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ORIGINAL ARTICLE

Reward positivity affects temporal interval production in a continuous timing task

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Abstract

The neural circuits of reward processing and interval timing (including the perception and production of temporal intervals) are functionally intertwined, suggesting that it might be possible for momentary reward processing to influence subsequent timing behavior. Previous animal and human studies have mainly focused on the effect of reward on interval *perception*, whereas its impact on interval *production* is less clear. In this study, we examined whether feedback, as an example of performance-contingent reward, biases interval production. We recorded EEG from 20 participants while they engaged in a continuous drumming task with different realistic tempos (1728 trials per participant). Participants received color-coded feedback after each beat about whether they were correct (on time) or incorrect (early or late). Regression-based EEG analysis was used to unmix the rapid occurrence of a feedback response called the reward positivity (RewP), which is traditionally observed in more slow-paced tasks. Using linear mixed modeling, we found that RewP amplitude predicted timing behavior for the upcoming beat. This performance-biasing effect of the RewP was interpreted as reflecting the impact of fluctuations in reward-related anterior cingulate cortex activity on timing, and the necessity of continuous paradigms to make such observations was highlighted.

KEYWORDS

continuous paradigm, event-related potential (ERP), feedback, reward positivity (RewP), timing

1 | INTRODUCTION

A cortico-striatal dopaminergic system in the brain underlies reward processing (Arias-Carrión et al., 2010; Corlett et al., 2022; Haber & Knutson, 2010; Schultz, 2007; Smith & Kieval, 2000). Interestingly, the same dopaminergic circuits have been implicated in the estimation of temporal intervals (hereafter referred to as interval timing), particularly when the interval is encoded relative to the beat (Coull et al., 2011; Grahn, 2009; Matell et al., 2003; Matell & Meck, 2004; Meck & Malapani, 2004; Rao et al., 2001; Teki et al., 2012). This overlap in functional circuits for reward and interval timing raises the possibility that phasic activation of reward circuits during reward processing can lead to temporary changes in timing behavior. Such interaction may be more prominent for sub-second (shorter than a second) than supra-second (longer than a second) interval timing, due to more intense activation of subcortical areas (Nani et al., 2019; Wiener et al., 2010).

It is commonly believed that interval timing includes interval perception and interval production[1] (also referred to as perceptual and motor timing, respectively). Although whether they share a common timing mechanism is still under debate (Ivry & Hazeltine, 1995; Merchant et al., 2013), some researchers believe that a common 'internal clock' mechanism controls the speed of both interval perception and production (Block & Zakay, 1996; Zakay & Block, 1996). Past literature has predominantly focused on the effect of reward on interval *perception*, while the effect of reward on interval *production* remains understudied. Animal studies demonstrated that direct manipulation of phasic dopamine signaling alters interval perception. For example, Soares et al. (2016) reported that spontaneous increase in phasic DA signaling leads to mice perceiving the same interval as shorter, and optogenetic manipulation is sufficient for reproducing such behavioral pattern. In humans, while some studies have found that pharmacologically blocking dopaminergic receptors shortens perceived duration (Meck, 1986), researchers typically studied the influence of externally administered reward on interval perception. It was shown that intervals associated with a positive monetary prediction error or reward were perceived as longer by human participants (Failing & Theeuwes, 2016; Toren et al., 2020), an effect partially attributable to attention and salience (Berridge & Robinson, 1998; Coull et al., 2004; Tse et al., 2010). However, these studies typically manipulated reward independently of performance, whereas in real life, reward is likely contingent on timing performance (Ariely & Zakay, 2001; Petter et al., 2018).

Feedback is an incidence of performance-contingent reward, and positive feedback on performance (e.g., 'accurate', 'hit', or 'on time') is known to elicit a reward response in the brain 200–300 ms post-stimulus (Cockburn & Holroyd, 2018; Proudfit, 2015; Tunison et al., 2019). While several previous studies used fMRI to study the continuous sub-second interval production with visual feedback (e.g., Lutz et al., 2000; Pope et al., 2005), it may be difficult to conduct a trial-by-trial fMRI analysis to capture the transient changes in reward circuit due to technical constraints on temporal resolution. EEG allows for fine-grained discrimination of such interplay at the level of milliseconds, making it especially suitable for studying the influence of reward on sub-second timing behavior. It has been well-established that reward, relative to non-reward, elicits a positive deflection in the scalp-reported event-related potential (ERP) in the frontocentral electrode sites around 250 to 350 ms after stimulus onset called the reward positivity (RewP) (Holroyd et al., 2006, 2011; Holroyd & Coles, 2002; Walsh & Anderson, 2012).[2] RewP variability is likely due to variability in the reward response rather than the non-reward response (Holroyd et al., 2008). One theory of the RewP highlights its link to the reward prediction error in reinforcement learning (Sutton & Barto, 2018), attributing the RewP to the influence of a phasic ventral striatal DA signal on the anterior cingulate cortex (Becker et al., 2014; Carlson et al., 2011; Holroyd & Coles, 2002; Luu et al., 2003), although the exact nature of this influence is still under debate (Ullsperger et al., 2014). This reward information is utilized by the anterior cingulate cortex to compute a need-for-control signal, facilitating cognitive control and effort exertion (Hassall et al., 2022; Shenhav et al., 2013; Vassena et al., 2017). Timing tasks and gambling tasks are well-suited for studying feedback processing, because participants are relatively uncertain about their performance or outcomes compared to other tasks that have a 'correct answer' and must rely on external feedback (Carlson et al., 2011; Miltner et al., 1997). Altogether, the RewP provides a non-invasive, temporally sensitive measure of reward prediction errors on the scalp.

In this study, we asked how reward affects sub-second interval production in a continuous timing paradigm with EEG recording. Participants were instructed to reproduce different drumming patterns at different tempos (fast, medium, and slow) using two keys on a keyboard, and received color-coded feedback (early, on time, or late) on their accuracy after each response. We hypothesized that on-time feedback would elicit a RewP relative to either early or late feedback, and examined whether the RewP could be reliably observed in all three tempos. We then hypothesized that trial-to-trial instantaneous fluctuations of RewP amplitude in response to on-time feedback bias subsequent interval production, using a linear mixed model. We reported that RewP was only stably observed in the medium (0.6 s interval) and slow (1.0 s interval) tempos. In the slow tempo, a larger RewP in response to 'on-time' feedback led to a longer produced interval on the next trial.

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[1] Some researchers proposed a third class of methods called interval reproduction, where the target interval is presented (e.g., as a sound or a visual stimulus), immediately followed by the participant reproducing this interval (Grondin, 2008). We believe interval reproduction may involve both interval perception and production and thus is not listed here alone.

[2] RewP is also termed feedback-related negativity (FRN) or error-related negativity (ERN) when the contrast is loss minus gain (Gehring, 2002; Luu et al., 2003; Miltner et al., 1997; Proudfit, 2015).

2 | METHODS

2.1 | Participants

Due to the novel nature of this paradigm, we did not conduct a prior power analysis; rather, we based our planned sample size on the number of participants needed to observe a reliable reward positivity. Previous comparable studies typically recruited 10–20 participants (Chase et al., 2011; Hassall et al., 2022; Holroyd & Krigolson, 2007). Given that this continuous paradigm may reduce the amplitude of observed reward positivity, we planned for $N = 20$ effective participants. Post hoc power calculation was conducted following the study (see Result 3.3, Supplementary Information [SI] S2).

