Don't Stop Me Now: Neural Underpinnings of Increased Impulsivity to Temporally Predictable Events

Inga Korolczuk[1,2,3], Boris Burle[1], Jennifer T. Coull[1], Halszka Ogińska[2], Michał Ociepka[2], Magdalena Senderecka[2]*, and Kamila Śmigasiewicz[1]*

Abstract

■ Although the benefit of temporal predictability for behavior is long-established, recent studies provide evidence that knowing when an important event will occur comes at the cost of greater impulsivity. Here, we investigated the neural basis of inhibiting actions to temporally predictable targets using an EEG–EMG method. In our temporally cued version of the stop-signal paradigm (two-choice task), participants used temporal information delivered by a symbolic cue to speed their responses to the target. In a quarter of the trials, an auditory signal indicated that participants had to inhibit their actions. Behavioral results showed that although temporal cues speeded RTs, they also impaired the ability to stop actions as indexed by longer stop-signal reaction time. In line with behavioral benefits of temporal predictability, EEG data demonstrated that acting at temporally predictable moments facilitated response selection at the cortical level (reduced frontocentral negativity just before the response). Likewise, activity of the motor cortex involved in suppression of incorrect response hand was stronger for temporally predictable events. Thus, by keeping an incorrect response in check, temporal predictability likely enabled faster implementation of the correct response. Importantly, there was no effect of temporal cues on the EMG-derived index of online, within-trial inhibition of subthreshold impulses. This result shows that although participants were more prone to execute a fast response to temporally predictable targets, their inhibitory control was, in fact, unaffected by temporal cues. Altogether, our results demonstrate that greater impulsivity when responding to temporally predictable events is paralleled by enhanced neural motor processes involved in response selection and implementation rather than impaired inhibitory control. ■

INTRODUCTION

In the temporal prediction literature, the behavioral benefits of acting to temporally predictable events are usually emphasized. The vast majority of studies have investigated the effects of temporal predictability using simple detection or discrimination tasks and have repeatedly demonstrated that responses are faster and more accurate when the time of target onset could be predicted in advance (Nobre & van Ede, 2018; Correa, Lupiáñez, & Tudela, 2006; Coull & Nobre, 1998). However, temporal predictability does not always serve an adaptive function. In fact, when an already initiated response needs to be inhibited or when responses require conflict resolution, temporal predictability might actually be detrimental to performance (Korolczuk, Burle, & Coull, 2018; Correa, Cappucci, Nobre, & Lupiáñez, 2010). For example, behavioral studies have shown that when participants knew when a target would appear, both correct and incorrect responses were more likely to be co-activated, making it harder to resolve any response conflict (Menceloglu, Suzuki, & Song, 2021). Online recordings of muscle activity have further demonstrated that whenever a temporally predictable target induces potentially conflicting responses, there were a greater number of fast activations of the incorrect response muscle. These erroneous muscle activations included both fully executed suprathreshold responses as well as subthreshold response impulses ("twitches"; Korolczuk, Burle, Coull, & Smigasiewicz, 2020). However, temporal predictability did not affect the ability to successfully suppress subthreshold erroneous twitches, allowing the participant to eventually execute the correct response. In other words, acting to temporally predictable yet conflicting events exacerbates the urge to act impulsively but does not weaken the corrective inhibitory processes.

In a recent EEG study, we identified the neural bases of the costs and benefits of temporal predictability for conflicting actions (Korolczuk, Burle, Coull, & Śmigasiewicz, 2022). By investigating the cortical markers of correct response activation and incorrect response inhibition before the response had even been initiated, we found that an EEG marker of incorrect response inhibition (Burle, Vidal, Tandonnet, & Hasbroucq, 2004; Vidal, Grapperon, Bonnet, & Hasbroucq, 2003) was differentially modulated depending on response choice complexity. For conflicting responses, this inhibitory activity was weaker for temporally predictable targets, which suggests that the behavioral costs of temporal predictability (e.g., more fast errors) are because of insufficient suppression

[1]Aix-Marseille University & CNRS, France, [2]Jagiellonian University, Kraków, Poland, [3]Medical University of Lublin, Poland
*Shared last authorship.

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of the incorrect action. Strikingly, activity in the very same inhibitory circuit was stronger when temporally predictable targets induced nonconflicting responses, indicating that the behavioral benefits of temporal predictability (e.g., speeded RT) are achieved by keeping an incorrect response in check. Thus, in the context of competing response alternatives, temporal predictability utilizes a parsimonious cortical inhibitory mechanism that operates right before the response is even initiated.

Yet, efficient adaptation not only requires suppression of the inappropriate action in favor of more goal-directed ones, but might also require suppression of any action at all (Ridderinkhof, Forstmann, Wylie, Burle, & van den Wildenberg, 2011; Mostofsky & Simmonds, 2008). Indeed, inhibiting the action in general (i.e., global response inhibition) has been demonstrated to be conceptually and empirically different than to suppressing a competing response alternative (Duque, Greenhouse, Labruna, & Ivry, 2017; Mostofsky & Simmonds, 2008; Verbruggen & Logan, 2008; Burle et al., 2004). First, suppression of the competing motor response is usually measured with stimulus–response incompatibility tasks, such as the Simon, Stroop, and flanker tasks. All of them require the ability to inhibit the processing of irrelevant information and to select the correct response (Beppi, Violante, Hampshire, Grossman, & Sandrone, 2020; Ridderinkhof et al., 2011). In contrast, global response inhibition is most frequently studied using the stop signal task. The task requires the ability to attend stop signals and to efficiently counteract the preplanned motor response (Verbruggen & Logan, 2008). All these paradigms undoubtedly share some common features, but they also tap into different subprocesses of response inhibition. Second, a recent meta-analysis of brain imaging studies of action control has revealed that selective response inhibition recruits distinct anatomical substrates than global response inhibition (Zhang, Geng, & Lee, 2017). More precisely, suppression of the competing motor response, relative to action withholding/cancellation, elicits stronger activation in the left supplementary area, precentral gyrus, and superior parietal gyrus. This suggests its close association with the response selection process. In contrast, action withholding/cancellation relies more pronouncedly on the fronto-striatal network, which implies it as a late phase of inhibitory process. Third, although psychopharmacological studies on different forms of inhibition are scarce, an emerging body of research suggests that inhibitory processes can be modulated by different neurotransmitter systems (Lamar et al., 2009; Eagle, Bari, & Robbins, 2008). More specifically, selective response inhibition appears more sensitive to serotonin, whereas action cancellation to noradrenaline (apart from dopamine).

As already mentioned, this more global form of inhibition is often studied with the so-called stop-signal paradigm (Verbruggen & Logan, 2008; Logan, Cowan, & Davis, 1984), in which participants perform a discrimination task and, in some of the trials, an auditory signal is presented to inform participants that they need to inhibit their responses completely (i.e., stop trials). The estimated time taken to stop a response, termed the stop-signal reaction time (SSRT), provides an index of the ability to stop actions that are no longer appropriate in a given context. In a recent behavioral study investigating the effects of temporal predictability on the ability to suppress inappropriate actions, we showed that SSRT was prolonged when participants knew in advance the time of target occurrence. In parallel, temporal cues led to faster RT (Korolczuk et al., 2018). Such results suggest that temporal predictability increases overall response activation, which leads to excessive response readiness, which might, in turn, indirectly hinder the ability to inhibit the response. However, the exact neural mechanisms that could explain the detrimental effects of temporal predictability on stopping unwanted actions remain unknown.

