

# Electrophysiological measures of conflict and reward processing are associated with decisions to engage in physical effort

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## Abstract

Anterior cingulate cortex (ACC), a key brain region involved in cognitive control and decision making, is suggested to mediate effort- and value-based decision making, but the specific role of ACC in this process remains debated. Here we used frontal midline theta (FMT) and the reward positivity (RewP) to examine ACC function in a value-based decision making task requiring physical effort. We investigated whether (1) FMT power is sensitive to the difficulty of the decision or to selecting effortful actions, and (2) RewP is sensitive to the subjective value of reward outcomes as a function of effort investment. On each trial, participants chose to execute a low-effort or a high-effort behavior (that required squeezing a hand-dynamometer) to obtain smaller or larger rewards, respectively, while their brainwaves were recorded. We replicated prior findings that tonic FMT increased over the course of the hour-long task, which suggests increased application of control in the face of growing fatigue. RewP amplitude also increased following execution of high-effort compared to low-effort behavior, consistent with increased valuation of reward outcomes by ACC. Although neither phasic nor tonic FMT were associated with decision difficulty or effort selection per se, an exploratory analysis revealed that the interaction of phasic FMT and expected value of choice predicted effort choice. This interaction suggests that phasic FMT increases specifically under situations of decision difficulty when participants ultimately select a high-effort choice. These results point to a unique role for ACC in motivating and persisting at effortful behavior when decision conflict is high.

## KEYWORDS

choice difficulty, effort selection, frontal midline theta, reward positivity, single-trial EEG, valuation

## 1 | INTRODUCTION

Should you take the elevator or the stairs? A growing literature of non-human animal studies indicates that such decisions are mediated partly by anterior cingulate cortex (ACC), a broad region of frontal midline cortex involved

in cognitive control and decision making (Holroyd & Verguts, 2021). In particular, ACC weighs the effort-related costs of choices against their expected rewards and appears critical for overcoming effort costs (Floresco & Ghods-Sharifi, 2007; Rudebeck et al., 2006; Salamone et al., 2003; Walton et al., 2002, 2009). For example, ACC

lesions cause rodents to shift their preference away from high-effort, high-reward choices to low-effort, low-reward choices (e.g., Floresco & Ghods-Sharifi, 2007; Hosking et al., 2014; Walton et al., 2002, 2009), and hinder monkeys' ability to sustain optimal behavior (Kennerley et al., 2006). These studies highlight a role for ACC in deciding specifically whether the expected benefit of an action is worth the incurred cost in effort, in contrast to other types of costs such as temporal delays (Cardinal et al., 2001; Rudebeck et al., 2006).

Human studies echo these findings. ACC lesions lead to apathy (Le Heron et al., 2019, for review) whereas electrical stimulation of ACC induces a subjective feeling of perseverance in the face of challenges (Caruana et al., 2018; Parvizi et al., 2013). Further, several human neuroimaging studies have revealed strong ACC activation when participants evaluate the predicted value of expending cognitive and physical effort against the incurred costs of the expenditure (e.g., Bonnelle et al., 2016; Chong et al., 2017; Croxson et al., 2009; Kurniawan et al., 2010; Skvortsova et al., 2014; Vassena et al., 2014), as well as when participants instigate effortful actions (e.g., Croxson et al., 2009; Bonnelle et al., 2016; c.f., Parvizi et al., 2013; Caruana et al., 2018). Computational theories have proposed a role for ACC in determining the value of applying effortful control and motivating the achievement of high-level task goals (Holroyd & McClure, 2015; Holroyd & Verguts, 2021; Holroyd & Yeung, 2012; Shenhav et al., 2013, 2017; Verguts et al., 2015). Although these theories generally agree that ACC is involved in regulating effortful control, especially when behavior is challenging, the precise mechanism of ACC function continues to be debated (Holroyd & Verguts, 2021; Vassena et al., 2017, 2020).

Measures of cognitive control and reward processing recorded from the human electroencephalogram (EEG) can help to answer this question (Holroyd & Umemoto, 2016; Umemoto, Inzlicht, & Holroyd, 2019). In particular, frontal midline theta (FMT), consisting of 4 to 8 Hz neural oscillations distributed over frontal-central regions of the human scalp, is commonly observed during cognitive control processes involving effort (e.g., Cavanagh & Frank, 2014; Holroyd & Umemoto, 2016). For example, brief, phasic changes in FMT power are often observed following receipt of negative feedback stimuli (e.g., Bernat et al., 2015; Foti et al., 2015), during value-based decision-making (Lin et al., 2018), and immediately following error commission and periods of response conflict (e.g., Cavanagh & Frank, 2014; Luu & Tucker, 2001). By contrast, more long-lasting FMT power is observed over extended periods of task performance involving sustained mental effort (Hsieh & Ranganath, 2014; Mitchell et al., 2008; Umemoto, Inzlicht, & Holroyd, 2019;

Wascher et al., 2014). Thus, phasic FMT appears to reflect transient reactivity to discrete, task-relevant events, whereas tonic FMT appears to be related to sustained cognitive processing. Source localization studies of FMT (both phasic and tonic) as well as intracranial recordings in humans and non-human animals point to ACC as the neural generator (see Holroyd & Umemoto, 2016 for review). These findings suggest that FMT activity generated by the ACC plays important roles in implementing control processes (Cavanagh & Frank, 2014; Verguts, 2017).

Further, the reward positivity (RewP), also called the feedback error-related negativity, is an event-related potential (ERP) component that is sensitive to the valence of external feedback (Miltner et al., 1997). RewP has been proposed to be elicited by phasic midbrain dopamine reward prediction error signals modulating ACC activity (Holroyd & Coles, 2002). A meta-analysis supports the proposal that the RewP indexes a reward prediction error signal (Sambrook & Goslin, 2015). Although the source of the RewP is controversial because of the inverse problem (Michel et al., 2004), the dominant hypothesis is that the RewP is produced in the ACC (Holroyd & Umemoto, 2016; Walsh & Anderson, 2012). Further, RewP amplitude appears to index subjective levels of reward valuation (Holroyd & Umemoto, 2016 for review). For example, RewP amplitude correlates positively with individual differences in reward sensitivity (Bress & Hajcak, 2013; Cooper et al., 2014; Liu et al., 2014; Umemoto & Holroyd, 2017), and negatively with individual differences in self-reported depression levels (e.g., Proudfit, 2015; Umemoto & Holroyd, 2017).

EEG studies on effort and reward integration have begun only recently, focusing mostly on cognitive effort (Harmon-Jones, Clarke, et al., 2020; Harmon-Jones, Willoughby, et al., 2020; Ma et al., 2014; Umemoto, Inzlicht, & Holroyd, 2019; see also Gheza et al., 2018). These studies hint at a reward-effort link, but the results are not straightforward. One study reported increased RewP amplitude with increased cognitive demand (Ma et al., 2014), whereas other studies showed a larger RewP to high-effort only within a high-effort condition (Harmon-Jones, Clarke, et al., 2020), or only when participants believed that their efforts were instrumental in bringing about the reward outcomes (Harmon-Jones, Willoughby, et al., 2020). Examining a slightly different question, Gheza et al. (2018) reported a larger RewP when participants could avoid expending effort (clicking with a mouse on dots on a computer screen), which was associated with higher participant ratings of pleasantness and relief. However, FMT in that study was not modulated by effort costs.

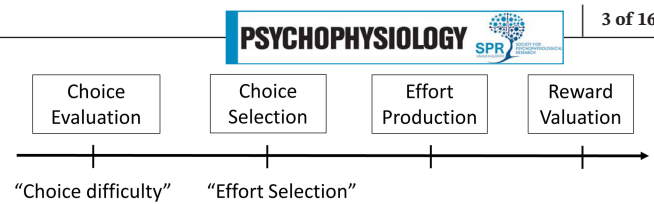
Although these studies provide some evidence that effort-related processing by ACC may interact with the

subjective valuation of reward outcomes, a number of important questions remain. Although decades of animal work on this issue have utilized physical effort (e.g., Floresco & Ghods-Sharifi, 2007; Rudebeck et al., 2006; Salamone et al., 2003; Walton et al., 2002, 2009; but see Hosking et al., 2014), most human research has involved cognitive effort, leaving open the possibility that physical effort could more strongly impact control and reward processing in humans. It is also unclear how effortful control might impact the subjective valuation of reward, as effort expenditure appears to increase the value of rewarded outcomes once obtained (i.e., Inzlicht et al., 2018, for a review). Conversely, the value of reward outcomes can influence the amount of effort participants invest in a task, as people tend to work harder for larger rewards (Frömer et al., 2021; Shenhav et al., 2013; Westbrook & Braver, 2015).

## 1.1 | Current study

The goal of this study was to clarify these questions. We examined neural signatures of effortful control (FMT power) and reward valuation (RewP amplitude) of subjects engaged in a physically demanding task: squeezing a hand-grip. Toward this end, we adapted the Effort-Expenditure for Rewards Task (Treadway et al., 2009), which has been used previously to examine individual differences in effort allocation (Geaney et al., 2015; Treadway et al., 2009, 2012), for an EEG experiment. This task allowed us to investigate both effort-related decision- and reward-processes. On each trial, participants chose between performing a low-effort behavior (a low-force squeeze on a hand-dynamometer) and a high-effort behavior (a high-force squeeze on the hand-dynamometer) to obtain smaller or larger rewards, respectively, and then to immediately carry out that behavior.

We considered two possibilities regarding the role of ACC in effortful control. First, the *choice difficulty* account relates ACC activity to the period of choice evaluation (Figure 1). Difficult task choices (for example, when the options are of equal subjective value) often manifest as increased ACC activity, regardless of whether a task requires physical or cognitive effort (e.g., Botvinick et al., 2001; Shenhav et al., 2016). This view predicts increased FMT power when the subjective values of the possible options are similar, for example, when deciding between a high-effort/high-reward option (100 push-ups for \$50) and a low-effort/low-reward option (1 push-up for 10 cents). Although the subjective values of the decisions cannot be directly observed, they give rise to increased reaction times (RTs) when participants choose between options with similar subjective values (Lin et al., 2018;



**FIGURE 1** Schematic illustrating hypothesized processes involved in effort- and reward-based decision making in the Effort-Expenditure for Rewards Task (Treadway et al., 2009). On each trial, participants were required to evaluate a high-effort and a low-effort choice (“Choice Evaluation”); select either choice (“Choice Selection”); squeeze a hand-dynamometer with an amount of force required by that choice (“Effort Production”); and see the outcome of that choice (“Reward Valuation”). The *Choice Difficulty* account relates FMT to the process of “Choice Evaluation”, whereas the *Effort Selection* account relates FMT to the process of “Choice Selection”. Arrow indicates direction of time on each trial.

Shenhav et al., 2014). Hence, on this view FMT power should correlate positively with decision RTs.

Second, the *effort selection* account relates ACC activity to effort regulation, namely the process of selecting effortful actions (Figure 1) (e.g., Holroyd & Umemoto, 2016; Shenhav et al., 2013; Vassena et al., 2017; Verguts et al., 2015). This view predicts increased ACC activity when participants choose a high-effort option irrespective of the subjective reward values of the options and the difficulty of the choice. Thus, in contrast to the choice difficulty account, this predicts enhanced FMT power when deciding between a high-effort/high-reward option (e.g., 100 push-ups for \$50) and a low-effort/low-reward option (1 push-up for 10 cents) only when the high-effort choice is in fact selected, but not when the low-effort choice is selected.

The results of prior FMT studies support both the task difficulty account (e.g., Lin et al., 2018; Pinner & Cavanagh, 2017) and the effort selection account (e.g., Umemoto, Inzlicht, & Holroyd, 2019; Wascher et al., 2014). We therefore tested these accounts by examining FMT power as a proxy for ACC activity. Specifically, we recorded FMT from participants making effort choices (prior to them carrying out the chosen options), and then tested whether FMT power is more sensitive to choice difficulty or effort selection. Because we were agnostic about whether these processes would manifest in phasic or tonic FMT, we examined both phenomena and compared different models using standard model selection criteria. Additionally, we explored whether FMT and its interaction with expected value (EV) may predict participants' choice behavior.

Lastly, we also explored how effort production interacted with reward valuation. That is, given the increased engagement of ACC in effortful behavior, we hypothesized that effort production would increase RewP amplitude, even after controlling for reward magnitude.

## 2 | METHOD

### 2.1 | Participants

Seventy-seven undergraduate students were recruited from the University of Victoria Department of Psychology subject pool to fulfill a course requirement or earn bonus credits. The sample size was determined based on the past study that we modified for the current study (Treadway et al., 2009). Because the current study was an EEG study, we recruited additional subjects, assuming that up to 15% of subjects may need to be excluded due to excessive motor artifacts and hardware problems. Further, we performed a sensitivity analysis using the summary-statistics-based power analysis method developed by Murayama et al. (2022), which suggests that given our sample size, we could detect at least  $d = 0.36$  (relatively small-to-medium effect sizes) with 80% statistical power (see Figure S1). All subjects (26 males, 8 left-handed, age range = 18–35 years, mean age =  $21.5 \pm 3.8$  years) had normal or corrected-to-normal vision. Each participant also received a monetary bonus in addition to the credits, the amount of which depended on their task performance (see below). All subjects provided informed consent as approved by the local research ethics committee. The experiment was conducted in accordance with the ethical standards prescribed in the 1964 Declaration of Helsinki, and approved by the Human Research Ethics Board at the University of Victoria.

### 2.2 | Grip force calibration

Physical effort expenditure was measured using a hand-dynamometer (Neulog, U.S.). Each participant's maximum grip force was assessed before the experiment began. The hand-dynamometer was affixed to the table in a straight-up position in front of the computer screen (approximately 36 cm from the participants and 18 cm from the computer screen). Participants exerted their maximum grip force for 2 s, 5 times for both their right hand and left hand. The largest force produced by each hand was then taken as the maximum grip force for that hand throughout the experiment. Participants also repeated this calibration procedure 3 times for each hand at the completion of the experiment.

### 2.3 | Procedure

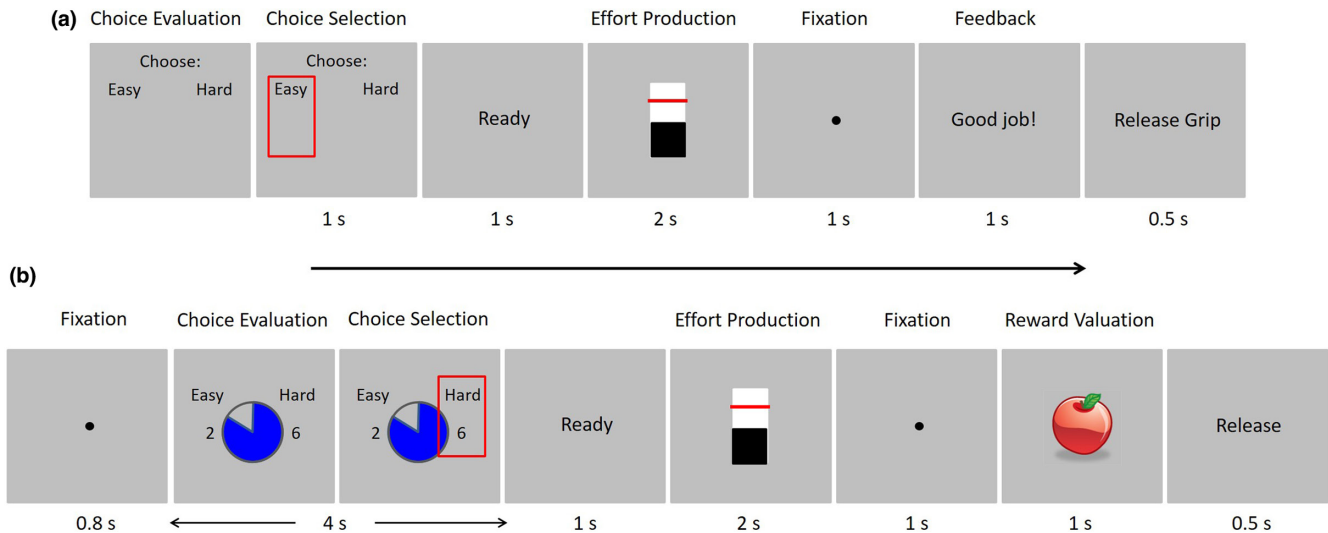
Participants were seated comfortably in front of a computer monitor (1024 by 1280 pixels) at a distance of about 60 cm in a dimly lit room. The task was programmed in MATLAB (MathWorks, Natick, MA, USA) using

the Psychophysics Toolbox extension (Brainard, 1997; Pelli, 1997). Instructions were given to participants both verbally and in a written format on a computer screen. Participants were told that they would be using a hand-dynamometer to perform a task, and that they would have an opportunity to win monetary rewards. This was followed by the calibration procedure to measure each participant's maximum grip force (see Section 2.2).

On each trial participants selected between a low-effort, small reward (“Easy”) choice and a high-effort, large reward (“Hard”) choice, as indicated by the words “Easy” and “Hard” presented in black against a gray background ( $0.4^\circ$  by  $1.1^\circ$  square visual angle each) (Figure 2a, 1st panel). The low-effort choice required participants to squeeze a hand-dynamometer with approximately 40% of their maximum grip force calibrated above plus trial-varying random jitter drawn from a standard normal distribution with a mean of 40 and a standard deviation of 1 (using the `randn` function of MATLAB). By contrast, the high-effort choice required participants to squeeze the device with approximately 85% of their maximum grip force plus trial-varying random jitter drawn from a standard normal distribution with a mean of 85% and a standard deviation of 1.

#### 2.3.1 | Practice phase

Participants practiced the task in two steps. First, participants were familiarized with the level of effort required to carry out the low-effort and high-effort choices for both hands. Participants were presented with the two choice options (Figure 2a, 1st panel), and selected one of the effort choices by pressing the right or the left arrow key. Their choice was then highlighted by a red frame for 1 s (Figure 2a, 2nd panel). The word “Ready” was then presented for 1 s (Figure 2a, 3th panel), after which a white rectangular bar bisected with a red horizontal line was presented ( $1.8^\circ$  square visual angle width; note that height depended on each subject's calibration force), which prompted the participants to squeeze the device (Figure 2a, 4th panel). The height of the white rectangular bar was adjusted to the maximum grip force for the responding hand of that participant, with the half-way point located at the center of the screen. The red horizontal line indicated the minimum grip force required to achieve a successful squeeze response for that trial. As participants squeezed the dynamometer, the base of the white bar was replaced with the color black, the height of which was proportional to the applied force, providing visual feedback to the subject on the strength of their response (Figure 2a, 4th panel). Participants were given 2 s maximum for their response



**FIGURE 2** An example trial during the initial Practice Phase (a) and during the actual task (b). During the Practice Phase, participants were first introduced to and practiced the low-effort (Easy) and high-effort (Hard) choice without reward and probability information. Successfully performing the required choice resulted in either “Good job!” or “Squeeze harder!” feedback. At the end of the Practice Phase, information about the reward offered and reward probability on each trial was also provided. The low-effort choice reward was always 2 cents, whereas the high-effort choice reward varied at random from 3 to 8 cents in 1 cent increments. The blue pie chart indicated reward probability of either 20%, 50%, or 80% (the pie chart in b indicates an 80% probability on this example trial). An image of an apple (shown in b) or an orange (not shown) indicated a receipt of reward offered or not (counterbalanced across subjects). To earn the reward, participants were required to squeeze the dynamometer at the effort level indicated by their choice. If participants successfully produced the required amount of effort, then they were provided with reward feedback according to the specified reward probability. During the actual task (b), the choice selection deadline was 4 s on each trial.

to exceed the threshold, after which the image was replaced with a fixation dot at the center of the screen for 1 s (Figure 2a, 5th panel). If the applied force exceeded the response threshold, then the words “Good job!” appeared at the center of the screen for 1 s, otherwise the words “Squeeze harder” were presented (Figure 2a, 6th panel). Finally, the instructions “Release Grip” appeared at the center of the screen for 500 ms to ensure that the participants relaxed their grip before starting the next trial (Figure 2a, last panel from left). The location of the effort choices (left or right side of the screen) and therefore mappings between the choice and the response finger were counterbalanced across participants but were maintained throughout the experiment for each participant. Participants practiced executing the low-effort and high-effort choices once each for each hand, for a total of four trials.

Second, participants were introduced to the potential rewards and reward probabilities. Participants were instructed that, following successful responses, the baseline low-effort option would always yield a chance to earn 2 cents reward, whereas the high-effort option would yield a chance to earn between 3 and 8 cents reward (in 1 cent increments for a total of 6 reward levels which were determined at random with equal probability on each trial) (see Figure 2b, 2nd panel, which shows an example for

the task proper). The rewards offered for the two effort choices were shown in black ( $0.4^\circ$  by  $0.4^\circ$  square visual angle) against a gray background underneath the words “Easy” and “Hard” on each trial. The probability of obtaining the reward, which varied among low (20%), medium (50%) and high (80%) values, was presented as a blue pie chart in the center of the screen ( $3.1^\circ$  by  $3.1^\circ$  square visual angle; each probability was equally likely to occur during practice) (Figure 2b, 2nd panel for example). Note that the probability for reward was the same irrespective of whether the low-effort or high-effort choice was selected. Participants selected their choice and then executed it as described above. For half of the participants the image of an apple indicated receipt of a reward and the image of an orange indicated receipt of a no-reward ( $3.1^\circ$  by  $3.1^\circ$  square visual angle. Figure 2b, 7th panel for example). This association was reversed for the other half of participants. Participants received a reward only if the applied force exceeded the response threshold, and according to the given reward probability for that trial. If the applied force did not exceed the response threshold, then a no-reward feedback stimulus was presented. Participants were given six practice trials (three trials with each hand) involving reward probability and amount. Participants were given their accumulated reward upon completion of the practice phase (between 5 and 25 cents).

### 2.3.2 | Task proper

Following the Practice Phase, the actual experiment began. The task proper (Figure 2b) was identical to the Practice Phase except that (1) each trial began with a fixation dot presented at the center of the screen (800 ms; Figure 2b, 1st panel from left), (2) the word “Choose:” and the cents sign “¢” did not appear during the choice panel, and (3) the choice deadline was extended to 4 s (Figure 2b, 2nd & 3rd panels from left). For example, if a participant made a response after 1 s, then his/her choice was highlighted for the remaining 3 s. If participants did not make a response within the response deadline, the message “Respond faster!” was presented for 500 ms and the same trial repeated (this occurred between 0–3 times per participant). Participants completed eight blocks of 39 trials each, which lasted approximately 1 hr in total. Importantly, due to a time constraint, trials with 20% and 80% reward probability occurred less (7 trials each per block) than trials with 50% reward probability (25 trials per block). The reward probability on each trial was randomly selected within this constraint (i.e., 18% chance that either the 20% and 80% reward probability would occur, and 64% chance that the 50% reward probability would occur). Each block lasted about 7 minutes with self-paced rest periods between blocks. Participants were told that the goal of the study was to perform the task as best as they could. Note that it was up to the participants which effort choice (high vs. low) to select and execute on each trial; therefore, this varied across participants. At the beginning of each block of trials instructions were presented on the computer screen indicating which hand they should use to grip the device for the upcoming block of trials (e.g., “RIGHT hand”), which alternated across blocks in order to minimize muscle fatigue (the first hand was determined randomly for each participant). After completing each block of trials the participants were queried on the computer screen about the correct mapping between the fruit images and reward feedback stimuli (i.e., “Press the 1 key if apple is the reward and press the 2 key if orange is the reward”), in order to ensure that they remembered the designated valences of the feedback stimuli. The summed total of their accumulated earnings for that block was also presented. Upon completion of the task, participants were shown the total amount of reward they had earned, which ranged between \$4 and \$8.80. At the end of the experiment each participant’s grip force was re-calibrated three times for each hand.

## 2.4 | EEG data acquisition and processing

EEG was recorded using a montage of 41 electrode sites in accordance to the extended international 10–20 system (Jasper, 1958). Signals were acquired using Ag/AgCl

ring electrodes mounted in a nylon electrode cap with an abrasive, conductive gel (EASYCAP GmbH, Herrsching-Breitbrunn, Germany). Signals were amplified by low-noise electrode differential amplifiers with a frequency response high cut-off at 50 Hz (90 dB–octave roll off) and digitized at a rate of 250 samples per second. Digitized signals were recorded to disk using Brain Vision Recorder software (Brain Products GmbH, Munich, Germany). Interelectrode impedances were maintained below 20 k $\Omega$ . Two electrodes were also placed on the left and right mastoids. The EEG was recorded using the average reference. Electrooculogram (EOG) was recorded for the purpose of artifact correction; horizontal EOG was recorded from the external canthi of both eyes, and vertical EOG was recorded from the suborbit of the right eye and electrode channel Fp2.

Analysis and data visualization were performed on MATLAB using the EEGLAB (Delorme & Makeig, 2004), ERPLAB (Lopez-calderon & Luck, 2014), and Fieldtrip (Oostenveld et al., 2011) toolboxes. The digitized signals were filtered using a second-order digital Butterworth filter with a high pass at 0.10 Hz. Ocular artifacts (eye blinks and movements) were removed using independent component analysis (ICA) on continuous EEG. The EEG data were re-referenced to the average of two electrodes placed on mastoid bones. Because participants were free to choose either the high- or low-effort choice on every trial, the data of several subjects did not contain enough trials to analyze the RewP for each effort condition (see Supporting Information for the trial count information). For this reason, we examined the single-trial EEG data instead of the averaged data (e.g., ERP) for all analyses.

Time-frequency analysis was performed using the Fieldtrip toolbox to compute FMT power during the decision phase. To avoid potential time-frequency decomposition edge artifacts, EEG data were segmented into long epochs of 9000 ms epoch extending from –2500 ms prior to 6500 ms time-locked to the onset of choice stimulus (Figure 2, “Choice Evaluation”). We used complex Morlet wavelets to compute power values for frequencies between 1 and 40 Hz, with the width (or cycles) of each frequency band increasing from 3 to 12 cycles between 1 and 40 Hz. Muscular and other artifacts were excluded according to the following criteria as implemented in EEGLAB (for detail see Delorme et al., 2007): (1) Linear trends with a maximum slope exceeding 150  $\mu$ V, (2) Data improbability exceeding 5 standard deviations (SD) based on the joint probability for each epoch at each electrode, (3) Spectral pattern that deviated from baseline by  $\pm$ 50 dB in the 0–2 Hz frequency window for detecting eye movements, and +25 dB and –100 dB in the 20–40 Hz frequency window for detecting muscle activity. FMT power was measured between 4 and 8 Hz at channel FCz, where it

generally reaches a maximum (e.g., Bernat et al., 2008; Foti et al., 2015; Umemoto, Inzlicht, & Holroyd, 2019). A time-window of interest was determined based on the average across all of the conditions across all participants (i.e., a collapsed localizer approach; Luck & Gaspelin, 2017). To measure phasic bursts of FMT (i.e., phasic FMT) during the period of choice evaluation and selection, average FMT power was calculated within 300 ms surrounding the maximum activity according to the grand average inspection above. Based on this procedure, we identified a time window from 60 to 340 ms during which phasic FMT was evaluated (down-sampled to 50 Hz for subsequent analyses, which reduced the time window from 300 ms to 280 ms). Data were baseline-corrected by subtracting from the average FMT power on each trial the mean FMT power during the  $-500$  to  $-300$  ms interval preceding choice onset. To measure ongoing FMT power (i.e., tonic FMT), average FMT power was calculated across the entire 4 s choice period without applying baseline correction.

For single-trial analysis of RewP amplitude, the data were segmented for an 800 ms epoch extending from 200 ms prior to 600 ms following the onset of reward and no-reward feedback on each trial. Data were baseline corrected by subtracting from each sample for each channel the mean voltage associated with that electrode during the 200 ms interval preceding feedback onset. The same artifact rejection procedure as for the time frequency analysis were applied, and data were low-pass filtered with 30 Hz (with a slope of 12 dB). Single-trial RewP amplitude was determined by averaging the mean voltage from 240 to 340 ms following feedback onset, measured at channel FCz, where it typically reaches maximum amplitude (Krigolson, 2018). To isolate the single-trial RewP from the P300, an ERP component that spatio-temporally overlaps with the RewP, we also measured P300 amplitude on single trials (Holroyd & Krigolson, 2007). Single-trial P300 amplitude was determined by averaging the voltages recorded at channel Pz from 440 to 540 ms following feedback onset, as determined based on the average across all of the conditions and all of the participants (Luck & Gaspelin, 2017).

## 2.5 | Data analysis

Trials with RTs less than 200 ms were removed. We also removed trials with long RTs using a robust median absolute deviation method (Leys et al., 2013; Lin et al., 2018). For each subject, this method first calculates a median RT, then identifies individual trials in which the RT was three or more median absolute deviations from the median RT. This resulted in removal of 7% of trials across all participants.

Classical frequentist statistical analyses were performed in R (code: <http://git.io/Jc9Iw>). The design was entirely within-subjects; unless stated otherwise, all estimates and statistics were obtained by fitting mixed-effects (multilevel or hierarchical) single-trial regression models (two levels: all factors and neurophysiological responses for each condition were nested within participants) with varying intercepts and slopes (unstructured covariance matrix) using the R package lme4 (Bates et al., 2014). Varying or random effects were modeled as supported by the data. We also included trial number in each model to account for increasing mental fatigue associated with time on task.<sup>1</sup> For models including FMT power, we tested the same model separately for phasic and tonic FMT. All continuous regressors were within-subject mean-centered (by subtracting the mean value for each participant from that participant's data) before being entered into a given model. Two-tailed probability values and degrees of freedom associated with each statistic was determined using the Satterthwaite approximation implemented in lmerTest (Kuznetsova et al., 2017).

### 2.5.1 | Behavior

#### *The baseline behavioral model*

First, we fitted a generalized mixed effects model to examine whether participants' choices on each trial varied as a function of reward offered, reward probability, expected value (EV: probability  $\times$  reward offered interaction), and trial number (i.e., time on task):

Choice made

= Reward offered + Probability + EV + Trial number

R syntax: `glmer(Choice ~ Reward offered + Probability + Reward offered: Probability + Trial number + [1 + Reward offered + Probability + Reward offered: Probability + Trial number || Subject] Family = "Binomial")`.

We predicted that higher values of reward offered, probability, and EV (which are all related to increasing reward value) would predict increased likelihood of high-effort choices, whereas time on task (i.e., trial number) would predict decreased likelihood of high-effort choices (Treadway et al., 2009).

<sup>1</sup>Although grip success (whether participants successfully executed a given choice; see Procedure) was significantly higher for the low-effort than the high-effort choice, it was not included in each model as a covariate in order for each model to converge. Importantly, there was no effect of grip success on any of the electrophysiological indices ( $ps > .37$ ).

### The behavioral model with FMT

We then explored whether FMT power and the interaction between FMT power and EV would be associated with participants' choices. We extended the baseline behavioral model described above by including FMT power and FMT×EV interaction:

$$\text{Choice made} = \text{Reward offered} + \text{Probability} + \text{EV} \\ + \text{Trial number} + \text{FMT} + \text{FMT} \times \text{EV}.$$

R syntax: `glmer(Choice~Reward offered + Probability + Reward offered: Probability + Trial number + FMT + Reward offered: Probability: FMT + (1 + Reward offered + Probability + Reward offered: Probability + Trial number + FMT + Reward offered: Probability: FMT || Subject) Family = "Binomial")`.

We examined whether increased FMT power and its interaction with EV was associated with more high-effort choices.

## 2.5.2 | Electrophysiology:

### The choice difficulty model of FMT

We tested whether FMT power varied as a function of choice difficulty (the *choice difficulty* account), which was captured by RT on each trial (during choice selection).<sup>2</sup> We also included reward offered, reward probability, EV, and trial number:

$$\text{FMT} = \text{Reward offered} + \text{Probability} + \text{EV} + \text{Trial number} + \text{RT}.$$

R syntax: `lmer(FMT~Reward offered + Probability + Reward offered: Probability + Trial number + RT + (1 + Reward offered + Probability + Reward offered: Probability + Trial number + RT || Subject))`.

<sup>2</sup>As an alternative approach to the RT measure, we also explored the Choice Difficulty Model by estimating subjective values (SV) of choice difficulty based on each subject's indifference point. To do this, we first calculated the difference in EV between the easy and the hard choice (EV-hard minus EV-easy) on each trial. We then used this EV difference to predict choice using logistic regression, and get an indifference point for each subject. To get a trial-by-trial estimate of SV of choice difficulty, we subtracted the indifferent point from the EV difference on each trial for each subject, and fit the model using this value in lieu of RT. Similar to the results with RT, there was no significant effect of SV on phasic FMT ( $t(3832) = -.43, p = .66$ ), and the model with tonic FMT failed to run due to a failure to converge.

We examined whether increased RT was associated with increased FMT power. Further, based on our prior work (Umemoto, Inzlicht, & Holroyd, 2019), we predicted that tonic FMT would increase with time on task.

### The effort selection model of FMT

We tested whether FMT power varied as a function of choice (high-effort vs. low-effort choice) (the *effort selection* account) by including participants' choice in lieu of RT. As with the Choice Difficulty Model of FMT above, we also included reward offered, reward probability, EV, and trial number:

$$\text{FMT} = \text{Reward offered} + \text{Probability} + \text{EV} \\ + \text{Trial number} + \text{Choice selected}.$$

R syntax: `lmer(FMT~Reward offered + Probability + Reward offered: Probability + Trial number + Choice + (1 + Reward offered + Probability + Reward offered: Probability + Trial number + Choice || Subject))`.

We examined whether selecting the high-effort choice was associated with increased FMT power. Similar to above, we predicted that tonic FMT would increase with time on task.

### The RewP model

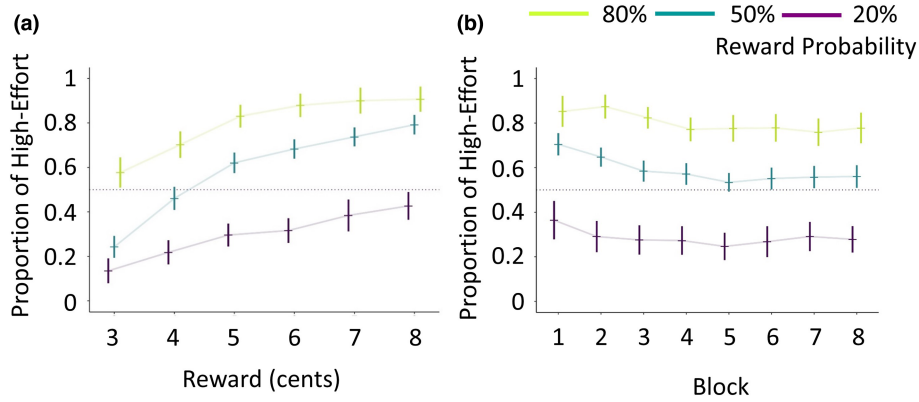
Finally, we tested whether effort choice influenced single-trial RewP amplitude. Reward outcome was entered as a binary variable (−0.5 = no-reward, 0.5 = reward), rather than as a continuous variable (see [Supporting Information](#) for an additional analysis), based on evidence that RewP encodes feedback outcomes in a binary manner (Hajcak et al., 2006). To control for the confounding effect of an overlapping ERP component (Krigolson, 2018), this model also included single-trial P300 amplitude. That is, we examined whether RewP varied as a function of choice (high-effort vs. low-effort choice), probability, binary reward outcome, probability×binary reward outcome, P300 amplitude, and trial number:

$$\text{Single-trial RewP} = \text{Choice selected} + \text{Probability} \\ + \text{Binary-reward outcome} + \text{Probability} \times \text{Binary} \\ - \text{reward outcome} + \text{Single-trial P300} + \text{Trial number}.$$

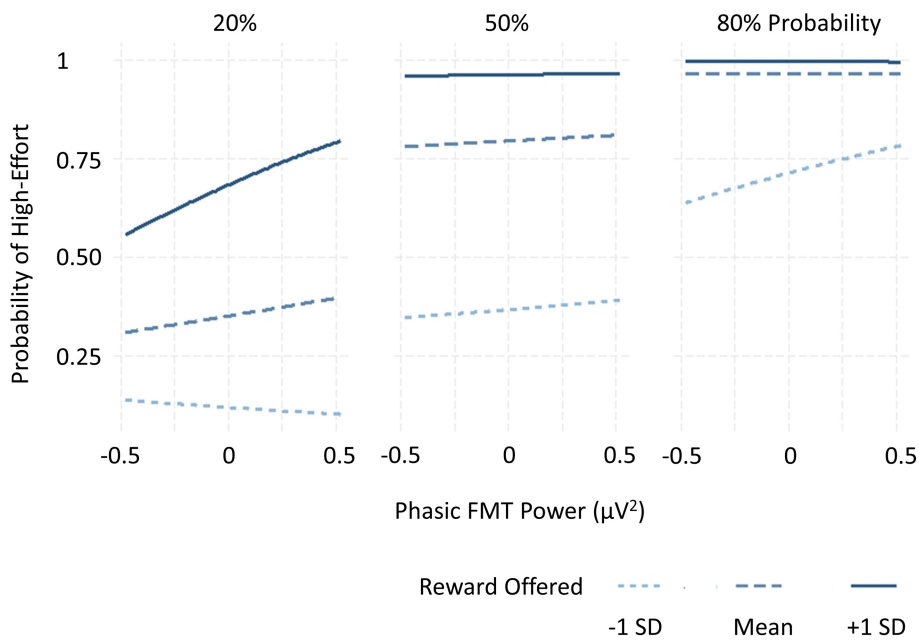
R syntax: `lmer(RewP~Choice + Probability + Binary-reward outcome + Probability: BINARY-reward outcome + P300 + Trial number + (1 + Choice + Probability + Binary-reward outcome + Probability: Binary-reward outcome + P300 + Trial number || Subject))`.

First, we examined whether selecting high-effort choices was associated with enhanced single-trial RewP amplitude. Second, we predicted that single-trial RewP amplitude





**FIGURE 3** Probability of the high-effort choice selected (y-axis) as a function of (a) reward offered from 3 to 8 cents (x-axis) and (b) block of trials (block 1 to 8, each containing 39 trials) for each reward probability of 20% (purple line), 50% (turquoise line), and 80% (light green line). The proportion of the high-effort choice was calculated as the number of high-effort choice selected divided by the sum of all the trials. Error bars indicate within-subject 95% confidence intervals.



**FIGURE 4** Phasic-FMT  $\times$  EV (expected value: reward offered  $\times$  probability) interaction on the probability of the high-effort choice selected. Each panel shows a relation between phasic-FMT power (x-axis) and the proportion of high-effort choice selected (y-axis) according to reward offered ( $\pm 1$  standard deviation (SD) from the mean of 5.5 cents) for 20% reward probability (left panel), 50% reward probability (middle panel), and 80% reward probability (right panel).

would be larger (i.e., more positive) following reward outcomes compared to no-reward outcomes, and following unexpected (i.e., low probability) outcomes compared to expected (high probability) outcomes. Third, we predicted a probability  $\times$  binary-reward outcome (no-reward vs. reward) interaction such that single-trial RewP amplitude would be more positive following unexpected reward outcomes, and more negative following unexpected no-reward outcomes. Lastly, in keeping with previous observations, we predicted that single-trial RewP amplitudes would decrease with time on task (Umemoto, Inzlicht, & Holroyd, 2019).

## 2.6 | Data exclusion

One participant discontinued the experiment. The data of another participant were excluded due to a low rate of successfully executing the high-effort choice, which was 3 standard deviations (SD) below the mean across all participants. The data of a third participant were excluded due to a technical problem. Finally, data sets in which more than 30% of the trials were contaminated by motor artifacts were excluded ( $n = 10$ ), resulting in a total of 64 participants' data analyzed.

