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ORIGINAL ARTICLE

Temporal unpredictability increases error monitoring as revealed by EEG–EMG investigation

I. Korolczuk^{1,2}  | B. Burle² | J. T. Coull² | H. Ogińska³ | M. Ociepka^{4,5} | M. Senderecka⁴  | K. Śmigasiewicz²

¹Department of Pathophysiology, Medical University of Lublin, Lublin, Poland

²Laboratoire de Neurosciences Cognitives, Aix-Marseille University & CNRS, Marseille, France

³Institute of Applied Psychology, Jagiellonian University, Kraków, Poland

⁴Institute of Philosophy, Jagiellonian University, Kraków, Poland

⁵Doctoral School in the Social Sciences, Jagiellonian University, Kraków, Poland

Correspondence

I. Korolczuk, Department of Pathophysiology, Medical University of Lublin, Jaczewskiego 8, 20-090 Lublin, Poland.

Email: inga.korolczuk@umlub.pl

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Abstract

Reacting in an unpredictable context increases error monitoring as evidenced by greater error-related negativity (ERN), an electrophysiological marker linked to an evaluation of response outcomes. We investigated whether ERN also increased when participants evaluated their responses to events that appeared in unpredictable versus predictable moments in time. We complemented electroencephalographic (EEG) analysis of cortical activity by measuring performance monitoring processes at the peripheral level using electromyography (EMG). Specifically, we used EMG data to quantify how temporal unpredictability would affect motor time (MT), the interval between the onset of muscle activity, and the mechanical response. MT increases following errors, indexing online error detection, and an attempt to stop incorrect actions. In our temporally cued version of the stop-signal task, symbolic cues predicted (temporally predictable condition) or not (temporally unpredictable condition) the onset of a target. In 25% of trials, an auditory signal occurred shortly after the target presentation, informing participants that they should inhibit their response completely. Response times were slower, and fewer inhibitory errors were made during temporally unpredictable than predictable trials, indicating enhanced control of unwanted actions when target onset time was unknown. Importantly, the ERN to inhibitory errors was greater in temporally unpredictable relative to temporally predictable conditions. Similarly, EMG data revealed prolonged MT when reactions to temporally unpredictable targets had not been stopped. Taken together, our results show that a temporally unpredictable environment increases the control of unwanted actions, both at cortical and peripheral levels, suggesting a higher subjective cost of maladaptive responses to temporally uncertain events.

KEYWORDS

action monitoring, ERP, error-related negativity (ERN), timing, uncertainty

M. Senderecka and K. Śmigasiewicz shared last authorship.

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1 | INTRODUCTION

Making an error can have negative consequences for successful adaptation and survival. Fortunately, humans have evolved to rapidly detect and evaluate behavior that differs from that desired. Error monitoring is one of the core cognitive functions that regulates behavior in complex environments. Importantly, environmental factors can reciprocally affect the processes involved in error monitoring. From an evolutionary perspective, maladaptive behavior can be even more dangerous in unpredictable situations due to the increased level of uncertainty and potential threats present in such environments (Frankenhuis et al., 2016). In these circumstances, individuals may have limited or unreliable information about the specific challenges they may face, making it difficult to predict and plan for appropriate responses. Additionally, the effectiveness of previously learned behaviors may be compromised, and individuals must rely on their ability to quickly adapt and respond to new challenges. Thus, maladaptive behaviors may even be harmful and can lead to negative consequences when facing unpredictable circumstances. In line with this view, acting in an unpredictable environment would require enhanced cognitive control. Indeed, recent studies have provided empirical support for this notion: unpredictable contexts increased error monitoring in adults (Jackson et al., 2015; Sandre & Weinberg, 2019) as well as in children and adolescents (Speed et al., 2017).

A key dimension of an ever-changing environment is time. Without accurate temporal predictions, we would not be able to drive a car safely or even dance to our favorite song. Over two decades of neural research on the temporal (un)predictability of events has revealed a fundamental role for timing in adaptive behavior (Nobre & van Ede, 2018). The ability to predict the onset of future events has been demonstrated to regulate action by improving accuracy (Correa et al., 2005; Martens & Johnson, 2005; Visser, 2014), reducing muscular effort (Hasbroucq et al., 1995; Mattes & Ulrich, 1997; Thomas et al., 2019; Van der Lubbe et al., 2004) and speeding responses (Correa et al., 2006; Coull & Nobre, 1998; Nobre, 2001). However, in more demanding situations, temporal predictability can lead to impulsive behavior (Correa et al., 2010; Korolczuk et al., 2018, 2020; Menciloglu et al., 2021). For example, our recent data showed that although temporal predictability enhanced cortical response selection and implementation, it indirectly made it harder to inhibit actions that were no longer appropriate (Korolczuk et al., 2023). Here, we re-analyzed these previously published data to examine whether the less impulsive behavior observed during temporally *unpredictable* situations could be explained

by increased cognitive control that would ensure adaptive behavior in uncertain situations.

