Time for Action: Neural Basis of the Costs and Benefits of Temporal Predictability for Competing Response Choices

Inga Korolczuk1,2, Boris Burle1, Jennifer T. Coull1, and Kamila Śmigasiewicz1

Abstract

The brain can anticipate the time of imminent events to optimize sensorimotor processing. Yet, there can be behavioral 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 intertrial 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 behavioral benefits of temporal predictability for nonconflicting 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.

INTRODUCTION

We often predict the temporal flow of external events to optimally guide our actions in accordance with current goals. The ability to utilize temporal information in the service of adaptive behavior is typically investigated with tasks requiring simple responses to unambiguous targets, and accurate temporal prediction has been repeatedly demonstrated to optimize motor processes (Thomas, French, Alizée, & Coull, 2019; Van der Lubbe, Los, Jaśkowski, & Verleger, 2004; Nobre, 2001; Coull & Nobre, 1998; Mattes & Ulrich, 1997). 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 (Menceloglu, Suzuki, & Song, 2021; Correa, Cappucci, Nobre, & Lupiáñez, 2010). 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, & Śmigasiewicz, 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 behavior in a dynamically changing world. These fundamental motor mechanisms involve the activation of an appropriate response and inhibition of an erroneous one (Ridderinkhof, Forstmann, Wylie, Burle, & van den Wildenberg, 2011; Mostofsky & Simmonds, 2008; Burle, Vidal, Tandonnet, & Hasbroucq, 2004). Indeed, when response choices necessitate inhibition of erroneous responses along with the activation of an appropriate one (e.g., in bimanual choice RT 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, whereas excitability of structures controlling the incorrect response decreases (Burle, Possamaï, Vidal, Bonnet, & Hasbroucq, 2002; Hasbroucq, Akamatsu, Burle, Bonnet, & Possamaï, 2000; see the work of 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., Praamstra & Seiss, 2005; Burle et al., 2004; Vidal, Grapperon, Bonnet, & Hasbroucq, 2003) by using current source density (CSD) through surface Laplacian estimation (Burle et al., 2015; Vidal et al., 2015; Babiloni et al., 1995; Nunez & Westdorp, 1994). 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 (Kayser & Tenke, 2015; Gevins, 1989). 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 et al., 2003). In parallel, a positive wave over the motor cortex ipsilateral to the response agonist corresponds to inhibition of the incorrect hand (Burle, van den Wildenberg, Spieser, & Ridderinkhof, 2016; Burle et al., 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 noncompeting 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 RTs into premotor times (PMTs; interval from target onset to EMG-locked response onset) and motor times (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 because of 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 msec before the onset of the EMG activity and so is termed the N40 component (Carbonnell et al., 2013; Vidal, Burle, Grapperon, & Hasbroucq, 2011; Vidal et al., 2005). This negative activity, likely generated by the SMA, is modulated by response choice demands (Carbonnell et al., 2013). Specifically, the N40 is larger for competing than noncompeting responses. Although the neural origins of the “activation/inhibition” pattern and the N40 are different, their exact functional relationship is still not well understood. In general, the N40 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 behavioral reports have revealed the detrimental effects of temporal predictability on response selection when a competing, erroneous response must be inhibited (Menceloglu et al., 2021; Korolczuk et al., 2018; Correa et al., 2010), 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 analyzing the role of N40 activity when participants were reacting to temporally predictable conflicting (or nonconflicting) 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 behavior. 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 hypothesized that faster RTs to temporally predictable events are because of a speeded MT, rather than speeded PMT. In other words, we expected that temporal predictability would facilitate the execution of the action. Second, we hypothesized 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, because SMA-driven ramping activity is less pronounced for less “effortful” responses (e.g., in compatible rather than incompatible trials), we hypothesized the N40 would be even further attenuated when compatible targets were temporally predictable versus unpredictable. In contrast, the N40 might be more pronounced when incompatible targets are temporally predictable, reflecting the difficulty of suppressing an inappropriate response in favor 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 women) 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 because of technical problems, high error rate (±2 SDs of the group average), or slow RTs (±2 SDs of the group average). Thus, the final sample was composed of 23 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 (Figure 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 on either 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 msec) whereas brightening of the larger, outer circle informed participants that a target would occur after a longer delay (1400 msec). These temporal cues were 100% valid. Participants 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 (Figure 1). Participants pressed one of them with their thumb as quickly as possible after target appearance.