21 participants completed the study. One participant (No. 12, female) was excluded due to the trigger cable being partially disconnected. The remaining 20 participants (15 female, 2 left-handed, mean age 25.85 ± 4.53) had normal or corrected-to-normal vision and had no known neurological impairments. Handedness was assessed by one item ('what is your dominant hand?') in the demographics survey before the experiment. All participants gave informed consent and were compensated for their participation and a performance bonus. This study was approved by the Medical Sciences Interdivisional Research Ethics Committee at the University of Oxford (R51132/RE002).

2.2 | Experimental task

Participants completed the drumming task along with two other unrelated tasks, the order of which was randomized between participants. Each task took approximately 20 min, and the entire study took around 60 min. The stimuli were presented using PsychoPy 3.6.6 (Peirce et al., 2019) on a monitor screen (60 Hz, 1920 by 1080 pixels, Acer XB270H) with size 59.9 cm (width) × 33.7 (height). Participants were seated approximately 66.0 cm from the display. In each block of the drumming task, participants listened to a drumming pattern for 24 beats and were asked to reproduce the pattern using the F and J keys on the keyboard (Figure 1a). The response sequence was self-initiated by pressing the first key, and participants were shown color-coded visual feedback for 50 ms after each subsequent key press response, indicating if their

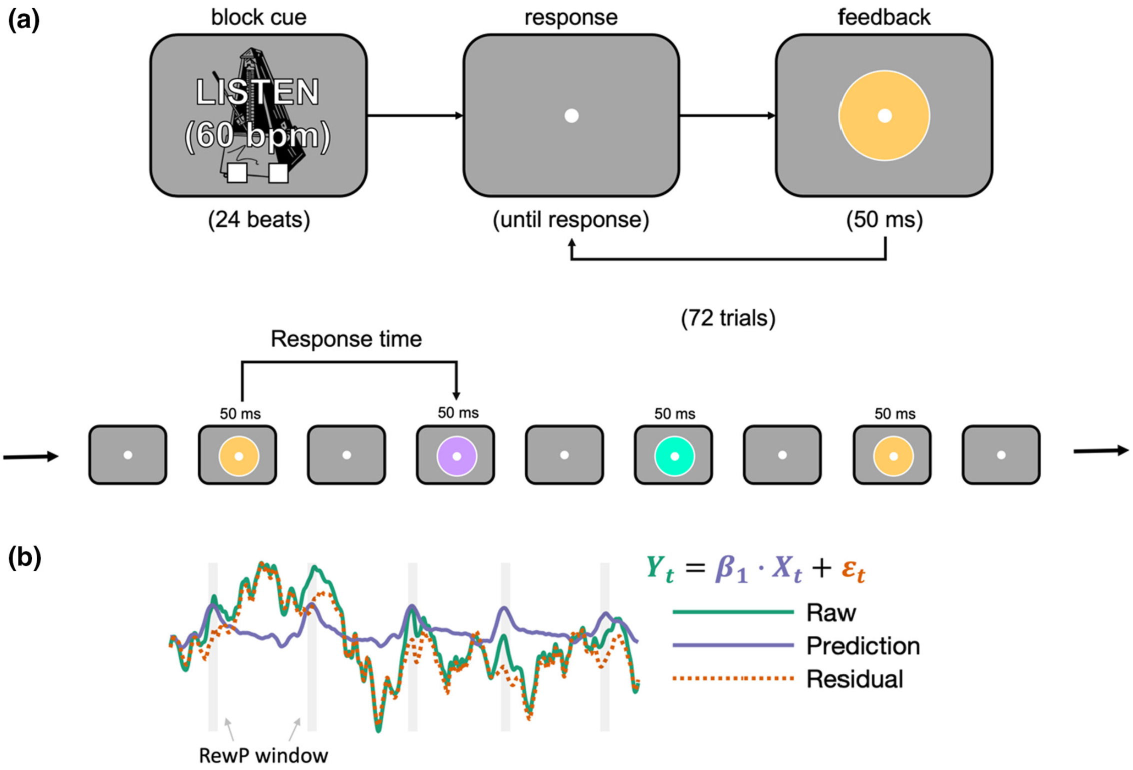

FIGURE 1 Task design and EEG data analysis. (a) The drumming task. In each block, participants were required to produce a drumming pattern using F and J keys on the keyboard. Each response was provided with color-coded visual feedback indicating if it was early, on time, or late. There were three tempos in the experiment: fast (0.4 s interval), medium (0.6 s interval), and slow (1.0 s interval). (b) The calculation of trial-to-trial residual RewP. The residual EEG was calculated by subtracting the predicted EEG amplitude from the regression analysis from the raw EEG amplitude at each time point. A trial's RewP was the average amplitude of residual EEG in the RewP time window, shown as gray rectangles in the figure.

response was fast, on time, or slow. The palette is color blind-friendly, and the correspondence between color and feedback was counterbalanced across participants. If the participant pressed a wrong button, a red 'X' appeared on the screen instead of the color-coded feedback for 50 ms. A participant was 'on time' if the produced interval fell into the target interval plus or minus a given margin. The margin had a starting width of 100 ms, and a staircase procedure was used to adjust the size of this margin by steps of 10 ms, so that in every block type, the 'on-time' feedback type composed approximately 50% of all feedbacks. The staircase procedure was used to control for the frequency of correct feedback given individual differences in timing accuracy. There were three tempo conditions: fast (150 beats per minute [BPM], target interval 0.4 s), medium (100 BPM, target interval 0.6 s), and slow (60 BPM, target interval 1.0 s). In each condition, there were two possible drumming patterns 'aaba/aaba/aaba…' (commonly referred to as '4/4 time') and 'aaabaa/aaabaa/aaabaa…' (commonly referred to as '6/8 time'). In both patterns, the starting hand (controlling beat 'a' above) is the dominant hand mainly determining the drumming speed. Therefore, to reduce the handedness effect, participants were instructed to use either the left or the right hand as the starting hand across different blocks of the same block type, the order of which is randomized in the task. Each participant completed 24 blocks in total (2 patterns × 3 tempos × 2 starting hands × 2 repetitions) in randomized orders. Participants received a bonus for their performance on the task. Twenty of the 21 participants completed 24 blocks (72 trials per block, 1728 trials in total) in total. One participant (No. 1, female) completed a pilot version of the task which included two identical repetitions of the task as performed by other participants, and only the first 1728 trials were included in the analysis.

This drumming task is continuous in the sense that participants self-paced the drumbeats and there was no artificial delay between events, making it relatively naturalistic. Because feedback stimulus occurred almost immediately (50 ms) after the timing response, signaling the start of the next timing interval, there were no 'trials' in the traditional sense. Instead, we defined a 'trial' in this paradigm as starting with feedback onset, followed by feedback-relayed neural responses, and until the subsequent button response. Similarly, we defined response time (RT) as each inter-beat interval between two drumbeats generated by key presses.

2.3 | Software

Pre-processing and analysis of EEG data was conducted in MATLAB R2020a (The MathWorks Inc., 2020), using EEGLAB v2023.0 (Delorme & Makeig, 2004). The results were then analyzed in RStudio (version 4.0.2, 2020-06-22). Linear mixed models were conducted using the R package *lme4* version 1.1-31 (Bates et al., 2014) and *lmerTest* version 3.1-3 (Kuznetsova et al., 2017), and effect size estimates were acquired using the R package *effectsize* version 0.8.2 (Ben-Shachar et al., 2020) and package *EMAtools* version 0.1.4. Data visualization is implemented using the R package *ggplot2* version 3.4.3 and the MATLAB plotting functions. All analysis and data visualization code are available on GitHub.

2.4 | Behavioral analysis

2.4.1 | Response time and its adjustment

Response time (RT) was defined as the time to press the button after the previous feedback onset. RT adjustment was calculated as the difference between RT in the current trial and in the last trial; a positive value suggests increasing RT, and a negative value suggests decreasing RT. To analyze timing performance, we first removed trials where participants pressed the wrong button, and excluded outliers of RT and RT adjustment in the top and bottom 1%. We conducted a one-sample t test comparing participants' average response time in each tempo to the target interval and reported Cohen's d (Cohen, 2013). We conducted a two-way ANOVA (3 tempos × 3 feedback types) on participants' average RT adjustment and reported the effect size partial eta squared (η_p^2).

2.4.2 | Hierarchical timing and chunking

During execution of movement sequences, participants tend to group consecutive movements together into 'chunks' and organize them in a hierarchical manner (Rosenbaum et al., 1984; Sternberg et al., 2018; Verwey & Dronkert, 1996; Verwey & Eikelboom, 2003). The chunking literature suggests that participants' movement is more fluent and efficient within a chunk than when they switch between chunks (Ramkumar et al., 2016; Verwey & Dronkert, 1996). Importantly, chunking has been linked to dopaminergic functioning in animals and humans (Tremblay et al., 2009, 2010) and thus may interfere with the reward-related activity estimated from the RewP. In this task, participants were explicitly instructed to drum at a specific pattern, so we used the current beat's location in the specific pattern as a proxy for chunking. We analyzed the effect of chunking on RT and its adjustment and controlled for chunking in the linear mixed models (for details, see Section 2.5.5).

2.4.3 | Regression to local mean

One possible concern with our RT adjustment measure is that it could partially reflect regression to the mean. A short RT could be followed by an apparent 'adjustment' in the right direction, simply because the next response is more likely to be closer to the mean RT (Jazayeri & Shadlen, 2010). To address this issue, we conducted a simulation by drawing response time (1728 draws per tempo) from a Gaussian distribution specified by the observed mean and standard deviation and derived apparent 'RT adjustment' as the difference between consecutive RT draws. If the observed RT adjustment following different feedbacks in this task is not different from the simulated null distribution, then we may conclude that the apparent RT adjustment observed in the study likely arose only from regression to the mean. Moreover, if RT adjustment is only due to regression to the mean, we should not observe any effect of neural processing of feedback such as RewP, nor any association between neural processing and behavioral adjustment.

Regression to the mean suggests that a larger deviation from the mean leads to larger subsequent adjustment in the opposite direction, resulting in a negative association between the two values. Moreover, it is likely that participants' performance drift over time, shifting the distribution from which the current RT is drawn. Therefore, regression to the mean ought to be quantified relative to the *local* mean (e.g., the recent trials), but not the grand mean (e.g., the mean RT in the current block or the target interval). This deviation-from-mean parameter was quantified as the difference between the RT on this trial and the local mean RT, which was the rolling mean averaged across the previous 10 trials. For the first 10 trials in a block where this rolling mean cannot be calculated, the deviation was calculated as the difference between RT and the target interval (0.4, 0.6, or 1 s). A positive value of this deviation variable suggests temporary slowing on this trial compared to recent history and a negative value suggesting temporary speeding. We demonstrated using simulation that when apparent RT adjustment solely arises from regression to the mean in a Gaussian distribution, this adjustment is negatively correlated with deviation from local mean, regression coefficient $B = -0.45$ (SI Figure S1.5a,b). Therefore, in the linear mixed models, we added deviation from the mean as a covariate to partial out the effect of regression to the mean on RT adjustment. Varying the time window for calculating the rolling mean or excluding the first trials where the rolling mean could not be calculated did not alter the main conclusions from the linear mixed model.

2.5 | EEG analysis

2.5.1 | EEG recording

32-channel EEG was recorded at 1000 Hz with a 280 Hz actiCHamp Plus anti-aliasing amplifier (Brain Products, GmbH, Gilching, Germany) using BrainVision Recorder (Version 1.23.0001, Brain Products, GmbH, Gilching, Germany). The EEG device featured active Ag/AgCl electrodes with per-electrode LED impedance feedback. 30 of the electrodes were arranged according to the international 10–20 system, and two additional electrodes were placed on the left and right mastoids. No additional EOG electrodes were included. The EEG recording was referenced to Fz online.

2.5.2 | Pre-processing

The EEG was pre-processed in MATLAB R2020a (MathWorks, Natick, USA) using EEGLAB v2023.0 (Delorme & Makeig, 2004). EEG data were down-sampled to 250 Hz, filtered by a 0.1–30 Hz band pass finite impulse response filter (-6 dB, hamming window) and a 50 Hz notch filter using the EEGLAB function *firfilt*, and re-referenced to the linked mastoids. Ocular artifacts were identified and removed from the continuous data by running an independent component analysis and then the *iclabel* function. On average, 1.65 ICA components (range: 1–4) were identified as ocular artifacts and removed from the data.

2.5.3 | Extraction of regression-based event-related potential

In this continuous task, each behavioral response was immediately followed by visual feedback, and the interval timing for the next beat immediately ensued without an inter-trial interval. Due to component overlap, this rapid design poses challenges to the traditional event-related approach to EEG analysis. We used a regression-based ERP (rERP) analysis method to extract waveforms from the overlapping signals using the *Unfold* toolbox in MATLAB (Ehinger & Dimigen, 2019; Smith & Kutas, 2015). We detected artifacts in the continuous EEG with a 150 μV threshold using the *basicrap* function from ERPLAB toolbox with 2000 ms window and 1000 ms step size (Lopez-Calderon & Luck, 2014). For each participant, we constructed a design matrix consisting of stick functions spanning −1500 to 1500 ms around the onset of visual feedback, for each feedback type and tempo, respectively. EEG sample and design matrix rows corresponding to artifacts were removed before solving the equation. We also conducted a traditional EEG analysis for comparison (SI Table S5.1, Figure S5.2).

2.5.4 | RewP amplitude quantification

To identify the scalp location of the RewP, we used the 'collapsed localizer' approach (Luck & Gaspelin, 2017), combining across tempos and incorrect feedback types (early or late) to form a single correct waveform and a single incorrect waveform for each electrode. We located the electrode (FCz) at which the RewP amplitude (collapsed correct minus collapsed incorrect) was maximal. RewP time window was selected as 240–340 ms according to a previous meta-analysis (Sambrook & Goslin, 2015). RewP was calculated as the difference wave between correct and incorrect feedback, and the amplitude is quantified as the mean amplitude in the RewP time window. We conducted one-sample t test comparing participants' average amplitude to 0 and reported Cohen's d (Cohen, 2013). We then conducted a two-way within-subject ANOVA (3 tempos × 2 feedback contrasts) on participants' average RewP amplitude, reporting the η_p^2. The average waveform and the topography were acquired by first averaging all trials within a participant, and then averaging across all 20 participants, for three tempos, respectively.

2.5.5 | Trial-by-trial analysis

After confirming the existence of RewP and localizing it to the electrode FCz, we asked the question whether the neural activity at this electrode site induced by reward (i.e., on-time feedback) affects subsequent timing. We used the trial-by-trial EEG amplitude during on-time trials in the RewP time window as a proxy for trial-to-trial fluctuations in reward-induced ACC activity, and use this amplitude to predict participants' behavioral adjustment in the next trial in a hierarchical manner, using all trials from each participant. This approach allowed us to capture the variability both from trial-to-trial and across participants, and get a better estimate by utilizing all available data, not just average values. We focused on the on-time trials for two reasons. First, there is evidence that RewP variability depends on the reward response but not the non-reward response (Holroyd et al., 2008; Proudfit, 2015). Second, reward feedback in this task ought to be unconfounded by the directional behavioral adjustments we would expect for 'early' and 'late' feedback (SI Table S1.1).