The goal of the current study was to examine the peripheral and cortical bases of impulsivity triggered by active prediction of the onset time of events. Importantly, we were interested in understanding how temporal predictability affects online action control occurring within the time-course of the action (after target presentation), rather than anticipatory action regulation (occurring before target presentation). These two aspects of action control, often used interchangeably, are distinct in terms of their neural bases, dynamics, and other factors like individual differences or task characteristics (Ridderinkhof et al., 2011). The vast majority of previous studies examining the neural bases of temporal predictability used simple RT tasks, in which participants could prepare their response in advance (e.g., Volberg & Thomaschke, 2017; Van Elswijk, Kleine, Overeem, & Stegeman, 2007; Miniussi, Wilding, Coull, & Nobre, 1999). In contrast, our temporally cued version of the stop-signal task allowed us to study the modulatory mechanism of temporal prediction involved in choosing the correct action and stopping responses that are no longer appropriate. Specifically, in this EEG–EMG investigation, we studied several action control mechanisms involved in both the selection and implementation of responses as well as inhibiting actions in general.

First, to reveal the effects of temporal predictability on neural response selection, we analyzed an electrophysiological marker of response selection, known as the N-40 component (Carbonnell et al., 2013; Vidal, Burle, Grapperon, & Hasbroucq, 2011; Vidal et al., 2003). This frontomedial negative activity peaks around 40 msec before EMG onset and is modulated by the difficulty of response choice demands (Burle, van den Wildenberg, Spieser, & Ridderinkhof, 2016; Carbonnell et al., 2013). More specifically, N-40 amplitude is greater for more difficult responses. Although previous neurophysiological data revealed no effect of temporal cues on the N-40 component in a Simon task (Korolczuk et al., 2022), we sought to further clarify whether temporal predictability might affect cortical response selection in the context of a bimanual choice task.

EMG recording allowed us also to measure peripheral markers of response activation, as indexed by EMG bursts in the muscles involved in the response. In turn, EEG additionally allowed us to study central markers of activation of the correct response hand and inhibition of the incorrect response hand—in choice RT tasks, this "activation/inhibition" pattern is observed over primary motor cortices (M1). Shortly before EMG onset, a negative wave develops over the motor cortex contralateral to the response agonist (activation of the correct response) and a positive wave is observed over the motor cortex ipsilateral to the response agonist (Vidal et al., 2003, 2011) that reflects inhibition of the incorrect response (Burle, Possamaï, Vidal, Bonnet, & Hasbroucq, 2002; Hasbroucq, Akamatsu, Burle, Bonnet, & Possamaï, 2000; see Burle et al., 2004, for a discussion). Importantly, the "activation/inhibition" pattern over the M1 cannot be equated to the lateralized readiness potential (LRP), a component known to reflect motor preparation. The LRP is calculated as a difference between the left and right motor areas of the brain (Gratton, Coles, Sirevaag, Eriksen, & Donchin, 1988), and thus does not allow the activity of the contralateral and ipsilateral motor cortex to be separated (Vidal et al., 2003; Eimer, 1999; Gratton, 1998). Moreover, the LRP is based on the monopolar data and so the activities recorded may stem from nonmotor remote areas making the motor interpretation of the LRP questionable. Instead, the "activation/inhibition" pattern is based on the current source density (CSD)-transformed signal (through Laplacian estimation). The CSD increases the spatial resolution of the EEG signal as if electrodes were placed on the surface of the cortex, and thus allows the sources of the signal to be successfully segregated (Kayser & Tenke, 2015; Gevins, 1989). In addition, by separating the activity of distinct neural generators, the CSD also improves the temporal resolution of the signal of interest (Burle et al., 2015; Law, Rohrbaugh, Adams, & Eckardt, 1993). In terms of the timing of the "activation/inhibition" pattern, the activities over M1 follow the N-40 negativity (Burle et al., 2016; Vidal et al., 2003), which would indicate the hierarchical organization of these areas involved in motor control. In other words, the M1 "activation/inhibition" pattern would be situated downstream of the SMA within a motor command hierarchy (Orgogozo & Larsen, 1979). Alternatively, the SMA and motor cortex might work in parallel during response selection (Woolsey et al., 1952). In this investigation, we aimed to examine the role of cortical selection of the response as well as motor activation and inhibition when acting to temporally predictable events.

EMG recordings can enhance the temporal resolution of cortical markers of interest by allowing us to identify brain activity right before the motor response is even initiated. Importantly, EMG can also be effectively utilized to measure motor processes directly at the peripheral level. Indeed, overt errors are only the tip of the iceberg and it is critical to also study covert indices of impulsive behavior. In the context of the stop-signal task, one can quantify subthreshold muscle activations in the stop trials, also called "partial responses," which have been suppressed and are thus not detectable in behavioral investigations (Van Boxtel, Van der Molen, Jennings, & Brunia, 2001; De Jong, Coles, Logan, & Gratton, 1990). Besides revealing covert response activations, such partial responses can be also used to reveal the correction processes directly at the peripheral level by computing the partial response correction ratio. It is calculated as the proportion of stop trials containing a partial response (i.e., a subthreshold activation of the correct hand) compared with all successfully stopped trials (including a partial EMG response or not). The correction ratio allows one to measure how often initial impulses to act are subsequently suppressed. Here, we aimed to investigate whether the increased impulsivity induced by temporal cues is indeed because of an impaired ability to suppress these partial responses by measuring the online inhibitory mechanisms that act to stop covert subthreshold impulses.

We formulated the following hypotheses. If temporal predictability leads to greater impulsivity by impairing global inhibitory processes, we would expect to see its effects on the direct index of the within-trial inhibition of subthreshold EMG activations that are no longer appropriate. Specifically, we would predict a lower partial response correction ratio in temporal versus neutral condition. Alternatively, the detrimental effects of temporal predictability on stopping impulsive responses could originate from an increased urge to act. In the context of a discrimination task, in which one cannot prepare a response in advance, the facilitative effects of temporal cues would be observed primarily within the time-course of the action (after target presentation). Such motor facilitation could stem from an easier selection and/or execution of the response. We would thus predict that at the brain level, the effects of temporal predictability would be reflected in easier response selection, empirically observed as attenuated N-40 activity. We would also predict that temporal predictability would affect execution of the selected response. Thus, right before response initiation, temporal predictability would either lead to increased activation of the correct response agonist and/or stronger suppression of the incorrect response agonist, resulting in less interference from the incorrect hand and, therefore, faster implementation of the correct action. These mechanisms would allow for rapid responding at precise moments in time but might increase the difficulty of stopping actions in general.

METHODS

Participants

We tested thirty-six participants (M_{age} = 22.1 years, SD = 2.8 years, 27 women) in the study approved by the

research ethics committee at the Institute of Applied Psychology at the Jagiellonian University (Kraków, Poland). The sample size was based on previous work (Korolczuk et al., 2018, 2022). All participants had normal or corrected-to-normal vision and no history of neurological or psychiatric disorders. All participants gave written informed consent. Data from seven participants were discarded from the analysis because of excessive artifacts (±2 *SD*s of the group average) in EEG recordings (two individuals) or noisy or "flat" EMG recordings (five individuals). The final sample consisted of 29 participants.

Experimental Task

Participants performed a temporally cued version of the stop-signal task (Korolczuk et al., 2018; Figure 1) controlled by PsychoPy (Peirce et al., 2019; Peirce, 2007). All stimuli were black, presented centrally on a gray background. Two concentric circles (1° eccentricity) were always present in the center of the screen (as a background display). Targets ("×" or "+") were 1° × 1° stimuli and appeared within the background display.

There were two cue conditions. In the temporal (T) condition, thickening of the line forming the smaller (inner) circle informed participants that a target would occur after a short delay or "foreperiod" (FP; 600 msec), whereas thickening of the larger (outer) circle informed participants that a target would occur after a longer interval (1400 msec). Temporal cues were always valid. In the neutral (N) condition, the lines forming both circles were thickened, thereby providing no temporally precise information, and targets occurred randomly after either short or long FPs. The cue (T or N) was presented for 500 msec, followed by presentation of the background display for 600 msec (short FP) or 1400 msec (long FP) and the target for 1000 msec.

