimoska & Johnstone, 2008; González-Villar, Bonilla, & Carrillo-de-la-Peña, 2016; Greenhouse & Wessel, 2013; Kok, Ramautar, De Ruiter, Band, & Ridderinkhof, 2004; Liotti, Pliszka, Perez, Kothmann, & Woldorff, 2005; Overtoom et al., 2002; Schmajuk, Liotti, Busse, & Woldorff, 2006; Wessel & Aron, 2015). Supporting the role of P300 as an index of inhibitory-control, several studies using the Stop-Signal Task have reported negative associations between P300 onset latency and Stop-Signal Reaction Time (SSRT) - the estimated speed of the stopping process derived from the response time distribution of Failed Inhibitions and Go trials – showing that individuals with faster stopping processes are likely to show shorter P300 onset latencies (Wessel, 2018).

Although P300 latency differences between Successful and Failed Inhibitions are consistently observed, it is debated whether it truly captures the onset of the inhibitory-control process (Huster, Enriquez-Geppert, Lavallee, Falkenstein, & Herrmann, 2013; Raud & Huster, 2017). Futhermore, amplitude differences between Successful and Failed Inhibitions are not unequivocal, with several studies reporting similar or even larger P300 amplitudes on Failed Inhibitions (Bekker, Kenemans, Hoeksma, Talsma, & Verbaten, 2005; Kok et al., 2004; Wessel, 2018). Although inhibitory-control has been extensively studied, there are still gaps in our knowledge about its electrophysiology. In this study, we aimed to extend our knowledge of P300 as an index of inhibitory-control beyond its binary categorisation of inhibition, by exploring its association with motor-output.

Several studies have used varying methods to examine co-variation between motor output and P300. In a Go/No-go task using a modified release-and-press response, we have discovered that partial failures to inhibit (erroneously initiated responses that were

cancelled before completion) also resulted in significant reductions in P300 amplitude (Nguyen et al., 2016). Motor output-related reductions in P300 have also been observed in comparisons between Count vs. Press Go/No-go Tasks and in motor-execution tasks (Novembre et al., 2018, 2019; Smith et al., 2008). On Successful Inhibitions, Wessel (2018) observed an association at the trial-level between P300 amplitude and motor-preparation as reflected by the lateralised readiness potential (LRP) amplitude in several variants of the Go/No-go task. They observed that higher levels of motor-preparation were associated with increased engagement of inhibitory-control (reflected by larger P300 amplitude). Collectively, there is some evidence suggesting a possible relationship between P300 and motor output, but the nature of this association remains to be examined.

In the current study, we conducted two experiments to investigate the relationship between P300 and motor output. In the first experiment, we examined inhibitory-control in a temporally controlled environment provided by the Anticipatory Timing Task. In the Anticipatory Timing Task, participants anticipated and synchronised the onset of their response to a fixed and predictable event, while inhibiting the response if a Stop-signal was presented shortly before the fixed event. This task is similar to the Stop-Signal Task in that it requires participants to cancel their response during the late phases of response preparation and execution. However, it differs in its anticipatory design, absence of a reaction to a separate Go stimulus, and the use of a fixed Stop-signal time. This design allows us to eliminate any differences in stimulus-presentation across inhibition trials and across participants, which may complicate the interpretation of modulations of the ERP. The fixed-response design also discourages delayed responding, preventing participants from strategically adapting to the task, even with prior knowledge about the timing of the Stop-signal. We also conducted an additional second experiment using an equiprobable Go/No-

go task to examine if the relationship between P300 and motor output can also be observed in a reaction-based inhibitory-control task. To encourage a pre-potent Go response, participants were required to initiate their response within 200 ms from the onset of the Go stimulus and a point reward system was implemented to encourage fast Go responses.

If inhibitory-control is reflected by the P300, the P300 should be modulated by the success of inhibition, producing enhanced and earlier P300s on Successful compared to Failed Inhibitions. If the P300 reflects the continuously varying engagement of inhibitory-control, we expected that P300 amplitude would be negatively related to the force of responses on Failed Inhibitions at the trial-level, where larger P300 amplitudes are associated with lower force, reflecting greater suppression.

2. Methods

2.1. Participants:

Two separate experiments were conducted in which 28 participants consisting of university students and volunteers were recruited for each study (56 participants across both experiments). Three participants were excluded from each study (6 in total) due to missing data or excessive EEG noise and artifacts (Exp. 1, final N = 25, M(SD) age = 21.16 (2.94) years, age range = 18-27 years; Exp. 2, final N = 25, M(SD) age = 21.56(3.31) years, age range = 18-30 years). The study was approved by the human research ethics committee of Curtin University (Approval code: HRE2016-0200) and all participants provided written informed consent before starting the experiment. All participants also reported being right-handed, having normal or corrected vision, and not having any known or diagnosed neurological conditions.

2.2. Experimental Tasks:

In this section we describe the Anticipatory Timing Task used in Experiment 1, directly followed by describing the Go/No-go Task used in Experiment 2.

2.2.1. Experiment 1: Anticipatory Timing Task

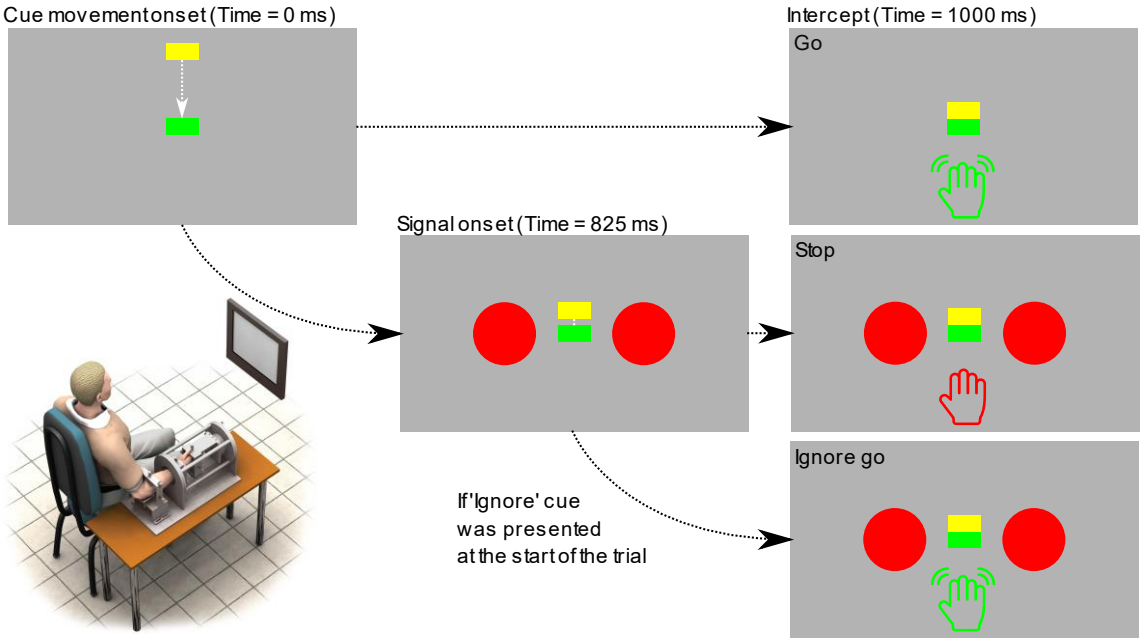

Figure 1. *Diagram of trial-events in the Anticipatory Timing Task. Participants were instructed to synchronise their response with the point when the yellow rectangle reaches the green target (Go trial), and to withhold their responses if a Stop-signal was presented (Stop trial). On Ignore Go trials, participants were presented with a cue at the beginning of the trial, instructing participants to respond to the trial despite the presentation of the Stop-signal. Participants responded by performing brief isometric wrist-extensions with their right-hand using the wrist-device shown.*