Previous studies (Jackson et al., 2015; Speed et al., 2017) have investigated the role of unpredictability on performance monitoring using an electrophysiological marker of error processing known as the error-related negativity (ERN) or error negativity (Ne) (Falkenstein et al., 1991; Gehring et al., 1993). The ERN is a negative frontocentral activity occurring 50–100 ms after the erroneous response and has been traditionally linked to the cingulate cortex (Brázdil et al., 2005; Dehaene et al., 1994). More recent studies, however, have demonstrated that the ERN signal can originate from the supplementary motor area (SMA) (Bonini et al., 2014; Iannaccone et al., 2015). Initially, studies reported that the amplitude of the ERN does not rely on the conscious detection of errors (Endrass et al., 2007; Nieuwenhuis et al., 2001; O'Connell et al., 2007). However, more recent data have challenged this conclusion, suggesting that the ERN's amplitude may indeed be influenced by conscious error detection (Ficarella et al., 2019; Hewig et al., 2011; Shalgi & Deouell, 2012; Wessel et al., 2011). The amplitude of the ERN also varies in line with the magnitude of the error such that the more salient or aversive the error, the larger the ERN (Hajcak et al., 2005; Hajcak & Foti, 2008). Most importantly for the present study, increased ERN amplitudes were observed for errors committed during unpredictable relative to predictable acoustic stimulation in a forced choice flanker task (Jackson et al., 2015; Speed et al., 2017). These findings suggest that performance monitoring processes are engaged to a greater extent in uncertain than certain contexts. Although the ERN is most pronounced for errors, the ERN is also observed to a somewhat smaller extent after correct responses, in which case it is called the correct response negativity (or CRN) (Coles et al., 2001; Vidal et al., 2000).

Although the ERN reflects a neurophysiological reaction to response outcome, error monitoring processes can also be measured before the erroneous response has even been made. The online attempt to stop actions that are no-longer appropriate can be accessed more directly by assessment of electromyographic (EMG) activity during responding. Specifically, individual reaction times (RTs) can be dissected on a trial-by-trial basis (Botwinick & Thompson, 1966) into premotor time (PMT), which corresponds to the time from target onset to the EMG-defined onset of the response, and motor time (MT), which corresponds to the time from the EMG-locked response onset to the mechanical response. Importantly, PMT and MT differ as a function of trial type. MT is slower for errors than correct responses, reflecting the attempt to stop inappropriate actions and thus is a

direct, within-trial marker of error detection and inhibition (Allain et al., 2004; Meckler et al., 2011; Rochet et al., 2014; Roger et al., 2014; Śmigasiewicz et al., 2020). PMT, on the other hand, is faster for errors than correct responses, reflecting a more rapid form of responding based on impulse.

In the current study, we examined how temporal unpredictability affects error monitoring. Specifically, we combined EEG and EMG methods to investigate cortical and peripheral markers of error monitoring when participants attempted to stop no longer appropriate responses to temporally unpredictable events. We manipulated temporal predictability by presenting visual cues that either predicted the timing of the subsequent target appearance (temporally predictable condition) or provided no specific timing information (temporally unpredictable condition). In the temporally predictable condition, participants could use this information to anticipate when the target would appear. However, in the temporally unpredictable condition, no precise timing information was provided, and the targets occurred randomly after either short or long intervals. Participants used temporal information conveyed (or not) by cues on a trial-by-trial basis to respond to a visual target (i.e., go trials). In a quarter of trials, an auditory signal informed participants that they had to stop their response completely (i.e., stop trials) (Logan & Cowan, 1984; Verbruggen & Logan, 2008). This hybrid temporally cued stop-signal task (Korolczuk et al., 2023) allowed us to study brain responses to inhibitory errors (i.e., unsuccessfully suppressed actions) in situations of temporal uncertainty.

We formulated the following hypotheses. Given that unpredictable situations lead to greater error monitoring (Jackson et al., 2015; Sandre & Weinberg, 2019; Speed et al., 2017), we expected that unpredictability of the time of target onset would similarly increase error monitoring. Specifically, we hypothesized that the ERN, an EEG marker of error monitoring, would be enhanced following inhibitory errors when targets were temporally unpredictable rather than predictable. In addition, we used EMG to reveal whether temporal uncertainty affects error monitoring processes occurring during the trial itself, before the erroneous response is even produced. More specifically, by fractionating response time into PMT and MT, we could investigate whether temporal unpredictability yielded similar effects on the initiation (PMT) or execution (MT) of responses that were either unsuccessfully inhibited during stop trials or correctly executed during go trials. We predicted that participants would initiate their responses more slowly to temporally unpredictable targets (Korolczuk et al., 2022), leading to longer PMT in both inhibitory errors and correct go responses. We assumed that although PMT would be faster for inhibitory errors

in general (Allain et al., 2004; Meckler et al., 2011; Rochet et al., 2014; Roger et al., 2014; Śmigasiewicz et al., 2020), temporal unpredictability should not further exacerbate this effect because it is thought to affect response initiation generally, regardless of whether the response is correct or incorrect (i.e., no interaction between predictability and response condition) (Menceloglu et al., 2021). In other words, the slowing down of response initiation in temporally unpredictable situations is expected to apply to both correct go responses and to inhibitory errors. More importantly, however, we expected that MT would be longer during inhibitory errors indicating an online attempt to inhibit incorrect actions (Allain et al., 2004; Meckler et al., 2011; Rochet et al., 2014; Roger et al., 2014; Śmigasiewicz et al., 2020), and this effect would be greater following temporally unpredictable targets (i.e., significant interaction between predictability and response conditions). This would provide direct evidence for enhanced error monitoring when reacting to temporally uncertain events.