Participants were encouraged to use the information provided by the temporal cue to speed their RTs to targets ("×" or "+"). In the neutral condition, they were encouraged to respond as quickly as possible to the targets although they could not predict when it would appear. Half of the participants responded with their left thumb to "×" and with their right thumb to "+" on a standard QWERTY keyboard (left "ctrl" and right "+" keys). These target–response pairings were reversed for the remaining participants. The target appeared within the circles and remained there for 1000 msec. During this time, participants gave their lateralized response according to target shape. The trial ended with presentation of the background display for a duration between 1000 and 1500 msec (random jitter of 100 msec).

In 25% of trials, an auditory stop signal (750 Hz, 50 msec) was presented a very short time after the target appeared, instructing participants to withhold their response (stop trials). There were never two stop-signal trials presented consecutively. The stop-signal delay (SSD) between target onset and the auditory beep was initially set at 100 msec and was adjusted continually using a staircase procedure. If the participant successfully suppressed their response, the SSD increased by 50 msec on the next stop trial. In turn, if the participant failed to inhibit their response, the SSD decreased by 50 msec on the next stop trial. These adjustments were made separately for temporal and neutral cues, and for short and long FPs, thus allowing the effects of cue and FP to be effectively disentangled. The SSD ranged from 50 to 400 msec across trials with a jitter of 50 msec.

The two cue conditions (T and N) were presented in two consecutive blocks in an alternating manner

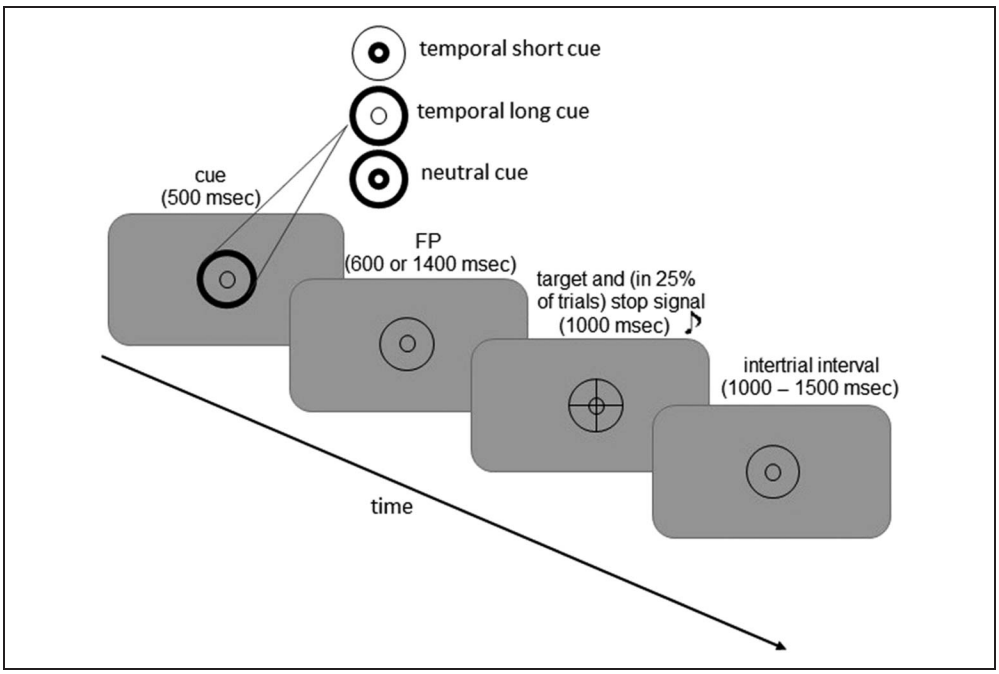

Figure 1. Temporally cued version of the stop-signal task. A cue (500 msec) either predicted (temporal condition) or not (neutral condition) the time of target onset. A background display was then presented for one of two FPs: short (600 msec) or long (1400 msec). Then, the target ("×" or "+") appeared centrally for 1000 msec during which participants gave their lateralized response depending on the shape of the target. In 25% of trials, an auditory stop signal was presented right after the target with a variable SSD, informing participants that they had to withhold their response. The intertrial interval was randomized between 1000 and 1500 msec.

(TT-NN-TT-NN or NN-TT-NN-TT), which allowed us to balance training effects and fatigue across the two cuing conditions. There were 128 trials per block, which resulted in 1024 trials altogether. In each block, the proportion of short and long FPs was 50:50, and the proportion of go to stop trials was 75:25. Thus, there were 192 trials for each of the four combinations of cue and FP in the go trials, and 64 trials for each of the four combinations of cue and FP in the stop trials. During an initial training session, participants performed 30 temporal and 30 neutral trials to familiarize themselves with the task.

EMG and EEG Recordings

We recorded electrophysiological data from 64 Ag/AgCl active pre-amplified electrodes (Biosemi Inc.) at a rate of 1024 Hz (analogue bandwidth limit: from direct current to 268 Hz, −3 dB at one fifth of the sampling rate). The electrodes were positioned in accordance with the extended 10–20 convention. Two electrodes lateral to the external canthi were used to record the EOG and measure horizontal eye movements. To measure vertical eye movements and blinks, we recorded activity from an electrode beneath the left eye and subtracted this activity from the FP1 electrode. In addition, we recorded the bipolar electromyographic activity of the flexor pollicis brevis from each hand also using Ag/AgCl active electrodes positioned 2 cm apart on the thenar eminence.

EMG and EEG Preprocessing

All the preprocessing steps and analysis of EMG and EEG data were conducted using BrainVision Analyzer 2.0 (Brain Products GmbH), MNE Python toolbox (Gramfort et al., 2013), and customized Python scripts (www.python.org).

To detect the onset and offset of EMG activity, we used a customized Python program (Spieser & Burle, 2022),[1] which is based on a combination of two algorithms: "integrated profile" (Liu & Liu, 2016; Santello & McDonagh, 1998) and a variance comparison (Hodges & Bui, 1996). Then, a naive observer, unaware of the trial type, manually corrected (if needed) the EMG onsets detected by the script. Based on this procedure, we distinguished and analyzed four types of trials: (1) pure correct go trials (i.e., go trials with a single suprathreshold EMG activation for the correct hand), (2) failed stop trials (i.e., stop trials with an overt behavioral response and a single suprathreshold EMG activation for the correct hand), (3) partial response stop trials (i.e., stop trials without an overt behavioral response but with a single subthreshold EMG activation after a stop signal for the correct hand), and (4) pure stop trials (i.e., stop trials without EMG activation). Partial response stop trials in which subthreshold EMG activity started before and finished after the stop signal were not analyzed because of an insufficient number of trials. Similarly, partial responses made with the incorrect hand were not analyzed because of an insufficient number of trials.

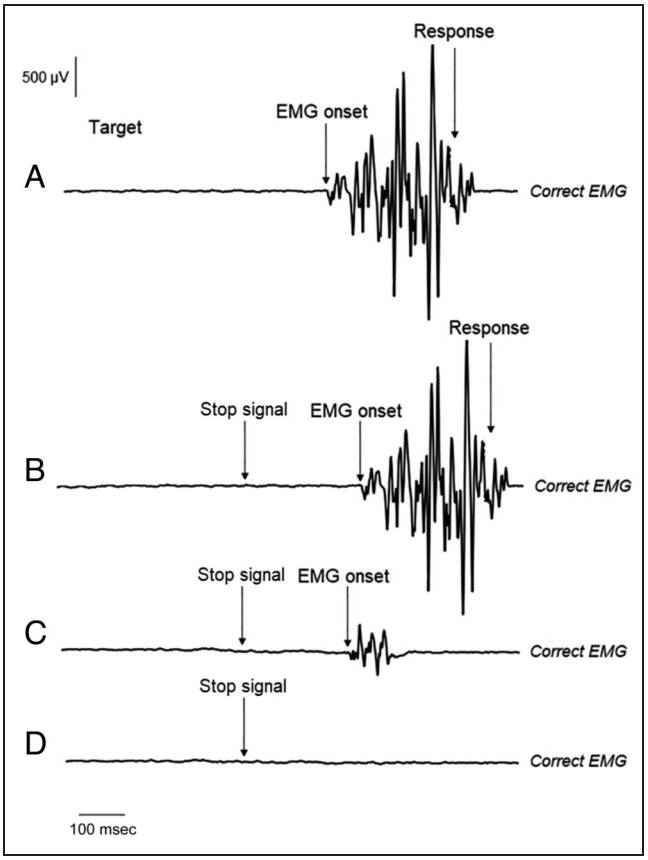

Figure 2. EMG trial types. (A) A pure correct response in a go trial. The EMG activity appeared only in the correct hand and resulted in an overt correct response. (B) A failed stop trial. The EMG activity appeared only in the correct hand and resulted in an overt unsuccessfully stopped response. (C) A partial response stop trial. The subthreshold EMG activity appeared only in the correct hand stop trials without an overt behavioral response. (D) A successfully stopped trial. No EMG activity was observed.