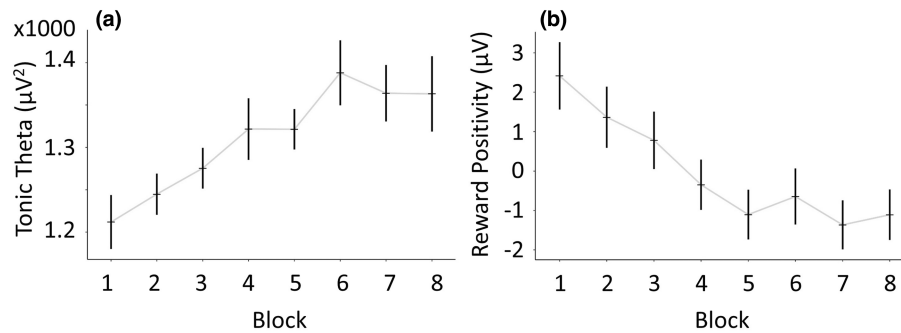


FIGURE 5 Effect of time on task (block) on (a) Tonic FMT power and (b) single-trial RewP. Error bars indicate within-subject 95% confidence intervals.

### 3 | RESULTS

#### 3.1 | Behavior

On average, participants nearly always produced the required effort for the selected choice ( $M = 97\%$ ,  $SD = 5\%$ ), with the success rate significantly higher for the low-effort choice ( $M = 99\%$ ,  $SD = 3\%$ ) than for the high-effort choice ( $M = 95\%$ ,  $SD = 8\%$ ),  $b = 3.60$ ,  $SE = 0.66$ ,  $z = -5.45$ ,  $p < .01$ .

##### 3.1.1 | The baseline behavioral model

The results from a generalized mixed model indicated that participants' choices varied as a function reward offered ( $b = 11.09$ ,  $SE = 0.97$ ,  $z = 11.42$ ,  $p < .01$ ), probability ( $b = 10.05$ ,  $SE = 0.81$ ,  $z = 12.37$ ,  $p < .01$ ), EV ( $b = 17.68$ ,  $SE = 2.93$ ,  $z = 6.03$ ,  $p < .01$ ), and trial number ( $b = -4.83$ ,  $SE = 1.27$ ,  $z = -3.80$ ,  $p < .01$ ). That is, participants were more likely to select the high-effort choice when reward offered and reward probability were higher (Figure 3a), and selected the high-effort choice less with time on task (Figure 3b), presumably due to increasing fatigue.

##### 3.1.2 | The behavioral model with FMT

This model extended the baseline behavioral model by including FMT power and the interaction between FMT and EV. As with the baseline model, the effects of reward offered, probability, EV, and trial number were significant ( $ps < .01$ ). Additionally, although the effects of phasic-FMT ( $p = .65$ ) or tonic-FMT ( $p = .19$ ) were not statistically significant, there was a significant phasic-FMT  $\times$  EV interaction ( $b = 24.09$ ,  $SE = 11.80$ ,  $z = -2.04$ ,  $p = .04$ ) on participants' choice. This interaction suggests that increased phasic FMT was associated with selecting the high-effort choice mainly on difficult decision trials (i.e., low probability and high reward offered, high probability and low reward offered) (Figure 4). For these difficult choices,

more FMT was associated with higher likelihood of selecting the effortful action.

#### 3.2 | Electrophysiology

##### 3.2.1 | The choice difficulty model of FMT

Phasic FMT: Phasic FMT power did not significantly vary as a function of RT ( $b < 0.01$ ,  $SE < 0.01$ ,  $t(50) = 0.01$ ,  $p = .99$ ) or any other variables ( $ps > .07$ ).

Tonic FMT: We found that tonic FMT varied as a function of trial number ( $b = 0.06$ ,  $SE = 0.01$ ,  $t(62) = 5.52$ ,  $p < .01$ ), such that tonic FMT increased with time on task (Figure 5a). There was a (non-significant) trend for the effect of RT ( $b < 0.01$ ,  $SE < 0.01$ ,  $t(55) = 1.99$ ,  $p = .051$ ).

##### 3.2.2 | The effort selection model of FMT

Phasic FMT: Phasic FMT did not vary as a function of choice ( $p = .53$ ), or other variables ( $ps > .06$ ).

Tonic FMT: We found a significant effect of trial number ( $b = 0.05$ ,  $SE = 0.01$ ,  $t(63) = 4.80$ ,  $p < .01$ ), such that tonic FMT increased with time on task (Figure 5a). There was no effect of choice ( $p = .64$ ), or other variables ( $ps > .15$ ).

##### 3.2.3 | The RewP model

Single-trial RewP amplitude was significantly modulated by choice ( $b = 0.01$ ,  $SE < 0.01$ ,  $t(61) = 3.31$ ,  $p < .01$ ), such that selecting the high-effort choice and executing it was associated with increased RewP amplitude. There was also a significant effect of P300 ( $b = 0.45$ ,  $SE = 0.02$ ,  $t(62) = 27.12$ ,  $p < .01$ ), such that a larger single-trial RewP amplitude was associated with a larger single-trial P300 amplitude. There was also a significant effect of trial number ( $b = -0.05$ ,  $SE = 0.01$ ,  $t(63) = -4.38$ ,  $p < .01$ ), such that

single-trial RewP amplitude decreased with time on task (Figure 5b). Finally, there was a significant interaction of reward probability and binary reward outcome on single-trial RewP amplitude ( $b = 0.02$ ,  $SE = 0.01$ ,  $t(17149) = 2.53$ ,  $p = .01$ ). That is, unexpected reward and no-reward were both more negative than expected reward and no-reward (Figure S3 in Supporting Information).

## 4 | DISCUSSION

Execution of goal-directed behavior depends on weighing expected rewards against the effort-related costs in acquiring the rewards. Although ACC has been suggested to play a key role in this process (Bonnelle et al., 2016; Chong et al., 2017; Croxson et al., 2009; Kurniawan et al., 2010; Skvortsova et al., 2014; Vassena et al., 2014), its exact role remains unclear. Here we examined electrophysiological signals related to the control and reward processing functions of ACC in order to investigate the contribution of ACC to carrying out physically effortful behavior. Toward this end, we measured single-trial FMT power and RewP amplitude from participants engaged in a modified Effort-Expenditure for Rewards Task (Treadway et al., 2009). Replicating previous observations, we found that participants were more likely to select the high-effort choice when reward offered and reward probability were higher, whereas they selected the high-effort choice less with time on task (Treadway et al., 2009).

Of central interest, we tested whether either phasic or tonic FMT were related to choice difficulty (using RT as a proxy) or to effort selection (using choice as a proxy). In fact, we did not find support for either hypothesis. Phasic FMT was not associated with RT, with selecting high-effort actions, nor with any other task variables. Tonic FMT, which is associated with sustained mental effort (Holroyd & Umemoto, 2016), did show a trend ( $p = .051$ ) for the effect of RT, suggesting that tonic FMT increased on trials when participants took longer to decide. However, given that this result is not statistically significant, it should be evaluated with caution.

Despite these findings, an exploratory analysis revealed a significant interaction of phasic FMT and EV on participants' choices, indicating an interplay between choice difficulty and effort selection (Figure 4). Visual inspection of this interaction reveals that, unsurprisingly, the probability of selecting the high-effort choice increased with reward probability (left, middle, and right panels), and increased with reward offered (dotted, dashed, and solid lines). Further, these choices were independent of phasic FMT for nearly all conditions (horizontal lines), except large rewards on low probability trials (solid line, left

panel) and small rewards on high probability trials (dotted line, right panel). In these cases, increased phasic FMT was associated with greater probability of selecting the high-effort choice. This interaction suggests that phasic FMT most influenced behavioral choices on difficult decision trials (i.e., low probability and high reward offered, high probability and low reward offered), with increased phasic FMT associated with a greater probability of selecting the high-effort choices. Notably, these results obtained despite phasic FMT being unrelated to decision difficulty (as indexed by RT) and effort selection.

Evidently, phasic FMT reflects an interaction between both processes: increased FMT is associated with selecting the effortful action only when the decision is difficult. For easy decisions, FMT is incidental to the action selection process. Thus, the amount of phasic FMT appears to matter most under conditions that demand increased control. When the effort-reward tradeoff is balanced between choices, increased control by ACC seems to tip the balance in favor of the high-effort choice. In this way, phasic FMT appears to regulate control specifically under situations of decision conflict, biasing the choice in favor of the high-effort/high-reward option.

Although phasic FMT has been well-studied in tasks requiring cognitive control (e.g., Cavanagh & Frank, 2014; Holroyd & Umemoto, 2016), its role in decision making (Lin et al., 2018; Pinner & Cavanagh, 2017) and effort (Umemoto, Lin, & Inzlicht, 2019) are under-studied. Lin et al. (2018) examined phasic FMT during an intertemporal choice task; they found that phasic FMT tracks subjective conflict in decision making, being largest when two options were similar in value, and, unexpectedly, when choice was easiest to make and attention-capturing (e.g., "\$15 today or \$15 in 30 days"). They interpreted these results as indicating that phasic FMT may reflect adaptive control during value-based choice. Further, Pinner and Cavanagh (2017) found that, although there was no effect of response conflict on risky decision making overall, individual differences in phasic FMT predicted this association. That is, individuals with increased phasic FMT showed reduced risky decision making under situations of increased response conflict, compared to individuals with decreased phasic FMT. Our present study adds to these findings by suggesting that phasic FMT adaptively biases decision making in order to motivate high-effort/high-reward behavior in the face of decision conflict.

Consistent with prior studies, tonic FMT increased with time on task, suggesting increased control application with increasing fatigue (Umemoto, Inzlicht, & Holroyd, 2019; Wascher et al., 2014; but see Arnau et al., 2021). Although prior studies examined tonic FMT as a sustained activity throughout a cognitively-fatiguing task (Umemoto, Inzlicht, & Holroyd, 2019;

Wascher et al., 2014, see also Tran et al., 2020), the present study restricted the measurement window to the decision period because of potential contamination of the EEG by motor-related artifacts. Nevertheless, we replicated the time-on-task effect of tonic FMT observed previously (Tran et al., 2020 for a review). Tonic FMT could also vary during other cognitive processing stages. For example, one study reported increased sustained FMT in anticipation of the deployment of cognitive effort, suggesting a preparatory control process (De Loof et al., 2019). Tonic FMT may also be enhanced during the actual production of effort (the Effort Production stage; Figure 1), given that ACC activity increases when physical effort is expended. Therefore, further investigations should assess tonic FMT during actual effort production (e.g., Umemoto, Lin, & Inzlicht, 2019) and other processing stages in effort-related decision-making tasks.

Replicating our previous finding, RewP amplitude decreased with time on task, suggesting that subjective reward value decreased over time (Umemoto, Inzlicht, & Holroyd, 2019). We examined whether effort-related process interacted with reward outcome valuation. This revealed a significant effect of effort choice on RewP amplitude, suggesting that selecting and instigating high-effort actions may have increased the subjective value of the reward received (Festinger, 1957; Norton et al., 2012). Importantly, this effect remained significant when controlling for the magnitude of the reward outcomes (Supporting Information), so that larger RewPs are associated with greater effort in obtaining the rewards rather than with the size of the rewards once obtained. Further, although the RewP was distributed over more posterior areas of the scalp (see Supporting Information), suggesting a possible confound with the overlapping P300 component, the effect of effort choice remained statistically significant even when controlling for P300 amplitude.

The finding that high-effort choice was associated with increased RewP amplitude is in line with prior studies examining the effect of cognitive effort on RewP (Harmon-Jones, Clarke, et al., 2020; Harmon-Jones, Willoughby, et al., 2020; Ma et al., 2014). A few possible mechanisms could be driving this effect. First, ACC activity is often associated with physical rather than cognitive demands of goal-directed performance (e.g., Caruana et al., 2018; Le Heron et al., 2019; Parvizi et al., 2013). Therefore, increased engagement of ACC during high-effort choices could result in a concomitant increase in ACC engagement when the reward outcomes of those choices are processed. Second, high-effort behavior is less predictive of successful performance. Consider which activity you would be more likely to complete: 5 push-ups or 500 push-ups? On this account, rewards for high-effort behaviors are less expected than rewards for low-effort behaviors, leading to

a larger RewP when reward for the former is in fact received. Nevertheless, this finding is tentative given the possible overlap of the RewP with the P300 (see below).

Finally, there was a significant interaction of reward probability and reward outcome (no-reward vs. reward) on RewP amplitude. At face value, this interaction appears consistent with the standard finding that RewP amplitude reflects reward prediction error signals (i.e., unexpected reward and no-reward feedback yield a larger difference in the ERPs compared to expected reward and no-reward feedback) (e.g., Holroyd et al., 2003; Holroyd & Krigolson, 2007; Sambrook & Goslin, 2015). However, a close inspection revealed that the values for unexpected reward and no-reward were both more negative than for expected reward and no-reward (Figure S3 in Supporting Information), which is inconsistent with that hypothesis. This discrepancy could be due to a few factors. First, RewP amplitude is not normally assessed using the single-trial regression approach, and although this analysis controlled for the influence of overlapping P300 component, the scalp topography of RewP was more posteriorly distributed than what is commonly observed, suggesting a possible confounding effect of the P300 on the RewP (Figure S2 in Supporting Information). Second, some studies have suggested that RewP amplitude is attenuated in more complex tasks. For example, when instructional information intervenes between response and reward feedback, informing subjects of what action to execute on the following trial, the RewP is disrupted (Baker & Holroyd, 2011). In the current study, participants were required to quickly integrate multiple types of information to decide what action to take on each trial (e.g., reward, probability, and required effort, in the presence of accumulating physical and mental fatigue). Note that we have successfully produced a standard RewP in our past studies using abstract feedback images (e.g., Baker et al., 2016; Baker & Holroyd, 2009; Heydari & Holroyd, 2016; Umemoto & Holroyd, 2017; Umemoto, Inzlicht, & Holroyd, 2019). Further, successful high-effort actions did not guarantee a reward, which was determined at random afterwards. Although the reward probability in interaction with small rewards (up to 8 cents) may have also affected the pattern of RewP, we have observed a standard RewP using similar task designs (Umemoto et al., 2017; Umemoto & Holroyd, 2017). Therefore, a combination of these factors may have contributed to our finding.

Taken together, several observations in the present study suggest a specific role for ACC in regulating effortful control for adaptive behavior. First, ACC appears to support task behavior for extended periods: During approximately 1 hour of a physically effortful task, participants appeared to apply greater effort (increased tonic FMT) with time while the rewards became increasingly

less rewarding (reduced RewP amplitude). Second, although our predictions about FMT's association with either choice difficulty or effort selection were not supported, an exploratory analysis revealed a more nuanced role of phasic FMT related to the interaction of the two processes. In particular, increased phasic FMT appeared to facilitate selection of the effortful behavior mainly when the decision between the high-effort and low-effort choices was especially difficult. Therefore, ACC's control levels seem to matter only for overcoming difficult decisions to motivate high-effort behavior. By contrast, under situations with little conflict (e.g., high reward and high probability, low reward and low probability), ACC's control levels are incidental to the action selection process. This is presumably because the signal is redundant with the output of other neural systems directly responsible for action selection, as suggested by computational simulations (Holroyd & McClure, 2015). Third, selection of the high-effort action was associated with increased RewP amplitude following the reward outcome. Possibly, increased engagement by ACC facilitating effort expenditure leads to increased processing by ACC of the subsequent reward. Alternatively, we speculate that the larger RewP reflects learning by the ACC of the reward value of effort investment, which could be used for future valuation of effort-related choices (Holroyd & McClure, 2015; Huw et al., 2021; Shenhav et al., 2013). These findings support a role for ACC not in evaluating conflict or motivating effortful behavior per se, but rather in overcoming conflict to motivate effortful behavior, precisely when conflict is highest (Holroyd & McClure, 2015; Kolling et al., 2016; Porter et al., 2019). In this way ACC may be uniquely positioned to motivate and persist at especially challenging goal-directed behaviors (Holroyd & Verguts, 2021).

#### AUTHOR CONTRIBUTIONS

**Akina Umemoto:** Conceptualization; data curation; formal analysis; methodology; visualization; writing – original draft; writing – review and editing. **Hause Lin:** Formal analysis; visualization. **Clay Holroyd:** Conceptualization; funding acquisition; methodology; supervision; writing – review and editing.

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#### DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in GitHub at <https://github.com/hauselin/eeg-uhl>.

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#### REFERENCES

- Arnau, S., Brümmer, T., Liegel, N., & Wascher, E. (2021). Inverse effects of time-on-task in task-related and task-unrelated theta activity. *Psychophysiology*, *58*, e13805. <https://doi.org/10.1111/psyp.13805>
- Baker, T. E., & Holroyd, C. B. (2009). Which way do i go? neural activation in response to feedback and spatial processing in a virtual t-maze. *Cerebral Cortex*, *19*(8), 1708–1722. <https://doi.org/10.1093/cercor/bhn223>
- Baker, T. E., & Holroyd, C. B. (2011). Dissociated roles of the anterior cingulate cortex in reward and conflict processing as revealed by the feedback error-related negativity and N200. *Biological Psychology*, *87*(1), 25–34. <https://doi.org/10.1016/j.biopsycho.2011.01.010>
- Baker, T. E., Wood, J. M. A., & Holroyd, C. B. (2016). Atypical valuation of monetary and cigarette rewards in substance dependent smokers. *Clinical Neurophysiology*, *127*(2), 1358–1365. <https://doi.org/10.1016/j.clinph.2015.11.002>
- Bates, D., Machler, M., Bolker, B. M., & Walker, S. C. (2014). Fitting linear mixed-effects models using lme4. *ArXiv Preprint ArXiv:1406.5823*.
- Bernat, E., Nelson, L., Holroyd, C. B., Gehring, W. J., & Patrick, C. (2008). Separating cognitive processes with principal components analysis of EEG time-frequency distributions. In *Advanced signal processing algorithms, architectures, and implementations XVIII* (Vol. 7074, pp. 240–249). SPIE. <https://doi.org/10.1117/12.801362>
- Bernat, E. M., Nelson, L. D., & Baskin-Sommers, A. R. (2015). Time-frequency theta and delta measures index separable components of feedback processing in a gambling task. *Psychophysiology*, *52*(5), 626–637. <https://doi.org/10.1111/psyp.12390>
- Bonnelle, V., Manohar, S., Behrens, T., & Husain, M. (2016). Individual differences in premotor brain systems underlie behavioral apathy. *Cerebral Cortex*, *26*(2), 807–819. <https://doi.org/10.1093/cercor/bhv247>
- Botvinick, M. M., Carter, C. S., Braver, T. S., Barch, D. M., & Cohen, J. D. (2001). Conflict monitoring and cognitive control. *Psychological Review*, *108*(3), 624–652. <https://doi.org/10.1037/0033-295X.108.3.624>
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, *10*, 433–436.
- Bress, J. N., & Hajcak, G. (2013). Self-report and behavioral measures of reward sensitivity predict the feedback negativity. *Psychophysiology*, *50*(7), 610–616. <https://doi.org/10.1111/psyp.12053>
- Cardinal, R. N., Pennicott, D. R., LakmaLi, C., Robbins, T. W., & Everitt, B. J. (2001). Impulsive choice induced in rats by lesions of the nucleus accumbens core. *Science*, *292*(5526), 2499–2501. <https://doi.org/10.1126/science.106081>

- Caruana, F., Gerbella, M., Avanzini, P., Gozzo, F., Pelliccia, V., Mai, R., Abdollahi, R. O., Cardinale, F., Sartori, I., Russo, G. L., & Rizzolatti, G. (2018). Motor and emotional behaviours elicited by electrical stimulation of the human cingulate cortex. *Brain*, *141*(10), 3035–3051.
- Cavanagh, J. F., & Frank, M. J. (2014). Frontal theta as a mechanism for cognitive control. *Trends in Cognitive Sciences*, *18*(8), 414–421. <https://doi.org/10.1016/j.tics.2014.04.012>
- Chong, T. T. J., Apps, M., Giehl, K., Sillence, A., Grima, L. L., & Husain, M. (2017). Neurocomputational mechanisms underlying subjective valuation of effort costs. *PLoS Biology*, *15*(2), 1–28. <https://doi.org/10.1371/journal.pbio.1002598>
- Cooper, A. J., Duke, E., Pickering, A. D., & Smillie, L. D. (2014). The influence of anhedonia on feedback negativity in major depressive disorder. *Frontiers in Human Neuroscience*, *8*, 213–220. <https://doi.org/10.1016/j.neuropsychologia.2013.11.023>
- Crosson, P. L., Walton, M. E., O'Reilly, J. X., Behrens, T. E. J., & Rushworth, M. F. S. (2009). Effort-based cost-benefit valuation and the human brain. *Journal of Neuroscience*, *29*(14), 4531–4541. <https://doi.org/10.1523/JNEUROSCI.4515-08.2009>
- De Loof, E., Vassena, E., Janssens, C., De Taeye, L., Meurs, A., Van Roost, D., Boon, P., Raedt, R., & Verguts, T. (2019). Preparing for hard times: Scalp and intracranial physiological signatures of proactive cognitive control. *Psychophysiology*, *56*(10), e13417. <https://doi.org/10.1111/psyp.13417>
- Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, *134*, 9–21. <https://doi.org/10.1016/j.jneumeth.2003.10.009>
- Delorme, A., Sejnowski, T., & Makeig, S. (2007). Enhanced detection of artifacts in EEG data using higher-order statistics and independent component analysis. *NeuroImage*, *34*(4), 1443–1449. <https://doi.org/10.1016/j.neuroimage.2006.11.004>
- Festinger, L. (1957). *A theory of cognitive dissonance* (Vol. 2). Stanford University Press.
- Floresco, S. B., & Ghods-Sharifi, S. (2007). Amygdala-prefrontal cortical circuitry regulates effort-based decision making. *Cerebral Cortex*, *17*(2), 251–260. <https://doi.org/10.1093/cercor/bhj143>
- Foti, D., Weinberg, A., Bernat, E. M., & Proudfit, G. H. (2015). Anterior cingulate activity to monetary loss and basal ganglia activity to monetary gain uniquely contribute to the feedback negativity. *Clinical Neurophysiology*, *126*(7), 1338–1347. <https://doi.org/10.1016/j.clinph.2014.08.025>
- Frömer, R., Lin, H., Dean Wolf, C. K., Inzlicht, M., & Shenhav, A. (2021). Expectations of reward and efficacy guide cognitive control allocation. *Nature Communications*, *12*(1), 1030. <https://doi.org/10.1038/s41467-021-21315-z>
- Geaney, J. T., Treadway, M. T., & Smillie, L. D. (2015). Expenditure for reward. *PLoS One*, *10*(6), 1–18. <https://doi.org/10.5061/dryad.nm13s>
- Gheza, D., De Raedt, R., Baeken, C., & Pourtois, G. (2018). Integration of reward with cost anticipation during performance monitoring revealed by ERPs and EEG spectral perturbations. *NeuroImage*, *173*, 153–164. <https://doi.org/10.1016/j.neuroimage.2018.02.049>
- Hajcak, G., Moser, J. S., Holroyd, C. B., & Simons, R. F. (2006). The feedback-related negativity reflects the binary evaluation of good versus bad outcomes. *Biological Psychology*, *71*, 148–154. <https://doi.org/10.1016/j.biopsycho.2005.04.001>
- Harmon-Jones, E., Clarke, D., Paul, K., & Harmon-Jones, C. (2020). The effect of perceived effort on reward valuation: Taking the reward positivity (RewP) to dissonance theory. *Frontiers in Human Neuroscience*, *14*, 1–8. <https://doi.org/10.3389/fnhum.2020.00157>
- Harmon-Jones, E., Willoughby, C., Paul, K., & Harmon-Jones, C. (2020). The effect of perceived effort and perceived control on reward valuation: Using the reward positivity to test a dissonance theory prediction. *Biological Psychology*, *154*, 107910. <https://doi.org/10.1016/j.biopsycho.2020.107910>
- Heydari, S., & Holroyd, C. B. (2016). Reward positivity: Reward prediction error or salience prediction error? *Psychophysiology*, *53*(8), 1185–1192. <https://doi.org/10.1111/psyp.12673>
- Holroyd, C. B., & Coles, M. G. H. (2002). The neural basis of human error processing: Reinforcement learning, dopamine, and the error-related negativity. *Psychological Review*, *109*(4), 679–709. <https://doi.org/10.1037//0033-295X.109.4.679>
- Holroyd, C. B., & Krigolson, O. E. (2007). Reward prediction error signals associated with a modified time estimation task. *Psychophysiology*, *44*(6), 913–917. <https://doi.org/10.1111/j.1469-8986.2007.00561.x>
- Holroyd, C. B., & McClure, S. M. (2015). Hierarchical control over effortful behavior by rodent medial frontal cortex: A computational model. *Psychological Review*, *122*(1), 54–83. <https://doi.org/10.1037/a0038339>
- Holroyd, C. B., Nieuwenhuis, S., Yeung, N., & Cohen, J. D. (2003). Errors in reward prediction are reflected in the event-related brain potential. *Neuroreport*, *14*(18), 241–281. <https://doi.org/10.1097/00001756-200312190-00037>
- Holroyd, C. B., & Umemoto, A. (2016). The research domain criteria framework: The case for anterior cingulate cortex. *Neuroscience and Biobehavioral Reviews*, *71*, 418–443. <https://doi.org/10.1016/j.neubiorev.2016.09.021>
- Holroyd, C. B., & Verguts, T. (2021). The best laid plans: Computational principles of Anterior Cingulate Cortex. *Trends in Cognitive Sciences*, *25*(4), 316–329. <https://doi.org/10.1016/j.tics.2021.01.008>
- Holroyd, C. B., & Yeung, N. (2012). Motivation of extended behaviors by anterior cingulate cortex. *Trends in Cognitive Sciences*, *16*(2), 122–128. <https://doi.org/10.1016/j.tics.2011.12.008>
- Hosking, J. G., Cocker, P. J., & Winstanley, C. A. (2014). Dissociable contributions of anterior cingulate cortex and basolateral amygdala on a rodent cost/benefit decision-making task of cognitive effort. *Neuropsychopharmacology*, *39*(7), 1558–1567. <https://doi.org/10.1038/npp.2014.27>
- Hsieh, L. T., & Ranganath, C. (2014). Frontal midline theta oscillations during working memory maintenance and episodic encoding and retrieval. *NeuroImage*, *85*, 721–729. <https://doi.org/10.1016/j.neuroimage.2013.08.003>
- Huw, J., Stevenson, I., Huynh, A. Q., Babbage, M., Coxo, J., & Chong, T. T. J. (2021). Effort reinforces learning. *Preprint*. <https://doi.org/10.31234/osf.io/rqjt3>
- Inzlicht, M., Shenhav, A., & Olivola, C. Y. (2018). The effort paradox: Effort is both costly and valued. *Trends in Cognitive Sciences*, *22*(4), 337–349. <https://doi.org/10.1016/j.tics.2018.01.007>
- Jasper, H. H. (1958). The ten-twenty electrode system of the International Federation. *Electroencephalography and Clinical Neurophysiology*, *10*, 370–375.
- Kennerley, S. W., Walton, M. E., Behrens, T. E., Buckley, M. J., & Rushworth, M. F. (2006). Optimal decision making and the anterior cingulate cortex. *Nature Neuroscience*, *9*(7), 940–947.