The trial structure was as follows. The cue (T or N) appeared for 500 msec. The background display was then presented either for a short (600 msec) or long (1400 msec) FP. The target appeared for 100 msec, after which the participants gave a lateralized response within a 1100-msec time window. Finally, the background display appeared for an intertrial interval (ITI) that was selected randomly.
from a uniform distribution between 900 and 1400 msec (random jitter of 100 msec).

There were 192 trials for each of eight 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 three consecutive blocks, in an 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 randomized using Mix software (van Casteren & Davis, 2006). Before an experimental session, participants completed a training session of 60 trials to familiarize themselves with the task.

EMG and EEG Recordings

Electrophysiological data were recorded continuously from 64 Ag/AgCl active pre-amplified electrodes at a rate of 1024 Hz (analogue bandwidth limit: from direct current to 268 Hz, −3 dB at 1/5th of the sampling rate). The electrodes were placed according to the extended 10–20 convention (Biosemi Inc.). The 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 electrodes (Biosemi Inc.) positioned 2 cm apart on the thenar eminence.

EMG and EEG Preprocessing

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

The onsets and offsets of EMG activity were detected using a customized 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 naive 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 analyzing only their behavioral 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. Because subsequent analysis steps included the CSD 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 the work of 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: PMT (time from target onset to EMG onset) and MT (time from EMG onset to mechanical response; Figure 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.

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 to 1600 msec relative to cue onset for short FP trials, and from −500 to 2400 msec for long FP trials. A precise interval from −200 msec 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 to 1100 msec after cue onset for short FP trials, and from 1600 to 1900 msec 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 analyzing the N40 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 to 500 msec time-locked to EMG onset. The
interval from −500 to −300 msec before EMG onset was used as a baseline. Then, the data were averaged for each of eight experimental conditions. The CSD computation was performed using BrainVision Analyzer 2.0 (Brain Products). 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° for the Legendre polynomial. The unit of EEG activity was μV/cm² (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 msec to 0 relative to the onset of the EMG. Peak values were analyzed 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 to 500 msec 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 to 0 msec, 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 customized Python script (www.python.org). The slopes were then analyzed 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 correlations to explore the relationship between performance and electrophysiological activity. Specifically, we correlated the normalized PMT 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 the work of 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 −2000 to 2500 msec relative to EMG onset. A continuous wavelet transformation (Morlet wavelet, length of four cycles) was applied to single-trial data for the frequency range 1–50 Hz, in 1-Hz steps, to calculate complex values. The intertrial phase coherence (ITPC) was computed by averaging the normalized 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 intertrial phase variability that is independent of the amplitude of oscillatory activity (Herrmann, Rach, Vosskuhl, & Strüber, 2014). These data were epoched from −500 to 500 msec 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 msec 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 correlations to explore the relationship between the relative strength of delta ITPC for incompatible versus compatible trials (I−C, z-scored) and MT for incompatible versus compatible trials (I−C, z-scored).

RESULTS

Behavioral 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, which shows the probability of the correct EMG activation as a function of latency, can be found in the work of Korolczuk et al. (2020).

Response Time Fractionation: PMT and MT

Although temporal predictability exacerbated impulsive responding, it also led to performance benefits such as faster correct RTs. To investigate whether these speeded responses were because of faster response initiation or more efficient motor execution, we analyzed PMT and MT.