Figure 2 presents an example of each trial type used in the analysis.

The EEG data were rereferenced to the average of the right and left mastoids, and the signal was band-pass filtered between 0.01 and 100 Hz using a second-order infinite impulse response Butterworth digital filter (slope: 12 dB/Oct). The MNE Python toolbox (Gramfort et al., 2013; Uusitalo & Ilmoniemi, 1997) was used to correct ocular artifacts. Data were then visually inspected for any remaining noise and artifacts. All electrodes were rejected even if only a small local artifact was present to allow for subsequent use of the CSD computation, which is particularly sensitive to local artifacts.

Data Analysis

Behavioral Data Analysis

The mean RT from correct go trials was calculated separately for each cue (temporal/neutral) and FP (short/long) condition. Similarly, the error rate in go trials (3%) was calculated for cue and FP conditions. The omission rate

(3.8%) was not further analyzed. The SSD was quantified for each cue and FP condition as the average delay between the target onset and the auditory stop signal onset for both successful and failed stop trials. The SSRT (the mean time to inhibit a response) was estimated using the integration method (Logan, 1994). First, the RTs from correct-only trials were rank ordered for each participant and for each of the four conditions (temporal/neutral cue; short/long FP). Then, the number of all responses in a given condition was multiplied by the probability of responding to a stop signal at a given delay [p(respond|signal)] to produce the critical RT. Subtracting the SSD from this RT provides an estimate of the SSRT. Importantly, this integration method of calculating the SSRT does not require the assumption of 50% inhibition (i.e., participants inhibit their responses in approximately half of stop trials), and so it provides a reliable measure of the ability to inhibit actions even when participants' probability of responding to a stop signal deviates from 50% (Logan, 1994).

To measure the effects of temporal predictability on performance, we conducted a series of two-way repeated-measures ANOVA involving Cue (temporal, neutral) and FP (short, long). We examined the effects of temporal predictability on go trial RT, go trial error rate, SSRT, SSD, SRRT (signal-response RT, i.e., RTs on failed stop trials), and [p(respond|signal)]. Based on our previous findings (Korolczuk et al., 2018), we expected to observe faster RT paralleled by longer SSRT in temporal versus neutral trials. Along with shorter SSD after temporal rather than neutral cues, these results would indicate greater impulsivity to temporally predictable targets. We further predicted that these findings would be strongest in short FP trials.

EMG Data Analysis

To investigate the covert mechanisms for inhibiting actions to temporally predictable targets, we measured the partial response rate and the partial response correction ratio (the equivalent of the correction ratio in choice RT tasks) in stop trials. The partial response was computed as the proportion of stop trials containing a partial response (i.e., a subthreshold activation of the correct hand) to all successfully stopped trials. The partial response correction ratio was computed by dividing the number of trials with partial responses by the overall number of incorrect activation trials (both failed stop trials and partial response trials). It indexes the ability to inhibit a response after it has been initiated.

Our paradigm included only two FPs and no catch trials. Therefore, if a target had not been presented at the short FP in the neutral condition, the participant knew it would necessarily have to appear at the long FP (Coull, Frith, Büchel, & Nobre, 2000). This is because of the influence of the hazard function, which is the increasing conditional probability of target appearance over time given that it has not already appeared (Luce, 1986; Durup & Requin, 1970; Elithorn & Lawrence, 1955). Because targets presented at the long FP were therefore 100% predictable in neutral as well as temporal conditions, temporal and neutral cues induced differential levels of temporal predictability at the short FP only. Therefore, the effects of temporal cueing on partial response rate and the correction ratio were evaluated by paired-samples *t* tests comparing temporal and neutral conditions at the short FP only (van Ede, Rohenkohl, Gould, & Nobre, 2020; Griffin, Miniussi, & Nobre, 2002).

EEG Data Analysis

The analysis of EEG data was conducted on short FP trials only. In go trials, we first analyzed the effects of temporal predictability on the frontocentral negativity known as the N-40 component, which has been shown to vary with the difficulty in response selection (Carbonnell et al., 2013; Vidal et al., 2003, 2011). Activity over the FCz electrode was segmented from −500 msec to 500 msec time-locked to EMG onset, and baseline correction (from −500 msec to −300 msec time-locked to EMG onset) was performed. Next, data for individual participants were averaged for each cue condition (temporal/neutral) for short FP trials only. We then performed the CSD computation using BrainVision Analyzer 2.0. The signal was interpolated using the spherical spline interpolation procedure (Perrin, Pernier, & Bertrand, 1989), setting the degree of spline to three. The second derivatives in two dimensions of space were calculated with a maximum of 15° for the Legendre polynomial. With the assumption of a head radius of 10 cm, the unit of EEG activity was $\mu V/cm^2$. Individual participants' peak values (i.e., the most negative values) were then extracted for the two cueing conditions, in a time window from −100 msec to 0 msec relative to the onset of the EMG. The statistical evaluation of these peak values was performed using paired-samples *t* tests (temporal short vs. neutral short). In addition, we conducted a between-participants Spearman's rho correlation analysis to explore the relationship between N-40 negativity and behavioral performance across participants. More specifically, we sought to determine the relationship between N-40 activity in temporal relative to neutral conditions (T-N) and the RT benefit of temporal cues (N-T).

To investigate whether temporal predictability modulated the motor cortex involved in activating the correct hand and inhibiting the incorrect one in go trials, we segmented the data separately for right- and left-hand responses in a time window from −500 msec to 500 msec time-locked to the EMG onset. This was done separately for the two cue conditions (temporal/neutral) for short FP trials only. Then, the averaged and CSD-transformed signal data were "collapsed" across the two hemispheres: Data from left hemisphere C3 electrodes during (contralateral) right-hand responses were averaged with data from right hemisphere C4 electrodes during (contralateral) left-hand responses (weighted average) to reflect the activity of the cortex involved in producing the correct

response. These averaged contralateral responses were attributed to the C3 electrode for visualization purposes. Similarly, data from left hemisphere C3 electrodes during (ipsilateral) left-hand responses were averaged with data from right hemisphere C4 electrodes during (ipsilateral) right-hand responses (weighted average) to reflect the activity of the cortex involved in producing an incorrect response. These averaged ipsilateral responses were attributed to the C4 electrode for visualization purposes. We analyzed activity shortly preceding muscle activation in a time window from −100 msec to 50 msec relative to the EMG onset. To obtain a baseline-independent index of phasic activity, we calculated the slopes of neural activity with a customized Python script by fitting a linear regression to the data in the time window of interest. Finally, statistical analysis of the slopes was conducted using paired-samples *t* tests (temporal short vs. neutral short). We also performed a Spearman's rho correlation analysis to test the relationship between ipsilateral motor cortex inhibition and behavioral performance across participants. More specifically, we investigated the relationship between the inhibitory motor cortex activity in temporal relative to neutral conditions (T-N) and the RT benefit of temporal cues (N-T/N). For EMG and EEG analyses, one-tailed tests were used whenever the directional hypotheses were drawn based on our previous findings. For the remaining contrasts, two-tailed tests were implemented.

