

Time for action: neural basis of the costs and benefits of temporal predictability for competing response choices

I Korolczuk, Boris Burle, J T Coull, K Smigasiewicz

▶ **To cite this version:**

I Korolczuk, Boris Burle, J T Coull, K Smigasiewicz. Time for action: neural basis of the costs and benefits of temporal predictability for competing response choices. Journal of Cognitive Neuroscience, 2022, 34 (2), pp.273-289. 10.1162/jocn_a_01795 . hal-03409679v2

HAL Id: hal-03409679
https://hal.science/hal-03409679v2

Submitted on 30 Apr 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

Journal of Cognitive Neuroscience, 34 (2) (2022), 273–289. DOI:10.1162/jocn_a_01795

Time for action: neural basis of the costs and benefits of temporal predictability for competing response choices☆

Korolczuk, I.[1,2,*], Burle, B.[1], Coull, J. T.[1], Smigasiewicz, K.[1]

[1] *Aix-Marseille Université, CNRS, LNC UMR 7291, 3 place Victor Hugo – 13331 Marseille cedex 3, France*

[2] *Institute of Applied Psychology, Jagiellonian University, Krakow, Poland*

Abstract

The brain can anticipate the time of imminent events to optimise sensorimotor processing. Yet, there can be behavioural costs of temporal predictability under situations of response conflict. Here, we sought to identify the neural basis of these costs and benefits by examining motor control processes in a combined EEG-EMG study. We recorded electrophysiological markers of response activation and inhibition over motor cortex when the onset-time of visual targets could be predicted, or not, and when responses necessitated conflict resolution, or not. If stimuli were temporally predictable but evoked conflicting responses, we observed increased inter-trial consistency in the delta range over the motor cortex involved in response implementation, perhaps reflecting increased response difficulty. More importantly, temporal predictability differentially modulated motor cortex activity as a function of response conflict before the response was even initiated. This effect occurred in the hemisphere ipsilateral to the response, which is involved in inhibiting unwanted actions. If target features all triggered the same response, temporal predictability increased cortical inhibition of the incorrect response hand. Conversely, if different target features triggered two conflicting responses, temporal predictability decreased inhibition of the incorrect, yet prepotent, response. This dissociation reconciles the well-established behavioural benefits of temporal predictability for non-conflicting responses as well as its costs for conflicting ones by providing an elegant mechanism that operates selectively over the motor cortex involved in suppressing inappropriate actions just before response initiation. Taken together, our results demonstrate that temporal information differentially guides motor activity depending on response choice complexity.

Keywords: temporal orienting, motor control, primary motor cortex, delta band, inter-trial phase coherence

INTRODUCTION

We often predict the temporal flow of external events to optimally guide our actions in accordance with current goals. The ability to utilise temporal information in the service of adaptive behaviour is typically investigated with tasks requiring simple responses to unambiguous targets, and accurate temporal prediction has been repeatedly demonstrated to optimise motor processes (Coull & Nobre, 1998; Mattes & Ulrich, 1997; Nobre, 2001; Thomas, French, Alizee, & Coull, 2019; Van der Lubbe, Los, Jaśkowski, & Verleger, 2004). Yet, we are immersed in a complex environment with events often triggering competing, potentially erroneous, responses. Efficient adaptation requires not only that appropriate responses are selected but also that erroneous tendencies are inhibited. Therefore, to fully understand how temporal information can be used to guide action, we must examine activity in action control circuits when more challenging tasks are being performed.

In tasks with stimuli affording competing response choices, knowing exactly when a target will appear can actually have detrimental effects on performance, experimentally observed as an increased difficulty in overcoming response conflict (Correa, Cappucci, Nobre, & Lupiáñez, 2010; Menceloglu, Suzuki, & Song, 2021). Empirically, this difficulty manifests itself as an increase in the number of fast impulsive errors (Korolczuk, Burle, & Coull, 2018). Concurrent EMG recording has further revealed that this impulsive responding stems from an exacerbated tendency to rapidly activate the prepotent, but incorrect, response effector, whether or not this response is then executed (Korolczuk, Burle, Coull, & Smigasiewicz, 2020). In parallel, if no conflict is present in the environment, temporal predictability benefits performance by speeding responses made by the correct response effector. The aim of the current study is to identify cortical mechanisms that could explain the differential effects of temporal predictability on performance when the correct response requires resolution of response conflict or not.

Action control acts through various mechanisms to ensure adaptive behaviour in a dynamically changing world. These fundamental motor mechanisms involve the activation of an appropriate response, and inhibition of an erroneous one (Burle, Vidal, Tandonnet, & Hasbroucq, 2004; Mostofsky & Simmonds, 2008; Ridderinkhof, Forstmann, Wylie, Burle, & van den Wildenberg, 2011). Indeed, when response choices necessitate inhibition of erroneous responses along with the activation of an

☆This is the version of the article accepted for publication in *Journal of Cognitive Neuroscience*

*Corresponding authors: Laboratoire des Neurosciences Cognitives UMR 7291, Aix-Marseille University, CNRS 3 Place Victor Hugo, 13331 Marseille cedex 3, France, Email: inga.korolczuk@univ-amu.fr (I. Korolczuk)

appropriate one (e.g., in bimanual choice reaction time tasks), an "activation/inhibition" pattern is observed over motor structures (primary motor cortices – M1). Specifically, a few tens of milliseconds before EMG onset, the excitability of motor structures controlling the response agonist increases, while excitability of structures controlling the incorrect response decreases (Burle, Possamaï, Vidal, Bonnet, & Hasbroucq, 2002; Hasbroucq, Akamatsu, Burle, Bonnet, & Possamaï, 2000, see Burle et al., 2004 for an overview). Importantly, these cortical markers of response activation and inhibition can be effectively measured using electroencephalography (EEG) (e.g., Burle et al., 2004; Praamstra & Seiss, 2005; Vidal et al., 2003) by using current source density (CSD) through surface Laplacian estimation (Babiloni et al., 1995; Burle et al., 2015; Nunez & Westdorp, 1994; Vidal et al., 2015). Indeed, by extracting the radial component of cortical current density, CSD reduces the volume conduction induced by the various layers of the head that the current must go through. It thereby provides a rudimentary "corticogram" to measure brain activity as if electrodes were placed on the surface of the cortex. As a consequence, spatial resolution is improved from 9–10 to 2–3 cm (Gevins, 1989; Kayser & Tenke, 2015). In parallel, by segregating scalp-recorded activity induced by the underlying neural generators, activity is better separated in both space and time, leading to better temporal resolution and, hence, a more temporally precise signal (Burle et al., 2015; Law, Rohrbaugh, Adams, & Eckardt, 1993). Specifically, for the current purposes, a negative wave over the motor cortex contralateral to the response agonist reflects activation of the motor cortex involved in executing the correct response and can be interpreted as the initial emission of the cortical motor command (Tandonnet, Burle, Vidal, & Hasbroucq, 2003; Vidal, Grapperon, Bonnet, & Hasbroucq, 2003). In parallel, a positive wave over the motor cortex ipsilateral to the response agonist corresponds to inhibition of the incorrect hand (Burle et al., 2016, 2004). In the current investigation, we used this approach to investigate whether temporal predictability acts by modulating cortical motor activation and/or inhibition in situations of competing and non-competing response choices.

The "activation/inhibition" pattern over motor cortex occurs shortly before overt muscle activation and is hence more precisely measured by supplementing EEG with concurrent EMG recording. EEG-EMG recording enables brain activity occurring right before the response is even initiated to be identified, thereby increasing temporal resolution for measurement of motor control processes. This procedure also circumvents the limitations imposed by response-locked investigations, in which brain processes are measured after muscle activity in the response agonist has already begun. In addition, EMG can be used to elucidate mechanisms underlying overt responses directly at the peripheral level. By fractionating individual reaction times (RTs) into premotor times (PMTs; interval from target onset to EMG-locked response onset) and motor time (MTs; interval from EMG onset to mechanical response) the time needed to initiate the response (PMT) or execute the response (MT) can be effectively separated on a trial-by-trial basis (Botwinick & Thompson, 1966). Therefore, EMG recording also allowed us to clarify whether faster RTs to temporally predictable events are due to faster response initiation or response execution.

Finally, concurrent EEG-EMG recording allowed us to measure another electrophysiological marker of motor control that occurs right before the response-related muscular activity (i.e., the EMG). In bimanual choice RT tasks, the selection of goal-directed responses is reflected in frontomedial ramping negativity that peaks around 40 milliseconds before the onset of the EMG activity and so is termed the N-40 component (Carbonnell et al., 2013; Vidal, Burle, Grapperon, & Hasbroucq, 2011; Vidal et al., 2003). This negative activity, likely generated by the supplementary motor area (SMA), is modulated by response choice demands (Carbonnell et al., 2013). Specifically, the N-40 is larger for competing than non-competing responses. Although the neural origins of the "activation/inhibition" pattern and the N-40 are different, their exact functional relationship is still not well understood. In general, the N-40 has been demonstrated to precede the motor cortex "activation/inhibition" pattern (Burle et al., 2016; Vidal et al., 2003) and so would be situated upstream of motor cortex 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). Although previous behavioural reports have revealed the detrimental effects of temporal predictability on response selection when a competing, erroneous response must be inhibited (Correa et al., 2010; Korolczuk et al., 2018; Menceloglu et al., 2021), neurophysiological evidence of such impairment in response selection is lacking. We therefore aimed to further clarify the effects of temporal predictability on response selection processes by analysing the role of N-40 activity when participants were reacting to temporally predictable conflicting (or non-conflicting) events.