As expected, PMT 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 PMT, \( F(1, 22) = 92.53, p < .001, \eta^2 = .81 \). PMTs were faster for compatible than incompatible targets. Results also showed a main effect of Cue, \( F(1, 22) = 5.63, p = .027, \eta^2 = .20 \), with faster PMTs after a temporal versus neutral cue. Importantly, there was a Cue × Compatibility interaction, \( F(1, 22) = 5.07, p = .035, \eta^2 = .19 \). The interaction was broken down by compatibility (Figure 3). Participants initiated their responses earlier when temporally cued, but only in compatible conditions (\( p = .04 \), Tukey-corrected, Cohen’s \( d = 0.56, 95\% \text{ CI} [21.9, 2.8] \)). On the contrary, no temporal cueing benefit was present when responding to incompatible targets (\( p = .324 \), 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 nonconflicting events. The Cue × FP interaction did not reach statistical significance, \( F(1, 22) = 3.41, p = .078, \eta^2 = .13 \). This may seem surprising because the RT benefits of temporal cues in simple (detection) RT tasks are greatly reduced at long FPs because of 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 (Korolczuk et al., 2018, 2020; Correa, Lupiáñez, & Tudela, 2006). No main effect of FP, \( F(1, 22) = 2.72, p = .113, \eta^2 = .11 \), nor an FP × Compatibility interaction, \( F(1, 22) = 0.60, p = .448, \eta^2 = .03 \), was found. In contrast, the analysis of MTs failed to reveal a main effect of Cue, \( F(1, 22) = 0.04, p = .834, \eta^2 = .002 \), or a Cue × Compatibility interaction, \( F(1, 22) = 1.23, p = .280, \eta^2 = .05 \). In other words, temporal cueing did not affect motor execution. Confirming previous results (Tandonnet, Burle, Vidal, & Hasbroucq, 2005; Hasbroucq, Akamatsu, & Seal, 1995), we found a main effect of FP, \( F(1, 22) = 20.22, p < .001, \eta^2 = .48 \), with faster MTs after short versus long FPs. Finally, a main effect of Compatibility, \( F(1, 22) = 7.22, p = .013, \eta^2 = .25 \), revealed that MT was slower for compatible than incompatible trials, although this was qualified by an FP × Compatibility interaction, \( F(1, 22) = 4.74, p = .041, \eta^2 = .18 \). MT was slower in compatible versus incompatible conditions only for long \( (p = .008, \text{Tukey-corrected}, \text{Cohen’s} d = 0.638, 95\% \text{ CI} [0.7, 3.9]) \), but not short, FP trials \( (p = .681, \text{Tukey-corrected}) \). These results are difficult to interpret. No other significant effects were identified. In summary, and importantly for our research question, the results of the ANOVA revealed that temporal cueing did not modulate MT. 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 Bayes factor [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 MT.

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 msec to 0 before 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 & Näätänen, 1981), we compared the averaged CNV amplitude before onset of the short FP target and long FP target separately. As predicted by prior investigations (Breska & Deouell, 2014, 2017; Praamstra, Kourtis, Hoi, & Oostenveld, 2006; Macar, Vidal, & Casini, 1999; Miniussi, Wilding, Coull, & Nobre, 1999), 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, $t(22) = 2.24$, $p = .018$, one-tailed, Cohen's $d = 0.47$, 95% CI [inf, −0.2] (Figure 4A). By contrast, in the long FP trials, the difference in CNV amplitude between temporal and neutral conditions did not reach significance, $t(22) = 0.45$, $p = .328$ one-tailed, Cohen's $d = 0.09$, 95% CI [inf, 1.07]), demonstrating that the hazard function mitigated temporal uncertainty in neutral long trials (Figure 4B). These CNV data confirmed that

**Figure 3.** Response time decomposed into premotor time and motor time. (A) Temporal cues speeded PMT in the compatible condition only. By contrast, incompatible targets cancelled out the benefit of temporal cueing on response initiation time. (B) MT was not modulated by temporal cues. (C) Thus, faster response time (published in the work of 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.
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 analyzed the frontocentral negative activity that is observed in choice RT tasks just before EMG onset (i.e., the N40 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 N40 for nonconflicting versus conflicting responses. More specifically, we expected that, for nonconflicting 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 N40 indicating more difficult response selection. We performed peak analysis in the time window from −100 msec to 0 (time-locked to the EMG onset) on CSD-transformed data.

First, results revealed a main effect of Compatibility, $F(1, 22) = 9.98, p = .005, \eta^2_p = .31$, 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 (Figure 5). Importantly, however, no Cue × Compatibility interaction was observed, $F(1, 22) = 0.44, p = .513, \eta^2_p = .02$, nor a main of Cue, $F(1, 22) = 0.07, p = .789, \eta^2_p = .003$, or FP, $F(1, 22) = 0.11, p = .739, \eta^2_p = .005$. 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 ($BF_{01f} = 6.07, BF_{01f} \text{ for } \text{Cue} \times \text{Compatibility interaction} = 3.9$, other interactions $BF_{01} > 4$). No other effects were noted.
Correct Response Activation

In order to investigate cortical activation of the correct hand, we analyzed 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 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 msec 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, $F(1, 22) = 0.5, p = .489, \eta^2_p = .02$. These results confirm that cortical response activation processes are resistant to response conflict manipulation. Contrary to our hypothesis, the Cue × Compatibility interaction was nonsignificant, $F(1, 22) = 0.25, p = .623, \eta^2_p = .01$. Furthermore, there was no main effect of Cue, $F(1, 22) = 0.8, p = .38, \eta^2_p = .04$. 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 nonsignificant.