RESULTS

Behavioral Results

Go Trials

We first aimed to establish whether participants used temporal predictions to speed their motor responses by analyzing RTs in go trials. A two-way repeated-measures ANOVA comprising Cue (temporal, neutral) and FP (short, long) revealed a main effect of Cue, $F(1, 28) = 9.76$, $p = .004$, $\eta_p^2 = .26$, and a main effect of FP, $F(1, 28) = 5.25$, $p = .03$, $\eta_p^2 = .16$, which were further qualified by a significant Cue × FP interaction, $F(1, 28) = 26.02$, $p < .001$, $\eta_p^2 = .48$. Post hoc comparisons showed the typical pattern of results: RTs were faster after temporal rather than neutral cues in short FP trials ($p < .001$), but not in long FP trials ($p = .206$; Figure 3). This replicates previous findings (Correa et al., 2006; Nobre, 2001; Coull & Nobre, 1998) and confirms that effects of temporal cueing on response speed are most pronounced at the short FP. Participants made more errors in go trials after temporal than neutral cues, $F(1, 28) = 11.68$, $p = .002$, $\eta_p^2 = .29$.

Stop Trials

Replicating our previous results (Korolczuk et al., 2018), we found that temporal cueing made it harder for participants to inhibit their actions. The estimated RT to stop an already activated response (SSRT) was longer in temporal versus neutral trials, $F(1, 28) = 5.43$, $p = .027$, $\eta_p^2 = .16$. Again, there was a Cue × FP interaction, $F(1, 28) = 4.61$, $p = .04$, $\eta_p^2 = .14$. Temporal cueing led to longer SSRT in short FP trials ($p = .004$), but not long FP trials ($p = .227$). In parallel, the analysis of the SSD revealed a main effect of Cue, $F(1, 28) = 9.61$, $p = .004$, $\eta_p^2 = .26$, and FP, $F(1, 28) = 4.99$, $p = .034$, $\eta_p^2 = .15$, which was explained by a significant Cue × FP interaction, $F(1, 28) = 8.86$, $p = .006$, $\eta_p^2 = .24$. The SSD was shorter after temporal cues only in short FP trials ($p < .001$), whereas long FP trials cancelled out this effect ($p = .178$). The analysis of the RT in failed stop trials further revealed main effects of Cue, $F(1, 28) = 9.22$, $p = .005$, $\eta_p^2 = .25$, and FP, $F(1, 28) = 5.26$, $p = .029$, $\eta_p^2 = .16$. As previously, these main effects were qualified by a significant Cue × FP interaction, $F(1, 28) = 6.73$, $p = .015$, $\eta_p^2 = .19$. RT in failed stop trials (SRRT) was

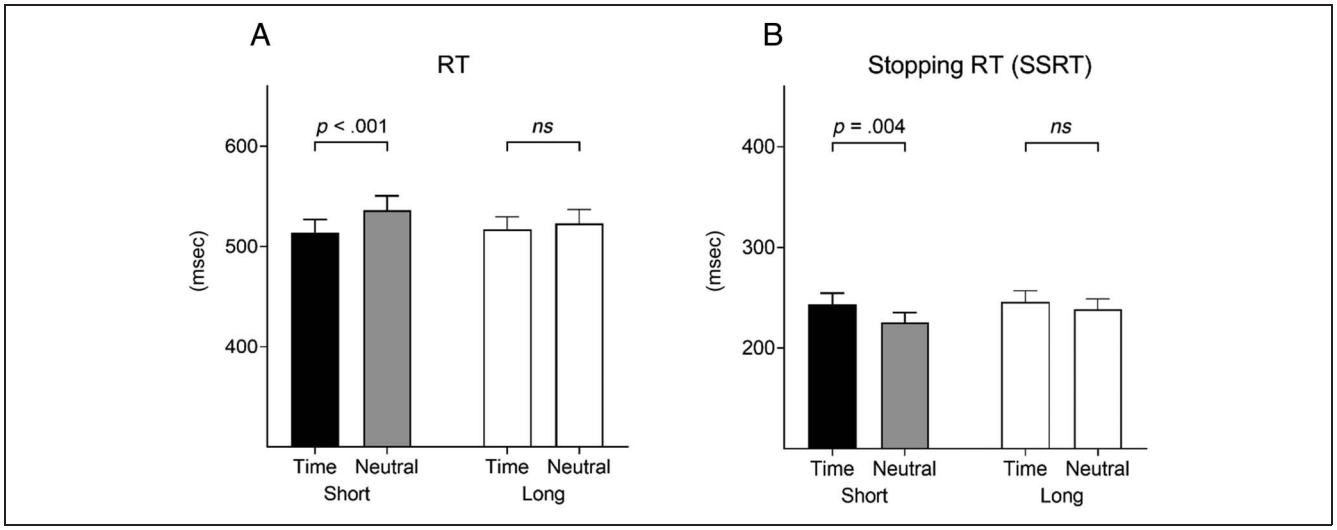

Figure 3. The effects of temporal cueing on RT in go trials and stopping RT (SSRT) in stop trials. (A) Temporal cueing speeded RTs in go trials. (B) In parallel, temporal cues led to slower SSRT in stop trials. As expected, these effects were most pronounced in short FP condition but not long FP condition. Error bars reflect standard errors.

Table 1. Behavioral and EMG Results

Measure		*Time*	*Neutral*
Behavioral	Go RT	514 (13)	536 (14)
	SSRT	243 (11)	225 (10)
	SSD	247 (16)	275 (15)
	SRRT	570 (15)	597 (13)
EMG	% Partial response (stop trials)	22.4 (2.0)	21.2 (1.8)
	Partial response correction (%)	31.2 (2.8)	29.7 (2.3)

Behavioral measures include: go RT, SSRT, SSD, and SRRT. EMG measures include: percentage of partial response and partial response correction rate in stop trials. Indices are provided with standard errors (msec) for short FP trials.

shorter in the temporal cue condition than in the neutral condition in short FP trials ($p < .001$) but not in long FP trials ($p = .131$). Finally, the analysis of the mean percentage of the failure to stop a response [p(respond|signal)] showed main effects of Cue, $F(1, 28) = 6.06$, $p = .02$, $\eta_p^2 = .18$, and FP, $F(1, 28) = 5.55$, $p = .026$, $\eta_p^2 = .17$. Again, these effect were explained by a Cue × FP interaction, $F(1, 28) = 5.66$, $p = .024$, $\eta_p^2 = .17$. The percentage of failures to stop a response was higher for the temporal versus neutral cue condition at the short FP ($p = .003$), but not at the long FP ($p = .209$).

Overall, the consistent pattern of Cue × FP interactions confirms that the differential effects of temporal predictability can be measured at the short FP only. Therefore, in all subsequent EMG and EEG analyses, we examined the effects of temporal cueing on short FP trials only. More importantly, behavioral results revealed a complementary influence of temporal predictability in go versus stop trials. Although temporal cueing facilitated responding as demonstrated by faster RTs in go trials, it also led to greater impulsivity as revealed by slower SSRT in stop trials (Figure 3).