The derivation of residual RewP

To derive the trial-by-trial RewP amplitude, we extracted a common feedback component for each participant's individual condition (fast, medium, slow) and feedback type (early, late, on time), using the rERPs acquired from the regression-based analysis above. The trial-to-trial 'residual RewP' was computed as the difference between the current trial's EEG amplitude and the predicted amplitude from the regression model, averaged within the prespecified RewP window (240–340 ms) at electrode FCz (Figure 1b). As a comparison, we also derived the trial-to-trial residual EEG from the traditional ERP by subtracting the grand mean ERP waveform from the trial-to-trial ERP (SI S5.3).

This experiment does not contain explicit practice trials; the first three blocks were considered as practice blocks and excluded from the analysis. We further truncated the top and bottom 1% of RT for each tempo, 1% of all RT adjustment, regression to the mean, and residual RewP amplitude from the data set, removing 7.0% of all trials. For sensitivity analysis, we varied the number of blocks counted as practice blocks and the percentage of outliers (see Results 3.3). Before exclusion, the range of RT was 0.001 to 25.573 s, the range of RT adjustment was −24.995 to 24.949 s, the range of deviation from the mean was −4.004 to 22.118 s, and the range of trial-to-trial EEG was −76.786 to 66.371 μV; after exclusion, the range of RT was 0.305 to 1.222 s, the range of RT adjustment was −0.290 to 0.283 s, the range of deviation from the mean was −0.419 to 0.391 s, and the range of trial-to-trial EEG was −28.593 to 28.777 μV.

Autocorrelation

To examine the temporal variation structure in the neural and behavioral data, we examined the autocorrelation of residual RewPs and the behavioral adjustment variables. Linear mixed models with lag = 1 were constructed with random intercept for each participant, as follows:

$$\text{value\_this\_trial} \sim 1 + \text{value\_last\_trial} + (1| \text{ participant})$$

A positive association would indicate that the variable of interest maintains similarity with the previous value.

Hierarchical regression model for predicting RT adjustment

To estimate the extent to which variations in residual RewP influence the behavioral adjustment in the subsequent trial, we constructed a series of linear mixed models, where each trial is nested within a participant. In these models, the common effect of predictor variables on all participants' all trials was estimated, while the intercepts were allowed to vary for each participant. Specifically, tempo, feedback type, residual

RewP, and their interactions were entered as group-level predictors for the RT adjustment (signed; positive value indicates slowing) on the next trial, while controlling for the effect of chunking and regression to the mean. We focused on the slow tempo, where the most prominent RewP was observed (Section 3.2), and on the on-time feedback type, because this is where the hypothesized fluctuations in phasic DA signaling occur. In practice, linear mixed model was constructed using the R function *lmer()* with random intercept for each participant:

$$\begin{aligned}&\text{rt\_adjustment} \sim 1 + \text{feedback} \times \text{tempo} \times \text{RewP}\\&+ \text{chunk\_location} + \text{deviation\_from\_the\_mean}\\&\times \text{tempo} + (1|\text{participant})\end{aligned}$$

Here, chunk location denotes the location of the current interval in the drumming pattern. The main effect of RewP on RT adjustment following on-time feedback within each tempo was acquired by relevelling the model to different tempos and re-running the model. Cohen's *d* was reported for all linear regressions.

Finally, to confirm the robustness and homogeneity of the effect across participants, we also estimated the regression coefficients for each participant individually. In practice, we fit a linear mixed model with random slope and intercept for every participant, while controlling for the group-level effect of chunking and deviation from the mean.

$$\begin{aligned}&\text{rt\_adjustment} \sim 1 + \text{chunk\_location}\\&+ \text{deviation\_from\_the\_mean} \times \text{tempo}\\&+ (\text{RewP} \times \text{tempo} \times \text{feedback} \mid \text{participant})\end{aligned}$$

The slope coefficient B was extracted for each participant, respectively, and we tested whether they are systematically greater than 0 in a one-sample *t* test.

2.5.6 | Post hoc power analysis

Post hoc power analysis was conducted using the R package *SIMR* (Green & MacLeod, 2016). Importantly, because the main finding was concerning the main effect of RewP on behavioral timing when the feedback was on time and the tempo was slow, we created a subset of data set containing only those trials and conducted a post hoc power analysis on the main effect of RewP in this subset of data. We did not conduct post hoc power analysis on other tempo and feedback types. Achieved power was obtained from the function *powerSim* with 100 simulations. We further tested how the sample size and the block number influenced the observed power, demonstrating that the current study achieved more than 90% post hoc power (SI Figure S3.1).

3 | RESULTS

3.1 | Systematic bias in interval production

Participants were relatively accurate in reproducing the target intervals (Figure 2a,b). One-sample *t* tests on participant's average RT indicated that participants were significantly faster than the target interval for the medium tempo (all RT below in seconds; mean = 0.570 s, $SD = 0.020$, $t_{(1,19)} = -6.867$, $p < .001$, Cohen's $d = -1.54$) and the slow tempo (mean = 0.933 s, $SD = 0.037$, $t_{(1,19)} = -7.884$, $p < .001$, Cohen's $d = -1.76$), but not for the fast tempo (mean = 0.402 s, $SD = 0.014$, $t_{(1,19)} = 0.661$, $p = .516$, Cohen's $d = 0.15$). Consistent with the systematic bias in RT, participants also received asymmetric proportion of 'early' and 'late' feedbacks, while the proportion of on-time feedback was approximately 50% due to the staircase procedure (SI Table S1.1). The margin used for the staircase adjustment procedure decreased over time within a block and across blocks, indicating improvement of performance accuracy, whereas the average margin size is still larger for slower tempos (SI Figure S1.2). Chunking was observed for both drumming patterns; participants' RTs were faster when they were within a chunk than when they moved to another chunk or switched hands (SI Figure S1.5c).

Two-way within-subject ANOVA (3 tempos × 3 feedback types) on participants' average RT adjustment suggested that RT adjustment significantly differed by feedback type ($F_{(2,38)} = 205.651$, $p < .001$, $\eta_p^2 = 0.92$) and tempo ($F_{(2,38)} = 28.213$, $p < .001$, $\eta_p^2 = 0.60$). The significant main effect of feedback type confirms that participants adjusted their behavior according to feedback, speeding up upon receiving 'late' feedback and slowing down upon receiving 'early' feedback (Figure 2c). There was also a significant interaction between feedback and tempo ($F_{(4,76)} = 21.280$, $p < .001$, $\eta_p^2 = 0.53$). Pairwise comparisons with Bonferroni adjustment further suggested that participants' RT adjustment following 'on-time' feedback was significantly more positive (suggesting slowing) for fast tempo than slow tempo (mean difference = 0.025 s, *t*-ratio = 3.957, $p_{\text{adjust}} < .001$, Cohen's $d = 1.83$). The biasing effect of tempo and feedback on RT was systematic across participants, although there were individual differences in their mean RT and RT adjustments (Figure 2d).