We sought, therefore, to investigate neural mechanisms of temporal prediction by bridging two distinct, yet related, cognitive domains – timing and action control. Specifically, we aimed to functionally reconcile the well-established benefit of temporal predictability with recent findings demonstrating its cost for more complex behaviour. In our combined EEG-EMG investigation, a temporally cued version of the Simon task allowed the onset time of the target to be predicted. Importantly, the target could elicit conflicting responses (incompatible condition) or not (compatible condition). First, we hypothesised that faster RTs to temporally predictable events are due to a speeded motor time, rather than speeded premotor time. In other words, we expected that temporal predictability would facilitate the execution of the action. Second, we hypothesised that right before response initiation, temporal predictability would increase activation over the motor cortex contralateral to the correct hand when participants were reacting to compatible targets, reflecting a more efficient emission of the motor command and thereby explaining faster response times (i.e., the benefit of temporal predictability). In turn, we expected that the difficulty in inhibiting prepotent action would be reflected in decreased inhibition over the motor cortex contralateral to the incorrect hand (i.e., the cost of temporal predictability). Finally, since SMA-driven ramping activity is less pronounced for less

"effortful" responses (e.g., in compatible rather than incompatible trials), we hypothesised the N-40 would be even further attenuated when compatible targets were temporally predictable versus unpredictable. In contrast, the N-40 might be more pronounced when incompatible targets are temporally predictable, reflecting the difficulty of suppressing an inappropriate response in favour of a more goal-directed one when the time of response has already been programmed in advance (Correa et al., 2010).

METHODS

Participants

Twenty-six healthy volunteers (mean age = 24.6 years, range = 18-38 years, 15 females) participated in the study. The local research ethics committee approved the experimental protocol (Comité de Protection des Personnes Sud Méditerranée 1 in Marseille, Protocol No. AFFSAPS B100968-30). All participants gave written informed consent. Three participants were excluded from the analysis due to technical problems, high error rate (±2 SD of the group average) or slow RTs (±2 SD of the group average). Thus, the final sample was composed of twenty-three participants. All participants had normal or corrected-to-normal vision and no history of neurological or psychiatric disorders.

Experimental task

All participants performed a temporally cued Simon task (Fig. 1) programmed in PsychoPy (Peirce et al., 2019). White centrally located concentric circles (1° eccentricity) were presented on a black background. The circles acted as visual cues that conveyed information about the time of target onset (temporal condition) or not (neutral condition). Diagonal ("×") or vertical ("+") crosses sized 1° visual angle acted as targets and were placed 3° of visual angle either on the right, or left, side of the cue.

The trial structure was identical in temporal and neutral conditions. In the temporal (T) condition, brightening of the smaller, inner circle informed participants that a target would appear after a short delay (600 ms) while brightening of the larger, outer circle informed participants that a target would occur after a longer delay (1,400 ms). These temporal cues were 100% valid. Subjects were instructed to use the information about the delay or "foreperiod" (FP) conveyed by temporal cues to prepare to respond to a target that would be presented at these predictable moments in time. By contrast, in the neutral (N) condition both small and large circles brightened, providing no temporally precise information and targets could appear randomly after either a short or long FP. In both conditions, participants were instructed to respond as quickly as possible with their left or right thumb according to the shape of the target ("×" or "+"). The target-response mappings were counterbalanced across participants. A target was presented equiprobably on either the right or left side of the screen and, therefore, the correct hand response could be either on the same (compatible condition) or opposite (incompatible condition) side as the target. Response buttons were two cylindrical handgrips (3 cm in diameter, 12 cm in height) fixed vertically to the table (Fig. 1). Participants pressed one of them with their thumb as quickly as possible after target appearance.

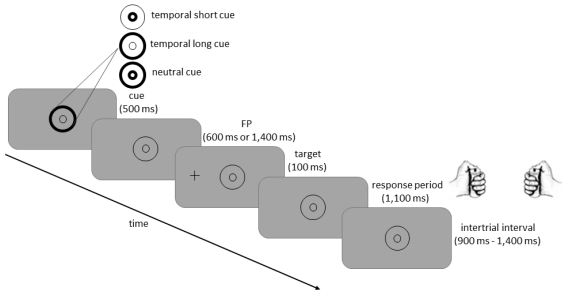


Figure 1: Temporally cued Simon task. A cue appeared for 500 ms predicting (temporal) or not (neutral) the onset time of a target. A background display was then presented for 600 ms or 1,400 ms (FP). Next, the target ("×" or "+") appeared for 100 ms on either the left or right side of the display. Participants made their lateralised response (left or right thumb depending on the shape of the target) within a 1,100 ms time window, during which the background display was presented. The intertrial interval was randomised between 900 ms – 1,400 ms.

The trial structure was as follows. The cue (T or N) appeared for 500 ms. The background display was then presented either for a short (600 ms) or long (1,400 ms) FP. The target appeared for 100 ms, after which the participants gave a lateralised response within a 1,100 ms time window. Finally, the background display appeared for an intertrial interval that was selected randomly from a uniform distribution between 900-1,400 ms (random jitter of 100 ms).

There were 192 trials for each of 8 combinations of cue, FP, and compatibility conditions, resulting in 1536 trials, which were administered in 12 blocks. Each of the two cue conditions (T and N) was presented in 3 consecutive blocks, in alternating manner (TTT-NNN-TTT-NNN or NNN-TTT-NNN-TTT). In each block, there was an equal proportion of compatible and incompatible trials, as well as short and long FPs, with both factors being randomised using Mix software (van Casteren & Davis, 2006). Before an experimental session, participants completed a training session of 60 trials to familiarise themselves with the task.

EMG and EEG recordings

Electrophysiological data were recorded continuously from 64 Ag/AgCl active flat pre-amplified electrodes at a rate of 1,024 Hz (analogue bandwidth limit: from DC to 268Hz, -3 dB at 1/5th of the sampling rate). The electrodes were placed according to the extended 10–20 convention (Biosemi Inc., Amsterdam, The Netherlands). The electrooculogram (EOG) was recorded using two electrodes lateral to the external canthi in order to measure horizontal eye movements, and by placing an electrode beneath the left eye and subtracting this activity from the FP1 electrode to measure vertical eye movements and blinks.

Bipolar electromyographic activity of the flexor pollicis brevis was recorded from each hand using Ag/AgCl active elec-

trodes (Biosemi Inc., Amsterdam, The Netherlands) positioned 2 cm apart on the thenar eminence.

EMG and EEG pre-processing

The pre-processing steps and analysis of EMG and EEG data were performed using BrainVision Analyzer 2.0 (Brain Products, Germany), MNE Python toolbox (Gramfort et al., 2013) and customised Python scripts.

The onsets and offsets of EMG activity were detected using a customised Python script (Spieser & Burle, 2021, soon to be released under open source license), and based on a combination of two algorithms: "integrated profile" (Liu & Liu, 2016; Santello & McDonagh, 1998) and a variance comparison (Hodges & Bui, 1996). The EMG onsets were then inspected visually and corrected manually by a naïve observer, unaware of the type of trial she/he was seeing. Based on this procedure, we identified three categories of trials: pure correct trials (i.e., trials with a single EMG activation for the correct hand), partial error trials (i.e., trials with two EMG activations: the first subthreshold activation for the incorrect hand, which is subsequently suppressed before a second suprathreshold EMG activation for the correct hand is produced) and error trials (i.e., trials with a single EMG activation for the incorrect hand). In this way we could effectively separate purely correct responses from other types of responses (e.g., partial errors), which would normally be merged together if we were analysing only their behavioural manifestation.

The EEG data were re-referenced to the left mastoid. 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). Ocular artifacts were detected and corrected with the use of functions implemented in the MNE Python toolbox (Gramfort et al., 2013; Uusitalo & Ilmoniemi, 1997). Data were then visually inspected for noise and artifacts. Since subsequent analysis steps included the Current Source Density computation, which is particularly sensitive to local artifacts, all electrodes were rejected even if only a small local artifact was present.

Data analysis

RT, accuracy and partial error methods and results were already published in Korolczuk et al. (2020). Here, the EMG and EEG analyses were focused on pure correct trials only.

EMG data analysis

EMG recordings allowed us to fractionate the mean response time (RT) into two subcomponents: premotor time (PMT; time from target onset to EMG onset) and motor time (MT; time from EMG onset to mechanical response) (Fig. 2). PMTs correlate strongly with RTs (Botwinick & Thompson, 1966) and thus serve an equally useful role in complementing the EEG results. The effect of temporal predictability on these two indices was assessed by a three-way repeated-measures ANOVA involving cue (temporal, neutral), FP (short, long), and compatibility (compatible and incompatible) factors.

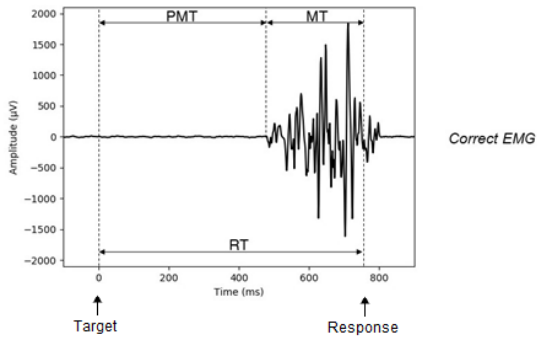


Figure 2: EMG activity and chronometric measures. The figure presents a pure correct trial: EMG activity results in a mechanical response in the correct response hand. PMT denotes premotor time (time since target onset to the onset of EMG activity), MT the motor time (time since onset of EMG activity to the mechanical response), RT the reaction time.

EEG data analysis

In order to confirm that temporal cues encouraged participants to form expectations about target onset, we first measured the CNV buildup in temporal versus neutral trials separately for short and long FP. Specifically, we expected to observe a more negative CNV before the target onset in temporal short than neutral short trials. For long FP trials, we expected that the hazard function would diminish this effect. The ERPs were epoched from -500 ms to 1,600 ms relative to cue onset for short FP trials, and from -500 ms to 2,400 ms for long FP trials. A precue interval from -200 ms to 0 was used as a baseline. The average CNV amplitude was then calculated within a time window shortly preceding the onset of the target (i.e., from 800 ms to 1,100 ms after cue onset for short FP trials, and from 1,600 ms to 1,900 ms after cue onset for long FP trials) over the FCz electrode. Planned contrasts were used to reveal the difference in CNV amplitude for temporal versus neutral trials.

The effects of temporal predictability on response selection processes were investigated by analysing the N-40 component. As this frontocentral negativity peaks shortly before EMG onset (Carbonnell et al., 2013; Vidal et al., 2011, 2003), we segmented activity over the FCz electrode from -500 ms to 500 ms time-locked to EMG onset. The interval from -500 ms to -300 ms before EMG onset was used as a baseline. Then, the data was averaged for each of eight experimental conditions. The CSD computation was performed using BrainVision Analyzer 2.0 (Brain Products, Germany). 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 computed with a maximum of 15 degrees for the Legendre polynomial. The unit of EEG activity was $\mu V/cm^2$ (assuming a head radius of 10 cm). Then, for each participant, the peak value was extracted for each of the eight experimental conditions from the averaged and CSD-transformed signal in the time window from -100 ms to 0 relative to the onset of the EMG. Peak values were analysed in a three-way repeated-measures ANOVA involving cue (temporal, neutral), FP (short, long), and compatibility (compatible and incompatible) as factors.

To examine whether temporal predictability modulated motor cortex activity related to activation of the correct hand and inhibition of the incorrect one, data from each of the eight experimental conditions were segmented from -500 ms to 500 ms relative to the EMG onset, separately for right and left hand responses. Epochs were averaged. Following the CSD transformation, data from left hemisphere electrodes during (contralateral) right-hand responses were averaged with that from right hemisphere electrodes during (contralateral) left-hand responses (weighted average), and correspondingly, data from left hemisphere electrodes from (ipsilateral) left-hand responses were averaged with the right hemisphere electrodes from (ipsilateral) right-hand responses. Consequently, the C3 electrode always corresponds to the electrode contralateral to the response hand (i.e., involved in activation of the correct response), whereas the C4 electrode represents the electrode ipsilateral to the response hand (i.e., involved in inhibition of the incorrect response). To track the neural activity immediately preceding peripheral muscle activation, we defined a window of interest for statistical analysis from -200 ms to 0 ms, time-locked to the onset of the EMG. We calculated slopes of neural activity within this window so as to provide a baseline-independent measure of phasic activity. The slopes were computed by fitting a linear regression to the signal in a predefined time window using a customised Python script (www.python.org). The slopes were then analysed in a three-way repeated-measures ANOVA involving cue (temporal, neutral), FP (short, long), and compatibility (compatible and incompatible) as factors. Additionally, for critical analyses, we performed Bayesian statistics with cue (temporal, neutral), FP (short, long), and compatibility (compatible and incompatible) as factors. We also used Spearman's correlations to explore the relationship between performance and electrophysiological activity. Specifically, we correlated the normalised premotor time temporal benefit (N-T/N) in compatible trials (log-transformed, z-scored) with the relative strength of motor inhibition in temporal versus neutral (T-N) compatible trials (z-scored). Also, we investigated the relationship between the costs of temporal cues (T-N) on error rate (published in Korolczuk et al., 2020) in incompatible trials (z-scored) and the relative strength of the motor cortex inhibition in temporal versus neutral (T-N) incompatible trials (z-scored) .

Finally, a phase-locking analysis was performed on data trials, segmented from -2,000 ms to 2,500 ms relative to EMG onset. A continuous wavelet transformation (Morlet wavelet, length of 4 cycles) was applied to single-trial data for the frequency range 1 to 50 Hz, in 1 Hz steps, to calculate complex values. The inter-trial phase coherence (ITPC) was computed by averaging the normalised complex values across trials for a given frequency and time. The ITPC (also called phase-locking factor or PLF) reflects the consistency of event-locked phase angles across trials for each time-frequency point and ranges from 0 (indicating randomly distributed phase angles) to 1 (indicating identical phase angles). Importantly, the ITPC provides a measure of inter-trial phase variability that is independent of the amplitude of oscillatory activity (Herrmann, Rach, Vosskuhl, & Strüber, 2014). These data were epoched from -500 to 500 ms relative to EMG onset, and then averaged and rectified (i.e., taking the absolute value). We collapsed the ITPC values for delta (1-4 Hz) and theta (4-7 Hz) frequency bands across right- and left-hand contralateral response trials (see the description of the ERP data analysis above) and examined phase consistency over the motor cortex involved in producing a correct response (i.e., contralateral to the response agonist) at the C3 electrode. The time window of interest was set from 0 to 300 ms time-locked to EMG onset. The ITPC values were submitted to a three-way repeated-measures ANOVA involving cue (temporal, neutral), FP (short, long), and compatibility (compatible and incompatible) as factors. Again, we used Spearman's correlations to explore the relationship between the relative strength of delta ITPC for incompatible versus compatible trials (I-C, z-scored) and motor time for incompatible versus compatible trials (I-C, z-scored).

RESULTS

Behavioural and EMG results

We replicated the classic Simon effect, comprising both slower RTs and a higher number of errors to incompatible versus compatible targets. Temporal predictability further speeded RTs and exacerbated erroneous responding. Detailed statistical analyses of RTs, accuracy, partial errors and EMG-informed Conditional Accuracy Function (EMG-CAF), which shows the probability of the correct EMG activation as a function of latency, can be found in Korolczuk et al., 2020.

Response time fractionation: premotor and motor time

Although temporal predictability exacerbated impulsive responding, it also led to performance benefits such as faster correct RTs. To investigate whether these speeded responses were due to faster response initiation or more efficient motor execution, we analysed premotor and motor times.

As expected, premotor time correlated strongly with response time ($r(21) = .834$, $p < .001$). Consistent with other reports (Salomone, Burle, Fabre, & Berberian, 2021; Spieser, Servant, Hasbroucq, & Burle, 2017), there was a main effect of compatibility on premotor time, $F(1, 22) = 92.53$, $p < 0.001$, $\eta_p^2 = 0.81$. Premotor times were faster for compatible than incompatible targets. Results also showed a main effect of cue, $F(1, 22) = 5.63$, $p = 0.027$, $\eta_p^2 = 0.20$, with faster premotor times after a temporal versus neutral cue. Importantly, there was a Cue × Compatibility interaction, $F(1, 22) = 5.07$, $p = 0.035$, $\eta_p^2 = 0.19$. The interaction was broken down by compatibility (Fig. 3). Participants initiated their responses earlier when temporally cued, but only in compatible conditions ($p = 0.04$, Tukey-corrected, Cohen's $d = 0.56$, 95% CI [21.9, 2.8]). On the contrary, no temporal cueing benefit was present when responding to incompatible targets ($p = 0.324$, Tukey-corrected). These findings provide evidence that faster response initiation underlies the performance benefits of temporal prediction, typically manifested as faster RTs but only when responding to non-conflicting events. The Cue × FP interaction did not reach statistical significance, $F(1, 22) = 3.41$, $p = 0.078$, $\eta_p^2 = 0.13$.

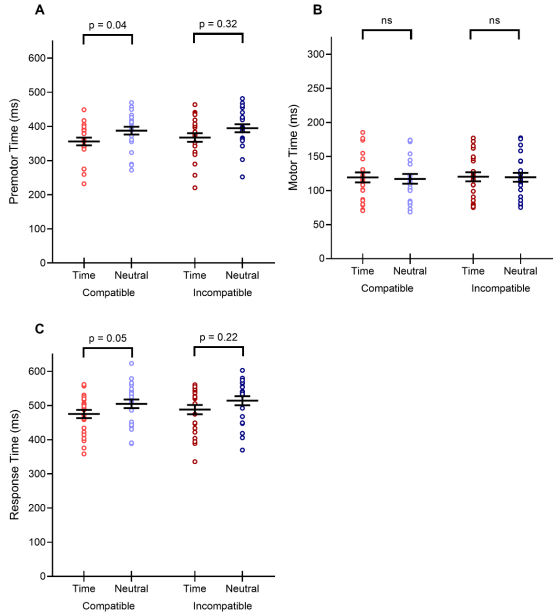


Figure 3: Response time decomposed into premotor time (PMT) and motor time (MT). (A) Temporal cues speeded premotor time in the compatible condition only. By contrast, incompatible targets cancelled out the benefit of temporal cueing on response initiation time. (B) Motor time was not modulated by temporal cues. (C) Thus, faster response time (published in Korolczuk et al, 2020) following temporal cues in the compatible condition is underpinned by faster response initiation (PMT) rather than response execution (MT). Solid lines reflect means with standard errors.

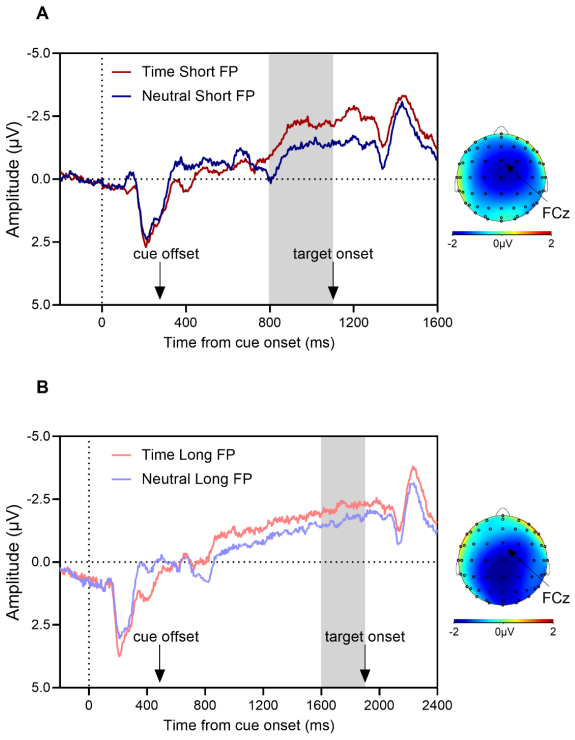


Figure 4: Group-averaged CNV activity in the FCz electrode, time-locked to cue onset. (A) In short FP conditions, the CNV amplitude was more negative in temporal than neutral trials just prior to the expected time of target onset. (B) In long FP conditions, the hazard function attenuated this effect, yielding no statistical difference in CNV amplitude between temporal and neutral trials. Scalp topographies show activity just before target onset separately for short (1,050-1,100 ms after cue onset) and long (1,850-1,900 ms after cue onset) FP conditions.

This may seem surprising since the RT benefits of temporal cues in simple (detection) RT tasks are greatly reduced at long FPs due to the influence of the 'hazard function' (i.e., the increasing conditional probability over time that a target will occur given that it has not already occurred) (Correa, Lupiáñez, & Tudela, 2006; Coull & Nobre, 1998). However, our result actually reinforces previous findings that the influence of the hazard function on response speed is less pronounced or even absent in choice RT tasks (Correa, Lupiáñez, & Tudela, 2006b; Korolczuk et al., 2018, 2020). No main effect of FP, $F(1, 22) = 2.72$, $p = 0.113$, $\eta_p^2 = 0.11$, nor a FP × Compatibility interaction, $F(1, 22) = 0.60$, $p = 0.448$, $\eta_p^2 = 0.03$, was found.

In contrast, the analysis of motor times failed to reveal a main effect of cue, $F(1, 22) = 0.04$, $p = 0.834$, $\eta_p^2 = 0.002$ or a Cue × Compatibility interaction, $F(1, 22) = 1.23$, $p = 0.280$, $\eta_p^2 = 0.05$. In other words, temporal cueing did not affect motor execution. Confirming previous results (Hasbroucq, Akamatsu, & Seal, 1995; Christophe Tandonnet, Burle, Vidal, & Hasbroucq, 2005), we found a main effect of FP, $F(1, 22) = 20.22$, $p < 0.001$, $\eta_p^2 = 0.48$, with faster motor times after short versus long FPs. Finally, a main effect of compatibility, $F(1, 22) = 7.22$, $p = 0.013$, $\eta_p^2 = 0.25$ revealed that motor time was slower for compatible than incompatible trials, although this was qualified by a FP × Compatibility interaction, $F(1, 22) = 4.74$, $p = 0.041$, $\eta_p^2 = 0.18$. Motor time was slower in compatible versus incompatible conditions only for long ($p = 0.008$, Tukey-corrected, Cohen's $d = 0.638$, 95% CI [0.7, 3.9]), but not short, FP trials ($p = 0.681$, Tukey-corrected). These results are difficult to interpret. No other significant effects were identified. In sum, and importantly for our research question, the results of the ANOVA revealed that temporal cueing did not modulate motor time. In order to interpret this null effect confidently, we ran an additional three-way repeated-measures Bayesian ANOVA involving cue (temporal, neutral), FP (short, long) and compatibility (compatible and incompatible) as factors. A BF01 (i.e., an exclusion BF, indicating the probability ratio between H0 and H1 models) was 5.56 for the main effect of cue and 3.81 for the Cue × Compatibility interaction. Therefore, there was moderate evidence for an absence of effect of temporal predictability on motor time.

EEG results

Preparatory activity

We examined the buildup of the CNV over the FCz electrode during the cue-target interval to measure preparation for the upcoming event (i.e., -300 ms to 0 prior to target onset) in temporal versus neutral conditions. To avoid any influence of the hazard function in long FP trials (i.e., the increasing probability of target occurrence given that it has not yet occurred; Niemi and Naatanen, 1981), we compared the averaged CNV amplitude prior to onset of the short FP target and long FP target separately. As predicted by prior investigations (Breska &

Deouell, 2014, 2017; Macar et al., 1999; Miniussi et al., 1999; Praamstra et al., 2006), we found a more negative deflection when the temporal cue predicted that the target would appear after a short FP as compared to a neutral cue (t(22) = 2.24, p = 0.018, one-tailed, Cohen's d = 0.47, 95% CI [inf, -0.2]) (Fig. 4A). By contrast, in the long FP trials, the difference in CNV amplitude between temporal and neutral conditions did not reach significance (t(22) = 0.45, p = 0.328 one-tailed, Cohen's d = 0.09, 95% CI [inf, 1.07]), demonstrating that the hazard function mitigated temporal uncertainty in neutral long trials (Fig. 4B). These CNV data confirmed that participants formed a temporal prediction about target onset following a temporal cue.

Response selection

To elucidate the modulatory effects of temporal predictability on response selection, we analysed the frontocentral negative activity that is observed in choice RT tasks just before EMG onset (i.e., the N-40 component) and is interpreted as a physiological marker of the response selection processes (Carbonnell et al., 2013; Vidal et al., 2011, 2003). We aimed to test the hypothesis that temporal predictability would differentially modulate the N-40 for non-conflicting versus conflicting responses. More specifically, we expected that for non-conflicting responses the negativity would be attenuated following temporal cues, suggesting easier response selection. In turn, the opposite pattern was expected for temporally predictable but conflicting targets, with an increased N-40 indicating more difficult response selection. We performed peak analysis in the time window from -100 ms to 0 (time-locked to the EMG onset) on CSD-transformed data. First, results revealed a main effect of compatibility, F(1, 22) = 9.98, p = 0.005, η_p^2= 0.31, which replicates previous reports (Burle et al., 2016; Carbonnell et al., 2013). Activity was more negative for the incompatible (i.e., more demanding response selection) than the compatible condition (Fig. 5). Importantly, however, no Cue × Compatibility interaction was observed, F(1, 22) = 0.44, p = 0.513, η_p^2= 0.02, nor a main of cue, F(1, 22) = 0.07, p = 0.789, η_p^2= 0.003, or FP, F(1, 22) = 0.11, p = 0.739, η_p^2= 0.005. No other effects were noted. These results indicate that neither the benefits nor the costs of temporal prediction can be attributed to more efficient or impaired response selection processes, respectively (at least in the context of response conflict tasks). This conclusion was further supported by the results of a three-way repeated-measures Bayesian ANOVA involving cue (temporal, neutral), FP (short, long) and compatibility (compatible and incompatible), which provided substantial evidence for the absence of effects of temporal predictability on response selection (BF01 for a cue = 6.07, BF01 for a Cue × Compatibility interaction = 3.9, other interactions BF01 > 4). No other effects were noted.

Correct response activation

In order to investigate cortical activation of the correct hand, we analysed negativity over the motor cortex contralateral to the response agonist. Specifically, we tested the hypothesis that when reacting to compatible targets, temporal predictability would increase the efficiency of the initial emission of the

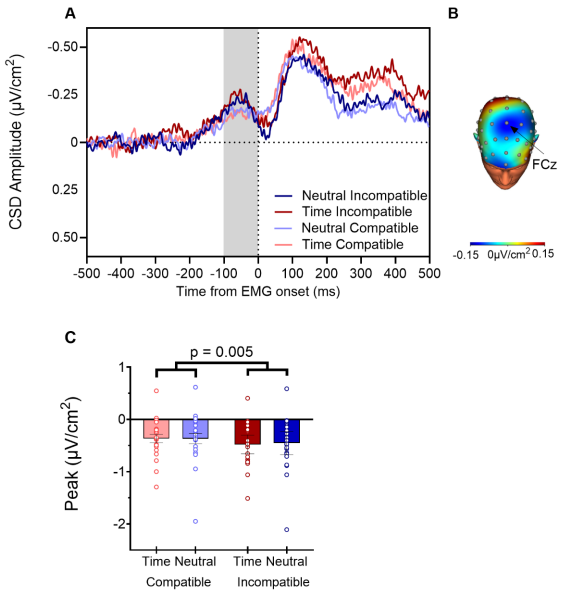


Figure 5: CSD-transformed group-averaged frontocentral negativity related to response selection (i.e., N-40 component), time-locked to EMG onset. (A) The N-40 component occurring just before EMG onset was more pronounced for incompatible (dark) conditions than compatible (light) conditions but was not modulated by temporal predictability. (B) Topography (CSD-transformed) recorded over the FCz electrode. (C) The statistical analysis of the peak revealed a significant compatibility effect.

cortical motor command. We performed a slope analysis on the CSD-transformed data to track the buildup of negativity starting shortly before the EMG onset (time window: -200 ms to 0 time-locked to the EMG onset).

Replicating previous results (Burle et al., 2016), we did not observe a significant main effect of compatibility, F(1, 22) = 0.5, p = 0.489, η_p^2= 0.02. These results confirm that cortical response activation processes are resistant to response conflict manipulation. Contrary to our hypothesis, the Cue × Compatibility interaction was non-significant, F(1, 22) = 0.25, p = 0.623, η_p^2= 0.01. Furthermore, there was no main effect of cue, F(1, 22) = 0.8, p = 0.38, η_p^2= 0.04. These results demonstrate that, rather counterintuitively, temporal predictability does not act by increasing the activation of the correct response. All other analyses were also found to be non-significant.

As this analysis was critical for the current investigation, we ran a three-way repeated-measures Bayesian ANOVA involving cue (temporal, neutral), FP (short, long) and compatibility (compatible and incompatible) as factors to quantify evidence in favour of the null effect. BF01 was 4.14 for the main effect of Cue, 6.37 for FP, 4.58 for Compatibility, and 4.1 for the Cue × Compatibility interaction. The BF01 values for other interactions were also substantial (BF01 > 4). We can thus accept a lack of effect of temporal predictability on the activation of the correct response with a fair degree of certainty.

To further examine the role of contralateral motor cortex in performing motor acts at temporally predictable moments, we measured phase locking in the delta-theta frequency range over the contralateral motor cortex, which has been proposed as a

marker of response execution (Popovych et al., 2016). Importantly, our EMG-coupled analysis enabled us to precisely trace neural activity after EMG onset, reflecting later stages of motor processing. These analyses are presented at the end of the Results section.

Incorrect response inhibition

A priori, we hypothesised that temporal predictability would selectively weaken cortical inhibition of the incorrect hand when participants were reacting to conflicting targets. To test our hypothesis, we performed a slope analysis of the positive-going CSD-transformed wave developing over the motor cortex contralateral to the incorrect response hand just prior to EMG onset (time window: -200 ms to 0 time-locked to the EMG onset).

First, we found a main effect of compatibility, F(1, 22) = 8.42, p = 0.008, η_p^2= 0.28. An increased positivity over the motor cortex involved in inhibiting the incorrect response indicated that potentially erroneous responses were more strongly inhibited for incompatible than compatible targets. Most importantly, the data revealed a pattern of results consistent with our hypothesis. Cortical inhibition was affected by an interaction between Cue and Compatibility, F(1, 22) = 6.2, p = 0.021, η_p^2= 0.22 (Fig. 6) Planned comparisons revealed that inhibition of the incorrect hand was weaker (i.e., less positive-going slope) when participants were reacting to temporally predictable incompatible targets, F(1, 22) = 10.2, p = 0.004, η_p^2= 0.32 (Fig. 6D). Strikingly, however, we obtained the opposite pattern for compatible trials. Here, inhibition was stronger (i.e., more positive-going slope) for temporally predictable targets, F(1, 22) = 5.25, p = 0.032, η_p^2= 0.19. These results indicate that temporal predictability acts by selectively engaging cortical motor inhibitory processes that are necessary for keeping an incorrect response in check. Notably, temporal predictability yields dissociable effects on cortical inhibition depending on whether or not response choices necessitate suppression of conflicting actions. This dissociation is the critical aspect of our findings, and is consistent with the behavioural benefits of temporal predictability for non-competing actions (paralleled by stronger motor cortex inhibition) as well as its costs for competing actions (paralleled by weaker motor cortex inhibition). In line with our interpretation of the data, there was a trend for a positive correlation between the relative strength of motor inhibition in temporal versus neutral (T-N) compatible trials (z-scored) and the normalised premotor time temporal benefit (N-T/N) in compatible trials (log-transformed, z-scored) (rs(21) = .327, p = .064, one-tailed). In other words, the stronger the motor cortex inhibition in temporal relative to neutral compatible trials, the greater the behavioural benefit of temporal cues. In parallel, we also found a trend for a negative correlation between the relative strength of motor cortex inhibition in temporal versus neutral (T-N) incompatible trials (z-scored) and the costs of temporal cues (T-N) on error rate in incompatible trials (z-scored) (rs(21) = -.299, p = .082, one-tailed). In other words, the weaker the motor cortex inhibition in temporal relative to neutral incompatible trials, the greater the behavioural cost of temporal cues on accuracy. No main effect of cue, F(1, 22) = 0.56, p = 0.463, η_p^2= 0.03, FP, F(1, 22) = 1.02, p = 0.324, η_p^2= .04 nor a FP × Compatibility, F(1, 22) = 2.17, p = 0.155, η_p^2= 0.09, or a Cue × FP × Compatibility F(1, 22) = 0.74, p = 0.40, η_p^2= 0.03 interactions was found.

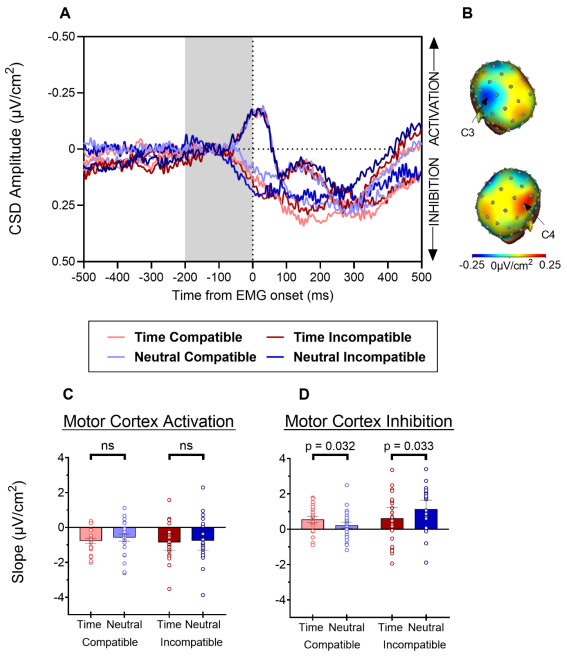


Figure 6: CSD-transformed group-averaged activity recorded over motor cortex involved in activation of the correct hand and inhibition of the incorrect hand, time-locked to EMG onset. (A) The time-course of response activation in contralateral motor cortex (negative-going slope) and inhibition in ipsilateral motor cortex (positive-going slope) for neutral compatible (light blue), temporal compatible (light red), temporal incompatible (dark red) and neutral incompatible (dark blue) conditions. (B) Topographies (CSD) at EMG onset for motor cortex activation (recorded over the C3 electrode) and motor cortex inhibition (recorded over the C4 electrode). Note that data from both response hands were collapsed such that C3 always reflects the electrode contralateral to the response hand (activation), whereas C4 reflects the electrode ipsilateral to the response hand (inhibition). (C) Statistical analysis of the slopes failed to reveal any significant effects of temporal predictability on contralateral motor cortex activation. (D) By contrast, temporal predictability yielded dissociable effects on ipsilateral motor cortex inhibition. Slopes were less negative-going for the temporal versus neutral condition, demonstrating weaker inhibition of the incorrect hand when responding to timely but conflicting targets. In turn, a different pattern was observed for compatible targets: the slopes were steeper for temporal compatible than neutral compatible trials, indicating stronger inhibition of the incorrect hand when reacting to temporally predictable, non-conflicting targets. Error bars reflect standard errors.

Phase locking over contralateral motor cortex

In order to further explore the role of contralateral motor cortex in temporally-guided action control, we conducted a complementary phase-locking analysis. Importantly, we focused on neural processes at the later stages of motor processing (i.e., execution of the correct response). More specifically, we measured the inter-trial phase coherence (ITPC, also referred to as a phase-locking factor or PLF) over the motor cortex contralateral to the correct response (i.e., over C3) in the time window corresponding to response implementation (0-300 ms after EMG onset) (Fig. 7). We primarily focused on the delta (1-4 Hz) and theta (4-7 Hz) frequency bands, which have been reported to

index preparation and execution of movement (Popovych et al., 2016). Since the delta phase in motor cortex has been demonstrated to be modulated by task load (Saleh, Reimer, Penn, Ojakangas, & Hatsopoulos, 2010), such that a more difficult task is accompanied by less variable phase consistency, we expected to observe stronger (i.e., less variable) phase consistency across trials in incompatible versus compatible conditions.

Delta phase locking.. As expected, the analysis of ITPC revealed a significant effect of compatibility, F(1, 22) = 9.20, p = 0.006, η_p^2= 0.30. ITPC was stronger in incompatible than compatible trials. Intriguingly, however, there was a significant interaction between Cue and Compatibility, F(1, 22) = 4.66, p = 0.042, η_p^2= 0.18. Post-hoc comparisons showed that in incompatible trials, phase locking was stronger following temporal rather than neutral cues (p = 0.050, uncorrected, Cohen's d = 0.41, 95% CI [0.001, 0.05). In contrast, no difference between temporal and neutral conditions was observed for compatible trials (p = 0.703). No other significant effects were identified. These results indicate that phase locking of low-frequency oscillations plays a functional role in the reaction to temporally predictable incompatible targets. In order to better understand the role of delta phase locking in action control, we used Spearman's correlation to examine the relationship between delta ITPC effects and motor time, which temporally overlap. We found a positive correlation between the relative strength of delta ITPC for incompatible versus compatible trials (I-C, z-scored) and motor time for incompatible versus compatible trials (I-C, z-scored). In other words, stronger delta ITPC for incompatible versus compatible trials was accompanied by longer motor times (rs(21) = .360, p = .046, one-tailed). We also ran a correlation between the N-40 effect (incompatible-compatible) and the delta ITPC (incompatible-compatible) at the participant-level. Results of the Spearman correlation indicated that these two measures were unrelated (rs(21) = .005, p = .984).

Theta phase locking.. The analysis of ITPC showed a main effect of compatibility, F(1, 22) = 17.57, p < 0.001, η_p^2= 0.44. ITPC was stronger for incompatible than compatible conditions indicating increased theta phase locking when executing a response under a situation of conflict. The interaction between Cue and Compatibility was non-significant, F(1, 22) = 1.24, p = 0.278, η_p^2= 0.05. These results demonstrate that although theta phase consistency is modulated by response conflict, it remains insensitive to the temporal predictability of events. No other significant effects were observed.