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 favor 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 hypothesized 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 before EMG onset (time window: −200 msec to 0 time-locked to the EMG onset).

First, we found a main effect of Compatibility, $F(1, 22) = 8.42, p = .008, \eta_p^2 = .28$. 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, $F(1, 22) = 6.2, p = .021, \eta_p^2 = .22$ (Figure 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, $F(1, 22) = 10.2, p = .004, \eta_p^2 = .32$ (Figure 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, $F(1, 22) = 5.25, p = .032, \eta_p^2 = .19$. 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 behavioral benefits of temporal predictability for noncompeting 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 normalized PMT temporal benefit (N-T/N) in compatible trials (log-transformed, z-scored; $r_s(21) = .327, p = .064$, one-tailed). In other words, the stronger the motor cortex

![Figure 6.](image-url)
inhibition in temporal relative to neutral compatible trials, the greater the behavioral 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 (z-scored; \( r_{s(21)} = -0.299, p = .082 \), one-tailed). In other words, the weaker the motor cortex inhibition in temporal relative to neutral incompatible trials, the greater the behavioral cost of temporal cues on accuracy. No main effect of Cue, \( F(1, 22) = 0.56, p = .463, \eta^2_p = .03 \); FP, \( F(1, 22) = 1.02, p = .324, \eta^2_p = .04 \); nor an FP × Compatibility, \( F(1, 22) = 2.17, p = .155, \eta^2_p = .09 \), or a Cue × FP × Compatibility, \( F(1, 22) = 0.74, p = .40, \eta^2_p = .03 \), interactions was found.

**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 ITPC (also referred to as a PLF) over the motor cortex contralateral to the correct response (i.e., over C3) in the time window corresponding to response implementation (0–300 msec after EMG onset; Figure 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). Because 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, \( F(1, 22) = 9.20, p = .006, \eta^2_p = .30 \). ITPC was stronger in incompatible than compatible trials. Intriguingly, however, there was a significant interaction between cue and compatibility, \( F(1, 22) = 4.66, p = .042, \eta^2_p = .18 \). Post hoc comparisons showed that in incompatible trials, phase locking was stronger following temporal rather than neutral cues (\( p = .050, \) 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. In turn, although ITPC in the theta range was stronger for incompatible than compatible targets, it remained unaffected by temporal predictability.
Table 1. Summary of EEG and EMG Results

| Variables       | Electrode Site              | Time Window                  | Modulated by Temporal Prediction? | Effect of Temporal Prediction                                      |
|-----------------|------------------------------|------------------------------|-----------------------------------|-------------------------------------------------------------------|
| PMT             | Over the flexor pollicis brevis | Between target onset and EMG onset | Yes/compatible trials only        | Faster PMT in compatible trials                                   |
| MT              | Over the flexor pollicis brevis | Between EMG onset and response | No                                 | N/A                                                               |
| CNV             | FCz                          | −300 msec to 0 before target onset | Yes                              | More negative amplitude at the short FP after temporal versus neutral cues |
| N40             | FCz                          | −100 msec to 0 before EMG onset | No                                 | N/A                                                               |
| Motor activation | C3 (contralateral to response) | −200 msec to 0 before EMG onset | No                                 | N/A                                                               |
| Motor inhibition | C4 (ipsilateral to response) | −200 msec 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 msec after EMG onset | Yes/incompatible trials only      | Increased ITPC in incompatible trials                           |
| Theta ITPC      | C3 (contralateral to response) | 0 to 300 msec after EMG onset | No                                 | N/A                                                               |

N/A = non-applicable.
observed for compatible trials ($p = .703$). 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 correlation to examine the relationship between delta ITPC effects and MT, 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 MT for incompatible versus compatible trials (I–C, z-scored). In other words, stronger delta ITPC for incompatible versus compatible trials was accompanied by longer MTs, $r_s(21) = .360$, $p = .046$, one-tailed. We also ran a correlation between the N400 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, $r_s(21) = .005, p = .984$.

**Theta Phase Locking**

The analysis of ITPC showed a main effect of Compatibility, $F(1, 22) = 17.57, p < .001, \eta_p^2 = .44$. 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 nonsignificant, $F(1, 22) = 1.24, p = .278, \eta_p^2 = .05$. 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. Table 1 summarizes the EMG and EEG results.