3.2 | RewP was observed only for the medium and the slow tempos

We derived rERPs for each tempo and feedback type (Figure 3a–c). The slower the tempo, the larger the

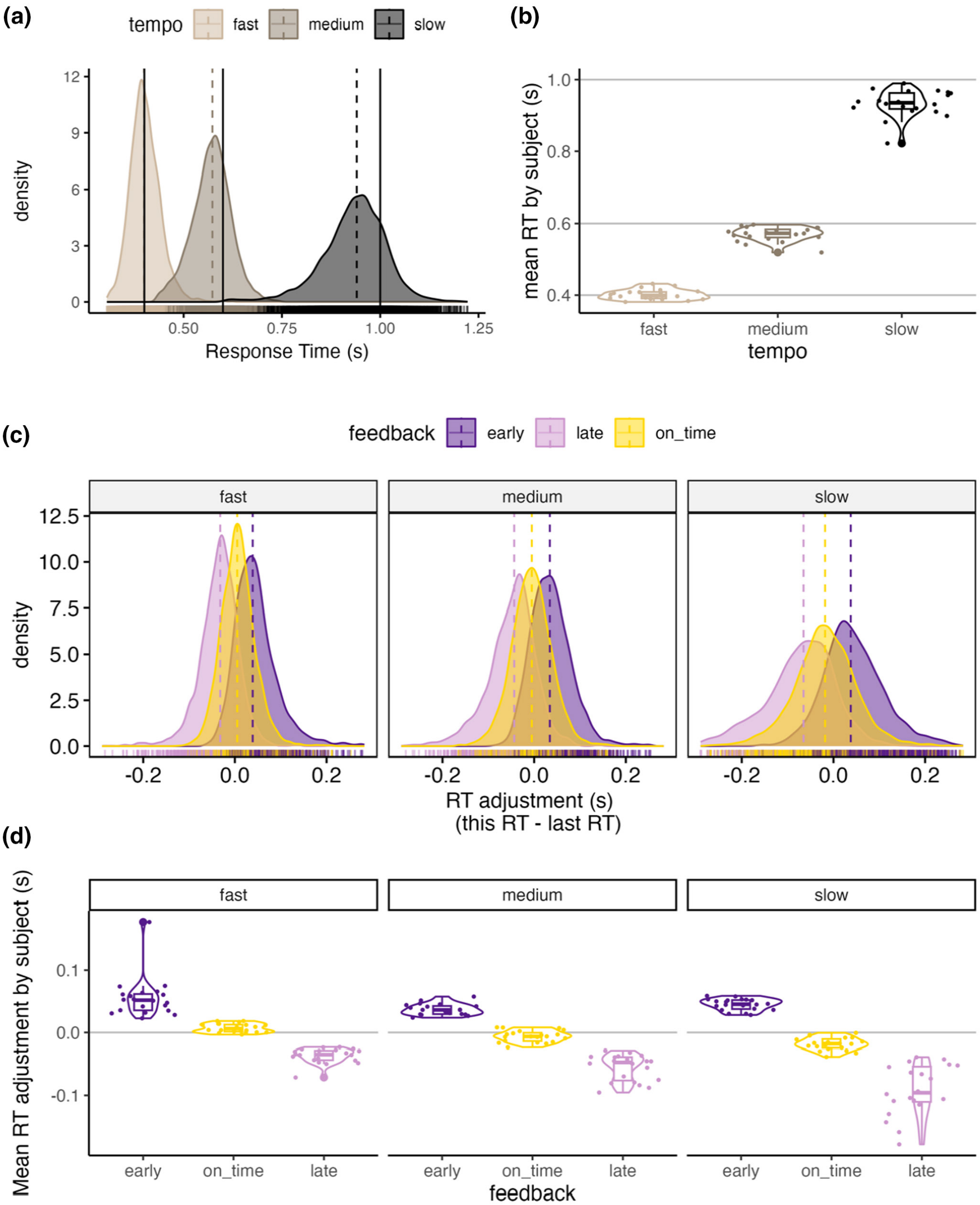

FIGURE 2 Participants relatively accurately reproduced different drumming patterns and adjusted their behavior following different feedbacks. (a) The distribution density of RT in each tempo, suggesting speeding in the medium and the slow tempo. The dotted line and the solid line indicated the population mean and the target interval, respectively. (b) The distribution of participants' average RT in each tempo. Each point represents one participant. The horizontal lines represent the target interval. (c) The distribution of RT adjustment in each tempo. The dotted lines showed the population mean. (d) The distribution of RT adjustment by feedback type in each tempo.

RewP observed, whether the early and late feedback types were separated (Figure 3d–f) or collapsed (SI Figure S1.3). In the slow tempo, a clear frontocentral gradient of scalp RewP amplitudes emerged that peaked at FCz (Figure 3g–i). Two-way within-subject ANOVA (3 tempos ×2 feedback contrasts) on the mean RewP amplitude for each participant suggested a significant main effect of tempo ($F_{(2,38)} = 7.560$, $p = .002$, $\eta_p^2 = 0.285$), but not feedback type ($F_{(1,19)} = 0.044$, $p = .837$, $\eta_p^2 = 0.002$). There was no interaction between tempo and feedback type ($F_{(2,38)} = 0.270$, $p = .765$, $\eta_p^2 = 0.014$) (SI Figure S1.5d). Pairwise *t* tests with Bonferroni corrections suggested

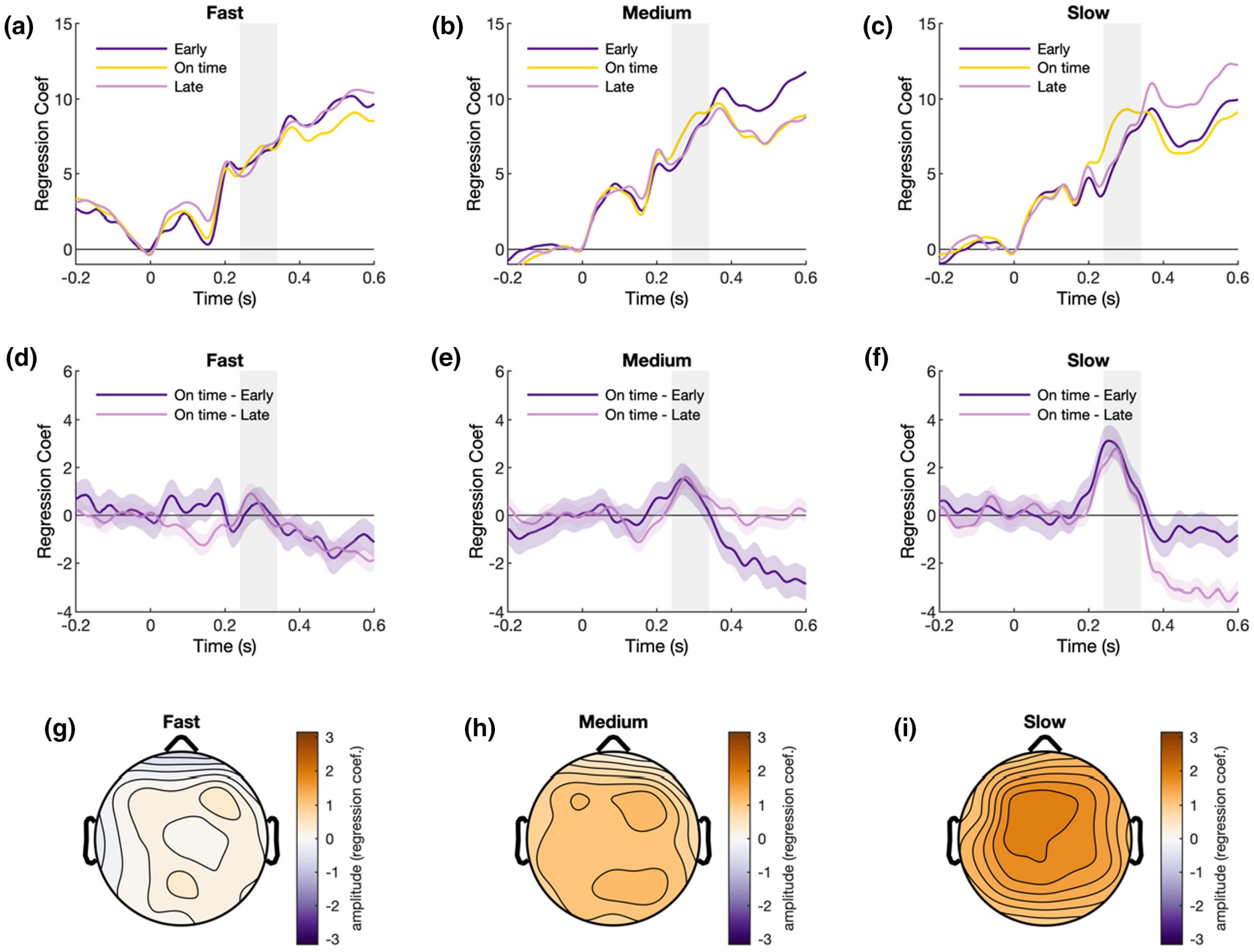

FIGURE 3 Reward positivity in the fast, medium, and slow tempo. (a–c) Regression-based ERP by tempo and feedback type. The RewP time window as reported in Sambrook and Goslin (2015) was highlighted in gray (240–340 ms). (d–f) The RewP wave was calculated as the contrast between correct (on time) and incorrect (early or late) feedback type. RewP amplitude increased as a function of target interval. (g–i) The topography of RewP as the average difference between correct and incorrect waveform in the 240–340 ms time window, averaged between early and late feedback type. In the slow tempo, the peak amplitude was located at electrode FCz.

that the RewP amplitude in the slow tempo was marginally significantly larger than in the medium tempo (mean difference = 0.931, $t_{(1,39)} = 2.474$, $p_{\text{adjust}} = .053$, Cohen's $d = 0.39$) and significantly larger than in the fast tempo (mean difference = 1.768, $t_{(1,39)} = 3.509$, $p_{\text{adjust}} = 0.003$, Cohen's $d = 0.55$); the RewP amplitude in the medium tempo was not significantly larger than that in the fast tempo (mean difference = 0.837, $t_{(1,39)} = 2.043$, $p_{\text{adjust}} = 0.143$, Cohen's $d = 0.32$). The 95% confidence interval of the RewP amplitude in the fast tempo included zero, and the 95% confidence interval of the amplitude from medium and slow tempo was greater than 0, suggesting that RewP could be reliably observed in the medium and slow tempo (Table 1).

To explore whether the effect of tempo on the RewP amplitude was due to increasing internal error monitoring as opposed to external feedback processing, we investigated the amplitude of the error-related negativity (ERN) under different tempos, an ERP signal implicated in internal error monitoring that peaks around 100 ms at electrode FCz after committing an error (Gehring et al., 2012). An ERN could be localized (SI Figure S4.1), although the erroneous trials were less frequent than other feedback types (SI Table S4.2). Participants had a greater (more negative) ERN amplitude in the fast tempo compared to the medium and the slow tempos (SI Figure S4.3).

3.3 | Trial-to-trial fluctuation in RewP amplitude influences timing in slow tempo

We examined the autocorrelation of RT adjustment and RewP using linear mixed models with random intercept

TABLE 1 Summary statistics of participants' mean RewP amplitude for each tempo and feedback type.

				95% CI		
Tempo	**Feedback contrast**	**Mean**	***SD***	**Lower**	**Upper**	**Cohen's *d***
Fast	On time–early	0.176	2.817	−1.142	1.495	0.06
	On time–late	0.289	1.656	−0.486	1.037	0.17
Medium	On time–early	1.032	1.617	0.275	1.789	0.64
	On time–late	1.106	1.780	0.273	1.940	0.62
Slow	On time–early	2.220	1.633	1.456	2.985	1.36
	On time–late	1.781	2.703	0.516	3.046	0.66

for each participant. Last trial's RT adjustment was negatively associated with RT adjustment on this trial, such that slowing on the last trial predicted speeding up on this trial, and vice versa (regression coefficient $B=-0.257$, $t=-61.281$, $p<.001$, Cohen's $d=-0.749$), suggesting regression to the mean. Last trial's RewP was not associated with this trial's RewP, $B=-0.0016$, $t=0.316$, $p=0.752$, Cohen's $d=0.004$, suggesting negligible baseline fluctuations in the RewPs across trials.

For initial visualization, we divided the RewP amplitudes into 10 bins with 10% of trial data in each bin and plotted the mean and standard error of RT adjustment for this RewP bin (Figure 4a,b). Visual inspection revealed a linear association between the RewP amplitude and RT adjustment. Next, we fitted a linear mixed model using the current trial's residual RewP (trial EEG subtracted by average EEG waveform) to predict RT adjustment on the next trial. The model converged successfully. Feedback type, tempo, regression to the mean, and chunk locations significantly predicted RT adjustment. In the slow tempo, trial-to-trial fluctuations in RewP in response to on-time feedback predicted RT adjustment on the next trial, such that larger (more positive) RewP led to a slowing of RT compared to the last trial ($B=2.9\times10^{-4}$, $t=4.341$, $p<.001$); the effect size of the biasing effect of RewP was modest, Cohen's $d=0.053$ (Figure 4c). This association between RewP and RT adjustment is specific to when the RewP temporarily precedes the RT adjustment, but not the other way around ($B=-4.76\times10^{-5}$, $t=0.372$, $p=.710$). Such timing-biasing effect of RewP fluctuations was not significantly observed for the fast ($B=1.2\times10^{-4}$, $t=1.892$, $p=0.058$, Cohen's $d=0.023$) or the medium tempo ($B=0.0\times10^{-4}$, $t=-0.002$, $p=0.999$, Cohen's $d<.001$). This observed time-biasing effect of the RewP in the slow tempo was also significant when using the traditional ERP approach; however, using the traditional approach, the trending positive association between RewP amplitude and RT adjustment became significant (SI S5.3). RewP fluctuations did not significantly affect timing following early or late feedback in any of the three tempos ($|t|<1.390$, $p>0.164$), although this may not be a fair test due to the unbalanced percentage of early and late feedback types. The entire linear mixed model, including effects of tempo and chunk location on RT adjustment, is shown in SI Table S1.4. The regression coefficient B of RewP was still significant when not including chunk location and regression to the mean by tempos as the covariates, $B=2.7\times10^{-4}$, $t=3.703$, $p<.001$, Cohen's $d=0.045$. Post hoc power analysis showed that the observed significant effect of RewP in the slow tempo, on-time feedback attained a power of 96.00% (95% CI: 90.07%–98.90%). Because participants would on average speed up following an on-time feedback in the slow tempo, as illustrated by the negative intercept in Figure 4b, a larger RewP on an on-time trial leads to the participants speeding up less and thus more likely to remain on time the next trial.

To confirm the finding that trial-to-trial RewP was not limited to the present exclusion criterion, we conducted sensitivity analysis by varying (1) the number of blocks considered as practice blocks and (2) the percentage of outliers in timing behavior and EEG. When no block was counted as practice block, the regression coefficient of RewP was still significant, $B=2.95\times10^{-4}$, $t=4.431$, $p<.001$, Cohen's $d=0.051$. When only the bottom and top 0.5% of RT, RT adjustment, deviation from the mean, and RewP amplitude were excluded (inclusion rate 95.76%), the regression coefficient was still significant, $B=2.8\times10^{-4}$, $t=3.742$, $p=.002$, Cohen's $d=0.042$. An additional sensitivity analysis targeting the impact of influential observations based on two diagnostic statistics, Studentized residuals and Cook's distance, revealed little influence of outliers on the main findings (SI Figures S2.1 and S2.2).

When fitting both random slope and random intercept for each participant in this model, all but two participants' slope estimates were larger than 0 ($\min=-0.18\times10^{-4}$, $\max=10.5\times10^{-4}$, $\text{Mean}=2.5\times10^{-4}$, $SD=2.6\times10^{-4}$) (Figure 4d, see also SI Figure S1.6). One-sample t test suggests that the slopes were significantly larger than 0 ($t_{(1,19)}=4.304$, $p<.001$, Cohen's $d=0.96$).

Finally, we explored other ERP windows associated with behavioral adjustment using permutation tests on the point-wise correlation coefficient for all time

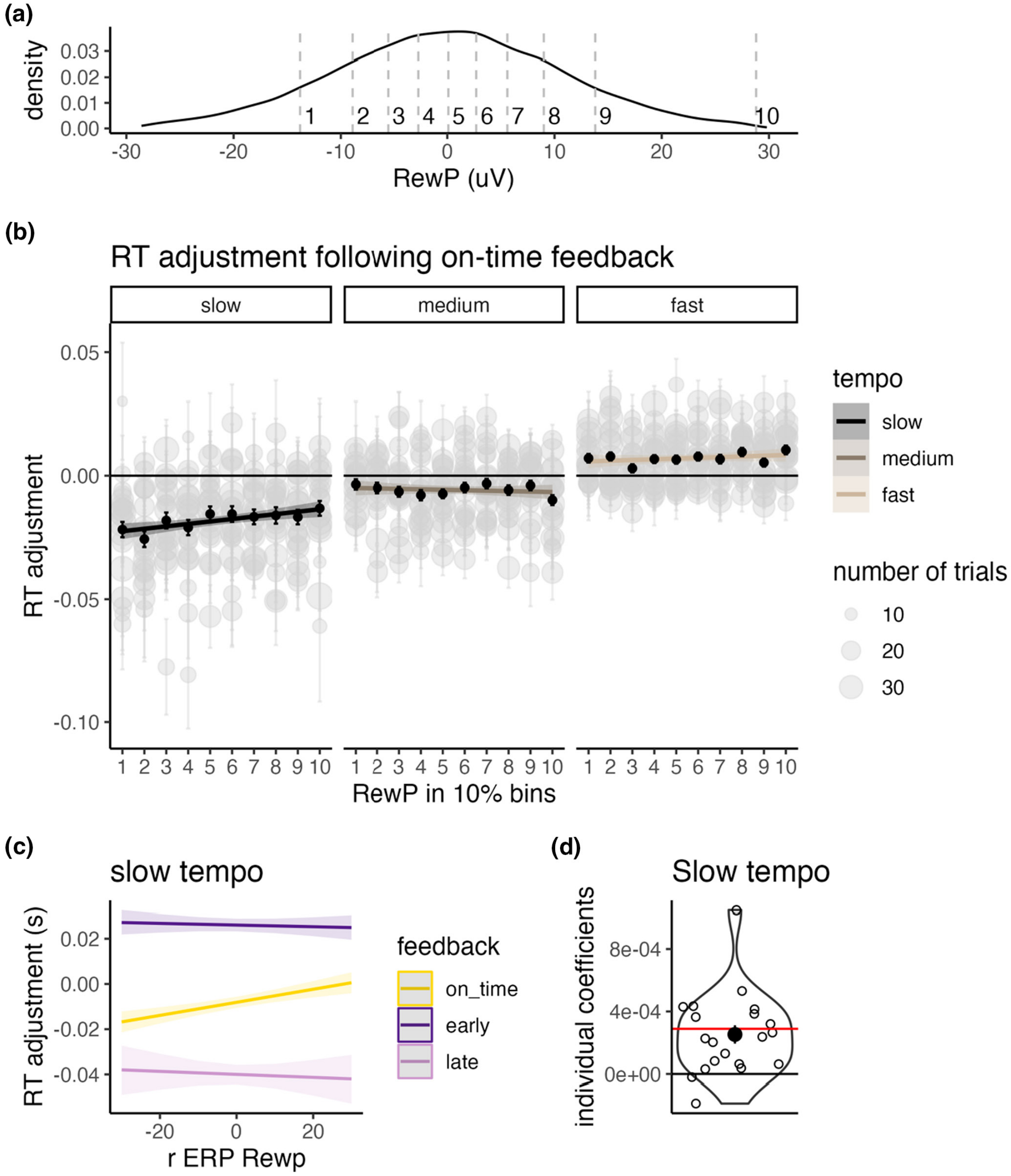

FIGURE 4 Reward response predicted timing behavior. To visualize RT adjustment as a function of RewP on the individual participant level, RewPs were divided into 10 bins of 10%. (a) The distribution density of RewP amplitude on the group level, and the range of the 10 bins. (b) Size of RT adjustment as a function of the RewP amplitude in response to on-time feedback. Each gray point represented one participant's data in this bin, with larger point size indicating more trials. The gray-colored error bars shown below indicated standard error of the subset of data represented by the gray point. The black points and error bars represent the group-level mean and standard error within each RewP bin. (c) The predicted values of RT adjustment in the slow tempo from the linear mixed model. (d) Individual regression coefficients *B* from a linear mixed model with random slopes and random intercept, in the slow tempo. Each open dot represents the regression coefficient of one participant, and the red horizontal line denotes the coefficient when the slope is fixed across participants.

points. It was revealed that in addition to RewP, trial-to-trial residual C1 and P3b may also predict longer RT on the next trial, suggesting a generic effect of external feedback processing on timing performance (SI Figure S6.1).

4 | DISCUSSION

This study investigated the influence of reward processing on interval production by looking at participants' reward positivity (RewP) in response to rapid feedback while they engaged with a continuous drumming task at different tempos. A continuous timing paradigm was used to gather larger number of observations compared to traditional trial-based paradigms. In the slow tempo (1.0 s expected interval), trial-to-trial EEG fluctuations in the RewP time window predicted timing adjustment on the next trial, such that a larger (more positive) RewP amplitude relative to the mean waveform forecasted longer produced interval on the next trial. Because participants had a general tendency to be too early in the slow tempo, a larger RewP was associated with producing a more accurate interval in the next trial. This study demonstrated the plausibility of using a rapid paradigm to acquire the RewP and showed that fluctuations in the RewP are associated with variations in interval production.

Considering previous studies that linked the RewP to a striatal reward prediction error relayed to the anterior cingulate cortex (ACC) (Holroyd & Coles, 2002; Holroyd & Yeung, 2012), our findings could be interpreted as a slowing effect of reward-related ACC activity on interval production. Previous studies have reported divergent results regarding the effect of reward on interval perception; while some studies reported that reward led to the same interval being perceived longer by human participants (Failing & Theeuwes, 2016; Toren et al., 2020), one study directly manipulating dopamine signaling in mice found the opposite effect (Soares et al., 2016). However, caution needs to be taken in comparing results on interval perception with those on interval production (Coull et al., 2013), although there is some evidence of shared psychological substrates (Ivry & Hazeltine, 1995; Keele et al., 1985). One prominent class of timing theories proposes that an 'internal clock', or pacemaker, determines the speed of psychological timing (Church, 1984). According to this theory, a slower pacemaker (emitting fewer pulses within an interval) is associated with compressed interval perception but extended production, although others report that individual difference factors like depression affect interval perception and production in the same direction (Block et al., 1998; Mioni et al., 2016). Under this framework, our observation that a larger RewP is associated with prolonged interval production seems to align with previous findings that a higher dopamine level is associated with compressed interval perception (Soares et al., 2016), but is at odds with other reports in humans where reward expanded interval perception (Failing & Theeuwes, 2016; Toren et al., 2020). However, one main difference between this and previous paradigms in humans is that reward here was administered as feedback to the produced interval, but not during the interval; therefore, the expanding effect of attention likely impacted the next interval to be produced, but not the previous interval to be perceived. It should also be noted that the RewP is an indirect measure of dopaminergic activity that reflects the suppression of ACC activity by reward (Proudfit, 2015). Thus, our findings may not be strictly comparable with those that directly manipulated midbrain dopaminergic neurons.

Considering that the RewP typically occurs 250–350 ms post-feedback, it may be surprising that we did not reliably observe a RewP in the fast tempo which had a target interval of 0.4 s, which is longer than the typical latency of the RewP. One possibility is that there might be a shift in timing strategies across different tempos. In the slower tempos, participants may rely more on a feedback-based, discrete interval timing system, while the fast tempo may tap into a more automatic and motoric timing system where participants rely more on sampling from their internal interval representation (Lewis & Miall, 2003; Petter et al., 2016; Wiener et al., 2011). In the supplementary analysis, we did find some evidence for stronger internal monitoring in the fast tempo by comparing ERN amplitudes (SI S4). Furthermore, feedback processing may interact with tempo speed; the richer the information that the feedback stimuli contain, the smaller the observed RewP amplitude might be (Cockburn & Holroyd, 2018). This study provided directional incorrect feedback (early and late) instead of a dichotomous right-or-wrong differentiation, which may require more feedback processing and reduce RewP amplitude in the faster tempos. Overall, this highlights the tradeoff between continuous timing paradigm and RewP amplitude due to a possible shift in timing strategy.

It was argued that the RewP is larger when the feedback is surprising or salient, and that surprise leads to larger behavioral adjustment (Holroyd & Krigolson, 2007; Talmi et al., 2013; but see: Heydari & Holroyd, 2016; Mulligan & Hajcak, 2018). The link between RewP fluctuations and subsequent behavioral adjustment in this study is unlikely to be confounded by surprise about the feedback. This is because the present study used a staircase procedure to ensure that on-time feedback always consisted of 50% of trials in each block, eliminating the impact of surprise due to rarity on the EEG amplitude in response to on-time feedback. Although such staircase adjustment may lead to divergent feedback for the exact same duration depending on the margin size, this divergence is unlikely to cause a strong conflict signal, since interval production is intrinsically noisy and it is unlikely that participants have strong confidence that the two produced intervals that they receive divergent feedback for are exactly the same (Oprisan & Buhusi, 2014). Thus, participants continuously adjust their behavior according to external feedback under this staircase regime. The different feedback types were also color-coded and randomized across participants to reduce the confound of perceptual salience.

However, due to a systematic bias in interval production (Figure 2a), the proportion of 'early' and 'late' feedback types were not strictly 25% each. Considering the saliency effect, this might have confounded the estimation of the RewP amplitude and led to a spurious difference in the RewP amplitude for the two contrasts (on time vs. early and on time vs. late) (Table 1). The finding concerning the influence of trial-to-trial RewP on RT adjustment is unlikely to be affected by this issue, because only the residual EEG in the on-time condition, but not the contrast wave with incorrect feedback types, was used.

This paper adds to the body of literature linking the RewP to subsequent behavioral adjustment, which mostly focused on between-subject level associations across the entire study with a few exceptions (Arbel et al., 2013; Cavanagh et al., 2010; Holroyd & Krigolson, 2007; Yasuda et al., 2004). Several studies that conducted within-subject, trial-based analysis reported non-significant associations between RewP amplitude and timing behavior (Castellar et al., 2010; Cockburn & Holroyd, 2018). Such results may not be contradictory to our findings. We estimated that each μV increase in RewP amplitude slows down the following produced interval by 0.29 ms, equating to a decrease of 0.029% for the 1.0 s target interval in the slow tempo. Given the modest effect size of this biasing effect, one possibility is that the limited number of trials from traditional trial-based paradigms (a few hundred trials compared to around 576 trials in the slow tempo of this task) may not have the power to detect such effects. Nevertheless, although the post hoc power analysis suggested that the observed effect was relatively robust, we acknowledge the small effect size and the exploratory nature of the findings. In addition, in an exploratory analysis across different ERP time windows, we found that an early visual component C1 and a later component P3b were also positively associated with RT adjustment in the on-time trials in the slow tempo. This suggests that the behavioral-biasing effect of ERP may not be limited to the time window of RewP, but may be relevant to other stages of external feedback processing (Castellar et al., 2010). Future studies should seek to replicate these results in a preregistered manner using various interval production paradigms, including traditional trial-based paradigms.

It should be noted that adjustment in timing behavior was not solely dependent on external feedback, but also on internal error monitoring (Coles et al., 2001; Danielmeier & Ullsperger, 2011; Miltner et al., 1997; Ullsperger & Von Cramon, 2003). The neural substrates for internal error monitoring and external reward monitoring are partially separable (de Bruijn et al., 2009). Participants have an internal model of timing which they use to update their belief and modify their behavior (Petter et al., 2016, 2018). Due to the continuous and ecological property of this paradigm, the internal model may integrate priors about both interval duration and rhythm. First, despite trial-by-trial feedback, participants in this study exhibited a systematic deviation from the target interval. This implies that participants have a prior that biased their produced tempo. Future studies can test this hypothesis by, for example, asking participants to drum with a certain pattern using visual cues without explicit instructions about the tempo speed and examine whether this natural drumming tempo has an interval below 0.6 s. Second, participants' internal models of rhythm may lead to deviation from target interval as a function of beat location in a pattern (Repp et al., 2011). This study aimed at reducing the influence of variations in internal rhythm by showing participants an explicit drumming pattern and varying the drumming pattern to be copied. Moreover, the linear mixed model took into considerations where the participant currently was in a pattern, thereby controlling for the influence of rhythm on RT adjustment.

In conclusion, the present study examined how fluctuations in reward processing-related neural activity bias subsequent performance in interval production. We used a continuous drumming paradigm and regression-based analysis to deconvolute overlapping EEG signals. RewP was reliably observed in the slow and medium tempos (target interval 1.0 s or 0.6 s) but diminished in the fast tempo (target interval 0.4 s). We found that more positive RewP response to on-time feedback predicts the production of longer interval on the next trial, only in the slow tempo where RewP was the largest. Since participants overproduced the slow tempo in this task, a larger RewP was also related to producing a duration closer to the target interval. The modest effect size of this behavior-biasing effect of reward highlights the necessity of using a continuous design that allows for more intensive data collection.

AUTHOR CONTRIBUTIONS

Yan Yan: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; software; visualization; writing – original draft; writing – review and editing. **Laurence T. Hunt:** Conceptualization; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; supervision; writing – original draft; writing – review and editing. **Cameron D. Hassall:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; supervision; visualization; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors (YY, LH, and CH) declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this article.

DATA AVAILABILITY STATEMENT

The EEG data are available at https://openneuro.org/datasets/ds004152/versions/1.1.2. Analysis scripts are available at https://github.com/chassall/drumtrainer.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1: Supporting Information

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