2 | METHOD

2.1 | Participants

Thirty-six participants ($M_{\text{age}} = 22.1$ years, $SD = 2.8$, 27 females) took part in the experiment. All volunteers provided written informed consent and the study was approved by the local research ethics committee (KEBN, Jagiellonian University, Krakow, Poland). All participants had normal or corrected-to-normal vision. No history of neurological or psychiatric disorders was noted among participants. Seven volunteers had excessive artifacts either in EEG (two subjects) or noisy or “flat” EMG recordings (five subjects) and were discarded from the analysis. The final sample was thus composed of twenty-nine ($M_{\text{age}} = 22$ years, $SD = 2.1$, 21 females) participants.

2.2 | Temporally cued version of the stop-signal task

We designed a temporally cued version of the stop-signal task (Korolczuk et al., 2023), in which a visual cue predicted (temporally predictable condition) or not (temporally unpredictable condition) the onset time of the target (Figure 1). A visual cue (1° eccentricity) was always displayed centrally on the screen and consisted of two concentric circles. In the temporally predictable condition, a brightening of a smaller, inner circle indicated that a target would occur after a short temporal interval or “fore-period” (600 ms). In turn, a brightening of a larger, outer

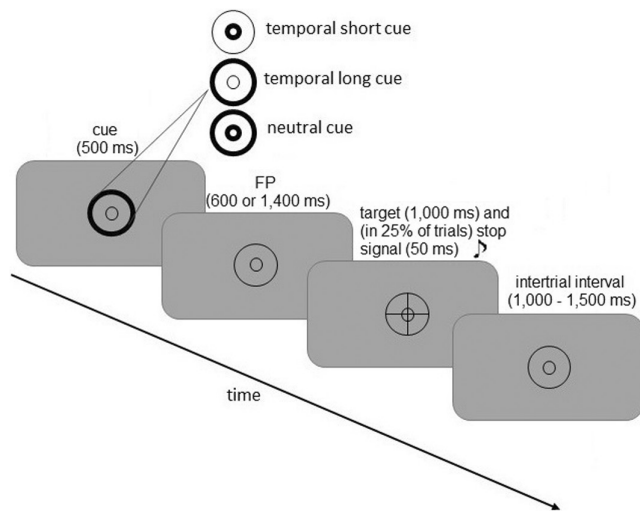


FIGURE 1 Temporally cued version of the stop-signal task. A temporal cue (500 ms) predicted (temporally predictable condition) or not (temporally unpredictable condition) the time of target onset. After the cue was presented, a background display appeared for one of two intervals (foreperiods or FP): short (600 ms) or long (1400 ms). Then, the target (“x” or “+”) appeared within the cue outline for 1000 ms, and participants gave a lateralized response according to the shape of the target. In 25% of trials, an auditory stop signal was presented shortly after the target, indicating that participants had to withhold their response. The intertrial interval varied between 1000 and 1500 ms.

circle indicated that a target would occur after a longer temporal interval (1400 ms). Temporal cues were always valid. In the temporally unpredictable condition, both circles brightened thus providing no temporally precise information, and targets occurred randomly after short or long temporal intervals. Participants were instructed to use the information provided (or not) by the cues to speed their RTs to targets that consisted of either “x” or “+” ($1^\circ \times 1^\circ$ eccentricity), which appeared superimposed within the outline of the cue. Participants responded with their left and right thumb according to the shape of the target. The target-response mappings were counterbalanced across participants.

On a random sample of 25% of trials, an auditory stop signal (750 Hz, 50 ms) was presented shortly after target presentation, informing participants that they had to withhold their response entirely. In these “stop trials,” the stop-signal delay (SSD) was initially set at 100 ms (i.e., the stop signal occurred 100 ms after target onset) and was adjusted continually using a staircase procedure. If the participant successfully suppressed their response, the SSD increased by 50 ms on the next stop trial. In contrast, if the participant failed to inhibit their response, the SSD decreased by 50 ms on the next stop trial. Importantly, these trackings were made separately for temporal and neutral cue trials, and for short and long foreperiod (FP) trials.

Consequently, the effects of cue and FP could be effectively disentangled. The SSD spanned from 50 to 400 ms (with a jitter of 50 ms).

The trial structure was as follows. First, the cue (temporally predictable or unpredictable) appeared for 500 ms. Following the cue, the background display was presented either for 600 ms (short FP) or 1400 ms (long FP). Then, the target was presented for 1000 ms, which defined the response window. In stop trials only, the target was followed by a stop signal (after a variable SSD, see above). All trials ended with the background display, presented for 1000–1500 ms (with a jitter of 100 ms).

The two predictability conditions (unpredictable and predictable) were presented in separate blocks. Each of the predictability conditions appeared in two consecutive blocks, in an alternating manner (UU-PP-UU-PP or PP-UU-PP-UU). There were eight blocks and each block consisted of 128 trials, which resulted in 1024 trials altogether. There were 192 trials for each of the four combinations of predictability and FP in the go trials and 64 trials for each of four combinations of predictability and FP in the stop trials. The experimental task was programmed in PsychoPy software (Peirce et al., 2019). Prior to testing, participants completed a training session, which consisted of 30 temporally predictable trials followed by 30 temporally unpredictable trials.

2.3 | EMG–EEG recording

The bipolar EMG activity of the flexor pollicis brevis was recorded from each hand using Ag/AgCl active electrodes positioned 2 cm apart on the thenar eminence. EEG data were recorded from 64 Ag/AgCl active pre-amplified electrodes (Biosemi Inc., Amsterdam, The Netherlands) at a rate of 1024 Hz (analogue bandwidth limit: from direct current (DC) to 268 Hz, -3 dB at 1/5th of the sampling rate). EEG electrodes were placed according to the extended 10–20 convention. The horizontal and vertical eye electrooculograms (EOGs) were recorded from electrodes lateral to the external canthi and below the left eye (and FP1 electrode), respectively.

2.4 | EMG–EEG processing

EMG and EEG data were analyzed using BrainVision Analyzer 2.0 (Brain Products, Germany), MNE Python toolbox (Gramfort et al., 2013), and customized Python scripts (www.python.org).

A high-pass filter of 10 Hz was applied offline to the EMG signal. The onsets and offsets of EMG activity were detected using a customized Python program

(Spieser & Burle, 2023).¹ This program is based on the combination of variance comparison (Hodges & Bui, 1996) and integrated profile (Liu & Liu, 2016; Santello & McDonagh, 1998) algorithms. The detected onsets were then corrected (if needed) by a naïve observer. Following this procedure, we extracted two types of trials critical for the current investigation: (1) correct go trials (i.e., go trials with a single suprathreshold EMG activation of the correct hand) and (2) unsuccessful stop trials (i.e., stop trials with a single suprathreshold EMG activation of the correct hand, which should have been suppressed).

The EEG data were re-referenced offline to the averaged left and right mastoids, band-pass filtered between 0.01 and 100 Hz using a second-order infinite impulse response Butterworth digital filter (slope: 12 dB/Oct) and corrected for the ocular artifacts using the MNE Python toolbox (Gramfort et al., 2013; Uusitalo & Ilmoniemi, 1997). Additional artifacts were visually inspected and rejected.

2.5 | Data analysis

Behavioral data have already been reported in Korolczuk et al. (2023). Here, we focused our analyses on EMG and EEG markers of performance monitoring. In our paradigm, the target was presented equiprobably after one of two FPs and there were no catch trials. So, if the target did not appear at the short FP, participants knew with 100% certainty that it had to occur at the long FP in both the temporally predictable *and* unpredictable conditions (Coull & Nobre, 1998). Therefore, the predictable and unpredictable conditions differ in terms of temporal predictability at the short FP only (Correa et al., 2006; Coull & Nobre, 1998; Nobre, 2001). Consequently, EMG and EEG analyses were conducted on short FP trials only (Griffin et al., 2002; van Ede et al., 2020).

2.6 | EMG–EEG analysis

To reveal the online peripheral mechanisms of activating, executing, and attempting to stop actions that are no-longer appropriate, at either unpredictable or predictable moments in time, we dissected the RT into two subcomponents: PMT (time from target onset to EMG onset) and MT (time from EMG onset to mechanical response) (Figure 2). This was done on a trial-by-trial basis separately for each of the predictability (unpredictable and predictable) and response (correct go and unsuccessful stop) conditions. The effect of temporal

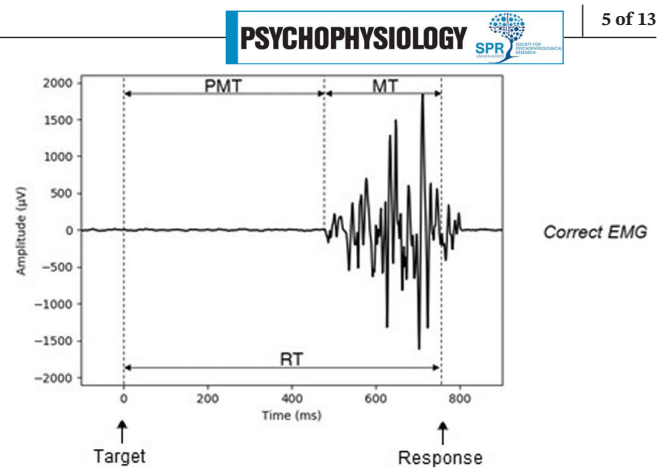


FIGURE 2 EMG activity and response time fractionation. Response time (RT) was decomposed on a trial-by-trial basis into premotor time (PMT), which indexes time from target onset to onset of EMG activity, and motor time (MT), which indexes time from onset of EMG activity to the mechanical response. This procedure was conducted for both unsuccessful stop and correct go responses.

unpredictability on PMT and MT was evaluated by a two-way repeated-measures ANOVA involving predictability (unpredictable, predictable) and response (correct go and unsuccessful stop) factors.

To examine whether temporal unpredictability modulated performance monitoring, we extracted EMG-locked epochs with a duration of 1000 ms and baseline corrected from -200 ms to 0 relative to the EMG onset. These signals were averaged within-participant. The error-related negativity was observed in unsuccessful stop trials (ERN unsuccessful stop), and the correct response negativity was observed in correct go trials (CRN go). The ERN and CRN were calculated as the mean amplitude between 0 and 150 ms after EMG onset at the FCz electrode, separately for temporally unpredictable and temporally predictable conditions. To reveal the effects of temporal unpredictability on EEG markers of error monitoring evaluation, a two-way repeated measures ANOVA comprising predictability (unpredictable, predictable) and response (unsuccessful stop, correct go) was conducted on the ERN/CRN amplitudes data.

