

Error-Induced Adaptability: Behavioral and Neural Dynamics of Response-Stimulus Interval Modulations on Posterror Slowing

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Response errors often cause individuals to slow down their subsequent reactions (posterror slowing [PES]). Despite intensive investigations on PES, the adaptive nature of PES remains unresolved. Here, we systematically examined this issue by manipulating response-stimulus intervals (RSIs) and examining their influence on behaviors and neural dynamics of PES. Behavioral and electrophysiological (EEG) measures were recorded while male and female human participants performed a four-choice flanker task as RSIs were manipulated. Behaviorally, PES showed maladaptive features at short RSIs but some adaptive features at long RSIs. EEG results indicated that RSIs did not affect basic error-related processing, indexed by the same pattern in the contrasts between flanker errors and correct responses on the error-related negativity (ERN), error positivity (Pe), or theta band, no matter at short or long RSIs. However, RSIs significantly influenced postflanker error attentional adjustment, motor inhibition, and sensory sensitivity. At short RSIs, compared with postcorrect trials, postflanker error trials elicited larger beta band power and smaller P1 amplitude but did not affect alpha band power, suggesting that motor processing was inhibited, and subsequent sensory processing was impaired, but no attentional adjustment occurred. By contrast, at long RSIs, postflanker error trials led to smaller alpha and beta band power but did not affect P1 amplitude, indicating that attentional adjustment but not motor inhibition occurred, and sensory processing was not impaired. Together with behavioral results, the current study demonstrated that PES was adaptive at long RSIs but maladaptive at short RSIs. We further discuss the role of central resources in the adaptability of PES.

Keywords: posterror slowing, error monitoring, event-related potential, time-frequency analysis

Error commission usually causes people to slow down their subsequent responses (Rabbitt, 1966), a phenomenon termed posterror slowing (PES). A popular view proposes that PES is adaptive and reflects a conservative strategy by which individuals use more time to obtain greater performance accuracy (Ridderinkhof, 2004). Notwithstanding, PES is often uncoupled from posterror improvement in accuracy (see Danielmeier & Ullsperger, 2011, for a review). Thus, the adaptive nature of PES remains questionable (Wessel, 2018). Ullsperger and Danielmeier (2016) proposed that PES is both adaptive and maladaptive: The increased decision bound immediately after error reflects an adaptive feature, whereas the decreased perceptual sensitivity on posterror trials indicates maladaptive aspects (see also Purcell & Kiani, 2016).

This hypothesis suggests that adaptive and maladaptive processing may occur in the same condition, but this remains unresolved. In the present study, we aimed to address this issue using behavioral and neural approaches. From existing study, it could be proposed that if PES was adaptive, a simultaneous improvement (at least, no impairment) in accuracy should be observed (Ullsperger, Danielmeier, & Jocham, 2014). Moreover, the neural correlates of motor inhibition (Amengual et al., 2013) or attentional adjustment would be observable, and impairment of sensory processing on posterror trials should not occur. In contrast, if PES was maladaptive, the above predictions would be reversed. In any case, basic error-related processing (e.g., error monitoring and error awareness) should appear, regardless of whether PES is adaptive or maladaptive.

Of note, previous studies have demonstrated that response-stimulus intervals (RSIs) substantially affect the adaptability of PES (Buzzell, Beatty, Paquette, Roberts, & McDonald, 2017; Jentsch & Dudschig, 2009; Van der Borgh, Braem, Stevens, & Notebaert, 2016). For instance, Jentsch and Dudschig (2009) reported that the amount of PES decreased with increasing RSI and was still significant at long RSIs, whereas posterror accuracy was decreased with short RSIs (50 ms) but did not change with long RSIs (1,000 ms). Thus, the present study would manipulate RSIs to examine the adaptability of PES.

Because of the accumulating event-related potential (ERP) evidence on error-related processing, electroencephalographic (EEG) data accompanying PES can be recorded to investigate its neural

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correlates. Two ERP components (error-related negativity [ERN] and error positivity [Pe]) have been associated with error-related processing (Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991). ERN may reflect error monitoring (Coles, Scheffers, & Holroyd, 2001) and Pe may correspond to error awareness (Nieuwenhuis, Ridderinkhof, Blom, Band, & Kok, 2001). Buzzell et al. (2017) observed that errors impaired subsequent sensory processing, indexed by attenuated P1 amplitude on following trials. Errors also affect cortical arousal, such as increased theta band (4–8 Hz) power, which has been associated with error monitoring and may reflect the degree of error responses deviating from correct responses (Tzur & Berger, 2007), and decreased alpha (8–13 Hz) power, which likely reflects higher arousal, engagement, or attention following error trials compared with correct trials (Carp & Compton, 2009). Importantly, increased beta band (12–24 Hz) power over the frontocentral and frontolateral scalp indicates motor inhibition in PES (Wessel et al., 2016). Therefore, cortical activation may provide valuable data to examine the above predictions.

Here, we used a variant of the flanker task (Eriksen & Eriksen, 1974; Maier, Steinhauser, & Hübner, 2008) to elicit correct and erroneous responses, where posterror and postcorrect behaviors and EEG responses were recorded and compared at short (200 ms) and long (1,000 ms) RSIs. As suggested by previous studies (Buzzell et al., 2017; Jentzsch & Dudschig, 2009), short RSIs would lead to insufficient central resources, whereas long RSIs would provide sufficient central resources. However, error monitoring always requires certain central resources (Welford, 1980). Therefore, we hypothesized that the maladaptive aspects of PES would be revealed at short RSIs, whereas adaptive ones would be observed at long RSIs. Further, we hypothesized that behavioral and EEG measurements in the two conditions would match the above predictions.

Materials and Methods

Participants

In total, 27 healthy volunteers (14 females, M age = 20.89 ± 1.58 years) participated in the experiment. All participants were right-handed, had normal or corrected-to-normal vision, and had no history of nervous system disease. All participants provided handwritten informed consent and were naive to the experimental purpose before the experiment. The study was approved by South-west University Human Ethics Committee for Human Research.

Apparatus and Stimuli

Participants were instructed to perform experiments in a sound-proof room. The experimental stimuli were presented on a 19-in. color monitor (85 Hz refresh rate, $1,024 \times 768$ pixels). Stimulus presentation and data acquisition were accomplished by programs designed with E-prime 2.0 (Psychology Software Tools, Inc., Pittsburgh, PA).

The experiment employed the modified flanker task (four-choice flanker task). Stimuli consisted of eight letters (B, K, P, R, M, V, W or X) and six neutral symbols (\$, %, &, #, or ?) which appeared in Arial font. Each stimulus array consisted of a central target letter (referred to as “target”) flanked by three identical

letters or neutral symbols (referred to as “flankers”) on each side. Participants were situated approximately 70 cm from the stimulus. The visual angle of each stimulus array was 4.1°. Four letter pairs (B and K, P and R, M and V, W and X) formed four possible target responses. For each of the eight possible target letters, six incongruent stimuli were composed of combining the respective target letter with one of six letters that was assigned to a different response than the target. For each of the eight possible target letters, six neutral stimuli were composed of combining the respective target letter with one of the six neutral symbols. In total, 48 incongruent stimuli and 48 neutral stimuli were constructed from all letters and neutral symbols.