**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 can actually impair performance when prepotent, yet undesirable, responses need to be inhibited in favor of more intentional ones (Menceloglu et al., 2021; Korolczuk et al., 2018, 2020; Correa et al., 2010). Yet, the neural mechanisms underlying the dual nature of the effects of temporal predictability on behavior 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 (Van Elswijk, Kleine, Overeem, & Stegeman, 2007; Miniussi et al., 1999). 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 nonconflicting 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 behavioral 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 behavioral 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 nonconflicting 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, time. 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, PMT 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 (van den Brink, Murphy, Desender, de Ru, & Nieuwenhuis, 2021; Bausenhart, Rolke, Seibold, & Ulrich, 2010) and the speed of perceptual processing and accumulation of sensory evidence in choice discrimination tasks (Rohenkohl, Cravo, Wyart, & Nobre, 2012; Vangkilde, Coull, & Bundesen, 2012). However, thus far, these effects have only ever been modelled for nonconflict response choice tasks. It would be informative in the 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 MTs, 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 before 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 synchronizing 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 before 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 (MT) measures of response execution. Finally, our findings further support the functional importance of delta phase in the behavioral effects of temporal predictability (Morillon, Arnal, Schroeder, & Keitel, 2019; Morillon & Baillet, 2017; Arnal, Doelling, & Poeppel, 2015). In particular, we add to literature showing that adjustments in the phase of delta oscillations mediate even nonrhythmic temporal predictions (Daume, Wang, Maye, Zhang, & Engel, 2021; Breska & Deouell, 2017) 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 (Menceloglu et al., 2021; Correa et al., 2010), our data did not support the notion that the behavioral costs of temporal predictability originate from detrimental effects on response selection processes. Although the frontocentral N40 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 toward 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 summarize, we aimed to examine the neural bases of the benefits of temporal predictability for nonconflicting actions (e.g., speeded RTs) as well as 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 behavioral 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.

Author Contributions
Inga Korolczuk: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Resources; Validation; Visualization; Writing—Original draft; Writing—Review & editing. Boris Burle: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Resources; Software; Supervision; Validation; Writing—Review & editing. Jennifer T. Coull: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Resources; Software; Supervision; Validation; Writing—Review & editing. Kamila Śmigasiewicz: Data curation; Formal analysis; Investigation; Methodology; Supervision; Validation; Writing—Review & editing.

Funding Information
This work was supported by the Polish Ministry of Science and Higher Education (https://dx.doi.org/10.13039/501100004569), grant number: 0050/DIA/2016/45, and by a postdoctoral fellowship from the Fyssen Foundation (https://dx.doi.org/10.13039/501100003135) 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-JET-004), and ANR (https://dx.doi.org/10.13039/501100001665), grant number: ANR-17-EURE-0029. The funding source had no impact on any part of this study.

Diversity in Citation Practices
A retrospective analysis of the citations in every article published in this journal from 2010 to 2020 has revealed 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 = .408, W(oman)/M = .335, M/W = .108, and W/W = .149, the comparable proportions for the articles that this authorship teams cited were M/M = .579, W/M = .243, M/W = .102, and W/W = .076 (Pulvio et al., JoCN, 33:1, pp. 3–7). 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 = .684; W/M = .105; M/W = .053; W/W = .158.

REFERENCES
Arnal, L. H., Doelling, K. B., & Poeppel, D. (2015). Delta-beta coupled oscillations underlie temporal prediction accuracy. Cerebral Cortex, 25, 3077–3085. https://doi.org/10.1093/cercor/bhu103, PubMed: 24846147
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, 35–45. https://doi.org/10.1007/BF01187668, PubMed: 8829389
Bausenhart, K. M., Rolke, B., Seibold, V. C., & Ulrich, R. (2010). Temporal prediction influences the dynamics of information processing: Evidence for early onset of information accumulation. Vision Research, 50, 1025–1034. https://doi.org/10.1016/j.visres.2010.03.011, PubMed: 20358190
Botwinick, J., & Thompson, L. W. (1966). Premotor and motor components of reaction time. Journal of Experimental Psychology, 71, 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, 1555–1571. https://doi.org/10.1162/jocn_a_00564, PubMed: 24392698
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, 1–30. https://doi.org/10.1371/journal.pbio.2001665, PubMed: 28187128
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, 324–336. https://doi.org/10.1007/s00426-002-0105-6, PubMed: 12466929
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, 210–220. https://doi.org/10.1016/j.ijpsycho.2015.05.004, PubMed: 25979156
Burle, B., van den Wildenberg, W. P. M., Spieser, L., & Ridderinkhof, K. R. (2016). Preventing (impulsive) errors:
