Disentangling Effort from Probability of Success: Temporal Dynamics of Frontal Midline Theta in Effort-Based Reward Processing

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Abstract

The ability to weigh a reward against the effort required to acquire it is critical for decision-making. However, extant experimental paradigms oftentimes confound increased effort demand with decreased reward probability, thereby obscuring neural correlates underlying these cognitive processes. To resolve this issue, we designed novel tasks that disentangled probability of success – and therefore reward probability – from effort demand. In Experiment 1, reward magnitude and effort demand were varied while reward probability was kept constant. In Experiment 2, effort demand and reward probability were varied while reward magnitude remained fixed. Electroencephalogram (EEG) data was recorded to explore how frontal midline theta (FMT; an electrophysiological index of mPFC function) and component P3 (an index of incentive salience) respond to effort demand, and reward magnitude and probability. We found no evidence that FMT tracked effort demands or net value during cue evaluation. At feedback, however, FMT power was enhanced for high compared to low effort trials, but not modulated by reward magnitude or probability. Conversely, P3 was sensitive to reward magnitude and probability at both cue and feedback phases and only integrated expended effort costs at feedback, such that P3 amplitudes continued to scale with reward magnitude and probability but were also increased for high compared to low effort reward feedback. These findings suggest that, when likelihood of success is equal, FMT power does not track net value of prospective effort-based rewards. Instead, expended cognitive effort potentiates FMT power and enhances the saliency of rewards at feedback.

Significance statement: The way the brain weighs rewards against the effort required to achieve them is critical for understanding motivational disorders. Current paradigms confound increased effort demand with decreased reward probability, making it difficult to disentangle neural activity associated with effort costs from those associated with reward likelihood. Here, we explored the temporal dynamics of effort-based reward (via frontal midline theta (FMT) and component P3) while participants underwent a novel paradigm that kept probability of reward constant between mental effort demand conditions. Our findings suggest that the FMT does not track net value and that expended effort enhances, instead of attenuates, the saliency of rewards.

Key words: Effort; subjective value; effort-based reward; cost / benefit estimation; frontal midline theta; motivation

Data availability: The datasets generated and analyzed during this study are available under https://osf.io/z5enb/.

Code availability: Scripts for all analyses are available through https://osf.io/z5enb/.

1. Introduction

Successful goal-directed behavior relies on the tracking of incentive values and their associated effort costs (Westbrook & Braver, 2015; Zald & Treadway, 2017). While extensive research has focused on developing neurocognitive tasks to measure the brain activity associated with the valuation of effort-based rewards, many experimental paradigms a) conflate effort with reward probability and/or b) limit analyses to early or late stages of reward processing, thereby limiting the interpretability of findings.

Specifically, the paradigms used to study the neural correlates of rewards requiring cognitive effort frequently report poorer performance for high, compared to low, effort tasks (Aridan et al., 2019; Giustiniani et al., 2015; Grodin et al., 2016; Ma et al., 2014; Umemoto et al., 2022; Wang et al., 2017; Westbrook et al., 2019; Yi et al., 2020), potentially confounding increased effort demand with reduced reward likelihood. This observation is critical for understanding the contribution of the dorsal anterior cingulate cortex (dACC) and surrounding medial prefrontal cortex (mPFC) in effort-based reward valuation, since the mPFC has been consistently implicated in signaling the subjective value of effort-based rewards (Lopez-Gamundi et al., 2021) and reward likelihood and uncertainty (Amiez et al., 2006; Monosov, 2017; Silvetti et al., 2013; Vassena, Krebs, et al., 2014). For example, activity in the mPFC has been shown to scale with prospective net value (Arulpragasam et al., 2018; Chong et al., 2017; Croxson et al., 2009; Massar et al., 2015; Skvortsova et al., 2014) and upcoming effort costs (Chong et al., 2017; Klein-Flügge et al., 2016; Prévost et al., 2010; Vassena, Silvetti, et al., 2014), but also signal the discrepancy between expected and actual rewards (Vassena et al., 2017, 2020). Furthermore, electrophysiological markers of mPFC functioning – specifically oscillatory activity frontal midline theta (FMT) and event-related potential feedback-related negativity / reward positivity (FRN/RewP) – have been shown to be sensitive to reward probability and uncertainty (Bellebaum et al., 2010; Silvetti et al., 2014; Smith et al., 2009; Yu et al., 2011), and outcome expectancy (Cavanagh et al., 2012; Hajihosseini & Holroyd, 2013; Mas-Herrero & Marco-Pallarés, 2014, 2016), but also to features of effort-based decision-making, such as reward incentive (Riddle et al., 2022), decision difficulty (Umemoto et al., 2022), and exerted effort (Umemoto et al., 2022). Therefore, one critical consideration when investigating the neural correlates of effort-based reward is controlling for demand-driven differences in reward probability.

Another important consideration is that the effect of effort may vary throughout the phases of reward processing. Specifically, neural activity in the early stages of reward processing (i.e., cue evaluation and decision making) is consistent with the effort discounting hypothesis, which posits that effort is a cost that diminishes the value of a reward (Salamone et al., 2009, 2015, 2018; Westbrook & Braver, 2015; Zald & Treadway, 2017). In later stages of reward processing (i.e., reward delivery), however, the effect of effort is less clear. For example, some functional magnetic resonance imaging (fMRI) studies have shown that exerted effort enhances hemodynamic responses in reward-related brain regions at the time of reward delivery (Dobryakova et al., 2017; Gaillard et al., 2019; Hernandez Lallement et al., 2014; Sullivan-Toole et al., 2019; Zink et al., 2004). Conversely, effort has been shown to increase amplitudes of encephalogram (EEG) indices of saliency and firing rates of midbrain dopamine neurons during performance feedback and reward delivery phases (Ma et al., 2014; Schevernels et al., 2014, 2016; Tanaka et al., 2019, 2021; Umemoto et al., 2022; Wang et al., 2017; Yi et al., 2020). Taken together, these findings support what has been coined the “paradoxical” effect of effort (Inzlicht et al., 2018a), where effort devalues reward during early processing stages but enhances sensitivity to reward at delivery. To date however, studies that are well-suited to directly test this hypothesis have either limited analyses to early or late time windows (M. Zhang & Zheng, 2022; Zheng et al., 2023) or have lacked adequate control for unequal reward rates between effort demand conditions (Ma et al., 2014; Wang et al., 2017; Yi et al., 2020).