The standard version of the flanker task contains congruent and incongruent stimuli, whereas the four-choice flanker task used neutral stimuli and incongruent stimuli. This is because the eight letters in a four-choice flanker task can only construct 48 incongruent stimuli and 16 congruent stimuli. This indicated that 16 congruent stimuli would be presented more frequently than 48 incongruent stimuli, which would lead to inconsistent stimulus proportions. It is worth noting that the response times and accuracy of neutral stimuli are closer to those of congruent stimuli than to those of incongruent stimuli (Spieler, Balota, & Faust, 2000). Therefore, using neutral stimulation could avoid this problem.

Procedure

Participants were instructed to respond to the central target letter, ignore the flankers on each side, and press “1” with the left middle finger, “2” with the left index finger, “9” with the right index finger, or “0” with the right middle finger (Figure 1A). Each trial began with the presentation of the stimulus array for 150 ms, followed by the appearance of a response screen for 2,000 ms (Figure 1B). Participants had to respond as quickly and accurately as possible to the target letter after the presentation of the stimulus array. Feedback on speed and accuracy was presented for 1,000 ms in the practice session, but no feedback was given in the formal experiment. When participants had given a response, the next trial started after a response-stimulus interval of 200 ms or 1,000 ms. RSI was manipulated in a block-wise fashion, and it was either short (200 ms) or long (1,000 ms). Each block comprised 96 trials, and each stimulus type was presented randomly in the block. Participants first completed two practice blocks of 96 trials. And they could begin the formal experiment, but only if the average error rate was less than 15%. The formal experiment included 12 blocks totaling 1,152 trials. The entire experiment took approximately 1 hr. If the average error rate fell below 15% in a block, participants were prompted to respond faster at the beginning of the next block.

Experimental Design and Statistical Analyses

Behavioral analysis. For all analyses, trials in which response times (RTs) for correct response, flanker error and nonflanker error deviated more than three standard deviations from the condition mean were removed from the analyses. The overall RT and accuracy were calculated. Based on previous studies, PES was defined as the difference between the RT of correct trials following errors and the RT of correct trials following correct responses (Danielmeier & Ullsperger, 2011; Jentzsch & Dudschig, 2009; Rabbitt,

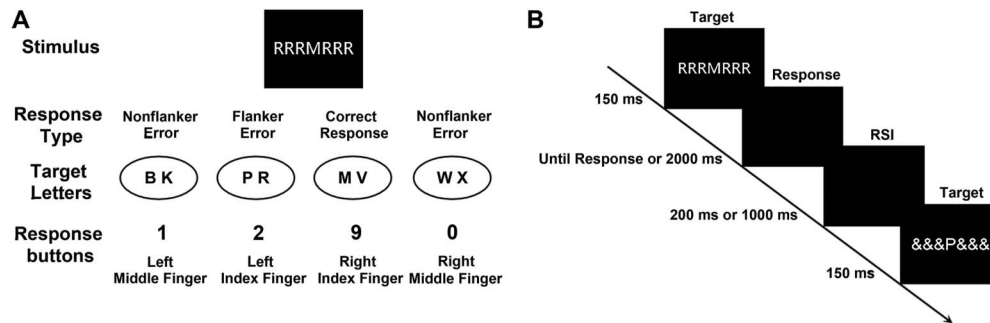


Figure 1. A: Stimulus-response mapping and response types in the four-choice flanker task. Each of the four response fingers corresponded to two target letters. In the shown example, if a response was given with the right index finger, it would be classified as a correct response. If a response was given with the left index finger, it would be classified as a flanker error. And a response with the remaining fingers would be classified as a nonflanker error. B: Task design. The sequence of a typical trial in the task. RSI = response-stimulus interval.

1966). Similarly, posterror accuracy was defined as the difference between the accuracy of trials following errors and the accuracy of trials following correct responses. RT and accuracy were analyzed using two-way repeated-measures analysis of variance (ANOVA) with within-subject factors of response type on trial $n-1$ (correct response, flanker error, and nonflanker error) and RSI (short RSIs, long RSIs), respectively. The unit of RT was ms.

EEG recording and preprocessing. EEG was recorded from standard 64 in-cap Ag/AgCl electrodes, following the extended international 10–20 system (Brain Products GmbH, Germany) and two additional electrodes placed over both mastoids. Vertical and horizontal electrooculograms (EOGs) were recorded from below the left eye and outer canthus of the right eye, respectively. The FCz was used as an online reference. The impedance of all electrodes was maintained below 5 k Ω throughout the recording process. EEG and EOG data were continuously collected at a sampling rate of 500 Hz and online filtered with a 0.1–100 Hz bandpass filter.

Following data recording, EEG data were preprocessed using EEGLAB v13.0.1 and MATLAB R2014a. Offline EEG data were rereferenced to the mean of both mastoids. Data were down-sampled to 250 Hz and filtered with a 0.1–30 Hz bandpass filter via a basic finite impulse response (FIR) filter. Continuous EEG was epoched from –200 to 800 ms for stimulus and response markers. The baseline window was from –200 ms to 0 ms before the stimulus. EOG artifacts were removed using the Automatic Artifact Removal toolbox, an eye movement correction program based on the linear regression method (Gratton, Coles, & Donchin, 1983). An epoch was automatically rejected whenever the voltage reached more than 100 μ V. In the next step, the Laplacian (current source density) transformation of the data was performed to reduce the impact of volume conduction by separating cortical sources, which allowed conducting the analyses of these temporally overlapping, but spatially different neural components (Buzzell et al., 2017; Beatty, Buzzell, Roberts, & McDonald, 2018; Kayser & Tenke, 2006). Considering that there may be a temporal overlap between error-related ERPs on trial $n-1$ and stimulus-related ERPs on trial n , we used the Laplacian transformation to separate error- and subsequent stimulus-induced ERPs, which led to amplitude values in μ V/m². In present study, we focused on flanker errors in

four-choice flanker task and take nonflanker errors as a comparison. This operation is based on the two considerations. One is that flanker errors mainly caused by insufficient selective attention are more pure errors than nonflanker errors caused by speed pressure or unspecific noise. The other is that flanker errors are interfered by flankers, whereas nonflanker errors are not. If all errors were due to speed pressure or unspecific noise, the relative frequency of flanker errors should be 33%. However, in the present study, the proportion of flanker errors on all errors were 41.2% (robustly exceeding 33%), which not only provided the evidence that flanker errors were due to insufficient selective attention but also ensured enough error trials for the reliable analysis (Maier et al., 2008). As a result, an average of 241 correct incongruent trials and 14 errors per condition were used for statistical analyses of ERP data. Of note, higher trial numbers are needed in various simulations according to Fischer, Klein, and Ullsperger (2017). In the present study, the average error trial number was 14 per condition, and it was also acceptable.

ERP analysis. Based on previous studies and grand mean mapping, response-locked ERN on trial $n-1$ was quantified as mean amplitude during a 40 ms window (–20–20 ms) at five fronto-central electrodes (Fz, FCz, Cz, F1, F2), and the average peak latency for the shown ERN somewhere was –12 ms ($SE = 2$ ms). Response-locked Pe on trial $n-1$ was calculated using a 100-ms window (80–180 ms) at fronto-central electrodes (Fz, FCz, Cz, F1, F2). Stimulus-locked P1 on trial n that was correct trial after either a correct or error response was computed using a time window of 70 ms (60–130 ms) at two lateral-occipital electrodes (PO7 and PO8). ERN, Pe, and P1 amplitudes were analyzed using two-way repeated-measures ANOVA with within-subject factors of response type on trial $n-1$ (correct response, flanker error and nonflanker error) and RSI (short RSIs, long RSIs), respectively. And the unit of ERP amplitude was μ V/m².

Time-frequency analysis. Epochs from –600 ms before to 1,000 ms after the stimulus and response were reextracted from the continuous EEG. The baseline window was from –600 ms to –100 ms before the stimulus and response. EEG data were converted into time-frequency domain data using continuous wavelet transform in Letswave Software (<https://www.letswave.org/>; Mouraux & Iannetti, 2008). The values of central frequency

(ω) and limit (σ) were set to 5 and 0.15, respectively, in the continuous wavelet transform. The range of time-frequency representation was 1–30 Hz, and the step was 0.58 Hz. Given the relatively low time resolution of time-frequency analysis, we used a relatively long baseline window for the analysis of time-frequency components (response-locked theta band, stimulus-locked alpha band, and stimulus-locked beta band). The time-frequency representation of a single trial would be obtained after wavelet transform. Mean time-frequency representations of each participant and condition were obtained by averaging the time-frequency representations of all trials per condition. The event-related spectral perturbation (ERSP) in time-frequency representation was calculated to obtain energy regulation of EEG rhythms. Generally, the ERSP was defined by $ER_{t,f} \% = [A_{t,f} - R_f]/R_f$, where $A_{t,f}$ was the energy of single-trial oscillation at a given time t and frequency f , and R_f was the mean of single-trial energy in the baseline time window (Pfurtscheller & Lopes da Silva, 1999). To avoid edge artifacts in wavelet transform, we used the baseline time window from –550 ms to –150 ms before the stimulus and response. The time-frequency regions of interest (TF-ROIs) and spatial regions of interest (S-ROIs) were determined by examining and then selectively testing the differences between conditions in the frequency spectrogram and scalp topography. The fronto-central area (Fz, FCz, Cz), occipital-parietal area (POz, Oz, PO3, PO4, PO7, PO8, O1, O2), and central area (C3, CP3, Cz, C4, CP4) were defined as S-ROIs. The mean time-frequency representations per condition were calculated in the defined S-ROIs. The selection of TF-ROIs must control the influence of false-positive observation (Maris & Oostenveld, 2007). For this purpose, the following two criteria needed to be met when selecting: 1) the selected time-frequency pixels were significantly different from those in the baseline time window ($p < .05$); 2) the TF-ROIs needed to contain at least 75 time points, which meant that the selected time intervals were at least 150 ms. To control for the problem of multiple comparisons correction, p values were corrected by false discovery rate (FDR). According to the above two criteria, three TF-ROIs that were response-locked theta band (4–7 Hz, 250–400 ms), stimulus-locked alpha band (8–13 Hz, 150–800 ms), and stimulus-locked beta band (15–22 Hz, 250–500 ms) were defined in the study. Frequency bands of interest (theta, alpha, and beta bands) were analyzed using two-way repeated-measures ANOVA with within-subject factors of response type on trial $n-1$ (correct response, flanker error, and nonflanker error) and RSI (short RSIs, long RSIs), respectively. And the unit of ERSP magnitudes was ER%.

Single trial analysis. To explore whether error-related processing (ERN/Pe) could predict the changes in subsequent sensory processing (the posterror P1) and posterror behavior (PES, posterror accuracy) on a single-trial level, similar to Buzzell et al. (2017) and Beatty et al. (2018), we conducted generalized linear mixed-effects analyses based on R statistical software, Version 3.6.3 (R Core Team, 2016), using the lme4 package, Version 1.1–21 (Bates, Mächler, Bolker, & Walker, 2015) and the lmerTest package, Version 2.0–32 (Kuznetsova, Brockhoff, & Christensen, 2016). In addition, considering the above feature of flanker errors, the single trial analysis was conducted only on the flanker errors.

Before performing each analysis, models were constructed with the continuous variables on flanker errors (ERN amplitude, Pe amplitude, P1 amplitude, RT) which were centered and scaled to

have a mean of 0 and SD of 1 across the data set, and the category variables (RSI, accuracy), which were entered using sum and contrast. The continuous variables were fit using linear mixed-effects analysis using the lmer function, with restricted maximum likelihood estimation. The categorical variables were fit using generalized linear mixed-effects models using the glmer function with logit link with maximum likelihood estimation.

In each model, the random effect was the variation in intercept within subjects, and the fixed effects were the effects of interest and their interactions (plus an intercept). The statistical significance of each fixed effect was calculated by lmerTest (Kuznetsova et al., 2016), using Satterthwaite's approximation to the denominator degrees of freedom. We defined the mixed effect model with the following formula:

$$Y = X\beta + Z\gamma + \varepsilon$$

Here Y is the response variable, X represents the fixed effect design matrix, β indicates the fixed effect coefficients, Z is the random effect design matrix, γ represents the random effect coefficients, and ε indicates the error term.

Using the syntax of the R Package lme4, the mixed-effects model was formed via:

```
lmer(dependent_var ~ 1 + (fixed_effect_1 * fixed_effect_2)
      + (1|Participant))
```

The code represents a model with a fixed effect for overall model intercept (the initial “1”), fixed effects for all independent variables of interest and their interactions, and a random effect for the variation in intercept per participant (“1 | Participant”).

We explored the effect of flanker error-related ERN or Pe and RSI bin (short vs. long) on subsequent trial activity, with separate models for postflanker error P1, postflanker error RT, and postflanker error accuracy. All models and analyses were limited to current trial errors, but the analyses of postflanker error P1 and postflanker error RT were also limited to pairs of trials in which the subsequent trial was correct.

Results

Behavioral Results

For behavioral analysis, trials were excluded if the response time of the choice response deviated more than three standard deviations from the condition mean. In total, 3.19% of the trials were excluded. The overall mean RT was 604 ($SE = 16$) and accuracy was 86.43% ($SE = 0.99\%$).

For PES effect analysis, a two-way repeated-measures ANOVA with response type on trial $n-1$ and RSI as within-subject factors was conducted. The results showed a main effect of response type on trial $n-1$, $F(2, 25) = 24.46$, $p < .001$, $\eta_p^2 = .66$, but the main effect of RSI did not reach significance, $F(1, 26) = 2.04$, $p = .165$. Critically, the two-way interaction between response type on trial $n-1$ and RSI was significant, $F(2, 25) = 12.92$, $p < .001$, $\eta_p^2 = .51$. Post hoc tests revealed that RTs on correct trials following flanker errors (at short RSIs: 707, $SE = 23$; at long RSIs: 651, $SE = 25$) and following nonflanker errors (at short RSIs: 663, $SE = 23$; at long RSIs: 648, $SE = 28$) were significantly slower than those on correct trials following correct responses (at short

RSIs: 597, $SE = 15$; at long RSIs: 604, $SE = 17$) at short and long RSIs (all $ps < 0.05$). And RTs on correct trials following flanker errors were significantly slower than following nonflanker errors at short RSIs ($p = 0.002$). In contrast, the RTs was not significantly different between correct trials following flanker errors and correct trials following nonflanker errors at long RSIs ($p = .865$; Figure 2A).