EMG Results

Partial Response Rate

Table 1 shows the effects of temporal predictability on EMG-derived measures. The analysis of the partial response rate showed that on approximately 22% of successfully stopped trials, participants emitted a subthreshold muscle activation in the correct response hand that was subsequently suppressed. However, temporal predictability did not affect the number of these activations, $t(28) = 0.61$, $p = .28$, one-tailed, Cohen's $d = 0.11$. Given that we have previously shown that temporal cues led to a greater likelihood of subthreshold muscle activations that were later inhibited in the context of the Simon conflict task (see Korolczuk et al., 2020), we ran an additional Bayesian paired-samples t test, to interpret the current null effect more confidently. A BF01 (i.e., an exclusion BF,

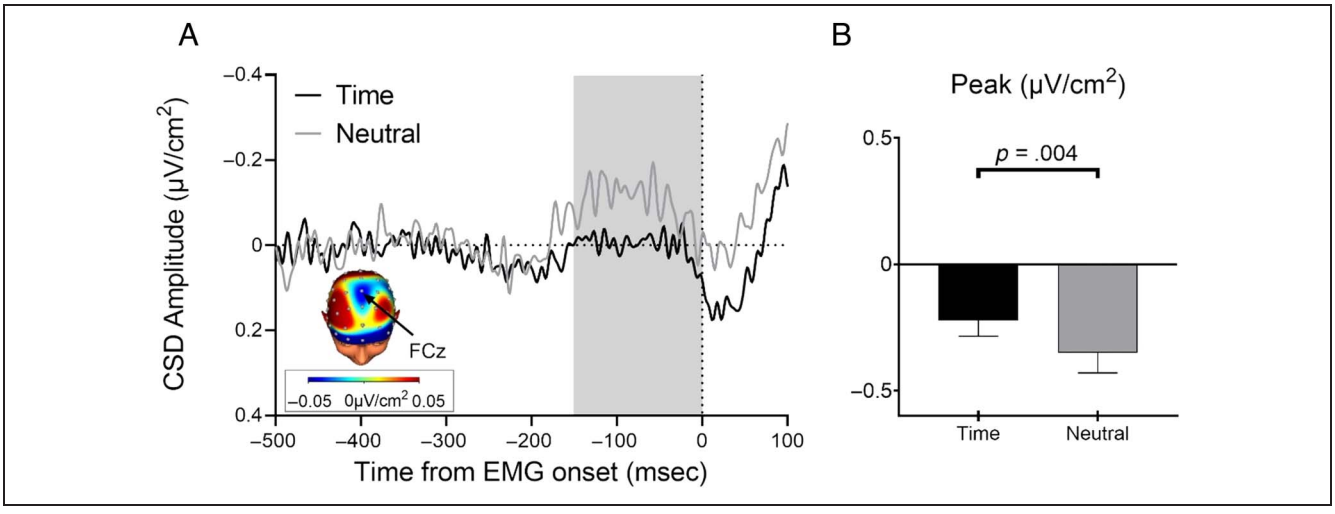

Figure 4. The frontocentral negativity indexing response selection (i.e., N-40 component) in go trials, CSD-transformed, time-locked to EMG onset. (A) The N-40 component was less pronounced for the temporal cue condition (black) than the neutral cue condition (gray), indicating that temporal predictability made it easier to select a response. Topography (CSD-transformed) was recorded over the FCz electrode. (B) The statistical analysis of the peak revealed a significant Cue effect.

indicating the probability ratio between H0 and H1 models) was 4.28, which indicated that there was substantial evidence for an absence of effect of temporal predictability on partial response rate.

Partial Response Correction Ratio

To examine whether temporal cues impaired the ability to suppress an already initiated response (i.e., partial response) in stop trials, we compared the partial response correction rate in temporal and neutral conditions. Importantly, and in line with our previous results (see Korolczuk et al., 2020), there was no difference between the two cue conditions, $t(28) = 0.53$, $p = .60$, two-tailed, Cohen's $d = 0.1$. To determine the evidence in favor of this null effect, we also conducted a Bayesian paired-samples t test. A BF01 was 4.45, which indicated that there was substantial evidence for the lack of an effect of temporal cueing on the partial response correction ratio.

Altogether, the EMG findings indicate that although temporal cueing makes it more difficult to stop a response by speeding response initiation, it does not impair the ability to interrupt a response once it has been initiated.

EEG Results

Response Selection

To examine the effects of temporal predictability on response selection, we measured the frontocentral negative activity (N-40 component), which occurs shortly before EMG onset in choice RT tasks. The N-40 has been found to be more pronounced (i.e., more negative) for more difficult response choice demands (Carbonnell et al., 2013; Vidal et al., 2003, 2011). We hypothesized that acting at predictable moments in time would facilitate response selection, which should be observed empirically as a smaller N-40 in temporal versus neutral

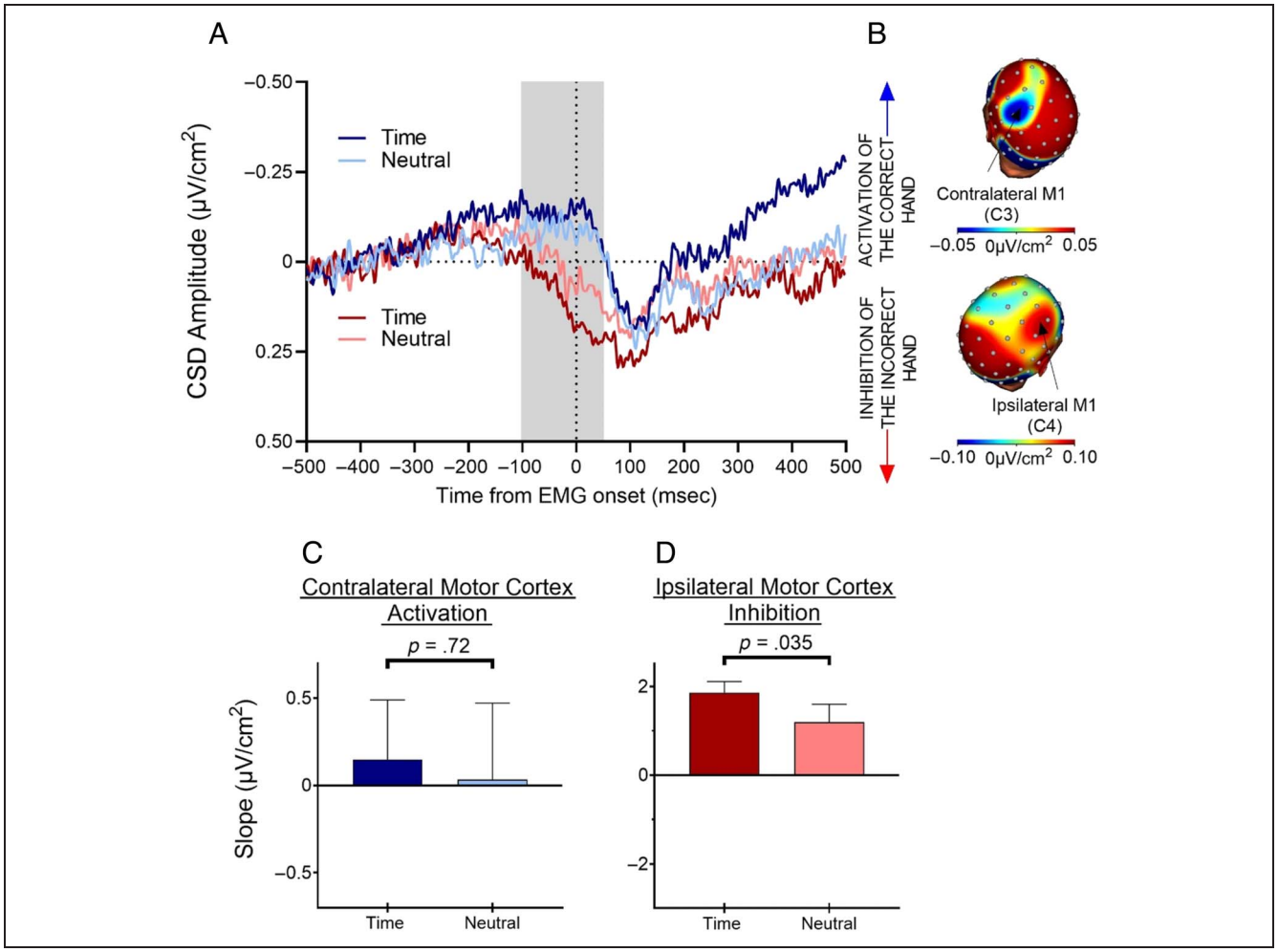

Figure 5. Motor cortex activation of the correct hand and inhibition of the incorrect hand shortly before EMG onset in go trials. (A) The negative-going slope indexes correct response activation in contralateral motor cortex for temporal (dark red) and neutral (light red) conditions, whereas the positive-going slope indexes incorrect response inhibition in ipsilateral motor cortex for temporal (dark blue) and neutral (light blue) conditions. (B) Topographies (CSD-transformed) around EMG onset for motor cortex activation (recorded over the C3 electrode) and motor cortex inhibition (recorded over the C4 electrode). (C) Temporal predictability did not affect motor cortex activation of the correct hand. (D) In contrast, motor cortex inhibition of the incorrect hand was stronger in the temporal condition, as demonstrated by steeper slopes following temporal than neutral cues. Error bars reflect standard errors.

cue conditions. We conducted peak analysis in the time window from −150 msec to 0 msec (time-locked to the EMG onset) on CSD-transformed data from the go trials.