3 | RESULTS

3.1 | Behavior

Table 1 summarizes the main behavioral results (see Korolczuk et al. (2023) for more details). Participants responded more slowly and more accurately to go targets in the temporally unpredictable, than predictable, condition. In stop trials, fewer responses were made after

¹Soon to be released under open source license.

the stop signal in the temporally unpredictable, than predictable, condition. Also, the time needed to inhibit a response (stop-signal reaction time or SSRT) was shorter for temporally unpredictable events, and this finding was paralleled by a shorter stop-signal delay (SSD), indicating better suppression of unwanted actions.

3.2 | EMG results

In order to better understand the online peripheral mechanisms of controlling actions to events occurring at unpredictable moments in time, we analyzed PMT and MT (Figure 3). The analysis of the PMT showed a main effect of predictability, $F(1, 28)=14.9$, $p<.001$, $\eta_p^2=0.35$, with slower PMT in the unpredictable than predictable condition. Confirming previous results (Korolczuk et al., 2022),

this finding shows that participants took longer to initiate their reactions to unpredictable targets. There was also a main effect of response, $F(1, 28)=58.28$, $p<.001$, $\eta_p^2=0.68$. PMT was faster for inhibitory errors than correct go responses, replicating numerous previous findings (Allain et al., 2004; Meckler et al., 2011; Rochet et al., 2014; Roger et al., 2014; Śmigasiewicz et al., 2020). No interaction between predictability and response conditions was observed, $F(1, 28)=0.2$, $p=.655$, $\eta_p^2=0.01$.

The analysis of MT revealed a main effect of predictability, $F(1, 28)=6.69$, $p=.015$, $\eta_p^2=0.19$, and a main effect of response, $F(1, 28)=295.03$, $p<.001$, $\eta_p^2=0.91$. Importantly, these main effects were further qualified by a significant Predictability \times Response interaction, $F(1, 28)=5.88$, $p=.022$, $\eta_p^2=0.17$. Post hoc comparisons revealed that for inhibitory errors, MT was longer for temporally unpredictable than temporally predictable targets

Measure	Unpredictable	Predictable	<i>t</i>	Cohen's <i>d</i>	<i>p</i>
Go RT	536 (14)	514 (13)	4.03	0.75	<.001
Go error rate	2.64% (0.53)	3.25% (0.58)	-2.44	-0.45	.021
Inhibitory error rate	41.8% (2.3)	44.5% (2.3)	-3.01	-0.56	.006
SSRT	225 (10)	243 (11)	-2.82	-0.52	.009
SSD	275 (15)	247 (16)	3.65	0.68	.001

TABLE 1 Behavioral results with standard errors (ms) for short FP trials: Go RT, go error rate, inhibitory error rate, stop-signal RT (SSRT), and stop-signal delay (SSD).

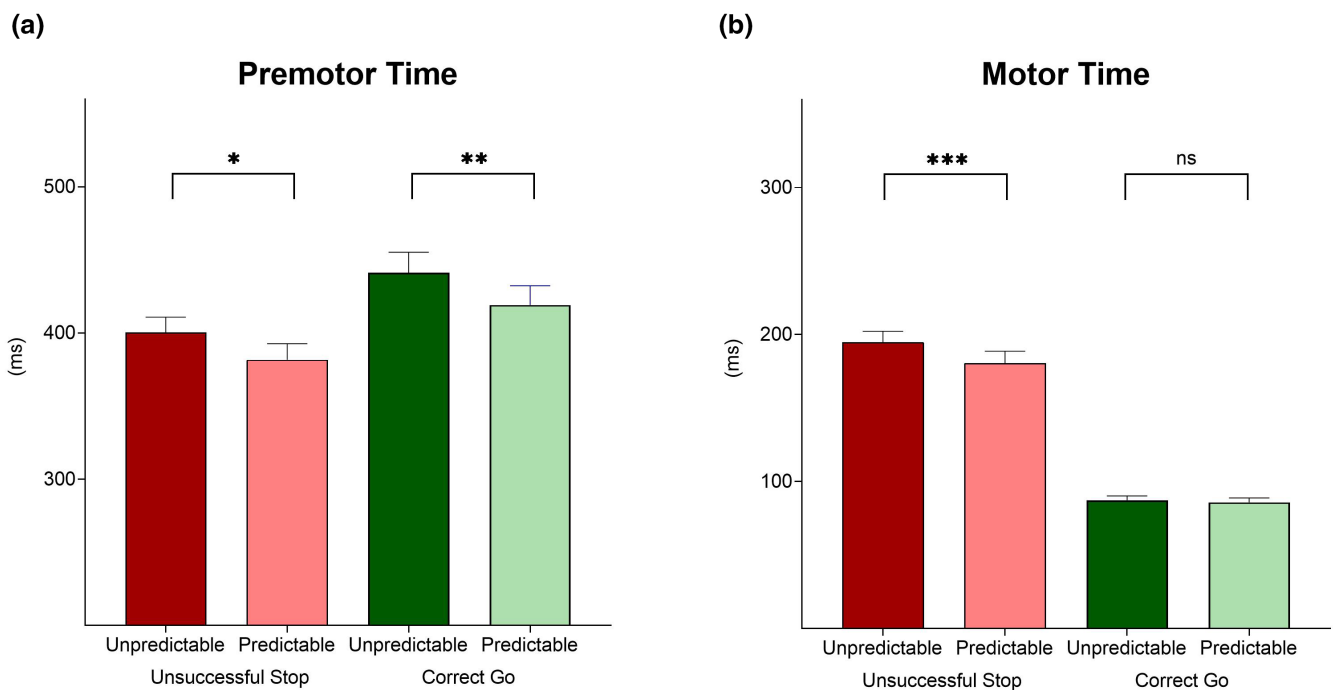


FIGURE 3 Premotor time and motor time in unsuccessful stop and correct go trials. (a) Premotor time was slower to unpredictable versus predictable targets, in both unsuccessful stop and correct go trials. (b) Motor time was longer to unpredictable versus predictable targets only in unsuccessful stop trials. No such effect was noted in correct go trials.