For accuracy, ANOVA revealed significant main effects of response type on trial $n-1$, $F(2, 25) = 10.20$, $p = .001$, $\eta_p^2 = .45$, and RSI, $F(1, 26) = 24.16$, $p < .001$, $\eta_p^2 = .48$. Moreover, there was a significant interaction between response type on trial $n-1$ and RSI, $F(2, 25) = 8.70$, $p = .001$, $\eta_p^2 = .41$. Post hoc tests showed that at short RSIs, the accuracy on trials following flanker errors (74.87%, $SE = 2.59\%$) and nonflanker errors (80.45%, $SE = 2.01\%$) was significantly lower than that on trials following correct responses (86.02%, $SE = 1.07\%$; both $ps < 0.01$), and the accuracy on trials following flanker errors was lower than that on trials following nonflanker errors ($p = 0.015$). But the accuracy did not differ among the response types (postcorrect trials: 88.04%, $SE = 0.92\%$; postflanker error trials: 86.56%, $SE = 2.09\%$; postnonflanker error trials: 88.30%, $SE = 1.64\%$) at long RSIs (all $ps > 0.41$; Figure 2B).

ERP Results

ERN. Analysis of the response-locked ERN component showed a main effect of response type on trial $n-1$, $F(2, 25) = 10.64$, $p < .001$, $\eta_p^2 = .46$, and the main effect of the RSI that was preceding the error/correct response where the ERN was measured was not significant, $F(1, 26) = 0.12$, $p = .734$. Importantly, the interaction between response type on trial $n-1$ and RSI reached a significant level, $F(2, 25) = 3.81$, $p = .036$, $\eta_p^2 = .23$. Post hoc tests showed that the correct-related negativity amplitude for correct responses (at short RSIs: -4.52 , $SE = 0.98$; at long RSIs: -4.94 , $SE = 1.77$) was smaller than for flanker errors (at short RSIs: -11.41 , $SE = 2.14$; at long RSIs: -9.55 , $SE = 2.60$) and nonflanker errors (at short RSIs: -7.66 , $SE = 1.67$; at long RSIs: -11.61 , $SE = 2.48$) at short and long RSIs (all $ps < 0.05$). The ERN amplitude evoked by flanker errors was greater than that evoked by nonflanker errors at short RSIs ($p = .036$), but the ERN

amplitudes for flanker errors and for nonflanker errors were not significantly different at long RSIs ($p = .360$; Figure 3B).

Pe. Analysis of the response-locked Pe component showed a main effect of response type on trial $n-1$, $F(2, 25) = 6.97$, $p < .01$, $\eta_p^2 = .36$, with greater Pe amplitude for flanker errors (4.21, $SE = 1.45$) and nonflanker errors (3.52, $SE = 1.28$) compared to correct responses (-0.14 , $SE = 0.69$; both $ps < 0.01$). However, neither the main effect of RSI, $F(1, 26) = 0.27$, $p = .608$ nor the interaction, $F(2, 25) = 0.16$, $p = .857$ was significant (Figure 3C).

P1. Analysis of the stimulus-locked P1 component revealed significant main effects of response type on trial $n-1$, $F(2, 25) = 3.83$, $p = .011$, $\eta_p^2 = .30$, and RSI, $F(1, 26) = 8.61$, $p = .007$, $\eta_p^2 = .25$. Crucially, the interaction between response type on trial $n-1$ and RSI was significant, $F(2, 25) = 5.37$, $p = .011$, $\eta_p^2 = .30$. Post hoc tests showed that the P1 amplitude following correct responses (17.75, $SE = 1.81$) was larger than flanker errors (4.04, $SE = 4.23$) and nonflanker errors (14.76, $SE = 2.31$) at short RSIs (both $ps < 0.05$). The P1 amplitude was smaller following flanker errors than nonflanker errors at short RSIs ($p = 0.030$). But the P1 amplitude following three response types did not differ (P1 following correct responses: 5.99, $SE = 1.67$; P1 following flanker errors: 6.45, $SE = 2.32$; P1 following nonflanker errors: 5.99, $SE = 2.34$) at long RSIs (all $ps > 0.80$; see Figure 4).

Time-Frequency Results

Theta band. The response type on trial $n-1 \times$ RSI repeated-measure ANOVA on the response-locked theta power revealed significant main effects of response type on trial $n-1$, $F(2, 25) = 10.13$, $p = .001$, $\eta_p^2 = .45$, indicating that theta power for correct responses (1.01, $SE = 0.09$) was significantly lower than for flanker errors (1.48, $SE = 0.15$; $p < .001$) and marginally significantly lower than for nonflanker errors (1.19, $SE = 0.11$; $p = .062$). However, neither the main effect of RSI, $F(1, 26) = 2.82$, $p = .105$, nor the interaction, $F(2, 25) = 1.16$, $p = .331$, was significant (see Figure 5).

Alpha band. Two-way repeated-measures ANOVA was conducted on the stimulus-locked alpha power in the occipital-parietal

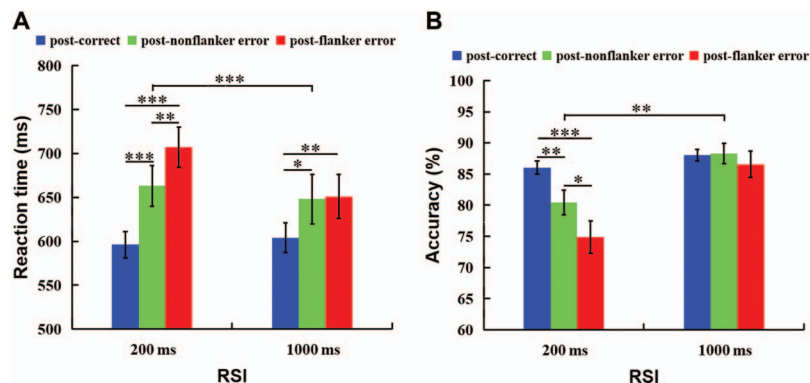


Figure 2. The reaction time (A) and accuracy (B) on trials following correct responses, flanker errors, and nonflanker errors. RSI = response-stimulus interval. Error bars denote standard error of the mean (SEM). * $p < .05$. ** $p < .01$. *** $p < .001$. See the online article for the color version of this figure.