To address this gap, we designed two novel paradigms that rewarded participants based on task performance but yielded similar reward rates for low and high levels of cognitive effort demand. Specifically, we investigated to what degree manipulations in effort demand, reward magnitude (Study 1), and reward probability (Study 2) modulate FMT – putative marker of mPFC activity – at both cue evaluation and feedback processing phases. FMT is an EEG oscillatory activity of 4-8 Hz that is distributed over fronto-central areas of the scalp and has been linked to a range of cognitive control (Cavanagh & Frank, 2014; Cavanagh & Shackman, 2015) and performance feedback functions (Doñamayor et al., 2012; Li et al., 2016, 2018; Mas-Herrero & Marco-Pallarés, 2014, 2016). Generated in the mPFC (Mas-Herrero & Marco-Pallarés, 2016), FMT has been hypothesized to reflect effortful control in goal-directed behavior (Cavanagh & Frank, 2014; Holroyd & Umemoto, 2016), improve behavioral performance via phase-amplitude coupling (Verguts, 2017), track task-relevant features (Hajihosseini & Holroyd, 2013), and correlate with trial-by-trial behavioral adjustments (Cavanagh & Shackman, 2015). Taken together, FMT is a candidate EEG signature for the allocation of control in effort-based reward. We hypothesized that if the mPFC tracks the motivational value of effort-based rewards, FMT activity would reflect an integrated effort and reward signal at both cue and feedback.

In parallel, we were interested in exploring the effect of effort on an established index of incentive salience: the P3 event-related potential (ERP; Glazer et al., 2018). This component is well-suited to test the effectiveness of our manipulations, as P3 amplitudes have been shown to be modulated by reward magnitude and probability at cue and feedback (Giustiniani et al., 2020; Hajcak et al., 2005, 2007; Pfabigan et al., 2014; Vignapiano et al., 2016). Furthermore, P3 amplitudes have been shown to be sensitive to effort demands during both anticipatory and consummatory phases of reward processing (Ma et al., 2014; Schevernels et al., 2014; Wang et al., 2017; M. Zhang & Zheng, 2022; Zheng et al., 2023), which suggests that the influence of effort on reward saliency can be effectively tracked through this component. Thus, if our manipulations were effective, we expected P3 to be enhanced for high magnitude and low probability rewards, and that these effects would be attenuated by prospective effort demands at the cue evaluation stage but enhanced by exerted effort at the time of reward delivery.

2. Methods

2.1. Study 1

2.1.1 Participants

Previous studies that have used similar repeated-measures EEG designs to explore effort-based reward have reported relatively small effect sizes in earlier (i.e. cue evaluation and reward anticipation) compared to later stages of reward processing (i.e. reward outcome) (M. Zhang & Zheng, 2022; Y. Zhang et al., 2017; Zheng et al., 2023). Consequently, sensitivity analyses yielded that a sample size of N=27 would be required to detect a conservative effect size of η_p^2= 0.06 with 80% statistical power. Subjects were excluded for current psychiatric diagnosis, color blindness, and lack of fluency in Spanish. 33 healthy adults (20 female, age: M= 27.24, SD=5.45) participated in the study. One subject was removed for low cue identification rate (<50%) in the catch questions and three subjects were removed for excessive motion artifacts, leaving a final sample of N=28.

2.1.2 Procedures

Upon arrival, participants reviewed and provided informed consent. Next, participants completed a series of self-report demographic and COVID-19 health questionnaires and then the Effort Valuation Task (see below). After the task, participants completed an end of session questionnaire (described below) before debriefing. All participants received a baseline payment of 20€ for participation, and additional earnings from the Effort Valuation Task, ranging from 5€ to

15€. This study was conducted in accordance with the ethical guidelines from the Declaration of Helsinki and was approved by the University of Barcelona ethics board.

2.1.2.2. Effort Valuation Task. The current Effort Valuation Task comprised of a variant of the reward effortful task used in Croxson et al. (2009), modified to use an effort component from Botvinick et al. (2009). The task was administered using PsychoPy software version 2 (Peirce et al., 2019). Subjects were seated approximately 50 cm away from the computer monitor and responded using a standard keyboard and mouse.

The schematic of the task is shown in Figure 1a. First, a cue signaling the prospective effort and reward of the upcoming trial was presented for 1.5 seconds. The shape of the cue (circle or square, counterbalanced across participants) indicated the effort requirement (low vs high) and the number of lines indicated the magnitude of reward on offer, with 1 line indicating low reward (5 points) and 5 lines indicating high reward (25 points).

In half of the trials, reward/effort cues were followed by an asterisk (1200 - 1500 ms, with 100 ms steps) and then aborted. As has been done in previous paradigms (Klein-Flügge et al., 2016; Kurniawan et al., 2013) we included abort trials in order to have sufficient power (i.e. enough trials) to analyze effects in the cue phase without making the task too tiring or excessively long. In the other half of the trials, cues were followed by a fixation cross (randomized time of presentation between 1200 and 1500 ms, with 100 ms steps) and then an effort exertion phase, which lasted 8 seconds. During the effort exertion phase, subjects viewed a series of numbers presented one at a time on the screen. Numbers ranged from one to nine, excluding five. If the number was blue, subjects were instructed to use the arrow keys to indicate if the number was even or odd. If the number was yellow, subjects were instructed to indicate whether the number was higher or lower than 5. In low effort trials, all judgments were of the same type. In the high effort trials, number color/judgment type alternated, requiring effortful cognitive set switches. Task set switching has been shown to be cognitively demanding (e.g., increased reaction time and reduced accuracy) and induce preference for tasks with less set switching (Kool et al., 2010). Furthermore, this same task has been widely used to manipulate cognitive effort in other paradigms (Botvinick et al., 2009; Croxson et al., 2009; Kool et al., 2010; Lopez-Gamundi & Wardle, 2018; Reddy et al., 2015). Participants were instructed to answer as quickly and as accurately as possible within the 8-second time frame. Immediately after the effort phase, another fixation cross appeared for 2000 to 2500 ms (steps of 100 ms), followed by a reward/performance feedback for 1000 ms. If participants correctly completed the task, a 5 or 25 was presented on the screen, matching the reward offer for the trial. If participants made more than 2 errors during the task or did not meet the calibrated decision threshold (see Training and Calibration for more detail), an X was presented indicating that the trial was not successful, and no points were being awarded. Another fixation cross marked the end of the trial. Intertrial intervals (ITIs) ranged from 2 to 3 seconds (with steps of 200 ms).

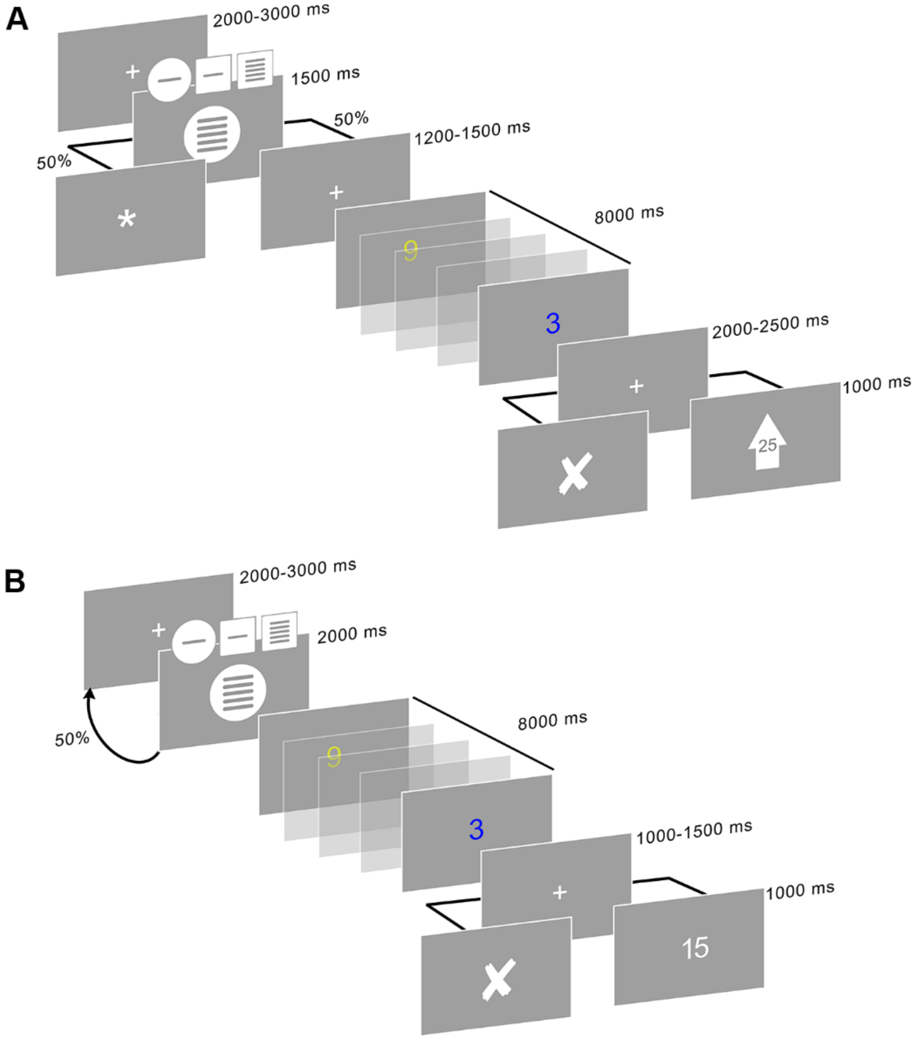

Figure 1. Schematic of tasks. A) *Schematic of Effort Valuation Task used in Study 1. Note that cues with one line indicate low reward on offer (5 points) while cues with five lines indicate high reward on offer (25 points). Note that in half of trials, cues were followed by asterisks, indicating that that trial would be aborted. In the other half of trials, cues were followed by fixation crosses and effort exertion.* ***B)*** *Schematic of the Probabilistic Effort Valuation Task used in Study 2. Note that cues with one line indicate that the trial has high probability of success (less responses are required). Cues with five lines indicate low probability of success (more responses are required). Note that half of trials were immediately aborted after cue presentation.*

To ensure that participants attended to the reward/effort cue, four abort trials in each block were followed by an identification question. Participants had to use the keypad to recall the meaning of the cue that had been presented at the beginning of the aborted trial; for example, if the cue was a circle with 1 line in it, the participant had to select the option that read "easy task worth 5 points". Participants were instructed that compensation depended partially on how accurate they answered these identification questions. Identification questions were self-paced and no feedback was provided until the break screen. Abort trials ended with the same fixation cross and ITI.

There were five blocks with 80 trials (40 effort, 36 abort, and 4 abort followed by an identification question) per block, totaling to 400 trials. Reward and effort conditions were intermixed and evenly distributed between effort/abort trials, so that in each block there were 10 effort trials and 10 abort trials for each of the 4 following cues: high reward/high effort, high reward/low effort, low reward/high effort and low reward/low effort. Trials were presented in pseudo-random order, such that there were no more than 2 consecutive no-effort trials. Participants were probed for fatigue, cue liking, and task difficulty (see Self-Report) after calibration, as well as halfway through and at the end of each block, making for 11 ratings total. After these questions, participants were given a self-paced break and provided with feedback about their cumulative points and their identification accuracy. Participants were able to earn up to 3000 points and were informed that 1000 points were equivalent to 5€, 2000 points to 10€, and 3000 points to 15€.

Self-Report Task Ratings. During the Effort Valuation Task, participants were probed, via 11-point Likert scales, for cue liking, task difficulty, and subjective experience of fatigue at baseline, as well as two times during each block. Participants were instructed to rate to which degree they liked the 4 reward/effort cues (0= did not like at all, 5= indifferent, 10= liked very much), how tired they felt (0=not tired at all and 10=very tired), and how difficult the High Effort and Low Effort tasks were (0=not difficult at all and 10=very difficult). Ratings for each block were composed of the average of the two block ratings.

Training and Calibration. Before beginning the Effort Valuation task, the participants were instructed on the different cue types, trial types, effort task rules, and compensation scheme. Next, participants completed a series of practice trials in blocks for each of the three trial types (e.g. low effort with all blue numbers, low effort with all yellow numbers, and high effort). Participants were told that they needed to correctly complete a minimum of 5 trials before they could move on to the real task. Although effort phases for practice trials were locked to 8 seconds, the cue and feedback presentation were self-paced in order to ensure that subjects understood the meaning of the presented stimuli.

Practice trials with greater than or equal to 85% accuracy (i.e. ≥85% correct choices within the 8-second time window) were considered successful and participants needed to correctly complete at least 5 practice trials of each effort type before moving on to the real task. Data from the practice trials was used to set the initial difficulty of high and low effort tasks. The number of correct decisions for each successful practice trial was stored in an array specific to each of the trial types. The number of correct decisions required to successfully complete a trial ("decision thresholds") for each trial type were then calculated by taking correct number of decisions above the lower 20th percentile. This method effectively fixed success rates of low and hard effort trials to 80%, making it equally probable to obtain reward under both levels of effort demands and minimizing the effect of probability discounting. These arrays were continuously updated during the task so that decision thresholds were recalculated for each trial based on performance on the previous 5 trials of that same trial type. Thus, decision thresholds decreased and increased based on poor or improved performance, respectively, on recent trials. This allowed our task to mitigate the effects of fatigue, which could diminish performance and reduce probability of reward, and learning of the effort task, which would improve performance and thereby increase (differentially) the probability of reward.

End of Session Questionnaire. At the end of the experiment, participants completed a 6-item survey to help us assess their understanding of the paradigm. Specifically, participants had to identify which cue signaled a 5- or 25-point offer and which cue signaled an upcoming high or low effort trial. We also asked participants to rate their perceived accuracy (from 0% to 100%) on the low and high effort tasks, separately.

2.1.2 Electroencephalographic activity recording and preprocessing

EEG data was continuously recorded from 33 standard scalp sites (Fp1/2, Fz, F3/4, F7/8, FCz (reference), FC1/2, FC5/6, FT9/10, Cz, C3/4, T7/8, CP1/2, CP5/6, Pz, P3/4, P7/8, O1/2, L/R Mastoids, ground at Fpz electrode) using active electrodes mounted on an ActiCap (Brain Products ©). EEG signal was amplified using BrainAmp amplifier, with a continuous sampling at a rate of 250 Hz, with a 0.01 Hz high-pass filter and 50 Hz notch filter. Eye movements were recorded with an electrode at the infraorbital ridge of the right eye. All electrode impedances were kept below 10kΩ.

EEG data were preprocessed and analyzed in MATLAB© using EEGLAB toolbox (Delorme & Makeig, 2004). EEG signals were first re-referenced to the average activity of the two mastoids (L/R). The EEG data were bandpass filtered between 0.01 Hz to 45 Hz. To analyze activity associated with cue and feedback phases, the signals were epoched from −2000 to 2000 ms relative to cue and feedback onset, respectively, with the activity from −200 to 0 ms serving as the baseline. All epoched data were screened manually for artifacts (e.g., spikes, channel-jumps, and non-biological signals). Independent components analysis (ICA) was then applied to the data and components reflecting motion artifacts (i.e. blinks/eye movement) were removed.

Finally, data were visually inspected again and remaining artifacts were removed. Analyses were then conducted on the remaining N=28 subjects (17 female, age: M= 27.89, SD=5.20) with viable EEG data. Due to unequal reward rates in Block 1 (see Behavioral results), analyses were conducted with Block 1 trials removed, resulting in an average of 299.25 trials (SD=10.99) for the cue phase and 117.79 trials (SD=9.45) for the feedback phase.

2.2. Study 2

2.2.1 Participants

Results from Study 1 suggested that a sample size of N=27 was adequate for detecting medium effect sizes in cue and feedback. However, to ensure that our final sample size was large enough, we recruited 37 healthy adults (20 female, age: M= 24.00, SD=5.77) to participate in Study 2. Two subjects were excluded due to low accuracy (<30%) on the catch identification trials and 3 participants were excluded for excessive motion artifacts, leaving a final sample of N=32.

2.2.2 Procedures

The behavioral paradigm and procedures for were similar to Study 1 except for the differences noted below.

2.2.2.1. Probabilistic Effort Evaluation Task. The paradigm was very similar to the task used in Study 1, but with a few key differences (see Figure 1b). First, instead of manipulating reward magnitude, we directly manipulated probability of success. Thus, potential rewards were fixed to 15 points per effort trial, but effort trials either had a high or low probability of success. Probability of success was manipulated by setting the decision threshold higher for low probability trials and lower for high probability trials. Specifically, decision thresholds for High Probability trials were set as in Study 1 (by taking correct number of decisions above the lower 20th percentile from the past 5 trials), while decision thresholds for Low Probability trials were to the number of correct decisions above the 60th percentile. This effectively locked probability to success to above 80% on High Probability trials and below 60% on Low Probability trials.

Second, we simplified the design of the task in the following ways. First, we set the Low Effort task to only one decision type (greater than/less than 5). This was done to simplify instructions and save time on the initial training/calibration. We selected the greater than/less than 5 decision rule because this task was rated as less difficult than the even/odd task, thereby allowing us to maximize the difference between low and high effort demand. Second, since FMT is hypothesized to signal the need to implement control (Cavanagh & Frank, 2014), it is possible that FMT activity in Study 1 was locked to the pre-effort fixation cross instead of the reward/effort cue since the pre-effort fixation was deterministic of future effort. To address this concern, we removed the pre-effort fixation cross from the task in Study 2. Instead, we extended the cue presentation to 2 seconds, which was then either followed by the corresponding effort exertion phase (effort trials) or the next trial (abort trials). Third, we shortened the pre-feedback ISI to 1000 to 1500 ms (steps of 100ms). All other trial and block structures remained the same as in Study 1. Fourth, we simplified the identification questions by asking participants to identify which cue image (as opposed to the meaning of the cue) was presented in the previous trial.

Self-Report Task Ratings. As in Study 1, participants were probed, via 11-point Likert scales, for cue liking and subjective experience of fatigue at baseline, as well as two times during each block. However, because we expected that probability of success would impact difficulty ratings, we decided to probe participants regarding how much effort was required to complete each task (0=No Effort, 10=Extreme Effort). Further, although participants were explicitly told which cues would signal high vs low probability of success, we also asked participants to rate how likely (0-100%) they were to correctly complete each task. As in Study 1, participants were asked for their ratings after the initial practice phase and twice during each block.

Training and Calibration. In Study 1 we saw that the calibration mechanism took longer than expected in stabilizing probability rates. In order to avoid tossing out the first trials, we extended the practice sessions so that participants had to correctly complete a minimum of at least 15 (as opposed to 5) trials of each effort type. We also interweaved the one-color and two-color tasks (as opposed to practicing in blocks) to better simulate the real task. Initial decision thresholds were based on the last five correct trials.

End of Session Questionnaire. At the end of the experiment, participants completed a 2-item survey to help us assess their understanding of cues and their effort demand contingencies. Specifically, participants had to identify which cue signaled an upcoming high or low effort trial.

2.2.3 Electroencephalographic activity recording and preprocessing

EEG data was continuously recorded from 32 standard scalp sites (Fp1/2, Fz (reference), F3/4, F7/8, FC1/2, FC5/6, FT9/10, Cz, C3/4, T7/8, CP1/2, CP5/6, Pz, P3/4, P7/8, O1/2, L/R Mastoids, ground at Fpz) using active electrodes mounted on an ActiCap (Brain Products ©). EEG signal was amplified using BrainAmp amplifier, with a continuous sampling at a rate of 500 Hz, with a 0.01 Hz high-pass filter and 50 Hz notch filter. Eye movements were recorded with an electrode at the infraorbital ridge of the right eye. As in Study 1, all electrode impedances were kept below 10kΩ.

EEG data were preprocessed and analyzed in MATLAB © using EEGLAB toolbox (Delorme & Makeig, 2004). EEG signals were first re-referenced to the average activity of the two mastoids (L/R). The EEG data were bandwith filtered with a bandpass of 0.01 Hz to 45 Hz. To analyze activity associated with cue and feedback phases, the signals were epoched from −2000 to 2000 ms relative to cue and feedback onset, respectively. All epoched data were screened manually for artifacts (e.g., spikes, channel-jumps, and non-biological signals). Independent components analysis (ICA) was then applied to the data and components reflecting motion artifacts (i.e. blinks/eye movement) were removed.

Finally, data were again visually inspected and remaining artifacts were removed. Three subjects were removed for excessive motion artifacts. Analyses were performed on the remaining N=32 subjects (28 female, age: M= 23.93, SD=5.24) with an average of 354.47 trials (SD=33.99) for the cue phase and 130.16 trials (SD=10.37) for the feedback phase.

2.3. Data Analysis

2.3.1. Event-Related Potentials

EEG data was again low-pass filtered at 20 Hz offline. Components in the cue phase and feedback phase were studied by epoching data time-locked to 200 ms before and 1000 ms after cue and feedback onset, respectively. Time windows and electrode sites for ERP components for each phase were selected by exploring waveforms and topographic maps across all conditions for each study separately. Cue-P3 was defined as the average amplitude from 350 and 500 ms after cue onset for Study 1 and 450 to 550ms after cue onset for Study 2. In Study 1, FB-P3 was defined as the mean activity between 300 and 400 ms following feedback onset, and 350 to 450ms in Study 2.

2.3.2. Time Frequency Analysis

Time-frequency analysis was performed per trial in 4 second epochs for cue and feedback phases (2 sec before cue/feedback through 2 sec after). In order to find the induced time-frequency activity, we convoluted single-trial activity using a complex Mortlet wavelet from 1 Hz to 40 Hz using 1Hz steps. We then computed the mean change in power with respect to baseline for each phase, defined as the 400 to 200ms before cue or feedback onset. To compare different conditions, trials associated with a specific Reward/Effort condition were averaged for each participant before performing a grand average. The mean increase/decrease in power for each condition was computed at Fz, Cz and Pz. Based on previous studies implicating theta in both effortful control (Cavanagh & Frank, 2014; Cavanagh & Shackman, 2015), we specifically focused on theta (4-8 Hz) in time windows where the effect of our manipulations appeared maximal (100 to 400 ms after cue and 200 to 550ms after feedback onset for both experiments).

2.3.3. Statistical Analysis

2.3.3.1. Behavioral Data. The novelty of the Effort Valuation and Probabilistic Effort Valuation tasks were that effort demands were continuously calibrated so that effort could be fully disassociated from reward probability. Thus, it was important for us to confirm that participants had similar success rates between high and low effort trials across the task. Thus, we used linear mixed-effects models (LMM) with Block, Effort, Reward (Study 1)/Probability (Study 2), and their interactions as fixed effects, Subject as a random effect, and trial success as the outcome to test if our calibration mechanism effectively locked success rates throughout the tasks. For our task to be valid, we also needed to confirm that high effort trials were more cognitively demanding than low effort trials. Since response times have been shown to increase as a function of task difficulty

(Dodonov & Dodonova, 2012; Wong et al., 2017), we used the number of decisions made per trial and the average speed of decisions as behavioral proxies of cognitive demand. The same fixed and random effects structure was used to fit two LMMs to the number of decisions made per trial and average speed of decision. Although we expected self-report fatigue to increase with time on task, we designed our calibration mechanism to adjust for declines in reward probability due to fatigue-related diminished performance. Thus, we first fit an LMM with self-report fatigue ratings at the dependent variable, Block as a fixed effect and subject as a random effect to see how fatigue changed throughout the task. We also used another LMM, with fatigue ratings, Block, and their interactions as fixed effects, subject as random effects, to predict block-wise mean trial accuracy.

With respect to self-report ratings, we expected that effort, reward probability, and time on task would affect appetitive responses to the cues (cue-liking) and subjective experience of task difficulty/effort. Again, we used two LMMs, with Block, Effort, Reward (Study 1)/Probability (Study 2), and their interactions as fixed effects and Subject as a random effect, to explore if self-report cue-liking and task difficulty/effort were modulated by our experimental manipulations. In the case of Study 2, we were interested in seeing how our probability manipulation impacted participants' perceived probability of successfully completing a trial. Thus, we first fit an LMM with the same fixed and random effects structure to the self-report probability of success data.

2.3.3.2. EEG Data. To study the effect of reward magnitude and probability and effort demands on midline ERP amplitudes and theta power, we conducted separate repeated-measures ANOVA with Effort (high and low), Reward Magnitude (high and low; Study 1) or Probability (high and low; Study 2) and Sensor (Fz, Cz, and Pz) as within-participant factors and time-locked ERP components and theta power as dependent measures. The Greenhouse-Geisser correction was applied in cases where the sphericity assumption was violated. Paired sample t-tests with Tukey HSD corrections for multiple comparisons were used to explore significant effects post-hoc. In the case where normality assumptions were violated, Wilcoxon signed rank tests were used.

Due to the limited research on the role of FMT in effort-based reward processing, we deemed it important to quantify null effects in cases where we failed to detect a significant effect of our manipulations on theta power. Since a "non-significant" *p*-value (*p*>.05) alone does not meaningfully support a null effect (Gelman & Stern, 2012), we employed Bayesian approaches which are better suited to quantify the amount of evidence in favor of the null hypotheses that Effort and Reward Magnitude/Probability do not have effects on theta power at cue. Specifically, we first replicated our original Frequentist analyses using Bayesian rmANOVA in JASPv0.17.1. In our case, we expected to replicate our original findings (described in the Results section) such that theta power during the cue phase would be best predicted by a model with only Sensor as a predictor. Bayes Factors (BFs) are computed to compare the probability of an alternative model relative to the probability of the null model. Inclusion Bayes factor (BF_{incl}), which contrasts the performance of a model with a given predictor against the performance of all models that exclude that predictor, were used to quantify the importance of a given predictor. Finally, we conducted Bayesian paired-sample t-tests to quantify the relative strength of evidence in favor of the simple null hypotheses (H_0) that 1) Effort and 2) Reward Magnitude/Probability do not have an effect on theta power at cue. A $BF_{01}>3$ (or $BF_{10}<1/3$) is interpreted as moderate evidence in support of the null hypothesis (Wagenmakers et al., 2011).

3. Results

3.1. Study 1

3.1.1. Behavioral and Self-Report Data

The primary aim of our paradigm was to experimentally isolate effort demand from reward probability. Thus, we had to first confirm that the likelihood of successfully completing the task, and therefore obtaining the reward, was equivalent for high and low effort trials throughout the task. LMM revealed significant Reward Magnitude (b=0.19, p<0.000) and Effort and Block interaction (b=-2.05, p=0.008; see Supplementary Table 1). As can be seen in Figure 2a, this interaction effect was driven by differential success rates in high vs low effort trials in Block 1. After exploring cumulative success rates in each subject, we concluded that the calibration mechanism created similar reward rates between high and low effort trials starting in Block 2. Thus, we decided to repeat the analysis excluding trials from Block 1. This LMM yielded non-significant effects of Effort (b= -0.18, p=0.883), Block (b=0.00, p=1.00), and Effort and Block interaction (b= 0.39, p=0.715), suggesting that reward rates were quantitatively similar between high effort (M=78.25%, SD=5.77) and low effort (M=78.44%, SD=5.04) trials. Therefore, trials from the first block were excluded from all remaining EEG analyses (see Study 1 Methods). Further, a significant positive effect of Reward Magnitude was found (b= 0.22, p<0.000), such that participants were overall slightly more accurate on high reward trials (M=80.6%, SD=9.3%) than low reward (M=76.1%, SD=9.6%) trials. All other Effort, Reward Magnitude, and Block interaction effects were non-significant (all p-values >0.3; see Supplementary Table 1).

Behavioral indices also indicate that our effort manipulation was effective. For example, if high effort trials were truly more difficult, we would expect that participants would make less judgements in the 8-second time window in high compared to low effort trials. As expected, LMMs revealed that participants were able to make less decisions (*b*=-2.84, *p*<0.000), and decide less quickly (*b*=0.30, *p*<0.000) in high effort vs low effort trials (see Figure 2b and 2c; Supplementary Tables 2 and 3). Furthermore, a significant effect of Block suggests that participants were able to make more decisions (*b*=0.35, *p*<0.000) in later blocks. Similarly, reaction times for decisions decreased with more time on task (Block: *b*=-0.05, *p*=<0.000), however this drop was more steep for high compared to low effort trials (BlockXEffort: *b*=-0.03, *p*=0.015). These data suggest that although probability of success remained relatively fixed in Blocks 2 to 5, participants improved with practice.