($p = .005$, Bonferroni-corrected). No differences between the two predictability conditions were observed for correct go responses ($p = 1.00$, Bonferroni-corrected).

3.3 | EEG results: ERN and CRN

To examine the effects of temporal unpredictability on cortical error monitoring, we analyzed the ERN/CRN components. The grand-averaged ERPs are shown in Figure 4. Results showed a main effect of predictability, $F(1, 28) = 16.39$, $p < .001$, $\eta_p^2 = 0.37$, and a main effect of response, $F(1, 28) = 14.15$, $p < .001$, $\eta_p^2 = 0.34$. Importantly, these main effects were qualified by a significant Predictability \times Response interaction, $F(1, 28) = 5.53$, $p = .026$, $\eta_p^2 = 0.17$. Post hoc comparisons revealed that for inhibitory errors, the ERN was more pronounced in the temporally unpredictable than predictable condition ($p = .006$, Bonferroni-corrected). In contrast, no differences in CRN amplitude were observed for temporally unpredictable versus predictable correct go trials ($p = .224$, Bonferroni-corrected). In parallel, the ERN and CRN differed significantly in unpredictable ($p < .001$) but not predictable condition ($p = .164$).

To investigate the potential impact of the number of inhibitory errors in predictable and unpredictable conditions, we conducted a follow-up ANCOVA, using the number of inhibitory errors as a covariate. As the ERN

amplitude is known to be affected by the frequency of errors, showing larger amplitudes with fewer errors (Fischer et al., 2017), the larger ERN observed in unpredictable trials might be attributed to a lower number of errors. By controlling for the number of inhibitory errors, we aimed to examine the specific impact of temporal unpredictability on the ERN amplitude, independent of any potential confounding effects related to error frequency. Importantly, ANCOVA also revealed a significant Predictability \times Response interaction, $F(1, 26) = 4.22$, $p = .0501$, $\eta_p^2 = 0.14$. Thus, the relatively lower inhibitory error rates in the unpredictable condition did not account for the effect of unpredictability on the ERN.

Furthermore, we conducted correlational analyses on an individual subject level to explore whether the difference in inhibitory error rate between the predictable and unpredictable conditions correlates with the difference in ERN amplitudes between these conditions. However, no significant relationship was found, $r(27) = .103$, $p = .595$.

4 | DISCUSSION

In the current investigation, we examined how temporal unpredictability influences error monitoring as measured by brain potentials and muscle activity. We demonstrate that (1) temporal unpredictability increased the ERN amplitude after failed attempts to stop actions that had