DISCUSSION

Performance benefits of temporal predictability have been repeatedly observed in simple RT detection tasks: if we know when an event is likely to happen we can respond to it more quickly and more accurately (Nobre & van Ede, 2018). However, events in our environment often trigger competing, and sometimes inappropriate, actions and temporal predictability

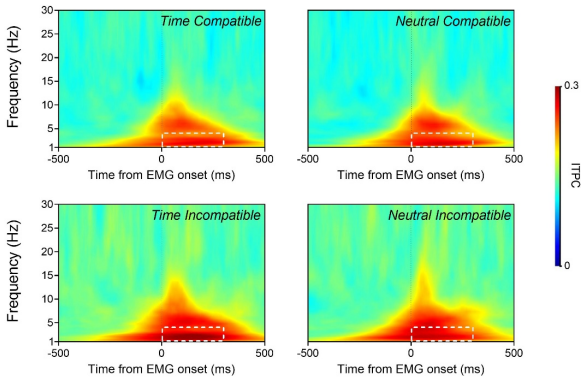


Figure 7: Inter-trial phase coherence (ITPC) over the primary motor cortex involved in response execution, time-locked to EMG onset. ITPC was calculated at the C3 electrode for the time period from 0 to 300 ms after the onset of the EMG, which corresponds to response implementation. Phase consistency in the delta frequency band was stronger for incompatible than compatible targets. Importantly, temporal predictability exacerbated this effect leading to even stronger phase locking when participants were reacting to incompatible targets. No differences between temporal and neutral conditions were observed for compatible trials. In turn, although ITPC in the theta range was stronger for incompatible than compatible targets, it remained unaffected by temporal predictability.

can actually impair performance when prepotent, yet undesirable, responses need to be inhibited in favour of more intentional ones (Correa et al., 2010; Korolczuk et al., 2018, 2020; Menceloglu et al., 2021). Yet, the neural mechanisms underlying the dual nature of the effects of temporal predictability on behaviour are unknown. We therefore used combined EEG-EMG recordings to probe activity of cortical regions involved in generating appropriate responses, or in inhibiting erroneous ones, to temporally predictable targets whose features either induced response conflict (incompatible targets) or not (compatible targets).

Although we expected the temporal predictability of compatible targets to increase activation over the contralateral motor cortex, our findings did not support this hypothesis. Activation over motor cortex involved in generating the correct response was unaffected by temporal predictability, regardless of whether response choices induced a response conflict or not. Notably, however, this null effect does not contradict previous findings that temporal prediction increases motor activation (Miniussi et al., 1999; Van Elswijk, Kleine, Overeem, & Stegeman, 2007). In fact, most studies examining the neural bases of temporal predictability used simple RT tasks in which the participant could prepare their motor response in advance. For example, a recent EEG study has shown modulatory effects of temporal prediction on effector-specific preparatory motor activity (i.e., before target presentation) when the probability of the hand to be used was known in advance (Volberg & Thomaschke, 2017). In contrast, in our choice RT task, the motor response could not be prepared in advance. Thus, a lack of effect on the motor cortex involved in activating the correct response suggests that temporal cueing does not flexibly modulate motor activation within the time course of the action (after

target presentation).

On the contrary, our data revealed a striking modulation of the inhibitory wave over the motor cortex involved in suppressing the incorrect response agonist, which varied as a function of response conflict. For non-conflicting responses to compatible targets, motor cortex inhibition of the incorrect hand was stronger when targets were temporally predictable, suggesting that the benefits of temporal predictability might originate from greater cortical inhibition of the incorrect response agonist right before response initiation. By contrast, when a goal-directed response required prepotent but erroneous tendencies to be suppressed, cortical inhibition of the incorrect hand was weaker for temporally predictable targets. Such attenuation of cortical inhibition for events that are temporally predictable, yet induce response conflict, is in line with previously published behavioural and EMG data (Korolczuk et al., 2018, 2020) demonstrating increased impulsive responding to such events. More importantly, the opposing effects of temporal predictability on the inhibition over ipsilateral motor cortex as a function of response conflict provides the neural mechanism underlying both the behavioural benefits and costs of temporal predictability in a choice response context. The temporal predictability of target onset attenuates inhibition over the (ipsilateral) motor cortex associated with an incorrect response if the target induces response conflict, thereby impairing performance. On the other hand, temporal predictability increases cortical inhibition for non-conflicting targets, thereby improving performance. Finally, given that in our task one could not predict which hand would be recruited before target occurrence, these results indicate that temporal predictability flexibly modulates inhibitory processes within the time course of the action in a highly specific way, rather than inducing an a priori global bias to increase or decrease inhibition.

Cortical EEG recordings were complemented by concurrent EMG measurements, which further unveiled otherwise hidden effects of temporal predictability on distinct stages of the motor command. Direct assessment of motor processes at the peripheral level revealed that faster responses to temporally predictable compatible targets originate from speeded premotor, rather than motor, times. It seems plausible that such an effect stems from stronger cortical inhibition of the incorrect hand, which then allows for downstream speeding in the initiation of the correct, goal-directed response. Rapid movement initiation at predictable moments in time has been observed in other reports (Menceloglu et al., 2021) and constitutes an important peripheral mechanism of temporal prediction. Of course, premotor time reflects many processes other than just response initiation, spanning from target identification to response selection and preparation. Indeed, formal modelling and electrophysiological data indicate that temporal predictability can accelerate the onset of the decision in simple RT detection tasks (Bausenhart, Rolke, Seibold, & Ulrich, 2010; van den Brink, Murphy, Desender, de Ru, & Nieuwenhuis, 2021) and the speed of perceptual processing and accumulation of sensory evidence in choice discrimination tasks (Vangkilde et al, 2012; Rohenkohl et al, 2012). However, thus far, these effects have only ever been modelled for non-conflict response choice tasks. It would be

Table 1: Summary of EEG and EMG results

Variables	Electrode site	Time window	Modulated by temporal prediction	Effect of temporal prediction
Premotor time (PMT)	Over the flexor pollicis brevis	Between target onset and EMG onset	Yes / compatible trials only	Faster PMT in compatible trials
Motor time (MT)	Over the flexor pollicis brevis	Between EMG onset and response	No	N/A
CNV	FCz	-300 ms to 0 before target onset	Yes	More negative amplitude at the short FP after temporal versus neutral cues
N-40	FCz	-100 ms to 0 before EMG onset	No	N/A
Motor activation	C3 (contralateral to response)	-200 ms to 0 before EMG onset	No	N/A
Motor inhibition	C4 (ipsilateral to response)	-200 ms to 0 before EMG onset	Yes / compatible & incompatible trials	- Stronger inhibition of incorrect hand in compatible trials - Weaker inhibition of incorrect hand in incompatible trials
Delta ITPC	C3 (contralateral to response)	0 to 300 ms after EMG onset	Yes / incompatible trials only	Increased ITPC in incompatible trials
Theta ITPC	C3 (contralateral to response)	0 to 300 ms after EMG onset	No	N/A

informative in future to model distinct sensory, decisional and motor components of response choice in situations of response conflict.

Although peripheral EMG recordings failed to reveal an effect of temporal predictability on the speed of motor times, we nevertheless sought to fully explore the possibility that temporal predictability could affect motor execution processes at the cortical level. Previous studies have found that movement execution is accompanied by phase-locking in delta and theta ranges over contralateral motor cortex (Popovych et al., 2016). We therefore supplemented our analysis of motor cortex activity prior to movement initiation by also assessing the variability of the cortical motor command over contralateral motor cortex during response execution. Importantly, and in contrast to previous reports (Popovych et al., 2016), in the current study we could precisely define when movement execution started by synchronising EEG activity to EMG onset. We found that delta and theta phase-locking over contralateral motor cortex was stronger (i.e., activity was less temporally variable) when goal-directed actions were executed in situations of response conflict. These findings are in line with local field potential data showing stronger delta phase-locking in human motor cortex (and specifically in the M1) for more demanding tasks (Saleh et al., 2010). More importantly, however, our results demonstrated that temporal predictability interacted with target compatibility, inducing even greater delta phase-locking when responses were executed under situations of response conflict. This effect suggests that temporal predictability imposes even greater difficulty when target characteristics trigger two conflicting response alternatives. Crucially, it also indicates that although inhibition over the ipsilateral motor cortex (which controls the incorrect response effector) is differentially modulated by temporal predictability prior to the initiation of the response, the activity over contralateral motor cortex (which controls the correct response effector) is modulated by temporal predictability at later stages of response implementation. This modulation is, however, restricted to the cortical level, at which response execution might be monitored, and does not extend to peripheral (motor time) measures of response execution. Finally, our findings further support the functional importance of delta phase in the behavioural effects of temporal predictability (Arnal, Doelling, & Poeppel, 2015; Morillon, Arnal, Schroeder, & Keitel, 2019; Morillon & Baillet, 2017). In particular, we add to literature showing that adjustments in the phase of delta oscillations mediate even non-rhythmic temporal predictions (Breska & Deouell, 2017; Daume, Wang, Maye, Zhang, & Engel, 2021) by demonstrating increased delta phase-locking when target onset-time could be predicted by an arbitrary visual cue.

Perhaps counterintuitively, and in contrast to previous postulations (Correa et al., 2010; Menceloglu et al., 2021), our data did not support the notion that the behavioural costs of temporal predictability originate from detrimental effects on response selection processes. Although the frontocentral N-40 component occurring tens of milliseconds before response initiation was indeed more pronounced when a conflicting response was selected, this effect was not further modulated by temporal cueing. In a recent study, Menceloglu et al. (2021) observed that during a reaching task, temporal predictability increased the curvature toward an incorrect response when participants were responding to conflicting targets, indicating greater co-activation of competing actions during response selection (Erb, Moher, Sobel, & Song, 2016). Although at first glimpse, these results might appear contradictory to our findings, they in fact suggest a similar pattern of data with an increased number of partial errors (which cannot be separated from correct responses in reaching tasks) when acting at temporally predictable moments (Korolczuk et al., 2020). Yet, the characteristics of the tasks and methods employed in these investigations need to be taken into consideration. Whereas in Menceloglu et al. (2021), participants reached towards the direction of the flanker's arrow by moving a mouse to either the left or right side of the screen, our task required participants to give a speeded response using left or right response buttons while muscular activity was continually recorded. Thus, unlike Menceloglu et al. (2021), we measured an index of response selection that occurs in the brain immediately before the response is even initiated. Nevertheless, given the multifaceted nature of action control mechanisms, it might be necessary to employ different methodological approaches to explore the nuances of the dynamic interplay of time and action.

To summarise, we aimed to examine the neural bases of the benefits of temporal predictability for non-conflicting actions (e.g., speeded RTs) as well its costs for conflicting ones (e.g., more fast errors). We provide evidence that temporal predictability functionally modulates inhibitory circuits over the motor cortex involved in suppression of incorrect actions. Most importantly, temporal prediction modulates these inhibitory pathways in a context-specific manner depending on whether the target elicits, or not, conflicting response alternatives. This elegant mechanism, which operates selectively over the motor cortex involved in inhibition of inappropriate responses just before response initiation, underlies both the behavioural benefits and costs of temporal predictability in a choice response context.

Acknowledgments

All participants gave written informed consent, and the study was approved by the Comité de Protection des Personnes Sud Méditerranée 1 in Marseille (Protocol No. AFFSAPS B100968-30). Reprint requests should be sent to Inga Korolczuk, Laboratoire de Neurosciences Cognitives UMR 7291, Aix-Marseille University, CNRS, 3 Place Victor Hugo, 13331 Marseille cedex 3, France, or via e-mail: inga.korolczuk@univ-amu.fr.

Funding Information

This work was supported by the Polish Ministry of Science and Higher Education grant (0050/DIA/2016/45) and by a postdoctoral fellowship from the Fyssen Foundation awarded to Inga Korolczuk. It has also received support from the French government under the Programme "Investissements d'Avenir", Initiative d'Excellence d'Aix-Marseille Université via A*Midex

funding (AMX-19-IET-004), and ANR (ANR-17-EURE-0029). The funding source had no impact on any part of the present study.

REFERENCES

Arnal, L. H., Doelling, K. B., & Poeppel, D. (2015). Delta-beta coupled oscillations underlie temporal prediction accuracy. *Cerebral Cortex, 25*(9), 3077–3085. https://doi.org/10.1093/cercor/bhu103

Babiloni, F., Babiloni, C., Fattorini, L., Carducci, F., Onorati, P., & Urbano, A. (1995). Performances of surface Laplacian estimators: A study of simulated and real scalp potential distributions. *Brain Topography, 8*(1), 35–45. https://doi.org/10.1007/BF01187668

Bausenhart, K. M., Rolke, B., Seibold, V. C., & Ulrich, R. (2010). Temporal preparation influences the dynamics of information processing: Evidence for early onset of information accumulation. *Vision Research, 50*(11), 1025–1034. https://doi.org/10.1016/j.visres.2010.03.011

Botwinick, J., & Thompson, L. W. (1966). Premotor and motor components of reaction time. *Journal of Experimental Psychology, 71*(1), 9–15. https://doi.org/10.1037/h0022634

Breska, A., & Deouell, L. Y. (2014). Automatic Bias of Temporal Expectations following Temporally Regular Input Independently of High-level Temporal Expectation. *Journal of Cognitive Neuroscience, 26*(3). https://doi.org/10.1162/jocn

Breska, A., & Deouell, L. Y. (2017). Neural mechanisms of rhythm-based temporal prediction: Delta phase-locking reflects temporal predictability but not rhythmic entrainment. *PLoS Biology, 15*(2), 1–30. https://doi.org/10.1371/journal.pbio.2001665

Burle, B., Possamaï, C.-A., Vidal, F., Bonnet, M., & Hasbroucq, T. (2002). Executive control in the Simon effect: an electromyographic and distributional analysis. *Psychological Research, 66*(4), 324–336. https://doi.org/10.1007/s00426-002-0105-6

Burle, B., Spieser, L., Roger, C., Casini, L., Hasbroucq, T., & Vidal, F. (2015). Spatial and temporal resolutions of EEG: Is it really black and white? A scalp current density view. *International Journal of Psychophysiology, 97*(3), 210–220. https://doi.org/10.1016/j.ijpsycho.2015.05.004

Burle, B., van den Wildenberg, W. P. M., Spieser, L., & Ridderinkhof, K. R. (2016). Preventing (impulsive) errors: Electrophysiological evidence for online inhibitory control over incorrect responses. *Psychophysiology, 53*(7), 1008–1019. https://doi.org/10.1111/psyp.12647

Burle, B., Vidal, F., Tandonnet, C., & Hasbroucq, T. (2004). Physiological evidence for response inhibition in choice reaction time tasks. *Brain and Cognition, 56*(2), 153–164. https://doi.org/10.1016/j.bandc.2004.06.004

Carbonnell, L., Ramdani, C., Meckler, C., Burle, B., Hasbroucq, T., & Vidal, F. (2013). The N-40: An electrophysiological marker of response selection. *Biological Psychology, 93*(1), 231–236. https://doi.org/10.1016/j.biopsycho.2013.02.011

Correa, Á., Cappucci, P., Nobre, A. C., & Lupiáñez, J. (2010). The two sides of temporal orienting: Facilitating perceptual selection, disrupting response selection. *Experimental Psychology, 57*(2), 142–148. https://doi.org/10.1027/1618-3169/a000018

Correa, Á., Lupiáñez, J., & Tudela, P. (2006). The attentional mechanism of temporal orienting: Determinants and attributes. *Experimental Brain Research, 169*(1), 58–68. https://doi.org/10.1007/s00221-005-0131-x

Coull, J. T., & Nobre, A. C. (1998). Where and when to pay attention: the neural systems for directing attention to spatial locations and to time intervals as revealed by both PET and fMRI. *Journal of Neuroscience, 18*(18), 7426–7435. https://doi.org/0270-6474/98/187426-10$05.00/0

Daume, J., Wang, P., Maye, A., Zhang, D., & Engel, A. K. (2021). Non-rhythmic temporal prediction involves phase resets of low-frequency delta oscillations. *NeuroImage, 224*, 117376. https://doi.org/10.1016/j.neuroimage.2020.117376

Erb, C. D., Moher, J., Sobel, D. M., & Song, J. H. (2016). Reach tracking reveals dissociable processes underlying cognitive control. *Cognition, 152*, 114–126. https://doi.org/10.1016/j.cognition.2016.03.015

Gevins, A. (1989). Dynamic functional topography of cognitive tasks. *Brain Topography, 2*(1–2), 37–56. https://doi.org/10.1007/BF01128842

Gramfort, A., Luessi, M., Larson, E., Engemann, D. A., Strohmeier, D., Brodbeck, C., … Hämäläinen, M. (2013). MEG and EEG data analysis with MNE-Python. *Frontiers in Neuroscience, 7*, 1–13. https://doi.org/10.3389/fnins.2013.00267

Hasbroucq, T., Akamatsu, M., Burle, B., Bonnet, M., & Possamaï, C. A. (2000). Changes in spinal excitability during choice reaction time: The H reflex as a probe of information transmission. *Psychophysiology, 37*(3), 385–393. https://doi.org/10.1017/S0048577200982052

Hasbroucq, T., Akamatsu, M., & Seal, J. (1995). Finger pairings in two-choice reaction time tasks: Does the between-hands advantage reflect response preparation? *Journal of Motor Behavior, 27*(3), 251–262. https://doi.org/10.1080/00222895.1995.9941715

Herrmann, C. S., Rach, S., Vosskuhl, J., & Strüber, D. (2014). Time-frequency analysis of event-related potentials: A brief tutorial. *Brain Topography, 27*(4), 438-450. https://doi.org/10.1007/s10548-013-0327-5

Hodges, P. W., & Bui, B. H. (1996). A comparison of computer-based methods for the determination of onset of muscle contraction using electromyography. *Electroencephalography and Clinical Neurophysiology, 101*(6), 511–519. https://doi.org/10.1016/s0013-4694(96)95190-5

Kayser, J., & Tenke, C. E. (2015). Issues and considerations for using the scalp surface Laplacian in EEG/ERP research: A tutorial review. *International Journal of Psychophysiology, 97*(3), 189–209. https://doi.org/10.1016/j.ijpsycho.2015.04.012

Korolczuk, I., Burle, B., & Coull, J. T. (2018). The costs and benefits of temporal predictability: impaired inhibition of prepotent responses accompanies increased activation of task-relevant responses. *Cognition, 179*, 102–110.

https://doi.org/10.1016/j.cognition.2018.06.006

Korolczuk, I., Burle, B., Coull, J. T., & Smigasiewicz, K. (2020). Mechanisms of impulsive responding to temporally predictable events as revealed by electromyography. *Neuroscience, 428*, 13–22. https://doi.org/10.1016/j.neuroscience.2019.12.022