In the first experiment, participants completed the Anticipatory Timing Task where they were instructed to synchronise the onset of their response with the intercept of the yellow and green rectangles (referred to as 'the intercept'), unless a Stop-signal was presented (Fig. 1). Participants responded by performing brief isometric wrist-extensions

with their right arm, which was secured inside a custom-built wrist-device (de Rugy, Loeb, & Carroll, 2012). The anticipatory design allowed us to overcome some of the methodological challenges associated with examining ERPs in Stop-Signal Tasks. In the Stop-Signal Task, the short time gap between the presentation of Go and Stop-signal stimuli is known to produce overlapping neural activity. Additionally, the relative timing of the Stop-signal also varies from trial-to-trial. These varied and overlapping activations can complicate the interpretation of changes in the ERP. By using the Anticipatory Timing Task, which does not present a Go stimulus that participants must react to, we were able to minimise effects associated with orienting and processing the Go stimulus, as well as eliminate variability in Stop-signal timings by using a fixed Stop-signal time. To ensure the task was difficult enough to elicit Failed Inhibitions, the Stop-signal was always presented 175 ms before the intercept, which has been shown to translate to ~50 % Successful Inhibitions across participants based on previous findings using the same task (Marinovic et al., 2009; Marinovic et al., 2010a; Marinovic et al., 2010b). The use of a fixed response time also discourages delayed responding, preventing participants from strategically adapting to the task, even with prior knowledge about the timing of the Stop-signal. To match the presentation of stimuli between Go and Stop-trials, an 'Ignore Go' condition was included where participants were instructed to ignore an upcoming Stop-signal. Ignore Go trials were used in the ERP analysis to calculate difference-waveforms for P300 onset latency detection.

The task was presented on an ASUS 24-inch LCD monitor (model: VG248QE, running at 1920 x 1080 resolution, 120 Hz) using MATLAB 2015b and Psychtoolbox version 3.0.11 (Brainard, 1997; Kleiner et al., 2013; Pelli, 1997). At the start of each trial, the text "*Relax*" was presented for 1000 ms. On Ignore Go trials, the text "*Ignore"* was presented for 1500ms, accompanied by an audible tone. Yellow and green rectangles (100 x 50 pixels)

were then presented at the top and middle of the display for 500 ms (Fig. 1). The yellow rectangle descended, intercepting with the green target after 1000 ms. On Stop and Ignore Go trials, two red circles (300-pixels diameter each) were presented on the left and right of the green box, 175 ms *before* the intercept (i.e. 825 ms after the yellow rectangle started moving). Visual feedback about temporal accuracy and force was presented for 500ms after the intercept for 1000 ms.

Movement onset and peak force (in Newtons) were the measures of response time and force. We measured responses using a custom-built wrist-device with a six-degree of freedom force/torque sensor (JR3 45E15AI63-A 400N60S, Woodland, CA) digitised using a National Instruments data acquisition device (USB-6229 BNC multifunctional DAQ). Although the sensors are capable of six degrees of freedom, only movements in the horizontal plane were required for this experiment. We calculated movement onset from the tangential speed time-series derived from the torque data using the algorithm recommended by Teasdale and colleagues (1993) (further details are provided in the Supplementary Materials section).

Participants completed two practice and three experimental blocks (10, 50 and 3 × 100 trials, respectively). The first practice block consisted of all Go trials, while all other blocks consisted of 40 % Go, 40 % Stop and 20 % Ignore Go trials, presented in a pseudo-random order. While the global percentage of response trials was 60 %, the conditional probability of standard Go and Stop-trials were equal, minimising the novelty-related effects which are known to influence the P300 and may confound inhibition-related effects (Debener, Makeig, Delorme, & Engel, 2005; Dimoska & Johnstone, 2008; Donkers & Van Boxtel, 2004; Ramautar, Kok, & Ridderinkhof, 2004). Participants were instructed to time

the onset of their responses such that it coincided with the intercept, and to produce moderate forces of at least 20 Newtons (N). As we wanted participants to focus on the timing of their responses, we only defined a moderate minimum force level and did not specify any additional constraints on force. Correct Go trials were identified as those with responses starting within -50 to 30 ms from the intercept, but participants were not explicitly informed of this criterion. A shorter post-intercept deadline was selected to discourage participants from delaying their responses in anticipation of the Stop-signal. Visual feedback was presented at the end of each trial (e.g. “Good”, “Too Early”, “Too Soft”). Numerical force values were only presented as feedback during practice blocks. On Go trials, participants were informed if responses were too early or late (-50 < RT > 30 ms), or too soft (< 20 N). Successful Inhibitions were defined as Stop-trials without a detectable response using the Teasdale et al. (2003) algorithm (refer to Supplementary Materials section for further details). Failed Inhibitions were defined as Stop-trials with a detectable response within -175 ms to 500 ms from the intercept. Responses initiated outside of this interval were considered out-of-bounds and were excluded from further analyses. The same feedback was presented for Failed Inhibition and out-of-bound trials, informing participants of an incorrect response.

2.2.2. Experiment 2: Go/No-Go Task

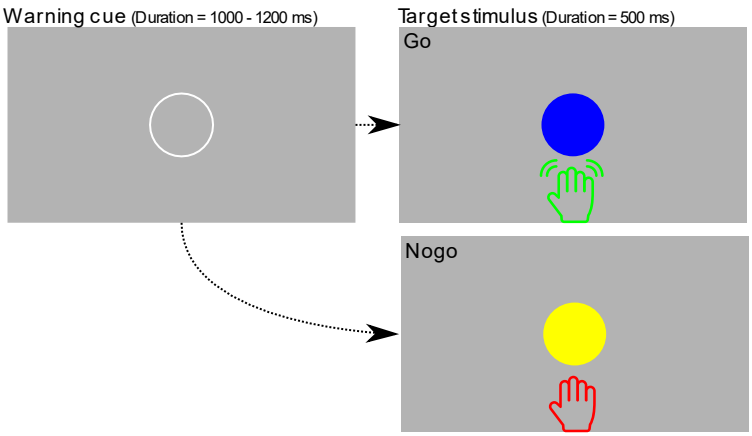

Figure 2. *Diagram of trial-events in the Go/No-go Task. Participants were instructed to quickly respond to Go stimuli (movement onset within 200 ms) while withholding responses to No-go stimuli. The coloured stimuli were counter-balanced across blocks for each participant.*

In the second experiment, participants completed the Go/No-go task where they were instructed to quickly respond to Go stimuli while withholding responses to No-go stimuli (Fig. 2). At the start of each trial, the text **"**Relax" was presented for 1000 ms, followed by a warning cue (hollow white circle, 300-pixel diameter) for a randomly varied duration between 1000 to 1200 ms. A Go or No-go stimulus (blue or yellow circle, 300-pixel diameter, counter-balanced across blocks and participants) was then presented for 500 ms, followed by visual feedback for 1000 ms.

Participants completed two practice and four experimental blocks (10, 24 and 4 × 80 trials, respectively). The first practice block consisted of all Go trials while all other blocks consisted of 50 % Go and No-go trials, presented in a pseudo-random order. An equiprobable task was used to match the design of the first experiment. Participants were instructed to initiate their response to Go stimuli within 200 ms to encourage the development of a pre-potent response, and to produce moderate forces of at least 20 N.

Correct Go trials were identified as those with responses starting within 200 ms of the stimulus. Visual feedback was presented at the end of each trial. On Go trials, participants were informed if their responses were too early or late (0 < RT > 200 ms), or too soft (< 20 N). On No-go trials, Successful Inhibition trials were defined as trials without a detectable response using the Teasdale et al. (2003) algorithm. Failed Inhibition trials were defined as No-go trials with a detectable response within 0 to 500 ms after stimulus onset. No-go trials with responses initiated outside of this window were considered out-of-bounds and were excluded from further analyses. To encourage fast responses, we awarded participants with 3 points for each Correct Go response and 1 point for each Successful Inhibition. No points were deducted for incorrect responses and the points were reset after each block. Points in the experiment were not recorded or analysed.

2.3. EEG Acquisition and Pre-Processing:

EEG data were recorded continuously for the duration of the experimental blocks. Data were acquired using a Biosemi ActiveTwo EEG system and ActiView (ver. 7.07) at a sampling rate of 1024 Hz with a DC – 100 Hz online filter. Data were recorded from 64 scalp electrodes arranged according to the 10-20 system with additional electrodes placed adjacent to the outer canthi of both eyes and on the left infraorbital region. For online referencing, the Biosemi EEG system uses active electrodes with common mode sense (CMS) and driven right leg (DRL) electrodes providing a reference relative to the amplifier reference voltage.

The EEG data were processed offline in MATLAB 2018a using EEGLAB (Delorme & Makeig, 2004), AMICA (Palmer, Kreutz-Delgado, & Makeig, 2011), SASICA (Chaumon, Bishop, & Busch, 2015), and ERPLAB (Lopez-Calderon & Luck, 2014) plugins. The data were

re-referenced to the average of the 64 scalp electrodes, down-sampled to 256 Hz and filtered from 0.1 – 40 Hz (-6 dB) using separate low- and high-pass Kaiser filters with transition widths of 0.2 and 2 Hz, a maximum passband deviation of .001, and filter orders of 4638 and 466.

Epochs were extracted for Go, Ignore Go, Successful and Failed Inhibitions, time-locked to the presentation of the Stop-signal/No-go/Go stimulus. Out-of-bound trials were excluded from further analysis. Epochs spanned from -1100 to 1200 ms, and baseline amplitudes were corrected to the 100 ms interval preceding the Stop-signal/No-go/Go stimulus. To correct for blinks artifacts, horizontal saccades and other artifacts, Independent Component Analysis was conducted and independent components (ICs) containing artifacts were manually identified with the guidance of SASICA and removed (Exp. 1: M(SD) = 13.4(7.3) ICs; Exp. 2: M(SD) = 12.6(7.2) ICs). Trials containing voltages exceeding ±100 μV were excluded (Exp. 1: M(SD) = 5(6.28) trials, max = 16 trials; Exp. 2: M(SD) = 3.57(2.82) trials, max = 8 trials). For Experiment 1, after trial rejection, the average number of trials retained for Standard Go, Ignore Go, Successful and Failed Inhibitions were 116.72(3.36), 58.00(1.83), 67.60 (18.97) and 51.52(18.97), respectively. For Experiment 2, the average number of trials retained for Go, Successful and Failed Inhibition conditions were 157.60 (2.35), 112.52 (25.66), and 39.80 (22.14), respectively. A Surface Laplacian filter was applied using algorithms described in Perrin and colleagues (1989) (smoothing factor = $1e^{-5}$, order of Legendre polynomial = 10) to reduce volume conduction effects in EEG sensor space, resulting in a $\mu V/mm^2$ voltage scale.

2.4. Measuring ERP Amplitude and Onset Latency:

We measured P300 at the frontocentral midline site (FCz) where P300 was maximal. Mean amplitudes were measured on Inhibition as well as Go trials at the trial-level over a 100 ms interval centred on the positive peak (200-500 ms after Stop-signal/No-go stimulus onset) of the grand-averaged Successful Inhibition waveform (Grey Shaded Area, Fig. 3).

Although no distinct P300 was evident on Go trials in the grand-averaged waveform, we measured P300 amplitude over the same time-window as Stop/No-go trials to investigate whether P300-force relationships were specific to inhibition trials and examine the potential role of general motor processes as highlighted in previous research (Neszmélyi & Horváth, 2017) (See Supplementary Materials for full results). The exploratory analysis showed that the P300-force relationship was also present on Go trials, but the size of the effect was smaller than Stop/No-go trials. Futher analyses accounting for motor-related activity in electrode C3 showed that general motor-related processes could not fully account for the P300-force effect on Inhibition-trials.

With respect to latency, we estimated the onset of inhibition-related activity on 'Stop minus Ignore Go' and 'No-go minus Go' difference waveforms using the 'Median Rule' described in Letham and Raij (2011). This method compares each point in the time-series with a threshold based on the median and the interquartile range of baseline activity. Onset latencies were estimated on individual-averaged difference waveforms due to difficulty in reliably detecting onsets at the trial-level. To reduce the chance of selecting transient noise spikes, we required 10 consecutive time-points to exceed threshold by 100 ms post-stimulus and onset latencies refer to the first point in this sequence. For Experiments 1 and 2 respectively, we excluded 5 and 4 participants where onset latency could not be identified

or participants who showed floor effects in both Successful and Failed Inhibitions. These participants were only excluded for the onset latency analysis.