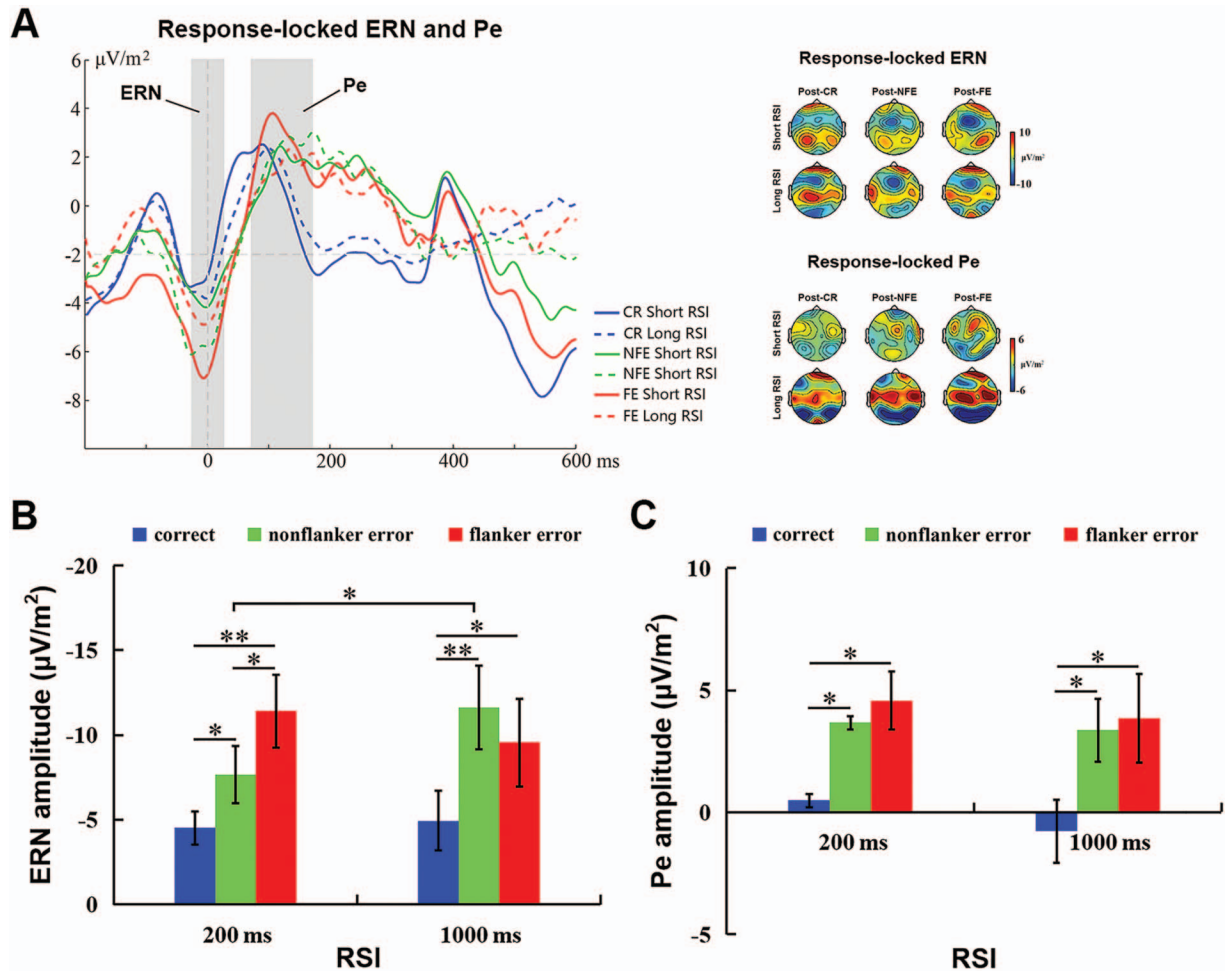


Figure 3. The error-related negativity (ERN) and error positivity (Pe) results in the four-choice flanker task. **A:** The ERN and Pe waveforms and topography distributions for correct responses (CRs), flanker errors (FEs), and nonflanker errors (NFEs) at short and long response-stimulus intervals (RSIs). The shaded regions represent the defined time windows of the ERN and Pe component, respectively. The topography distributions represent average amplitude in the time windows. **B:** The amplitude evoked by CRs, FEs, and NFEs at short and long RSIs for ERN component in the four-choice flanker task. **C:** The amplitude evoked by CRs, FEs, and NFEs at short and long RSIs for Pe component in the four-choice flanker task. Error bars denote *SEM*. * $p < .05$. ** $p < .01$. See the online article for the color version of this figure.

area revealed that response type on trial $n-1$, $F(2, 25) = 3.04$, $p = .066$, and RSI, $F(1, 26) = 2.11$, $p = .158$, were not significant. However, the interaction was significant, $F(2, 25) = 3.84$, $p = .035$, $\eta_p^2 = .24$. Post hoc test revealed that for short RSIs, the alpha power following three response types did not differ (alpha power following correct responses: 1.60, $SE = 0.05$; alpha power following flanker errors: 1.52, $SE = 0.13$; alpha power following nonflanker errors: 1.48, $SE = 0.11$; all $ps > 0.21$). For long RSIs, the alpha power was lower following flanker errors (1.51, $SE = 0.12$) than following correct responses (1.84, $SE = 0.11$) and nonflanker errors (1.89, $SE = 0.18$; both $ps < 0.05$), but it did not differ following correct responses and nonflanker errors ($p = .723$; see Figure 6).

Beta band. The response type on trial $n-1 \times$ RSI repeated-measures ANOVA on the stimulus-locked beta power revealed that response type on trial $n-1$, $F(2, 25) = 0.23$, $p = .796$ and RSI,

$F(1, 26) = 0.57$, $p = .458$ were not significant. Crucially, the interaction between response type on trial $n-1$ and RSI was significant, $F(2, 25) = 8.78$, $p = .001$, $\eta_p^2 = .41$. Post hoc test revealed that the beta power following flanker errors (0.71, $SE = 0.17$) was higher than following correct responses (0.39, $SE = 0.05$) at short RSIs ($p = .045$). And the beta power following flanker errors (0.44, $SE = 0.16$) was lower than following correct responses (0.94, $SE = 0.30$) and following nonflanker errors (0.67, $SE = 0.21$; both $ps < 0.05$) at long RSIs (see Figure 7).

In addition, considering that alpha band was a good neural marker to reflect arousal level, we analyzed stimulus-locked alpha power as a function of RSI for correct trials that were preceded/followed by another correct response. The results revealed that stimulus-locked alpha (at short RSIs: 1.61, $SE = 0.05$; at long RSIs: 1.69, $SE = 0.10$) was no differences between short and long RSIs, $t(1,26) = 0.88$, $p = .385$.

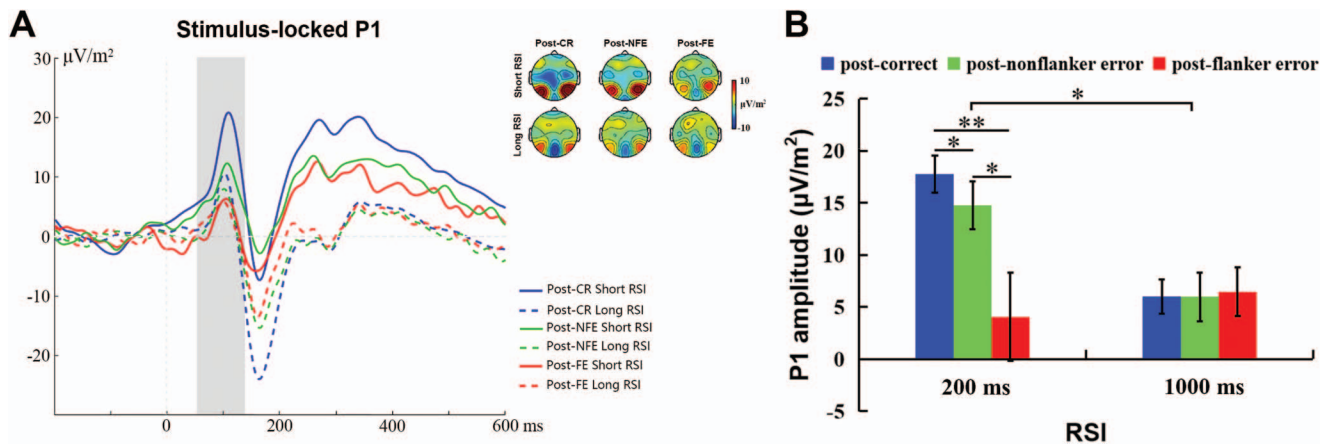


Figure 4. The P1 results in the four-choice flanker task. A: The event-related potential (ERP) waveforms and topography distributions for the P1 component following correct responses, flanker errors, and nonflanker errors at short and long response-stimulus intervals (RSIs). The shaded regions represent the defined time windows of the P1 component. The topography distributions represent average amplitude in the time windows. Post-CR = postcorrect response; Post-NFE = postnonflanker error; Post-FE = postflanker error. B: The amplitude following correct responses, flanker errors, and nonflanker errors at short and long RSIs for P1 component in the four-choice flanker task. Error bars denote *SEM*. * $p < .05$. ** $p < .01$. See the online article for the color version of this figure.