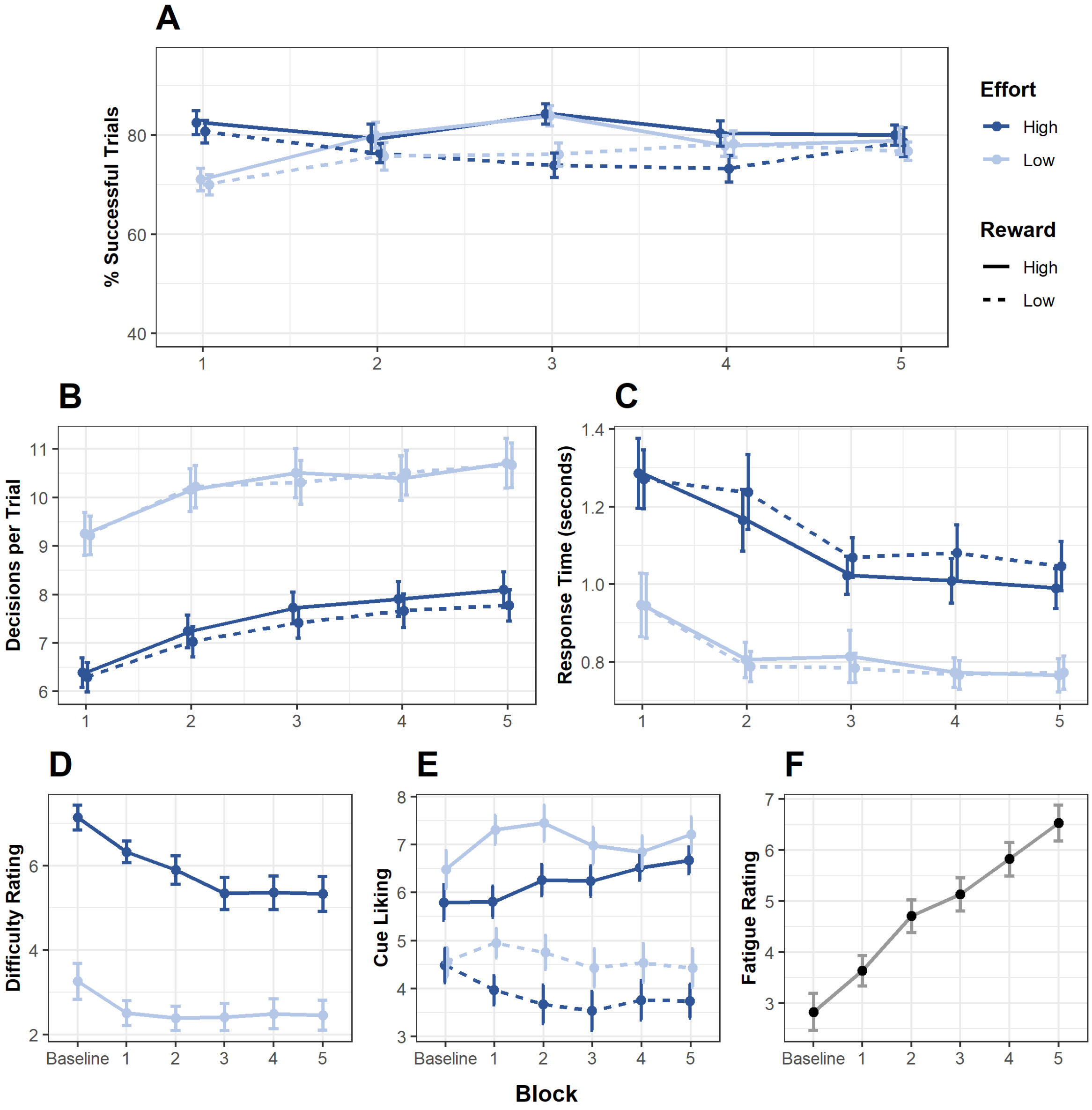

Figure 2. Effort Valuation Task adequately manipulates mental effort demands and disassociates it from reward probability. A) *Mean percentage of successful trials between high and low effort trials across the task. Success rates for low effort trials are significantly lower in Block 1 than those for high effort trials, but become statistically equivalent in later blocks.* ***B)*** *Average number of decisions made in the 8-second time window for high and low effort trials.* ***C)*** *Average response time (in seconds) for each decision made in the high vs low effort cue set-switching tasks.* ***D)*** *Subjective reports of difficulty for the 2 color (high effort) and 1 color (low effort) task; larger values indicate increased self-report difficulty ratings. Please note that in Study 1, participants were not asked to consider potential reward magnitude when giving difficulty ratings.* ***E)*** *Effect of reward and effort on subjective ratings of cue liking; higher values indicate higher appetitive responses to cue. Error bars represent the standard error of the mean.* ***F)*** *Self-report ratings of fatigue at each block; larger values indicate increased self-report fatigue ratings.*

In addition to behavioral indices, participants also rated the high effort task as more difficult than the low effort task (*b*=3.31, *p*= 0.163). Further, both high and low effort tasks were rated as less difficult as time went on (*b*=-0.218, *p*<0.000), presumably due to practice effects (Supplementary Table 4). Conversely, we were concerned that despite practice-related improvements in the task, participants would perform worse in later trials due to fatigue. The calibration method, however, was designed to mitigate the effect of fatigue on effort performance, so that reward probability would not be dependent on current fatigue state. LMMs revealed that although participants reported increased fatigue with time on task (*b*=0.73, *p*<0.000), there was no relationship between fatigue ratings and average block accuracy (*b*=-0.002, *p*=0.707; Supplementary Table 5). Thus, taken together, these findings suggest that our paradigm successfully manipulated effort demand while keeping reward probability constant throughout the task.

As shown in Figure 2e, participants also reported liking cues for high reward trials more than low reward trials (*b*=0.12, *p*<0.000) and low effort cues significantly more than high effort cues (*b*=-0.79, *p*<0.000; Supplementary Table 1). Moreover, we detected a significant interaction between Reward Magnitude and Block (*b*=0.01, *p*=0.003), indicating that high reward cues are liked more as the task progresses, while liking for low reward cues diminishes with time (see Figure E).

In the end of session questionnaire, 100% of participants correctly identified which cues signaled 5-point, 25-point, low effort, and high effort trials. Overall, participants reported having higher success rates on low (M=75.62%, SD=9.11) compared to high effort trials (M=66.72%, SD=10.46). Wilcoxon signed-rank tests revealed that participants reported being more accurate on low vs high effort trials (*Z*= -3.13, *p*= 0.002, *r*=0.58), despite the fact that real accuracy rates were not different between these conditions.

3.1.2. Cue Evaluation Phase

Repeated measures ANOVA revealed a significant effect of sensor at cue (F(1.38, 37.18)=19.82, *p*<0.000), such that theta was maximal at Fz. However, contrary to our hypothesis, we found no effect of either Reward (F(1, 27)=1.85, *p*=0.185, η_p^2 =0.0) or Effort (F(1, 27)=3.15, p=0.087, η_p^2=0.10) on cue theta (see Figure 3a and Supplementary Table 8). Bayesian rmANOVAs and pairwise t-tests were then used to quantify the evidence in favor of these null effects. Specifically, our findings were replicated by model comparison of Bayesian rmANOVAs, which identified that the data was best predicted by a model with Sensor as the sole predictor variable. Averaging across all models there is strong evidence in favor of including Sensor (BF_{incl}=16396.45) and weak evidence of including Effort, Reward Magnitude, and their interactions (all BF_{incl}<0.494; Supplementary Table 7). Nevertheless, Bayesian pairwise t-tests revealed only anecdotal evidence in favor of a null effect of

Effort (BF_{01}= 0.34) and Reward Magnitude (BF_{01}= 2.17). Thus, while FMT was generally present and no effect of Effort or Reward Magnitude were detected, we cannot conclusively deduce that FMT power was not modulated by our task features during the cue evaluation phase.