The N-40 activity was less negative following temporal than neutral cues, $t(28) = 3.02$, $p = .005$, two-tailed, Cohen's $d = 0.56$ (Figure 4). Thus, being able to predict when a target will occur results in more efficient cortical response selection within the time course of the action. The facilitative effects of temporal predictability on response selection are in line with temporal performance benefits such as faster RTs and premotor times.

Correct Response Activation

We then tested whether temporal predictability acts by modulating cortical activation of the correct hand as indexed by the negativity developing over the motor cortex contralateral to the response agonist immediately before EMG onset (Burle et al., 2004; Vidal et al., 2003). The slope analysis was conducted on the CSD-transformed data from go trials in a time window from −100 msec to 50 msec, time-locked to the EMG onset.

Replicating previous results using the Simon response conflict paradigm (Korolczuk et al., 2022), there was no effect of temporal predictability on motor cortex activation, $t(28) = 0.36$, $p = .72$, two-tailed, Cohen's $d = 0.07$ (Figure 5).

Incorrect Response Inhibition

We next analyzed the effects of temporal predictability on cortical inhibition of the incorrect hand as indexed by the positivity developing over the motor cortex ipsilateral to the response agonist (i.e., contralateral to the incorrect response hand) before EMG onset. Again, slope analysis was performed in the time window of −100 msec to 50 msec, time-locked to the EMG onset, on the CSD-transformed data from go trials.

Given our previous results using the Simon response conflict task (Korolczuk et al., 2022), we expected to observe stronger motor cortex inhibition of the incorrect hand (more positive-going neural activity) when reacting to temporally predictable targets. Confirming our hypothesis, the slopes were more positive-going for temporal than neutral trials, $t(28) = 1.89$, $p = .035$, one-tailed, Cohen's $d = 0.35$ (Figure 5). These findings indicate that temporal predictability recruits a cortical inhibitory mechanism that keeps an incorrect response in check to ensure rapid initiation of the appropriate response.

Brain–Behavior Correlations

Finally, we correlated task performance and cortical motor control indices across participants. We hypothesized that the behavioral benefits of temporal predictability such as faster RT are linked to improved cortical response selection and stronger inhibition of the incorrect hand in the temporal, relative to neutral, condition.

We thus correlated the RT benefit of temporal cues (N-T, with higher values reflecting greater temporal benefits), with (1) the relative attenuation of the negative activity indexing response selection processes at the cortical level (N-40) for temporal cues (T-N, with more positive values reflecting easier response selection in temporal than neutral condition), and (2) the relative increase of cortical inhibition of the incorrect response hand for temporal

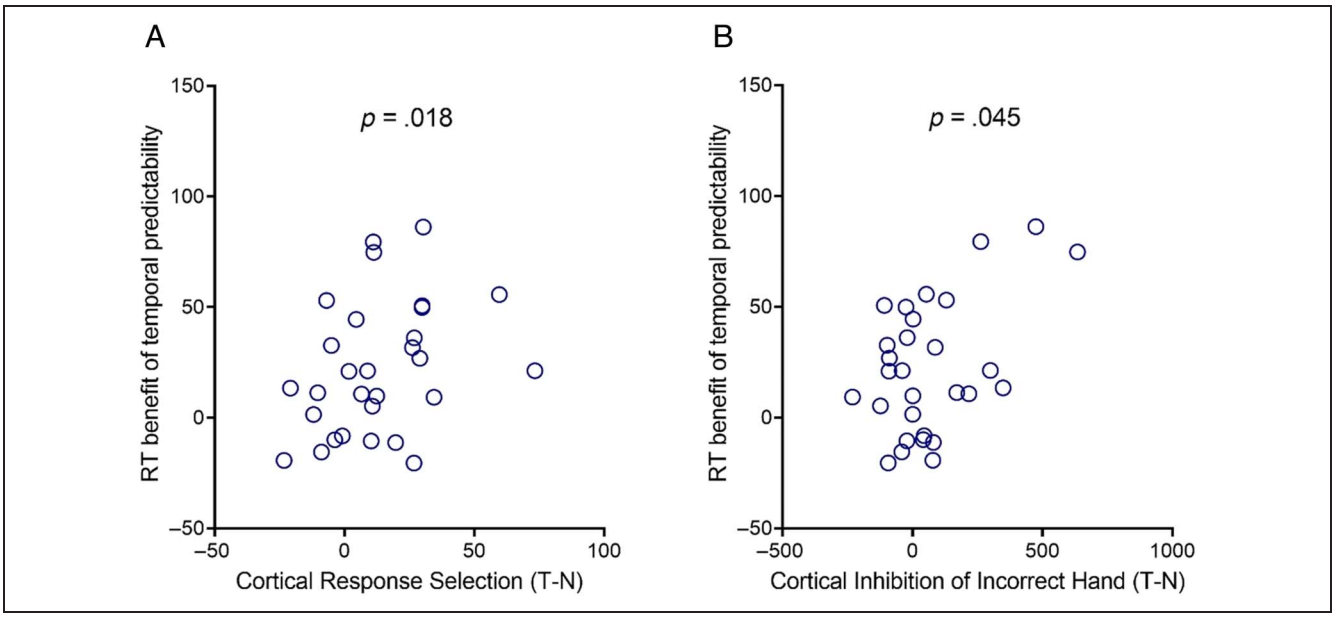

Figure 6. Brain–behavior correlations. Each point represents an individual participant. (A) Improvements in cortical response selection following temporal cues (more positive values for temporal/T than neutral/N condition) correlated positively with RT benefits of temporal predictability. (B) Similarly, stronger cortical inhibition of the incorrect hand in temporal, relative to neutral, trials, correlated positively with the RT benefit of temporal predictability.

cues (T-N, with more positive values reflecting stronger inhibition of the incorrect response hand in temporal than neutral condition).

In line with our interpretation of the findings, there was a positive correlation between the reduction in response selection negativity (N-40 component) in temporal, versus neutral, trials, and the RT benefit of temporal cues, $r(27) = .392$, $p = .018$, one-tailed (Figure 6A). In other words, if a participant had a greater difference in amplitude of the N-40, they also had a greater difference in performance.

Similarly, there was also a positive correlation between the increase in the strength of motor cortex inhibition in the temporal, relative to neutral, condition, and the RT benefit of temporal predictability, $r(27) = .322$, $p = .045$, one-tailed (Figure 6B). In other words, if a participant had a greater difference in the strength of cortical inhibition of the incorrect response hand, they also had a greater difference in performance.

DISCUSSION

Being able to predict when an event is going to occur optimizes motor processes. However, temporal predictability can also increase impulsivity when a prepotent response needs to be inhibited. We used a temporally cued version of the stop-signal task to reveal cortical and peripheral mechanisms of both reacting and stopping those reactions at predictable moments in time. First, we confirmed that temporal cues both speeded RT and exacerbated impulsive behavior, with the latter being indexed by the longer time needed to inhibit a response (SSRT). To identify the neural bases of impulsive responding to temporally predictable events, we examined cortical activity right before the response was even initiated. EEG results showed that temporal predictability facilitated response selection. In parallel, inhibition of motor cortex involved in the incorrect response agonist was stronger following temporal cues. Importantly, however, EMG data demonstrated that temporal predictability did not impede the ability to withhold the to-be-stopped response once it has started to be executed (partial false alarm).