Single Trial Analysis Results

The linear mixed-effects model of ERN and RSI on postflanker error P1 revealed an effect of ERN (estimate = 0.391, $SE = 0.129$, $df = 742.52$, $t = 3.027$, $p < .01$), suggesting that a larger (more negative) ERN was associated with a smaller P1, and an effect of RSI (estimate = -0.208, $SE = 0.071$, $df = 738.35$, $t = -2.933$, $p < .01$), suggesting that shorter RSIs evoked larger P1. Critically, there was a significant interaction in which ERN amplitude predicted P1 amplitude as a function of RSI (estimate = -0.214, $SE = 0.075$, $df = 745.74$, $t = -2.846$, $p < .01$; **Figure 8**). And the interaction indicated that increased ERN amplitude predicted decreased P1 amplitude at short RSIs, but not long RSIs. The linear mixed-effects model of Pe and RSI on postflanker error P1 revealed an effect of RSI (estimate = -0.209, $SE = 0.071$, $df = 738.92$, $t = -2.940$, $p < .01$), suggesting that short RSIs produced larger P1 compared with long RSIs, with no main effect of Pe and no interaction between Pe and RSI (both $ps > 0.12$).

The model of ERN and RSI on postflanker error RT revealed an effect of RSI (estimate = 0.143, $SE = 0.068$, $df = 725.83$, $t = 2.114$, $p = .035$), suggesting that longer RSI was associated with a faster response on the postflanker error trial, whereas neither the main effect of ERN nor the interaction between ERN and RSI was significant (both $ps > 0.69$). The model of Pe and RSI on postflanker error RT revealed an effect of RSI (estimate = 0.144, $SE = 0.067$, $df = 726.06$, $t = 2.146$, $p = .032$), suggesting that postflanker error RT was faster for trials in which RSIs were longer, with no main effect of Pe and no interaction between Pe and RSI (both $ps > 0.17$).

The model of ERN and RSI on postflanker error accuracy revealed an effect of RSI (estimate = 0.082, $SE = 0.027$, $z = 1.03$, $t = 3.041$, $p < .01$), suggesting that postflanker error accuracy was higher for trials in which RSIs were longer, with no main effect of ERN and no interaction between ERN and RSI (both $ps > 0.39$).

The model of Pe and RSI on postflanker error accuracy revealed an effect of RSI (estimate = 0.080, $SE = 0.027$, $z = 1.03$, $t = 2.966$, $p < .01$), suggesting that longer RSI was associated with a higher postflanker error accuracy, whereas neither the main effect of Pe nor the interaction between Pe and RSI was significant (both $ps > 0.81$).

Discussion

The present study systematically investigated the adaptability of PES by examining its behavioral and neural correlates across short and long RSIs. Behaviorally, RSIs significantly influenced participants' performance on subsequent trials. At short RSIs, postflanker error RT and accuracy were worse than those after correct responses, which is in line with the orienting account of PES (Notebaert et al., 2009), indicating maladaptive features. At long RSIs, although postflanker error RT was still slower than that after correct responses, the accuracy did not differ between the two response types, which may be due to that the postflanker error accuracy had reached the ceiling based on the previous studies (Maier et al., 2008; Maier, Yeung, & Steinhauser, 2011). Thus, performance at long RSIs exhibited adaptive features. Consistent with our predictions, PES at short RSIs was maladaptive, and increased RSIs may lead PES to embody adaptive features. For EEG results, for ERN, Pe, or theta band, the contrasts between flanker errors and correct responses followed the same pattern no matter at short or long RSIs. Because these EEG indexes have been associated with error-related processing such as error monitoring (Coles et al., 2001; Tzur & Berger, 2007) and error awareness (Nieuwenhuis et al., 2001), the current results suggest that RSIs did not affect basic error-related processing. Therefore, the behavioral differences between the two RSIs could not be attributed to differences in basic error-related processing. Crucially, alpha power for correct trials that were preceded/followed by another

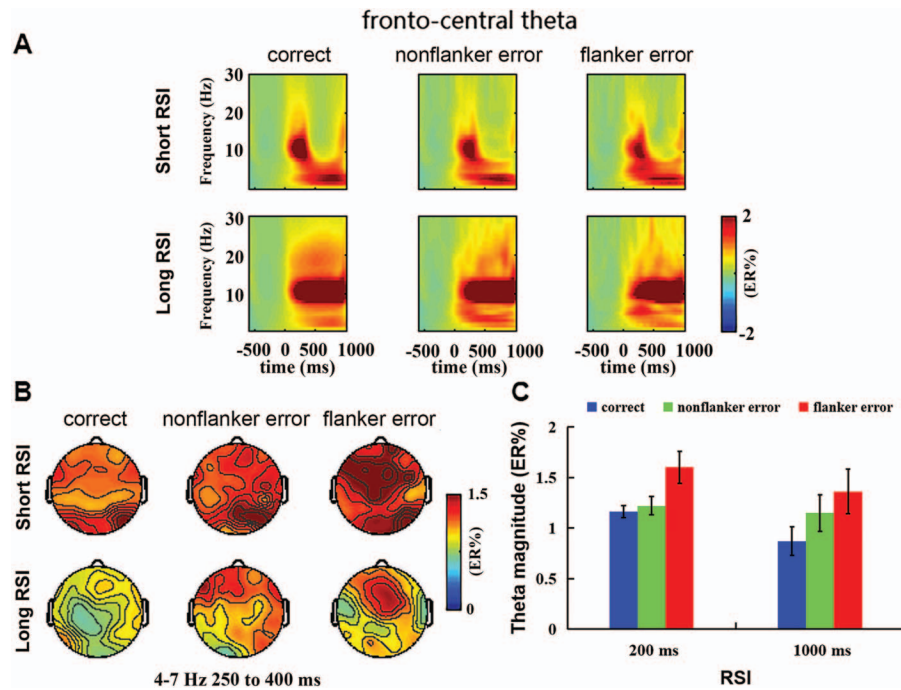


Figure 5. The time-frequency results for theta band in the four-choice flanker task. A: The grand-average time-frequency representations in the fronto-central area (Fz, FCz, Cz) for correct responses, flanker errors, and nonflanker errors at short and long response-stimulus intervals (RSIs) for theta band. B: The scalp topographies of event-related spectral perturbation (ERSP) magnitudes for correct responses, flanker errors, and nonflanker errors at short and long response-stimulus intervals within the defined time-frequency regions of interest (TF-ROI; theta band). C: The ERSP magnitudes (expressed as ER%) for theta band (4–7 Hz, 250–400 ms) in the four-choice flanker task. Error bars denote *SEM*. See the online article for the color version of this figure.

correct response was not different between short and long RSIs, indicating that there was no difference in arousal across blocks, and the current results were specific to error-related interactions with RSI.

In addition, compared with the correct responses, the results of nonflanker errors were similar to flanker errors on RT, accuracy, ERN, Pe, and P1, but different from flanker errors on theta band, alpha band, and beta band. On the whole, error monitoring and posterror adjustments on flanker errors were stronger than on nonflanker errors, which may be due to the different error intensity determined by the features of both error types.