Law, S. K., Rohrbaugh, J. W., Adams, C. M., & Eckardt, M. J. (1993). Improving spatial and temporal resolution in evoked EEG responses using surface Laplacians. *Electroencephalography and Clinical Neurophysiology/ Evoked Potentials, 88*(4), 309–322. https://doi.org/10.1016/0168-5597(93)90055-T

Liu, J., & Liu, Q. (2016). Use of the integrated profile for voluntary muscle activity detection using EMG signals with spurious background spikes: A study with incomplete spinal cord injury. *Biomedical Signal Processing and Control, 24*, 19–24. https://doi.org/10.1016/J.BSPC.2015.09.004

Macar, F., Vidal, F., & Casini, L. (1999). The supplementary motor area in motor and sensory timing: Evidence from slow brain potential changes. *Experimental Brain Research, 125*(3), 271–280. https://doi.org/10.1007/s002210050683

Mattes, S., & Ulrich, R. (1997). Response force is sensitive to the temporal uncertainty of response stimuli. *Perception & Psychophysics, 59*(7), 1089–1097. https://doi.org/10.3758/BF03205523

Menceloglu, M., Suzuki, S., & Song, J. H. (2021). Revealing the effects of temporal orienting of attention on response conflict using continuous movements. *Attention, Perception, and Psychophysics, 83*, 1463–1478. https://doi.org/10.3758/s13414-020-02235-4

Miniussi, C., Wilding, E. L., Coull, J. T., & Nobre, A. C. (1999). Orienting attention in time: Modulation of brain potentials. *Brain, 122*(8), 1507–1518. https://doi.org/10.1093/brain/122.8.1507

Morillon, B., Arnal, L. H., Schroeder, C. E., & Keitel, A. (2019). Prominence of delta oscillatory rhythms in the motor cortex and their relevance for auditory and speech perception. *Neuroscience and Biobehavioral Reviews, 107*, 136–142. https://doi.org/10.1016/j.neubiorev.2019.09.012

Morillon, B., & Baillet, S. (2017). Motor origin of temporal predictions in auditory attention. *Proceedings of the National Academy of Sciences, 114*(42), E8913–E8921. https://doi.org/10.1073/pnas.1705373114

Mostofsky, S., & Simmonds, D. (2008). Response inhibition and response selection: two sides of the same coin. *Journal of Cognitive Neuroscience, 20*(5), 751–761. https://doi.org/10.1162/jocn.2008.20500

Niemi, P., & Naatanen, R. (1981). Foreperiod and simple reaction time. *Psychological Bulletin, 89*(1), 133–162. https://doi.org/10.1037/0033-2909.89.1.133

Nobre, A. C., & van Ede, F. (2018). Anticipated moments: Temporal structure in attention. *Nature Reviews Neuroscience, 19*(1), 34–48. https://doi.org/10.1038/nrn.2017.141

Nobre, A. C. (2001). Orienting attention to instants in time. *Neuropsychologia, 39*(12), 1317-1328. https://doi.org/10.1016/S0028-3932(01)00120-8

Nunez, P. L., & Westdorp, A. F. (1994). The surface laplacian, high resolution EEG and controversies. *Brain Topography, 6*(3), 221–226. https://doi.org/10.1007/BF01187712

Orgogozo, J. M., & Larsen, B. (1979). Activation of the supplementary motor area during voluntary movement in man suggests it works as a supramotor area. *Science, 206*(4420), 847–850. https://doi.org/10.1126/science.493986

Peirce, J., Gray, J. R., Simpson, S., MacAskill, M., Höchenberger, R., Sogo, H., … Lindeløv, J. K. (2019). PsychoPy2: Experiments in behavior made easy. *Behavior Research Methods, 51*(1), 195–203. https://doi.org/10.3758/s13428-018-01193-y

Perrin, F., Pernier, J., & Bertrand, O. (1989). Spherical splines for scalp potential and current density mapping. *Electroencephalography and Clinical Neurophysiology, 72*(2), 184-187. https://doi.org/10.1016/0013-4694(89)90180-6

Popovych, S., Rosjat, N., Toth, T. I., Wang, B. A., Liu, L., Abdollahi, R. O., … Daun, S. (2016). Movement-related phase locking in the delta–theta frequency band. *NeuroImage, 139*, 439–449. https://doi.org/10.1016/j.neuroimage.2016.06.052

Praamstra, P., Kourtis, D., Hoi, F. K., & Oostenveld, R. (2006). Neurophysiology of implicit timing in serial choice reaction-time performance. *Journal of Neuroscience, 26*(20), 5448–5455. https://doi.org/10.1523/JNEUROSCI.0440-06.2006

Praamstra, P., & Seiss, E. (2005). The neurophysiology of response competition: Motor cortex activation and inhibition following subliminal response priming. *Journal of Cognitive Neuroscience, 17*(3), 483–493. https://doi.org/10.1162/0898929053279513

Ridderinkhof, R. K., Forstmann, B. U., Wylie, S. A., Burle, B., & van den Wildenberg, W. P. M. (2011). Neurocognitive mechanisms of action control: Resisting the call of the Sirens. *Wiley Interdisciplinary Reviews: Cognitive Science, 2*(2), 174–192. https://doi.org/10.1002/wcs.99

Saleh, M., Reimer, J., Penn, R., Ojakangas, C. L., & Hatsopoulos, N. G. (2010). Fast and slow oscillations in human primary motor cortex predict oncoming behaviorally relevant cues. *Neuron, 65*(4), 461–471. https://doi.org/10.1016/j.neuron.2010.02.001

Salomone, M., Burle, B., Fabre, L., & Berberian, B. (2021). An electromyographic analysis of the effects of cognitive fatigue on online and anticipatory action control. *Frontiers in Human Neuroscience, 14*, 1–15. https://doi.org/10.3389/fnhum.2020.615046

Santello, M., & McDonagh, M. J. (1998). The control of timing and amplitude of EMG activity in landing movements in humans. *Experimental Physiology, 83*(6), 857–874. https://doi.org/10.1113/expphysiol.1998.sp004165

Spieser, L., Servant, M., Hasbroucq, T., & Burle, B. (2017). Beyond decision! Motor contribution to speed–accuracy trade-off in decision-making. *Psychonomic Bulletin and Review, 24*(3), 950–956. https://doi.org/10.3758/s13423-016-1172-9

Tandonnet, C., Burle, B., Vidal, F., & Hasbroucq, T. (2003). The influence of time preparation on motor processes assessed by surface Laplacian estimation. *Clinical Neuro-*

physiology, 114(12), 2376–2384. https://doi.org/10.1016/S1388-2457(03)00253-0

Tandonnet, C., Burle, B., Vidal, F., & Hasbroucq, T. (2005). An electromyographic examination of response execution and inhibition in between-hand choice reaction time. *Journal of Psychophysiology, 19*(4), 330–336. https://doi.org/10.1027/0269-8803.19.4.330

Thomas, E., French, R., Alizee, G., & Coull, J. T. (2019). Having your cake and eating it: Faster responses with reduced muscular activation while learning a temporal interval. *Neuroscience, 410*, 68–75. https://doi.org/10.1016/J.NEUROSCIENCE.2019.05.003

Uusitalo, M. A., & Ilmoniemi, R. J. (1997). Signal-space projection method for separating MEG or EEG into components. *Medical and Biological Engineering and Computing, 35*(2), 135–140. https://doi.org/10.1007/BF02534144

van Casteren, M., & Davis, M. H. (2006). Mix, a program for pseudorandomization. *Behavior Research Methods, 38*(4), 584–589. https://doi.org/10.3758/BF03193889

van den Brink, R. L., Murphy, P. R., Desender, K., de Ru, N., & Nieuwenhuis, S. (2021). Temporal expectation hastens decision onset but does not affect evidence quality. *The Journal of Neuroscience, 41*(1), 130–143. https://doi.org/10.1523/JNEUROSCI.1103-20.2020

Van der Lubbe, R. H. J., Los, S. A., Jaśkowski, P., & Verleger, R. (2004). Being prepared on time: On the importance of the previous foreperiod to current preparation, as reflected in speed, force and preparation-related brain potentials. *Acta Psychologica, 116*(3), 245–262. https://doi.org/10.1016/j.actpsy.2004.03.003

Van Elswijk, G., Kleine, B. U., Overeem, S., & Stegeman, D. F. (2007). Expectancy induces dynamic modulation of corticospinal excitability. *Journal of Cognitive Neuroscience, 19*(1), 121–131. https://doi.org/10.1162/jocn.2007.19.1.121

Vidal, F., Burle, B., Grapperon, J., & Hasbroucq, T. (2011). An ERP study of cognitive architecture and the insertion of mental processes: Donders revisited. *Psychophysiology, 48*(9), 1242–1251. https://doi.org/10.1111/j.1469-8986.2011.01186.x

Vidal, F., Burle, B., Spieser, L., Carbonnell, L., Meckler, C., Casini, L., & Hasbroucq, T. (2015). Linking EEG signals, brain functions and mental operations: Advantages of the Laplacian transformation. *International Journal of Psychophysiology, 97*(3), 221–232. https://doi.org/10.1016/j.ijpsycho.2015.04.022

Vidal, F., Grapperon, J., Bonnet, M., & Hasbroucq, T. (2003). The nature of unilateral motor commands in between-hand choice tasks as revealed by surface Laplacian estimation. *Psychophysiology, 40*(5), 796–805. https://doi.org/10.1111/1469-8986.00080

Woolsey, C. N., Settlage, P. H., Meyer, D. R., Spencer, W., Hamuy, T. P., & Travis, A. M. (1952). Patterns of localisation in precentral and "supplementary" motor areas and their relation to the concept of a premotor area. *Research Publications- Association for Research in Nervous and Mental Disease, 30*, 238–264.