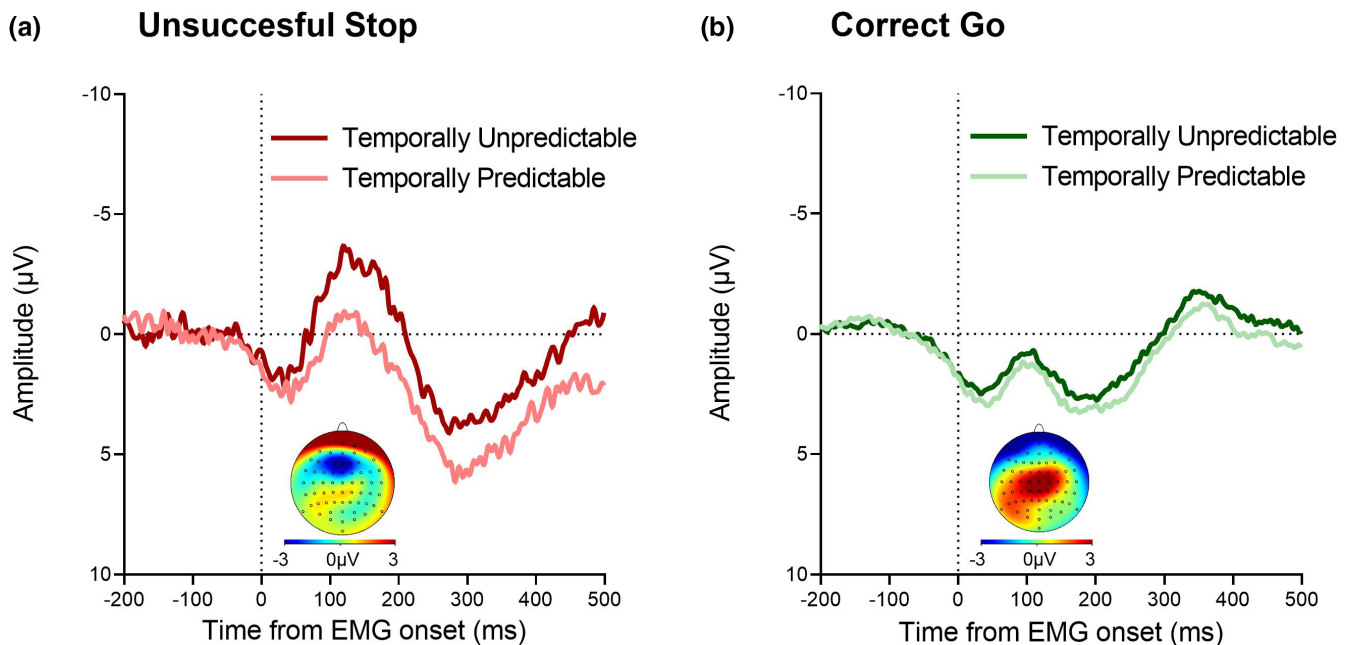


FIGURE 4 Grand-averaged ERP waveforms at the FCz electrode showing the ERN to inhibitory error in unsuccessful stop trials and the CRN in correct go trials, time-locked to EMG onset. (a) For inhibitory errors, the ERN was more pronounced in the temporally unpredictable (dark red) than temporally predictable (light red) condition. (b) No difference between temporally unpredictable (dark green) and temporally predictable (light green) trials was observed for correct go responses. The topography (150 ms after EMG onset) shows a negativity over FCz for inhibitory errors (ERN) and positivity over FCz for correct go responses (CRN).

already been initiated, (2) this result remained significant when controlling for differences in the number of failed stops in unpredictable and predictable conditions, (3) temporal unpredictability lengthened the MT of the responding hand.

Our findings show that a brain response to erroneous actions (the ERN) is potentiated when events are temporally unpredictable. By contrast, temporal unpredictability had no effect on the equivalent waveform for correctly executed actions (the CRN). Our results are therefore consistent with previous data showing that uncertain contexts are associated with enhanced performance monitoring (Jackson et al., 2015; Sandre & Weinberg, 2019; Speed et al., 2017) and further demonstrate, for the first time, that the inability to predict the onset of salient targets leads to an increased cortical response to undesired action outcomes. Thus, our study goes one step further by demonstrating that unpredictability of the *time* of future events boosts the need to enhance cognitive control. In line with Herry et al. (2007), who showed increased attentional bias along with greater activation of amygdala when processing temporal unpredictability, we interpret our findings as an indication that temporal uncertainty renders errors even more aversive and salient (Gehring et al., 1993; Hajcak et al., 2005; Jackson et al., 2015). Indeed, the interaction between time and action has increasingly been recognized, and neural signatures of temporal processing have often been observed in action circuits of the brain (Bella et al., 2015; Coull et al., 2012, 2016; Coull & Droit-Volet, 2018; Cravo et al., 2011; Kononowicz & van Rijn, 2015; Meck, 1996; O'Reilly et al., 2008; Soares et al., 2016; Thaut et al., 1996). Interestingly, the SMA, which is implicated in action monitoring (Bonini et al., 2014; Emeric et al., 2010; Fu et al., 2018; Purcell et al., 2012; Stuphorn et al., 2000) has also been consistently linked to timing (Coull, 2004; Coull et al., 2015; Nani et al., 2019; Protopapa et al., 2019; Wiener et al., 2010). Specifically, SMA has been claimed to be involved in estimating the temporal duration of events. One may thus hypothesize that after making a temporally informed response, the SMA is in a privileged position to obtain a quick access to action outcomes. In contrast, temporal unpredictability may make the integration of temporal and motor signals more difficult explaining the need for enhanced error monitoring. Nevertheless, the evidence presented here demonstrates increased engagement of performance monitoring processes when participants cannot prepare their actions at predictable moments in time.

Indeed, temporal unpredictability may have introduced higher uncertainty and variability in participants' responses. As a result, individuals may become more attentive to their errors as a means to adapt and enhance their performance. This heightened error monitoring could act

as a compensatory mechanism, enabling individuals to stay on track with their timing behavior, particularly in situations where temporal intervals are less predictable. Behavioral data further supported the notion that temporal unpredictability increased cautious responding: Participants made less errors and were slower to react to temporally unpredictable go targets. In stop trials, the number of inhibitory errors (unsuccessfully inhibited responses) was also lower following temporally unpredictable events, showing that participants were better able to suppress their impulsive tendencies. Importantly, however, the lower number of inhibitory errors did not account for the effect of temporal unpredictability on the ERN, which typically exhibits larger amplitudes with fewer errors. This emphasizes that the increase in the ERN amplitude (toward more negative values) cannot be solely attributed to the decrease in errors in temporally unpredictable situations. In the context of sensorimotor processing, our data suggest that temporal unpredictability heightens the response threshold. In other words, in an uncertain context, individuals may increase their response threshold to reduce the likelihood of making incorrect responses and to improve overall performance. Alternatively, though not mutually exclusively, temporal uncertainty can result in higher noise in evidence integration due to distraction. Formal modeling and electrophysiological evidence support the notion that temporal *predictability* can have a significant impact on various aspects of sensorimotor processing (Nobre & van Ede, 2023). Studies have shown that in simple reaction time (RT) detection tasks, temporal predictability can accelerate the onset of decision-making (Bausenhart et al., 2010; van den Brink et al., 2021). Additionally, in choice discrimination tasks, temporal predictability can increase the speed of perceptual processing and the accumulation of sensory evidence (Rohenkohl et al., 2012; Vangkilde et al., 2012). In contrast, in situations of temporal *unpredictability*, participants may experience increased distractions and difficulties in accurately processing sensory information (Gresch et al., 2021; van Ede et al., 2018). These distractions could lead to greater variability in the evidence integration process, making it harder to distinguish between correct and incorrect responses. As a result, individuals might be more attentive to their errors to identify potential lapses in performance caused by increased noise in the evidence integration process.

To complement EEG data, we used EMG recordings to obtain a direct measure of within-trial detection and suppression of incorrect actions to temporally uncertain events. We observed significantly longer MT for inhibitory errors in the unpredictable condition. In the context of our temporally cued stop-signal task, lengthened MTs reflect the detection and (unsuccessful) attempt to stop a

response that has suddenly become inappropriate, right down to the very last limit once the muscular response has already been initiated. Therefore, our results clearly demonstrate that temporal unpredictability heightens *online* performance monitoring processes, also at the peripheral level.

Although it was not a primary goal of our study, we also analyzed PMT, which indexes the time needed to initiate a response. Consistent with the EMG literature (Allain et al., 2004; Korolczuk et al., 2020; Meckler et al., 2011; Rochet et al., 2014; Roger et al., 2014), our results showed the main effect of response-type with faster PMT for inhibitory errors than correct go responses, suggestive of impulsivity during failed stop trials. However, when events were temporally unpredictable, PMT was relatively slower for both correct go responses and failed stops, indicating slower response initiation during situations of temporal unpredictability. As PMT involves processes all along the information processing chain, from target onset to response onset, these results lend further support to formal modeling (Bausenhardt et al., 2010; Rohenkohl et al., 2012; Vangkilde et al., 2012) and EEG work (Korolczuk et al., 2023) showing that temporal unpredictability can impede target identification and/or response selection. Temporal unpredictability not only affects manual responses but also oculomotor responses, including pupil dilation (Akdoğan et al., 2016; Shalev & Nobre, 2022) and microsaccades (Abeles et al., 2020; Amit et al., 2019; Badde et al., 2020; Dankner et al., 2017). For example, using pupillometry, Shalev and Nobre (2022) demonstrated that temporal uncertainty increased arousal levels. Since tonically elevated arousal allows for greater sustained attention to behaviorally relevant events, this finding aligns with our interpretation of heightened cognitive effort and control in temporally unpredictable situations.

By revealing the modulatory effects of temporal unpredictability on performance monitoring, our study complements the recent literature demonstrating that humans possess an ability to monitor their timing errors better than chance (Kononowicz et al., 2018; Öztel & Balci, 2022; Riemer et al., 2019). This metacognitive capability has been even found in rodents, suggesting the evolutionary significance of temporal error judgments (Balci, 2022; Kononowicz et al., 2022). Metacognitive assessment of timing performance can be achieved by monitoring *when* a response is made. By contrast, in our study, we measured how the predictability of the temporal context influenced monitoring of *whether* a response was made (left or right hand). In both cases, participant monitors their performance but in the former case they are monitoring temporal errors and in the latter

case they are monitoring motor execution errors. In the context of our study, increased monitoring of inhibitory error in temporally unpredictable situations may indicate a higher level of metacognitive awareness in temporally uncertain contexts. Consequently, individuals could adeptly assess and fine-tune their responses when faced with varying levels of uncertainty in event timing, leading to improved error monitoring. Additionally, temporal unpredictability imposes greater cognitive demands, requiring individuals to exert increased effort in monitoring and adjusting their responses to maintain accuracy. Consequently, individuals may exhibit heightened vigilance toward their inhibitory errors, aiming to avoid mistakes and optimize performance. Together, understanding how individuals adapt their timing behavior and error monitoring in unpredictable temporal contexts provides valuable insights into the underlying mechanisms of metacognition and its role in time perception and judgment.

5 | CONCLUSION

In the current study, we show that the unpredictability of the *time* of future events potentiates error monitoring at both cortical and muscular levels. When participants cannot form a temporal expectancy about the onset time of the event they are responding to, the neural processing of errors is boosted as indexed by the greater ERN. In parallel, at the peripheral level, temporal unpredictability leads to prolonged MT during inhibitory errors, indicating a stronger unsuccessful attempt to stop an action that has suddenly become inappropriate and hence, an enhanced online evaluation. Our findings are in line with recent evidence demonstrating increased error monitoring in uncertain contexts (Jackson et al., 2015; Sandre & Weinberg, 2019; Speed et al., 2017) and highlight time as a key dimension for the control of error monitoring. Together, EEG and EMG results suggest that a failure to inhibit actions in a temporally unpredictable environment is more costly.

AUTHOR CONTRIBUTIONS

I. Korolczuk: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; visualization; writing – original draft; writing – review and editing. **B. Burle:** Conceptualization; formal analysis; investigation; methodology; resources; software; supervision; validation; writing – original draft; writing – review and editing. **J. T. Coull:** Conceptualization; formal analysis; funding acquisition; investigation; methodology; resources; software; supervision; validation; visualization; writing

– original draft; writing – review and editing. **H. Ogińska:** Conceptualization; data curation; formal analysis; investigation; methodology; supervision; validation. **M. Ocieplka:** Conceptualization; data curation; investigation; methodology; software; validation. **M. Senderecka:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; supervision; validation; visualization; writing – original draft; writing – review and editing. **K. Śmigajewicz:** Conceptualization; formal analysis; investigation; methodology; software; supervision; validation; visualization; writing – original draft; writing – review and editing.

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DATA AVAILABILITY STATEMENT

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

ORCID

I. Korolczuk  <https://orcid.org/0000-0001-7985-951X>

M. Senderecka  <https://orcid.org/0000-0002-2098-5180>

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