Importantly, RSIs significantly interacted with response type for alpha and beta bands, and P1 amplitude. First, the alpha power following flanker errors was significantly lower than following correct responses at long RSIs but not at short RSIs. Notably, alpha suppression often indicates increased arousal and selective attention (Haegens, Händel, & Jensen, 2011; van Ede, de Lange, Jensen, & Maris, 2011). Moreover, spectral Granger causality analysis revealed that bottom-up (from occipital cortex to medial prefrontal cortex) synchronous oscillation is observed mainly in the alpha band (Cohen, van Gaal, Ridderinkhof, & Lamme, 2009). Similarly, an experiment conducted on monkeys revealed that bottom-up synchronous oscillation is observed in alpha band (Buschman & Miller, 2007). Therefore, alpha suppression on flanker errors suggest that when RSI is relatively long, attentional adjustment appeared that favors adaptive posterror adjustments.

Second, beta power following flanker errors was significantly larger than following correct responses at short RSIs, but the pattern was reversed at long RSIs. The beta band is generated in sensorimotor areas (Tzagarakis, West, & Pellizzer, 2015) and has been suggested to be more strictly related to motor functions (Kilavik, Zaepffel, Brovelli, MacKay, & Riehle, 2013). Importantly, the decrease in beta band is often considered to be a marker of motor processing (e.g., motor preparation or motor execution; Marshall, O'Shea, Jensen, & Bergmann, 2015; McFarland, Miner, Vaughan, & Wolpaw, 2000; Pfurtscheller, Pregener, & Neuper, 1994; Yang, Leung, Plank, Snider, & Poizner, 2015), whereas the increase in beta power inhibits prepared actions (Rosin et al., 2011; Swann et al., 2011, 2012; Wessel et al., 2016). Consistent with Fischer, Nigbur, Klein, Danielmeier, and Ullsperger (2018), following a longer RSI they found significantly faster choices which were associated with reduced beta power lateralization. Thus, motor processing was inhibited at short RSIs but was facilitated at long RSIs. Third, P1 amplitude on postflanker error trials was significantly attenuated relative to that on postcorrect trials at short RSIs, but it did not differ between the two types of trials at long RSIs. As one of the earliest ERP components, P1 reflects the earliest effect of spatial attention on visual processing (Hillyard, Vogel, & Luck, 1998). ERP studies have identified an early marker of impairments in visual sensory processing in the form of a decrement in the P1 component of the visual evoked potential (VEP; Butler et al., 2001, 2005; Haenschel et al., 2007; Schechter

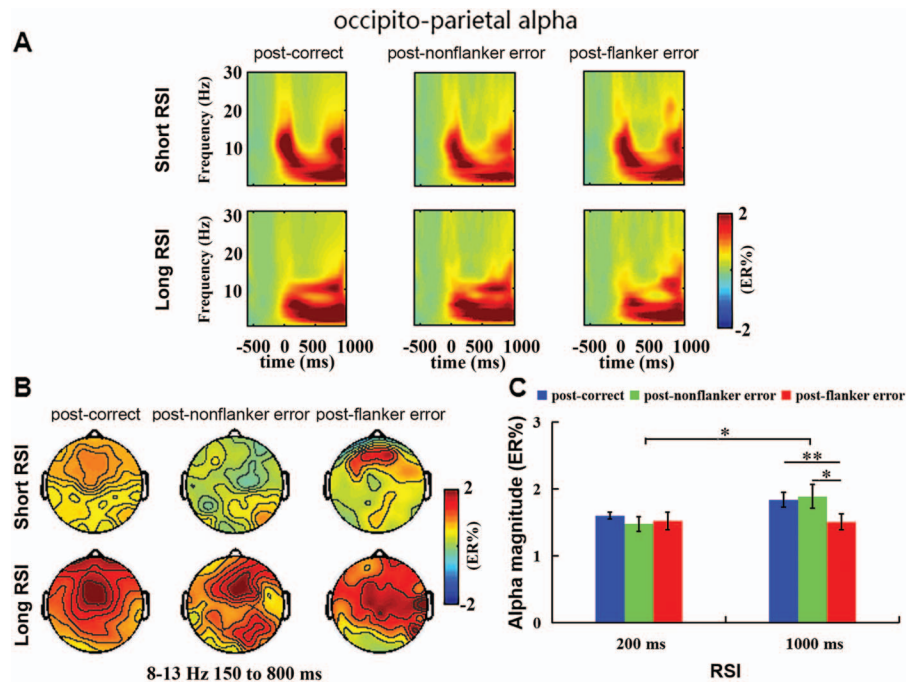


Figure 6. The time-frequency results for alpha band in the four-choice flanker task. A: The grand-average time-frequency representations in the occipital-parietal area (POz, Oz, PO3, PO4, PO7, PO8, O1, O2) for correct responses, flanker errors, and nonflanker errors at short and long response-stimulus intervals (RSIs) for alpha band. B: The scalp topographies of event-related spectral perturbation (ERSP) magnitudes for correct responses, flanker errors, and nonflanker errors at short and long RSIs within the defined time-frequency regions of interest (TF-ROI; alpha band). C: The ERSP magnitudes (expressed as ER%) for alpha band (8–13 Hz, 150–800 ms) in the four-choice flanker task. Error bars denote *SEM*. * $p < .05$. ** $p < .01$. See the online article for the color version of this figure.

et al., 2005). Thus, short RSIs impaired the sensitivity of sensory processing on subsequent trials, but long RSIs did not.

Collectively, these results showed that at short RSIs, motor processing was inhibited soon after flanker errors, sensory processing on subsequent trials was impaired, and there was no attentional adjustment. Thus, PES at short RSIs was maladaptive, which is consistent with the current behavioral results. By contrast, at long RSIs, motor processing was not inhibited but was facilitated by flanker errors, and there was no impairment of sensory processing on subsequent trials. Moreover, attentional adjustment occurred significantly after flanker errors. Therefore, PES at long RSIs was adaptive.

The supply of central resources seems critical for the adaptability of PES. Error monitoring is generally thought to be resource intensive (Buzzell et al., 2017; Hochman & Meiran, 2005; Jentzsch & Dudschig, 2009; Lavro & Berger, 2015; Welford, 1980), which may not only lead to insufficient central resources for posterror adjustments, but also disturb next-trial sensory processing and attentional processes (Houtman & Notebaert, 2013; Van der Borgh et al., 2016). A significantly lower P1 following flanker error compared to that following correctness at short RSIs indeed indicated impaired task-related sensory processing on postflanker error trials. Meanwhile, for flanker errors, the effects of PES on ERN and theta power did not differ between short and long RSIs, suggesting that error monitoring may consume a similar amount of central resources at both RSIs. In this case, the subsequent supply

of central resources is crucial for the appearance of later adaptive adjustments. In the present study, at short RSIs, the subsequent supply of central resources may have been insufficient, because stimuli of subsequent trials appeared very soon (200 ms) after flanker errors, where processing for stimuli overlapped with post-flanker error adjustments. Therefore, they may compete for central resources, which may aggravate the insufficiency of central resources for both sensory processing (attenuated P1 amplitude) and attentional adjustment (null effect on alpha power). Insufficient central resources may lead to inhibition of motor processing after flanker errors (larger beta power). These responses would contribute to impaired performance on RT and accuracy after flanker error and could be responsible for the maladaptive PES.