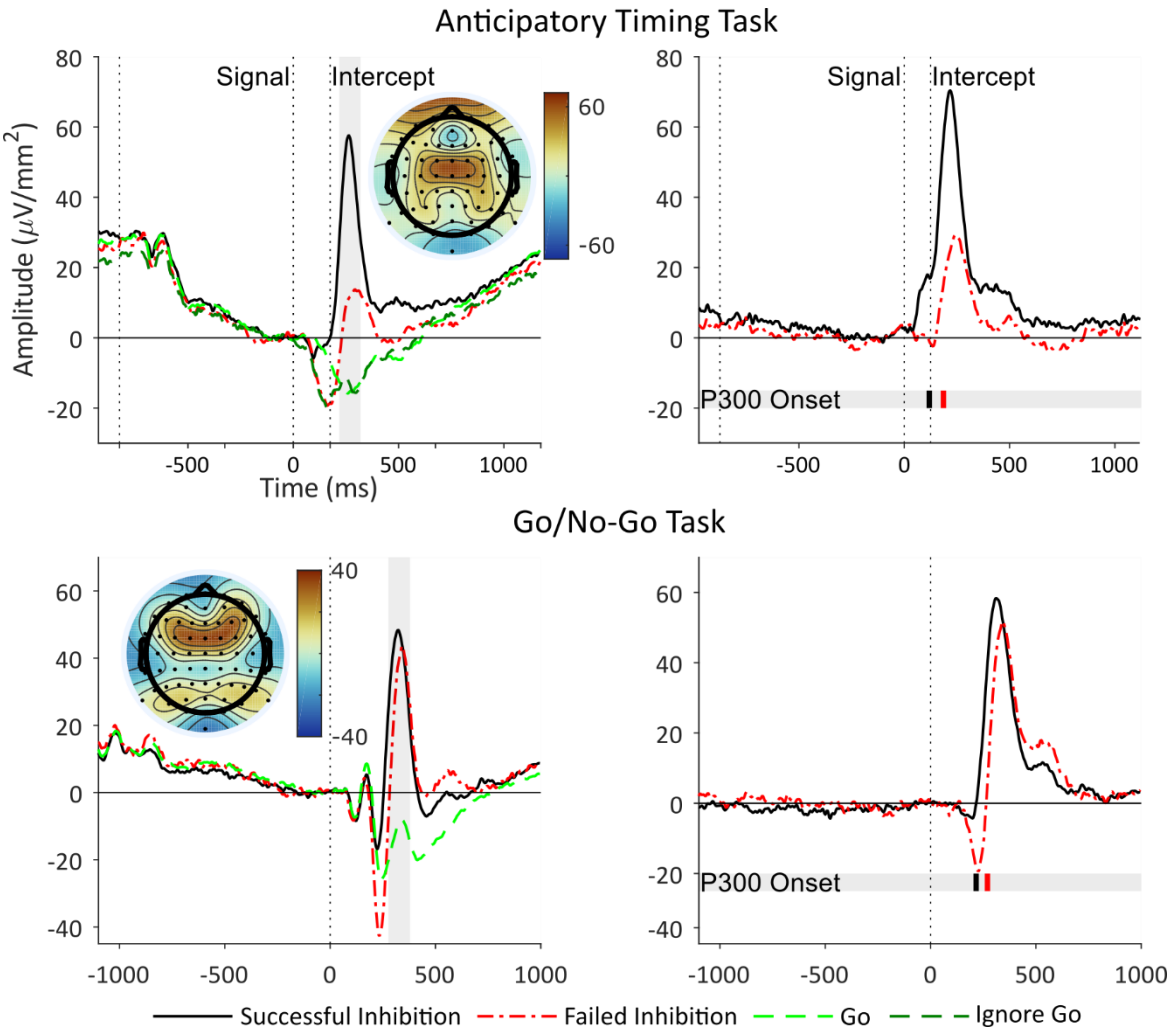

Figure 3. *Plots showing simple (left) and difference (right) grand-averaged waveforms at FCz in the Anticipatory Timing Task (top) and the Go/No-go Task (bottom). Difference waveforms depict 'Successful and Failed Inhibition minus Ignore Go' and 'Successful and Failed Inhibition minus Go' for Experiment 1 and 2, respectively. The grey shaded areas show measurement intervals for P300. Scalp maps show the distribution of activity over the P300 measurement interval on Successful Inhibitions.*

2.5. Statistical Analysis:

All statistical analyses were conducted using R statistics. First, we contrasted behavioural response measures (movement onset, peak force, peak force latency, rate of force development) between Go and Failed Inhibitions. This was done by comparing their estimated marginal means using the 'emmeans' function from the 'emmeans' package (Lenth, Sigmann, Love, Buerkner, & Herve, 2019). We presented the results of these pairwise categorical comparisons as *t*-ratios (mean difference estimate divided by standard error) with degrees-of-freedom estimated using the Kenward-Roger method. We also examined the association between peak force and movement onset time on Failed Inhibitions at the trial-level using linear mixed models (see below for specific details). Movement onset and peak force were scaled by participant (z-score, M = 0, SD = 1) in this analysis to reduce scale differences between the two variables.

Second, using the same method, we contrasted our electrophysiological response measures (P300 mean amplitude and P300 difference onset latency) between Successful and Failed Inhibitions. Third, we conducted two analyses comparing the onset timing of the P300 and the behavioural response. This was to examine the suggestion that markers of inhibitory-control should precede the expected behavioural response or inhibitory effects on the response to failed inhibitions, as it is debated whether the P300 occurs too late to reflect inhibitory-control (Huster et al., 2013; Raud & Huster, 2017). Specifically, we contrasted P300 difference onset latency on Successful Inhibitions with movement onset time on Go trials, and P300 difference onset latency on Failed Inhibitions with peak force latency on Failed Inhibitions.

Fourth, we examined the trial-level relationship between P300 amplitude and peak force on Failed Inhibitions. This was conducted using linear mixed models in R, with the

'lmer' function from the 'lmerTest' package (Kuznetsova, Brockhoff, & Christensen, 2017). We modelled P300 mean amplitude as the dependent variable and peak force as a fixed-effects, with participant intercepts modelled as a random effect. We presented the results as F values using the Satterthwaite's approximation method (Satterthwaite, 1941) with the 'anova' function. We used the 'summ' function in the 'jtools' package (Long, 2019) to calculate the estimated regression-weights (β), and used the 'r2beta' function from the 'r2glmm' package to calculate effect size as Partial R^2 (R_p^2) (Jaeger, 2017).

Lastly, we examined whether peak force can completely account for the P300 amplitude effect between Successful and Failed Inhibitions. To do this, we compared three models of P300 mean amplitude on all inhibition trials (Successful and Failed Inhibitions) with peak force and binary inhibition-success (Successful, Failed) as sole and combined predictors. Peak force was scaled (*z*-score, M = 0, SD = 1) by participant in this analysis to focus on relative changes in force within-individuals.

3. Results

3.1. Behavioural Data:

Participants successfully inhibited their responses on 56.33(15.81) % and 70.33(16.04) % of trials in the Anticipatory Timing and Go/No-go Tasks, respectively. Inhibition accuracy in the Anticipatory Timing Task was consistent with our estimates based on previous studies using a range of stop-signal presentation times (Marinovic et al., 2009; Marinovic et al., 2010a; Marinovic et al., 2010b). Unsuccessfully inhibited responses were initiated significantly earlier than Go responses (Fig. 4; Movement onset - Exp. 1: -43.32(54.50) vs. 1.19(63.16) ms relative to the intercept, *t-ratio*(24) = 8.91, $p < .001$; Exp. 2: 154.14(64.89) vs. 209.4(62) ms relative to stimulus-onset, *t-ratio*(24) = 16.14, $p < .001$). The

time in which peak force was reached was also significantly earlier on Failed Inhibitions than on Go trials (Peak force latency - Exp. 1: 88(33.18) vs. 167(69.71) ms, *t-ratio*(24) = 7.12, $p < .001$; Exp. 2: 251.48(36.07) ms vs. 337.26(39.55), *t-ratio*(24) = 9.13, $p < .001$).

With respect to motor output, peak force and peak rate of force development were both significantly lower on Failed Inhibitions compared to Go trials (Fig. 4; Peak Force – Exp. 1: 17.08(12.99) vs. 32.07(13.4) N, *t-ratio* (24) = 10.94, $p < .001$; Exp. 2: 9.99(11.71) vs. 37.32(13.1) N, *t-ratio*(24) = 12.51, $p < .001$; Peak rate of force development – Exp. 1: 226.90(97.46) vs. 375.56(155.01) N/s, *t-ratio*(24) = 7.20, $p < .001$; Exp. 2: 168.06(85.97) vs. 535.51(159.23) N/s, *t-ratio*(24) = 14.03, $p < .001$).

When examining the association between movement onset and peak force on Failed Inhibitions, we found a negative relationship between response time and force in the Anticipatory Timing Task, indicating that earlier responses were likely to be more forceful ($F(1,1286) = 27.60$, $p < .001$, $R^2_p = 0.02$, $\beta = -0.14$). However, this association was not statistically significant in the Go/No-go Task ($F(1,993) = 2.20$, $p = 0.139$, $R^2_p = 0.002$, $\beta = -0.05$).

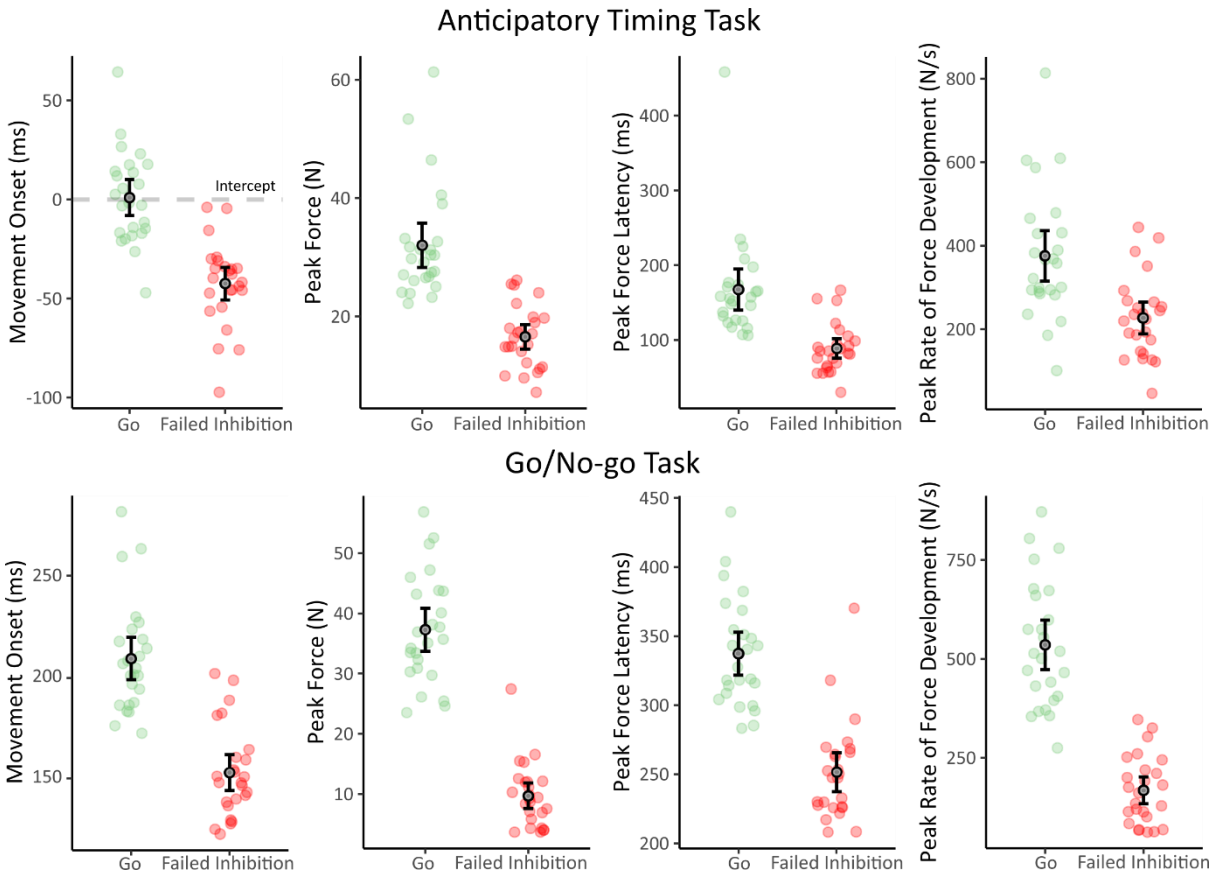

Figure 4. *Plots depicting individual- and grand-average values for movement onset, peak force, peak force latency, and peak rate of force development with 95% confidence interval error-bars. Movement onset and peak force latency in the Anticipatory Timing Task are relative to the intercept shown by the dashed grey line, whereas timings in the Go/No-go task are relative to the onset of the Go and No-go stimuli.*

3.2. Electrophysiological Data: P300 Mean Amplitude and Difference Onset Latency:

In categorical contrasts between Successful and Failed Inhibitions (Fig. 5), P300 mean amplitude was significantly reduced on Failed Inhibitions (Exp. 1: 8.47(22.98) vs. 45.04(22.02) $\mu V/mm^2$, *t-ratio*(24) = 8.95, $p < .001$; Exp. 2: 26.95(22.89) vs. 39.25(23.80) $\mu V/mm^2$, *t-ratio*(24) = 4.84, $p = .001$). P300 difference onset latency was also significantly

delayed on Failed Inhibitions (Exp. 1: 229.69(47.79) vs. 160.74(50.01) ms relative to Stop-Signal, *t-ratio*(17) = 5.19, $p < .001$; Exp. 2: 269.72(50.12) vs. 216.15(50.09) ms relative to No-go stimulus, *t-ratio*(20) = 3.40, $p = .002$).

When comparing the relative timing of electrophysiological and behavioural responses, our results showed that P300 onset did not differ significantly from movement onset in both experiments (Exp. 1: 160.74(50.01) vs. 176.25(22.88) ms, *t-ratio*(17) = 1.26, $p = .222$; Exp. 2: 216.15(52.09) vs. 204.56(24.18) ms, *t-ratio*(20) = 0.94, $p = .360$). However, we found that P300 onset on Failed Inhibitions occurred before the erroneous response reached its peak force in the Anticipatory Timing, but not the Go/No-go Task (Exp. 1: 229.68(47.79) vs. 268.74(33.82) ms, *t-ratio*(19) = 3.03, $p < .006$; Exp. 2, 269.72(50.12) vs. 247.43(34.33) ms, *t-ratio*(20) = 1.91, $p = .070$).

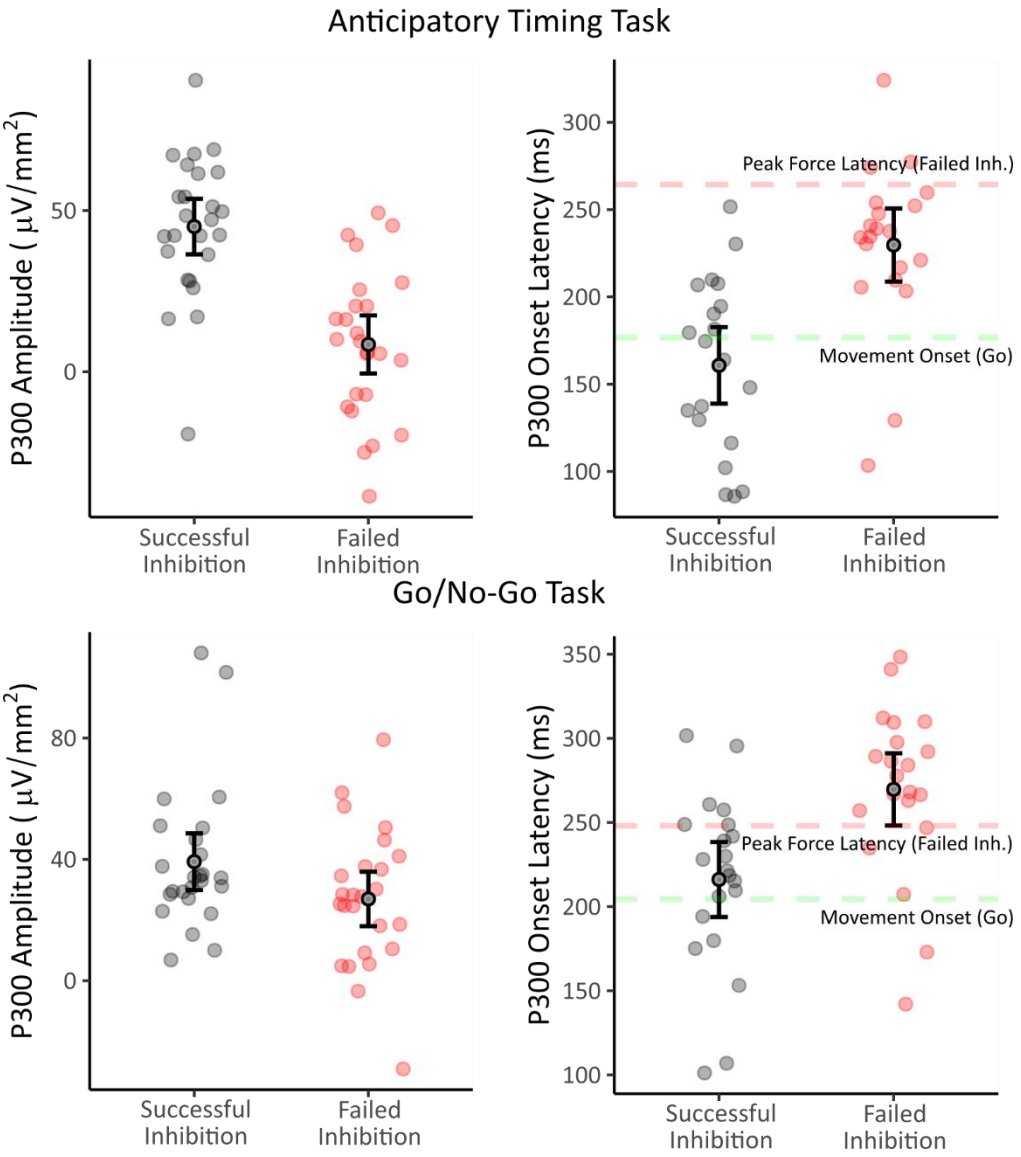

Figure 5. *Plots depicting individual- and grand-averaged values for P300 mean amplitude and P300 difference onset latency, with 95% confidence interval error-bars. Onset latencies are relative to the onset of the Stop/No-go stimulus. Dashed green and red lines represent the mean Go response time and Peak Force Latency, respectively, showing the relative timing between the P300 onset and the motor response.*

3.3. Association between P300 Mean Amplitude and Peak Force:

When examining the association between P300 mean amplitude and peak force on Failed Inhibitions, we found that peak force was a significant negative predictor of P300

amplitude, where smaller forces (reflecting a higher degree of suppression) were associated with larger P300 amplitudes (Exp. 1, $F(1,1256.4) = 24.39$, $p < .001$, $\beta = -6.95$, $R^2_p = .027$; Exp. 2, $F(1,968.85) = 120.91$, $p < .001$, $\beta = -14.44$, $R^2_p = .111$).

3.4. Does Peak Force completely account for P300 amplitude differences between Successful and Failed Inhibitions?

We contrasted three models predicting P300 amplitude on Successful and Failed Inhibitions with peak force and binary inhibition success as sole and combined predictors (Fig. 6). The analyses yielded a few notable findings. Firstly, peak force was found to be a significant predictor of P300 amplitude in both sole and combined predictor models, highlighting that it captures a robust and unique linear relationship with P300. Secondly in the combined predictor model of P300 in the Anticipatory Timing Task, binary inhibition success still remained a significant predictor of P300, accounting for more variance in the data than force. This indicates that while force is able to capture some P300 variability on Failed Inhibitions, there is P300 variation on Successful Inhibitions that force does not account for. However, in the combined predictor model of P300 in the Go/No-go Task, binary inhibition success was no longer significant when force was accounted for. The inability to detect the binary effect in the Go/No-go task could be due to the smaller difference in P300 between Successful and Failed Inhibitions, and may reflect the influence of task parameters.

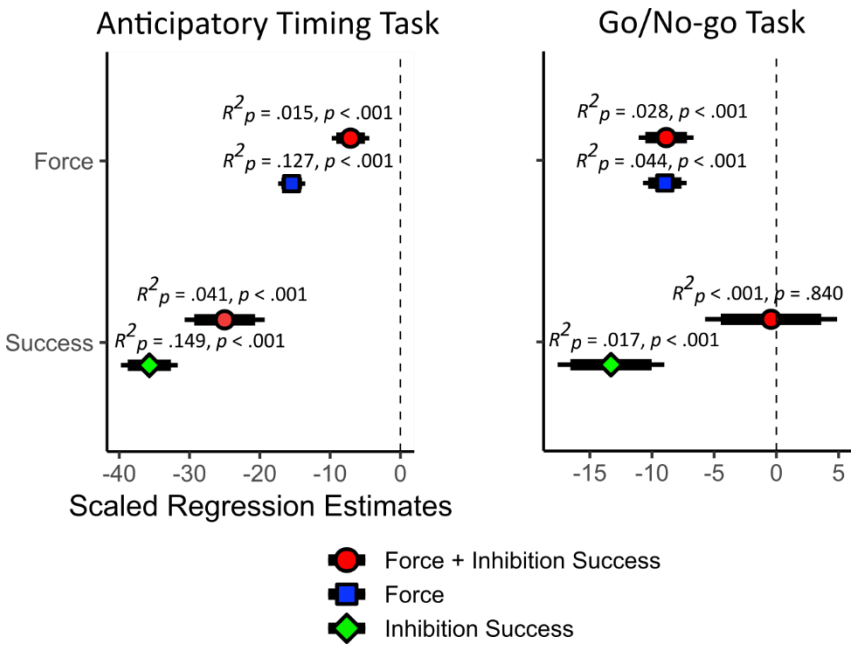

Figure 6. *Plot depicting estimated regression weights and variance explained by peak force and binary inhibition success from three models predicting P300 mean amplitude on Successful and Failed Inhibition trials in the Anticipatory Timing Task and the Go/No-go Task. Peak force and binary inhibition success as sole predictors are depicted in blue squares and green diamonds, respectively. Estimates for the combined model are depicted by red circles. The thick and thin black bars show 95% and 99% confidence intervals.*

4. Discussion

In this study, we sought to investigate the nature of the relationship between motor output and P300. Using the Anticipatory Timing Task and the Go/No-go Task, we measured the output and timing of the motor response, and the amplitude and latency of the P300. In our analyses, we characterised the behavioural and electrophysiological response to Failed Inhibitions, and examined the relationship between peak force and P300 amplitude on Failed Inhibitions. If inhibitory-control is reflected by the P300, we expected that P300 should be modulated by the success of inhibition showing enhanced and earlier P300s on

Successful compared to Failed Inhibitions. Regarding motor output, if P300 reflects the continuously varying engagement of inhibitory control, we expected P300 amplitude on Failed Inhibitions to be negatively related to force, where larger P300 amplitudes are associated with lower force, reflecting greater suppression.

Characterising the response to Failed Inhibitions, our analysis of the behavioural response showed that unsuccessfully inhibited responses were less forceful (reduced peak force and peak rate of force development) than Go responses, highlighting that there was some degree of response suppression on Failed Inhibitions which is consistent with previous studies examining response force (Ko, Alsford, & Miller, 2012; Scheffers et al., 1996). We also found that unsuccessfully inhibited responses reached their peak force earlier than Go responses, possibly indicating an interruption of the erroneous response. With respect to response timing, movement onset also occurred earlier for Failed Inhibitions compared to Go responses, suggesting that they were more highly prepared and more likely to escape inhibition.

Characterising the electrophysiological response, we found that P300 was modulated by the success of inhibition. In line with our predictions, P300 in both experiments was significantly reduced and delayed on Failed compared to Successful Inhibitions. To investigate the idea that markers of inhibitory-control should precede the response or inhibitory effects in the response during Failed Inhibitions (Huster et al., 2013; Raud & Huster, 2017), we examined whether onset timing of the P300 on Successful Inhibitions preceded the average Go response, and whether P300 onset on Failed Inhibition preceded the time where force reaches its peak, reflecting the time the motor action was interrupted. The results showed that P300 onset preceded peak force latency on Failed

Inhibitions in the Anticipatory Timing Task, providing some support for the inhibitory-control account. However, the other latency findings were non-conclusive showing that P300 onset and movement onset timing did not differ statistically, highlighting the close timing of the two onsets.

Although the categorical P300 amplitude and latency effects were largely consistent with our expectations, there were a few observations which require further consideration. Firstly, the magnitude of the P300 amplitude effect in Successful and Failed Inhibitions was notably smaller in the Go/No-go compared to the Anticipatory Timing Task. One possibility is that these discrepancies may be related to task differences in response preparation, influencing engagement of inhibitory-control required. In the Anticipatory Timing Task, the anticipatory nature of responding to a known event facilitates advanced response-preparation, thereby increasing the amount of inhibitory-control required to suppress highly prepared responses. Comparatively, the presentation of the Go stimulus is jittered and thus relatively uncertain in the Go/No-go task, which may reduce preparation and thereby decreasing the amount of control required. Similarly, previous comparisons between the Stop-Signal and Go/No-go tasks have reported larger P300 amplitudes in the Stop-Signal task, where the Go stimulus precedes the Inhibitory stimulus, allowing for the advance preparation and execution of the response (Enriquez-Geppert, Konrad, Pantev and Huster, 2010).

Secondly, P300 difference onset latencies in the Anticipatory Timing Task (~160 ms) were notably shorter than P300 onsets latencies commonly observed in typical Stop-Signal studies, but this timing is similar to inhibition-related effects in corticospinal excitability assessed using transcranial magnetic stimulation and EMG activity (Coxon, Stinear, &

Byblow, 2006; Raud & Huster, 2017). The relatively short P300 onset latencies in the Anticipatory Timing Task could be due to the use of a fixed and predictable Stop-Signal timing, facilitating the processing the Stop-Signal compared to other tasks which use unpredictably timed Stop-Signals. Additionally, this could be due to the requirement for participants to respond very shortly after the Stop-Signal (175 ms) in the Anticipatory Timing Task compared to standard Stop-Signal Tasks where average Go responses are less constrained, with average Go RTs ranging from 400-600 ms. The observation of earlier P300s could reflect a shift in the engagement of inhibitory-control to match task differences in the execution of Go responses.

Regarding the relationship between P300 and motor output, our analyses of Failed Inhibition trials revealed a significant negative relationship where greater force (reflecting a higher degree of error) was associated with smaller P300 amplitude. The relationship between motor output and P300 is consistent with our predictions and with previous work on partial inhibitions and recent work examining motor output (Nguyen et al., 2016; Novembre et al., 2018, 2019). This is also in line with P300-LRP associations at the trial-level suggesting that larger P300s are associated with greater engagement of inhibitory-control (Wessel, 2018).

To further examine the nature of the P300-force relationship, we examined whether force could completely account for the P300 amplitude effect between Successful and Failed Inhibitions. When both force and binary inhibition success were modelled together, both predictors significantly predicted P300 and binary inhibition success in the Anticipatory Timing Task. This indicates that while force is able to capture some P300 variability on Failed Inhibitions, force alone does not completely account for the difference in P300 amplitude

between Successful and Failed Inhibitions. However in the Go/No-go Task, binary inhibition success was no longer significant when force was accounted for. This indicates that P300 differences between Successful and Failed Inhbitions were largely attributed to P300 variability on Failed Inhibitions which could be explained by motor-output. While binary P300 amplitude effects may vary across experiments, possibly due to differences in the engagement of inhibition required in each task, force-related effects appeared to be more consistent.

In the Anticipatory Timing Task, the observation of a significant effect of binary inhibition success over-and-above force indicates that Successful Inhibitions are also associated with a range of larger P300 amplitudes that cannot be accounted for by force. The variation in P300 on Successful Inhibitions cannot be accounted for by force because no observable behavioural response is produced on these trials. Although there is no observed behaviour, we think that variation in P300 amplitude on Successful Inhibitions reflects the engagement of inhibitory-control process, extending from the P300-force assocaitions seen on Failed Inhibitions.

To illustrate our conceptualisation of how force may be modelled in inhibitory-control, and how binary effects may manifest from a continuous P300-force relationship, we developed an activation model with interacting preparatory response and inhibitory processes (Fig. 7). The model shows the development of the preparatory and inhibitory processes over the course of the trial and their combined net activation, reflecting the opposing interaction. The presence of a response is determined by whether net activation crosses the initiation threshold, but more importantly, the force of the response is reflected

by the extent that the initiation threshold is crossed. If the threshold is greatly exceeded, larger forces are produced and visa versa.

In Figure 7A, we show an illustration of the time course of processes during a Failed Inhibition trial and how the weak engagement of the inhibitory-control process fails to suppress and keep net activation below the initiation threshold, leading to a measurable response. In Figure 7B, we show how the P300 increases and force decreases as the hypothetical engagement of inhibitory-control increases. Notably, as the engagement of inhibitory-control increases, force decreases until net activation no longer exceeds initiation-threshold. Once this threshold is reached, the response is completely suppressed. Any further increases in the engagement of inhibitory-control is only reflected by P300, but not motor output (measurable force). In Figure 7C, we present two examples of Successful Inhibitions where there are higher but different levels of inhibitory-control engagement. This would lead to different P300 amplitudes but the same behavioural result. We think that the observation of the binary inhibition success effect over-and-above force in the Anticipatory Timing Task reflects these trials where inhibition was engaged more strongly than required.

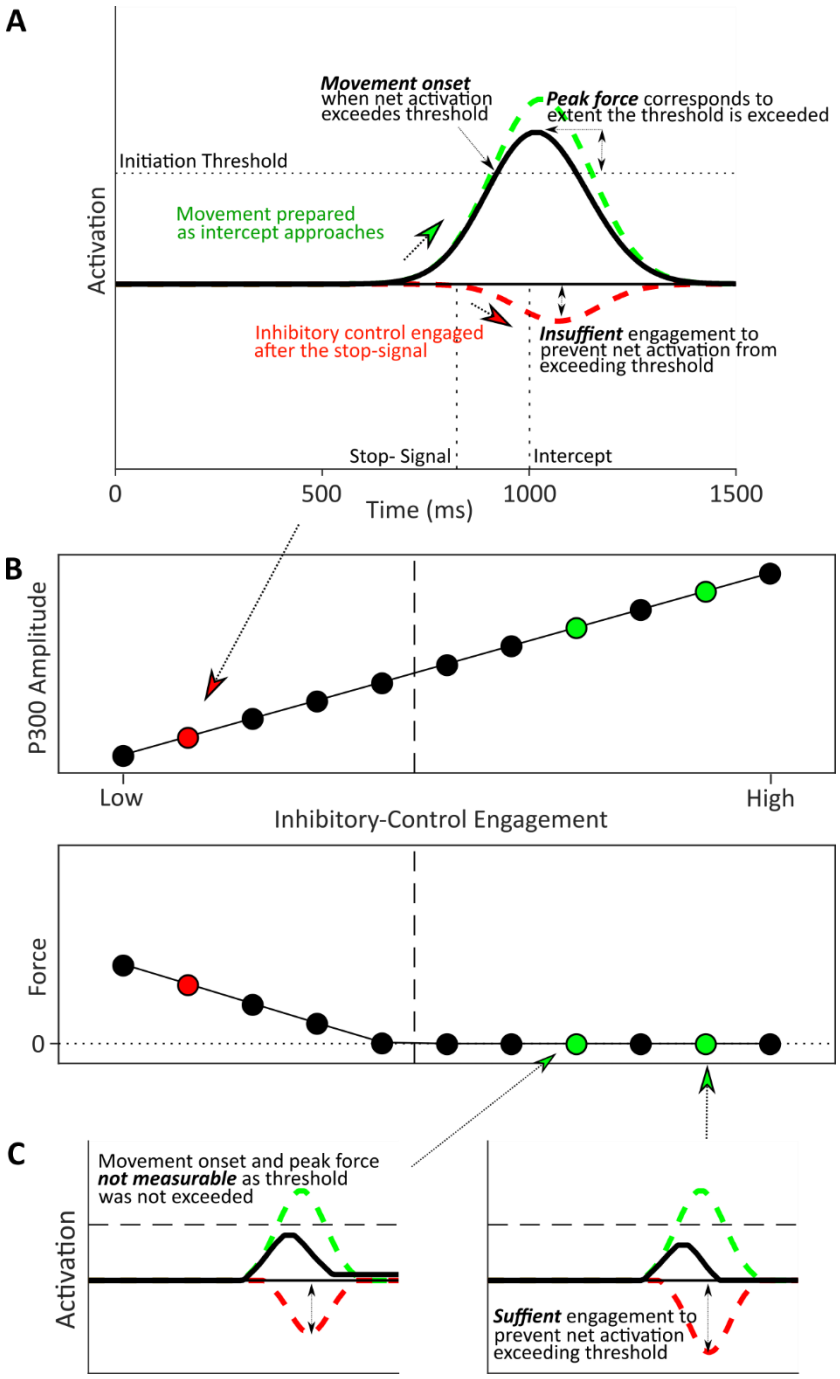

Figure 7. (**A**) *A graphical depiction of the Force Activation Model of Inhibitory-Control for the Anticipatory Timing Task, showing the activity of opposing preparatory (dashed green) and inhibitory processes (dashed red), and their combined signal (net activation, solid black). A response is initiated if net activation crosses the initiation threshold, and its timing and force are determined by the point at and the extent to which the threshold is crossed.* (**B**) *For a given level of response preparation, the model shows the relationship between the*

level of inhibitory-control engagement, P300 amplitude and peak force, and how Failed and Successful Inhibitions manifest. (**C**) Two examples of Successful Inhibitions which differ in their engagement of inhibitory-control, producing different P300 amplitude but not force.

Although we only described changes relating to the inhibitory-control process, it is possible for the amplitude and timing of both preparatory and inhibitory process to vary on a continuum from trial-to-trial as expectancies about whether the upcoming trial will be a Go or Stop trial may fluctuate over the experiment. Given the opposing interaction of two processes, the amount of inhibitory-control required to successfully inhibit the response depends on the engagement level of the preparatory response process.

Compared to other threshold models of inhibitory-control, the use of activation models and the idea that preparatory and inhibitory processes interact has been previously described in other models of inhibitory-control (e.g. Activation-to-threshold model of selective inhibition; MacDonald, McMorland, Stinear, Coxon, & Byblow, 2017; Interacting Horse-Race Model, Boucher et al., 2007). However, the primary difference is that existing models only consider the binary outcome of inhibition (Successful, Failed) and do not explicitly model the force of responses during inhibition failures. In the interacting horse-race model (Boucher et al., 2007), the activation of Go and Stop processes are only modelled until the winning process reaches the decision threshold. It is implied that once the threshold is reached, the following processes are ballistic and cannot be interrupted (i.e. the response is all-or-none). In some accounts of the horse-race model, it has been suggested that if the inhibitory process is completed shortly after the preparatory response process, the inhibitory process is able to modulate the outgoing response, but force is not explicitly specified. The explicit modelling of force of responses in the activation model was

inspired by previous studies using an activation model in the Anticipatory Timing Task to explain vigour and response time effects due to loud acoustic stimulation (Marinovic, de Rugy, Lipp, & Tresilian, 2012; Marinovic, Tresilian, de Rugy, Sidhu, & Riek, 2014; Tresilian & Plooy, 2006). The goal of the current model is not to compete with existing and more developed models of inhibitory-control, but to illustrate how motor-output can be incorporated in future model development.

5. Conclusion

Collectively, the results provide evidence that the P300 may reflect the continuously varying engagement of inhibitory-control, adding to current literature which largely focuses on P300 modulations across binary Failed and Successful Inhibition categories, conceptualising inhibition as an all-or-none process. Our findings have several implications for our current understanding and the future examination of inhibitory-control processing. Firstly, it highlights the utility of the Anticipatory Timing Task because of the control it provides over both the timing of the Stop-signal and expected response time, which allowed for the study of inhibitory-control in a high difficulty setting while maintaining a high level of control over the stimulus-environment. Secondly, it underscores the importance of studying the spectrum of motor outputs and its potential to provide further insights regarding the functional significance of other event-related brain signals (Huster, Schneider, Lavallee, Enriquez-Geppert, & Herrmann, 2017). Lastly, it draws attention to the fact that future models of inhibitory-control need to account for motor output, and not just the presence and absence of the response. Our model offers an extension to the existing frameworks for describing the implementation of inhibition-control over highly prepared motor responses that accounts for motor output.

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