Behavioral Costs and Benefits of Temporal Predictability

As predicted, RT was faster after temporal than neutral cues, which demonstrates once again the behavioral benefits of temporal predictability. This was, however, accompanied by an increased number of incorrect responses in go trials, revealing a speed-accuracy trade-off. On the other hand, temporal predictability made it harder to stop responses, as indexed by longer stopping RT (SSRT). Altogether, these results demonstrate that temporal prediction exacerbates the urge to act, which increases impulsivity in tasks requiring a flexible adjustment of actions. One facet of the impulsive behavior triggered by temporal prediction depends on the specific motor context. In response conflict tasks, in which one response needs to be inhibited in favor of another, temporal predictability increases the tendency to initiate a fast and incorrect response (Korolczuk et al., 2020, 2022; Menceloglu et al., 2021; Correa et al., 2010). In turn, in tasks that require the response to be withheld entirely, such as the stop-signal task, a priori temporal expectancies make it harder to flexibly stop actions (Korolczuk et al., 2018). Importantly, this behavioral pattern (i.e., longer SSRT along with shorter RT) appears to be specific to explicit temporal prediction induced by temporal cues rather than any form of preparation in general. In fact, higher motor preparation has been demonstrated to correlate negatively with both RT and SSRT such that the higher the motor preparation, the shorter the RT and SSRT (Wang et al., 2018).

Notably, although one may argue that temporal predictability impairs inhibitory processes, previous results have not supported this hypothesis (Korolczuk et al., 2020). On the contrary, it appears that a link between timing and impulsivity comes from the effects of temporal predictability on response activation rather than impairment of corrective inhibitory processes. Likewise, in the current study, both accelerated RT and slower SSRT following temporal cues were likely underlined by an excessive response readiness. Thus, the inability to stop prepotent responses can be explained by the increased level of activation caused by the prediction of the time of the event. The neural correlates of such increased activation are discussed below.

Temporal Predictability Enhances Response Selection as Indexed by the Frontocentral N-40 Component

EEG analyses revealed that the N-40 component, which covaries with response selection difficulty (Carbonnell et al., 2013), was modulated by temporal predictability. More specifically, the negative activity became less pronounced when participants were about to make a temporally guided response, which might indicate easier response selection after temporal cues. The N-40 component, reflecting response selection process, arises before the "activation/inhibition" pattern (Burle et al., 2016; Vidal et al., 2003); the facilitative effects of temporal cues are situated upstream in the motor command hierarchy (at least in the context of a discrimination task; Orgogozo & Larsen, 1979).

Incidentally, at first glimpse, these findings are at odds with previous EEG data suggesting that temporal predictability does not act by modulating the selection of responses (Korolczuk et al., 2022). In the prior investigation using a temporally cued Simon conflict task, we found that although N-40 amplitude varied as a function of response choice difficulty with more pronounced activity for conflicting rather than nonconflicting responses, it remained insensitive to temporal characteristics of the task. Importantly, however, the current study employed

a nonconflict choice task. It could be that increased activity because of conflict induces a ceiling effect preventing a genuine cue effect to appear. Alternatively, although not mutually exclusively, spatial certainty might be necessary for the beneficial effects of temporal cues to be observed. Indeed, previous EEG data have demonstrated that the effects of temporal predictability are more pronounced when the location of the target is known in advance (Rohenkohl, Gould, Pessoa, & Nobre, 2014; Doherty, Rao, Mesulam, & Nobre, 2005). Hence, in a spatially certain stop-signal task, the consequences of temporal predictability for response selection might be stronger than in a spatially uncertain Simon task. Our data support this notion and link the behavioral benefits of temporal cues to more effective cortical response selection.

The Motor Cortex Involved in Inhibiting the Incorrect Hand Is Modulated by Temporal Prediction

Following response selection, a correct response is activated over contralateral motor cortex and an incorrect response is inhibited over ipsilateral motor cortex (Burle et al., 2004). Prior EEG results showed that temporal predictability does not act by increasing the activation of the correct response hand in a response conflict task (Korolczuk et al., 2022). The current data replicated and extended this observation: Activation over the motor cortex involved in generating the correct action remained insensitive to the temporal structure of the task at hand also in a nonconflict choice RT paradigm. It should be noted, however, that this finding does not contradict prior investigations, indicating that temporal predictability increases motor activation. Whereas most of the EEG reports examined the effects of temporal predictability using a simple RT task (Van Elswijk et al., 2007; Miniussi et al., 1999) or when a response hand was known in advance (Volberg & Thomaschke, 2017), in our task, participants could not prepare a motor response in advance. Consequently, our results provide insight into the neural mechanisms by which temporal prediction modulates neural motor processes after target presentation. Within this context, we demonstrate that the modulatory effects of temporal predictability do not include cortical activation of the correct action.

More importantly, however, temporal predictability modulated the motor cortex involved in suppressing the incorrect action. Right before the action was even initiated, the positive activity in the ipsilateral motor cortex associated with an incorrect response hand was more pronounced following temporal cues, indicating stronger inhibition of incorrect response (Burle et al., 2004; Vidal et al., 2003) when acting to temporally predictable events. Such an exclusive effect of temporal cues on cortical inhibition lends further support to the notion that performance benefits are achieved by stronger inhibition of the incorrect hand (Korolczuk et al., 2022), possibly by ensuring faster initiation and execution of the correct action. Indeed, the strength of the inhibition of the ipsilateral motor cortex involved in the suppression of erroneous actions correlated positively with the RT benefit of temporal cues. Taken as a whole, these data indicate that in the context of choice RT tasks (both conflicting and nonconflicting), temporal prediction utilizes inhibitory circuits over the motor cortex involved in keeping an incorrect response in check to ensure a timely and rapid response.

Temporal Predictability Leaves the Ability to Correct Subthreshold Impulses Intact

To complement the EEG data, we used EMG recordings to obtain a direct measure of peripheral processes involved in suppressing actions at temporally precise moments. The partial response correction ratio—a direct, online marker of response inhibition—was unaffected by temporal prediction. This null effect is an important aspect of our findings, which demonstrates that impulsive behavior following temporal cues does not originate from impaired inhibitory processes per se. Instead, our results showed that increased motor readiness prompted more rapid responding, which exacerbated the difficulty in stopping actions in general. Finally, it might seem contradictory that temporal predictability did not increase the number of subthreshold responses but, at the same time, it made it harder to stop a response completely. These findings can be explained in terms of all-of-none type of impulsivity, which is triggered by temporal predictions. In other words, temporal predictability leads to more overt false alarms (makes it harder to stop the error completely), but it does not increase the number of subthreshold responses nor it affects the ability to correct an impulsive error for a more appropriate response.

To conclude, our results provide compelling evidence for the dual nature of temporal predictability on action control. On one hand, acting at temporally predictable moments enhanced cortical facilitation of response selection and led to stronger suppression of the incorrect response hand. Yet, temporal predictability led to performance costs when activated responses needed to be stopped. Importantly, however, the online inhibition of these impulsive activated actions was not impaired by temporal predictability. Taken together, our results demonstrate that costs of temporal predictability for stopping unwanted actions are paralleled by enhanced neural motor processes rather than impaired response inhibition.

Reprint requests should be sent to Inga Korolczuk, Laboratoire des Neurosciences Cognitives UMR 7291, Federation 3C, Aix-Marseille University & CNRS, 3 Place Victor Hugo, 13331 Marseille cedex 3, France, or via e-mail: inga.korolczuk@univ-amu.fr.

Data Availability Statement

Materials, data, and analysis script will be made available upon request to the lead author.

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Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience* (*JoCN*) during this period were M(an)/M = .407, W(oman)/M = .32, M/W = .115, and W/W = .159, the comparable proportions for the articles that these authorship teams cited were M/M = .549, W/M = .257, M/W = .109, and W/W = .085 (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance. The authors of this article report its proportions of citations by gender category to be as follows: M/M = .64; W/M = .08; M/W = .08; W/W = .2.

Note

1. Soon to be released under open source license.

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