Previous studies have indicated that the inhibitory activity of the motor cortex indexes a conservative strategy (e.g., Botvinick, Braver, Barch, Carter, & Cohen, 2001; King, Korb, von Cramon, & Ullsperger, 2010), which favors an increase in subsequent accuracy and is therefore adaptive. Strictly, if a response is thought to be strategic, it is thought to reflect an active and intentional response (Emeric et al., 2007; Verbruggen & Logan, 2009). From the current results, we nevertheless propose that the inhibited motor cortex may be an automatic and passive response to error commission, which is likely due to insufficient central resources that caused by the lack of attentional adjustment and the competition in central resources between posterror adjustments and sensory processing in a short time. This point is supported by the fact

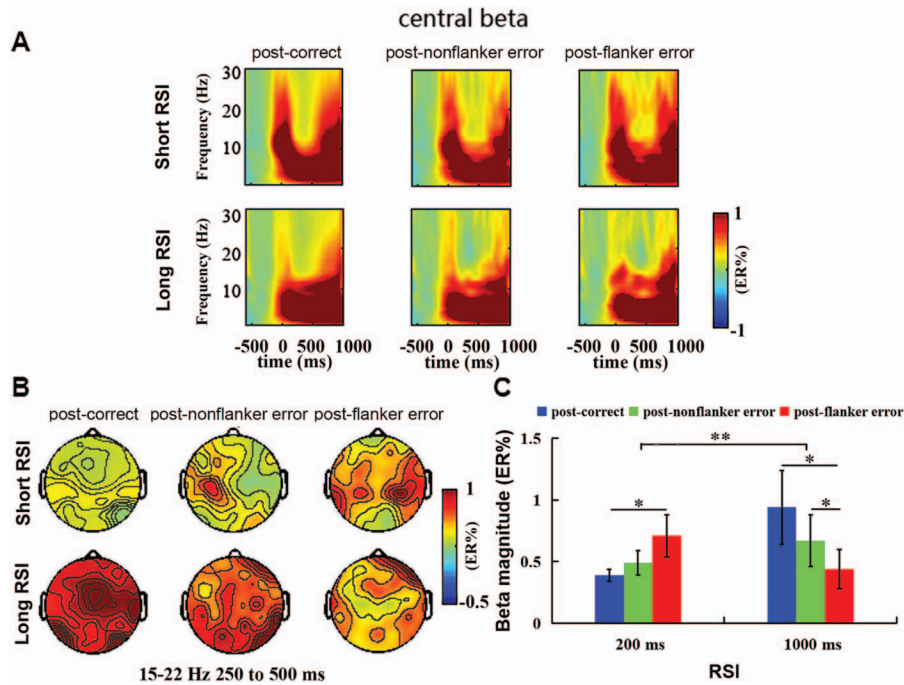


Figure 7. The time-frequency results for beta band in the four-choice flanker task. **A:** The grand-average time-frequency representations in the central area (C3, CP3, Cz, CP4, C4) for correct responses, flanker errors, and nonflanker errors at short and long response-stimulus intervals (RSIs) for beta band. **B:** The scalp topographies of event-related spectral perturbation (ERSP) magnitudes for correct responses, flanker errors, and nonflanker errors at short and long RSIs within the defined time-frequency regions of interest (TF-ROI; beta band). **C:** The ERSP magnitudes (expressed as ER%) for beta band (15–22 Hz, 250–500 ms) in the four-choice flanker task. Error bars denote *SEM*. * $p < .05$. ** $p < .01$. See the online article for the color version of this figure.

that inhibition of the motor cortex occurred at short RSIs but not at long RSIs.

Single trial analyses revealed that for flanker errors, ERN amplitude but not Pe amplitude predicted P1 amplitude as a function of RSI. This finding in a response conflict (four-choice flanker) task was consistent with the result by Beatty et al. (2018) that ERN predicted P1 decrements in a response conflict (Simon) task. Therefore, decreased P1 amplitude on postflanker error trials was predicted by increased ERN amplitude, implying that reduced sensory sensitivity stems from ERN at short RSIs and suggesting that early error monitoring in the medial frontal cortex (ERN) was directly involved in eliciting adaptive attentional adjustments (Steinhauser & Andersen, 2019). As analyzed above, error monitoring may consume most central resources at short RSIs, which may impair subsequent sensory processing. These results suggested that insufficient central resources indexed by attenuated P1 amplitude may be due to resource consumption by error monitoring. Nevertheless, Buzzell et al. (2017) reported that P1 amplitude was significantly correlated with Pe but not ERN in an attentionally demanding visual discrimination task. To resolve this, we suggest that the time windows of response-locked Pe and stimulus-locked P1 are response-locked 200–500 ms (Falkenstein, Hoormann, Christ, & Hohnsbein, 2000) and stimulus-locked 80–100 ms (Hillyard et al., 1998), which should be considered. The overlapping time windows may lead to confusion between the two components, especially at short RSIs.

Based on above results, we propose that PES is mainly attributable to error monitoring. In fact, for flanker errors, there is still significant PES at long RSIs where central resources could be supplemented, suggesting that supplemented resources in addition to central resources consumed by error monitoring could not eliminate PES. Moreover, at short RSIs, the single trial analysis between ERN and P1 suggested that error monitoring may be a direct cause impairing sensory processing on subsequent trials. Recent opinions of Wessel and Aron (2017) could explain the current results well that unexpected events (e.g., action errors) interrupt action and impact cognition by recruiting a fronto-basal-ganglia network (global suppressive network) for stopping. This network includes specific prefrontal cortical nodes and is posited to project to the subthalamic nucleus, with a putative global suppressive effect on basal-ganglia output.

In summary, the present study systematically examined the adaptability of PES by changing the supply of central resources, and it should be the most systematic study for error-induced processing up to now. We provided evidence to clarify under what conditions PES was adaptive and under what conditions it was maladaptive and elaborated the specific behavioral and neural manifestations when PES was adaptive and maladaptive. At short RSIs, error monitoring needs to occupy central resources following flanker errors, indexed by the larger ERN and theta power, which leads to insufficient resources for subsequent processing: inhibiting motor processing (indexed by greater beta power) and disturb-

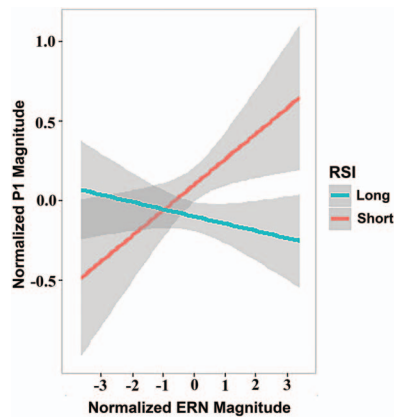


Figure 8. Relations between single-trial error-related negativity (ERN), P1, and response-stimulus interval (RSI) on flanker errors. Predicted values for the post-flanker error P1, relative to ERN and RSI (short vs. long). The ERN and RSI interact, such that the influence of ERN magnitude on postflanker error P1 differs between short and long RSIs. Shaded region around each line represents SE. See the online article for the color version of this figure.

ing next-trial performance (indexed by attenuated P1). At long RSIs, more central resources may be available for subsequent processing, indexed by suppressed alpha power following flanker errors, hence improving performance on subsequent tasks. Thus, the central resources that the cognitive system could supply in a specific scenario may determine the adaptability of PES in that context.

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