- Kolling, N., Wittmann, M. K., Behrens, T. E. J., Boorman, E. D., Mars, R. B., & Rushworth, M. F. S. (2016). Value, search, persistence and model updating in anterior cingulate cortex. *Nature Neuroscience*, *19*(10), 1280–1285. <https://doi.org/10.1038/nn.4382>
- Krigolson, O. E. (2018). Event-related brain potentials and the study of reward processing: Methodological considerations. *International Journal of Psychophysiology*, *132*, 175–183. <https://doi.org/10.1016/j.ijpsycho.2017.11.007>
- Kurniawan, I. T., Seymour, B., Talmi, D., Yoshida, W., Chater, N., & Dolan, R. J. (2010). Choosing to make an effort: The role of striatum in signaling physical effort of a chosen action. *Journal of Neurophysiology*, *104*(1), 313–321. <https://doi.org/10.1152/jn.00027.2010>
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, *82*(13), 1–26. <https://doi.org/10.18637/jss.v082.i13>
- Le Heron, C., Holroyd, C. B., Salamone, J., & Husain, M. (2019). Brain mechanisms underlying apathy. *Journal of Neurology, Neurosurgery and Psychiatry*, *90*(3), 302–312. <https://doi.org/10.1136/jnnp-2018-318265>
- Leys, C., Ley, C., Klein, O., Bernard, P., & Licata, L. (2013). Detecting outliers: Do not use standard deviation around the mean, use absolute deviation around the median. *Journal of Experimental Social Psychology*, *49*(4), 764–766. <https://doi.org/10.1016/j.jesp.2013.03.013>
- Lin, H., Saunders, B., Hutcherson, C. A., & Inzlicht, M. (2018). Midfrontal theta and pupil dilation parametrically track subjective conflict (but also surprise) during intertemporal choice. *NeuroImage*, *172*, 838–852. <https://doi.org/10.1016/j.neuroimage.2017.10.055>
- Liu, W., Wang, L., Shang, H., Shen, Y., Li, Z., Cheung, E. F. C., & Chan, R. C. K. (2014). The influence of anhedonia on feedback negativity in major depressive disorder. *Neuropsychologia*, *53*(1), 213–220. <https://doi.org/10.1016/j.neuropsychologia.2013.11.023>
- Lopez-calderon, J., & Luck, S. J. (2014). ERPLAB: An open-source toolbox for the analysis of event-related potentials. *Frontiers in Human Neuroscience*, *8*, 213. <https://doi.org/10.3389/fnhum.2014.00213>
- Luck, S. J., & Gaspelin, N. (2017). How to get statistically significant effects in any ERP experiment (and why you shouldn't). *Psychophysiology*, *54*, 146–157. <https://doi.org/10.1111/psyp.12639>
- Luu, P., & Tucker, D. M. (2001). Regulating action: Alternating activation of midline frontal and motor cortical networks. *Clinical Neurophysiology*, *112*(7), 1295–1306. [https://doi.org/10.1016/S1388-2457\(01\)00559-4](https://doi.org/10.1016/S1388-2457(01)00559-4)
- Ma, Q., Meng, L., Wang, L., & Shen, Q. (2014). I endeavor to make it: Effort increases valuation of subsequent monetary reward. *Behavioural Brain Research*, *261*, 1–7. <https://doi.org/10.1016/j.bbr.2013.11.045>
- Michel, C. M., Murray, M. M., Lantz, G., Gonzalez, S., Spinelli, L., & Grave De Peralta, R. (2004). EEG source imaging. *Clinical Neurophysiology*, *115*(10), 2195–2222. <https://doi.org/10.1016/j.clinph.2004.06.001>
- Miltner, W. H. R., Braun, C. H., & Coles, M. G. H. (1997). Event-related brain potentials following incorrect feedback in a time-estimation task: Evidence for a “generic” neural system for error detection. *Journal of Cognitive Neuroscience*, *9*(6), 788–798. <https://doi.org/10.1162/jocn.1997.9.6.788>
- Mitchell, D. J., McNaughton, N., Flanagan, D., & Kirk, I. J. (2008). Frontal-midline theta from the perspective of hippocampal “theta”. *Progress in Neurobiology*, *86*(3), 156–185. <https://doi.org/10.1016/j.pneurobio.2008.09.005>
- Murayama, K., Usami, S., & Sakaki, M. (2022). Summary-statistics-based power analysis: A new and practical method to determine sample size for mixed-effects modeling. *Psychological Methods*. <https://doi.org/10.1037/met0000330>
- Norton, M. I., Mochon, D., & Ariely, D. (2012). The IKEA effect: When labor leads to love. *Journal of Consumer Psychology*, *22*(3), 453–460. <https://doi.org/10.1016/j.jcps.2011.08.002>
- Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience*, *2011*, 1–9. <https://doi.org/10.1155/2011/156869>
- Parvizi, J., Rangarajan, V., Shirer, W. R., Desai, N., & Greicius, M. D. (2013). The will to persevere induced by electrical stimulation of the human cingulate gyrus. *Neuron*, *80*(6), 1359–1367. <https://doi.org/10.1016/j.neuron.2013.10.057>
- Pelli, D. G. (1997). The videotoolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*, 437–442.
- Pinner, J. F. L., & Cavanagh, J. F. (2017). Frontal theta accounts for individual differences in the cost of conflict on decision making. *Brain Research*, *1672*, 73–80. <https://doi.org/10.1016/j.brainres.2017.07.026>
- Porter, B. S., Hillman, K. L., & Bilkey, D. K. (2019). Anterior cingulate cortex encoding of effortful behavior. *Journal of Neurophysiology*, *121*(2), 701–714. <https://doi.org/10.1152/jn.00654.2018>
- Proudfit, G. H. (2015). The reward positivity: From basic research on reward to a biomarker for depression. *Psychophysiology*, *52*, 449–459. <https://doi.org/10.1111/psyp.12370>
- Rudebeck, P. H., Walton, M. E., Smyth, A. N., Bannerman, D. M., & Rushworth, M. F. S. (2006). Separate neural pathways process different decision costs. *Nature Neuroscience*, *9*(9), 1161–1168. <https://doi.org/10.1038/nn1756>
- Salamone, J. D., Correa, M., Mingote, S., & Weber, S. M. (2003). Nucleus accumbens dopamine and the regulation of effort in food-seeking behavior: Implications for studies of natural motivation, psychiatry, and drug abuse. *Journal of Pharmacology and Experimental Therapeutics*, *305*(1), 1–8. <https://doi.org/10.1124/jpet.102.035063>
- Sambrook, T. D., & Goslin, J. (2015). A neural reward prediction error revealed by a meta-analysis of ERPs using great grand averages. *Psychological Bulletin*, *141*(1), 213–235. <https://doi.org/10.1037/bul0000006>
- Shenhav, A., Botvinick, M. M., & Cohen, J. D. (2013). The expected value of control: An integrative theory of anterior cingulate cortex function. *Neuron*, *79*(2), 217–240. <https://doi.org/10.1016/j.neuron.2013.07.007>
- Shenhav, A., Musslick, S., Lieder, F., Kool, W., Griffiths, T. L., Cohen, J. D., & Botvinick, M. M. (2017). Toward a rational and mechanistic account of mental effort. *Annual Review of Neuroscience*, *40*, 99–124. <https://doi.org/10.1146/annurev-neuro-072116-031526>

- Shenhav, A., Straccia, M. A., Botvinick, M. M., & Cohen, J. D. (2016). Dorsal anterior cingulate and ventromedial prefrontal cortex have inverse roles in both foraging and economic choice. *Cognitive, Affective, & Behavioral Neuroscience*, *16*(6), 1127–1139. <https://doi.org/10.3758/s13415-016-0458-8>
- Shenhav, A., Straccia, M. A., Cohen, J. D., & Botvinick, M. M. (2014). Anterior cingulate engagement in a foraging context reflects choice difficulty, not foraging value. *Nature Neuroscience*, *17*(9), 1249–1254. <https://doi.org/10.1038/nn.3771>
- Skvortsova, V., Palminteri, S., & Pessiglione, M. (2014). Learning to minimize efforts versus maximizing rewards: Computational principles and neural correlates. *The Journal of Neuroscience*, *34*(47), 15621–15630. <https://doi.org/10.1523/JNEUROSCI.1350-14.2014>
- Tran, Y., Craig, A., Craig, R., Chai, R., & Nguyen, H. (2020). The influence of mental fatigue on brain activity: Evidence from a systematic review with meta-analyses. *Psychophysiology*, *57*(5), 1–17. <https://doi.org/10.1111/psyp.13554>
- Treadway, M. T., Buckholtz, J. W., Cowan, R. L., Woodward, N. D., Li, R., Ansari, M. S., Baldwin, R. M., Schwartzman, A. N., Kessler, R. M., & Zald, D. H. (2012). Dopaminergic mechanisms of individual differences in human effort-based decision-making. *Journal of Neuroscience*, *32*(18), 6170–6176. <https://doi.org/10.1523/JNEUROSCI.6459-11.2012>
- Treadway, M. T., Buckholtz, J. W., Schwartzman, A. N., Lambert, W. E., & Zald, D. H. (2009). Worth the “EEfRT”? The effort expenditure for rewards task as an objective measure of motivation and anhedonia. *PLoS One*, *4*(8), 1–9. <https://doi.org/10.1371/journal.pone.0006598>
- Umemoto, A., HajiHosseini, A., Yates, M. E., & Holroyd, C. B. (2017). Reward-based contextual learning supported by anterior cingulate cortex. *Cognitive, Affective, & Behavioral Neuroscience*, *17*(3), 642–651. <https://doi.org/10.3758/s13415-017-0502-3>
- Umemoto, A., & Holroyd, C. B. (2017). Neural mechanisms of reward processing associated with depression-related personality traits. *Clinical Neurophysiology*, *128*(7), 1184–1196. <https://doi.org/10.1016/j.clinph.2017.03.049>
- Umemoto, A., Inzlicht, M., & Holroyd, C. B. (2019). Electrophysiological indices of anterior cingulate cortex function reveal changing levels of cognitive effort and reward valuation that sustain task performance. *Neuropsychologia*, *123*, 67–76. <https://doi.org/10.1016/j.neuropsychologia.2018.06.010>
- Umemoto, A., Lin, H., & Inzlicht, M. (2019). Cost-benefit analysis in physical effort expenditure: An electrophysiological registered report (preprint). *Cortex* (Registered Report Stage 1). <https://doi.org/10.31234/osf.io/mc4by>
- Vassena, E., Deraeve, J., & Alexander, W. H. (2020). Surprise, value and control in anterior cingulate cortex during speeded decision-making. *Nature Human Behaviour*, *4*(4), 412–422. <https://doi.org/10.1038/s41562-019-0801-5>
- Vassena, E., Holroyd, C. B., & Alexander, W. H. (2017). Computational models of anterior cingulate cortex: At the crossroads between prediction and effort. *Frontiers in Neuroscience*, *11*, 1–9. <https://doi.org/10.3389/fnins.2017.00316>
- Vassena, E., Silvetti, M., Boehler, C. N., Achten, E., Fias, W., & Verguts, T. (2014). Overlapping neural systems represent cognitive effort and reward anticipation. *PLoS One*, *9*(3), e91008. <https://doi.org/10.1371/journal.pone.0091008>
- Verguts, T. (2017). Binding by random bursts: A computational model of cognitive control. *Journal of Cognitive Neuroscience*, *29*(6), 1103–1118. <https://doi.org/10.1162/jocn.2017.01103>
- Verguts, T., Vassena, E., & Silvetti, M. (2015). Adaptive effort investment in cognitive and physical tasks: A neurocomputational model. *Frontiers in Behavioral Neuroscience*, *9*, 57. <https://doi.org/10.3389/fnbeh.2015.00057>
- Walsh, M. M., & Anderson, J. R. (2012). Learning from experience: Event-related potential correlates of reward processing, neural adaptation, and behavioral choice. *Neuroscience and Biobehavioral Reviews*, *36*(8), 1870–1884. <https://doi.org/10.1016/j.neubiorev.2012.05.008>
- Walton, M. E., Bannerman, D. M., & Rushworth, M. F. S. (2002). The role of rat medial frontal cortex in effort-based decision making. *The Journal of Neuroscience*, *22*(24), 10996–11003. <https://doi.org/10.1523/JNEUROSCI.22-24-10996.2002>
- Walton, M. E., Groves, J., Jennings, K. A., Croxson, P. L., Sharp, T., Rushworth, M. F. S., & Bannerman, D. M. (2009). Comparing the role of the anterior cingulate cortex and 6-hydroxydopamine nucleus accumbens lesions on operant effort-based decision making. *European Journal of Neuroscience*, *29*(8), 1678–1691. <https://doi.org/10.1111/j.1460-9568.2009.06726.x>
- Wascher, E., Rasch, B., Sanger, J., Hoffmann, S., Schneider, D., Rinkenauer, G., Heuer, H., & Gutberlet, I. (2014). Frontal theta activity reflects distinct aspects of mental fatigue. *Biological Psychology*, *96*, 57–65. <https://doi.org/10.1016/j.biopsycho.2013.11.010>
- Westbrook, A., & Braver, T. S. (2015). Cognitive effort: A neuroeconomic approach. *Cognitive, Affective, & Behavioral Neuroscience*, *15*, 395–415. <https://doi.org/10.3758/s13415-015-0334-y>

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