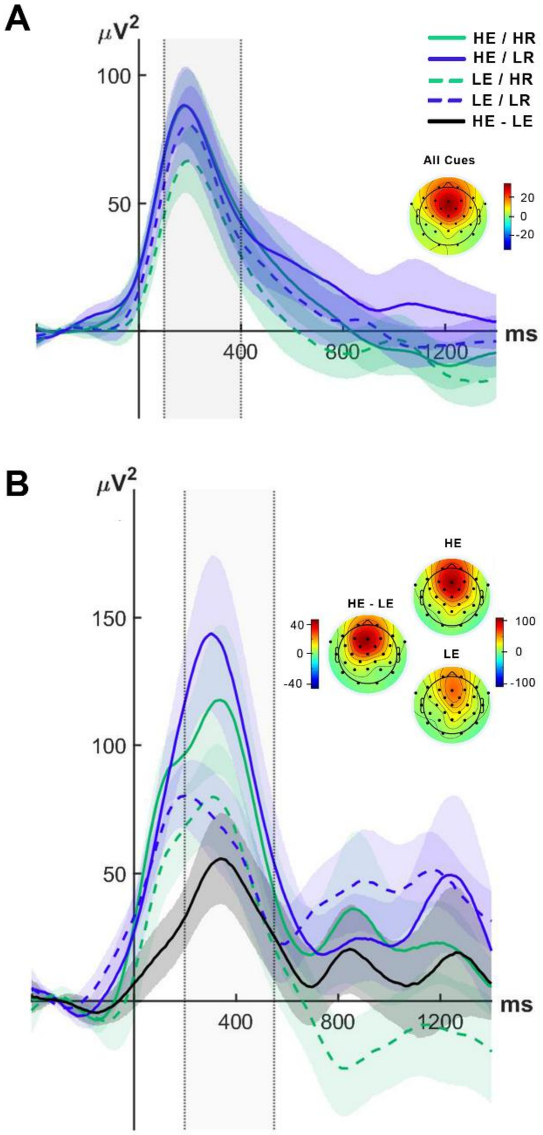

Figure 3. FMT during cue evaluation and feedback phases of the Effort Valuation Task. A) *Time course (in milliseconds) of theta power (µV2) during cue presentation. Shaded regions about the lines represent 95% confidence intervals while the shaded panel represents the time window selected for analysis. Inset shows the topographic distribution of theta power across all cues 100 to 400ms after cue onset.* ***B)*** *Time course (in milliseconds) of theta power (µV2) during correct feedback. Shaded regions about the lines represent 95% confidence intervals while the shaded panel represents the time window selected for analysis. Insets show the topographic distribution of theta power 200 to 300ms after correct feedback onset.* ***HR****=High Reward,* ***LR****=Low Reward,* ***HE****=High Effort,* ***LE****=Low Effort,* ***HE-LE****= Difference between High Effort and Low Effort conditions.*

ERP data, however, suggests that P3 signals reward magnitude of upcoming trial. Specifically, repeated-measures ANOVA detected a significant effect of Reward (F(1, 27)= 43.47, *p*<0.000, η_p^2=0.62), such that cue-P3 amplitudes were significantly larger for High Reward (M= 4.78, SD=2.34) compared to Low Reward cues (M=3.40, SD=1.87). We also detected significant effects of Sensor (F(1.30, 35.06)= 112.85, *p*<0.000, η_p^2=0.81), and a significant Reward and Sensor interaction (F(1.32, 35.58)= 18.92, *p*<0.000, η_p^2=0.41; Supplementary Table 9). As shown in Figure 4a, post-hoc pairwise t-tests indicate that cue-P3 amplitudes were significantly larger for High compared to Low Reward cues in parietal and central midline sensors (Cz: *t*(28)= 5.44, *p*<0.000, *p-adj.*<0.001; Pz: *t*(28)=6.36, *p*<0.000, *p-adj.*<0.001), but that this difference decreased as it approached frontal Fz (*t*(28)=4.14, *p*<0.001, *p-adj.*=0.11) Notably, no effect of Effort (F(1,27)=0.24, *p*=0.63, η_p^2=0.01) or effort-related interactions (EffortXReward: F(1, 27)=0.22, *p*=0.65, *ηp²*=0.01, EffortXSensor: F(1.46, 39.49)=0.12, *p*=0.82, η_p^2=0.01) were detected, suggesting that expected effort did not enhance cue-related salience.

3.1.3. Feedback Phase

In contrast to the cue evaluation phase, both FMT and P3 tracked expended effort at feedback (see Supplementary Tables 10 and 11). Specifically, repeated-measures ANOVA revealed a significant effect of Sensor (F(1.20, 32.35)=9.22, *p*=0.003, η_p^2=0.26) and an Effort and Sensor interaction (F(1.73, 46.83)=6.18, *p*=0.006, η_p^2=0.19) on FMT, such that theta power was significantly enhanced for rewards after high compared to low effort at Fz (*Z*=-2.90, *p*=0.004, *p-adj.*=0.046, *r*=0.55), but not Cz (*Z*=-2.42, *p*= 0.016, *p-adj.*=0.68, *r*=0.46) or Pz (*Z*= -0.91, *p*=0.362, *p-adj.*=0.99, *r*=0.17). Figure 3b illustrates the effect of effort on theta power at Fz.

Repeated-measures ANOVA also revealed a significant effect of Effort (F(1,27)= 31.95, *p*<0.000, η_p^2=0.54) and Reward (F(1,27)= 43.94, *p*<0.000, η_p^2=0.62) on fb-P3. As seen in Figure 4b, P3 amplitudes were larger after receiving positive feedback for High (M=13.16, SD=5.13) vs Low Effort (M=10.49, SD=4.00) and for High (M=13.10, SD=4.84) vs Low Reward (M=10.55, SD=4.23). We also detected significant effects of Sensor (F(1.26,33.99)= 35.81, *p*<0.000, η_p^2=0.57) and a significant Reward and Sensor interaction (F(1.26,34.10)= 9.95, *p*<0.000, η_p^2=0.27). Post-hoc paired t-tests revealed that although fb-P3 amplitudes were enhanced for high vs low rewards across all midline sensors, this difference was maximal at Pz (*t*(27)=8.18, *p*<0.000, *p-adj.*<0.001). Finally, we also detected a significant effect three-way interaction between Effort, Reward and Sensor (F(1.37, 36.88) = 5.269, *p*=0.018, η_p^2=0.16), however post-hoc 2x2 repeated measures ANOVAs for each sensor did not yield any significant effect of Effort and Reward (all *p*-values>0.4), thus we concluded that this interaction was driven by slight differences in the magnitude – but not direction – of reward- and effort-related effects in each sensor.

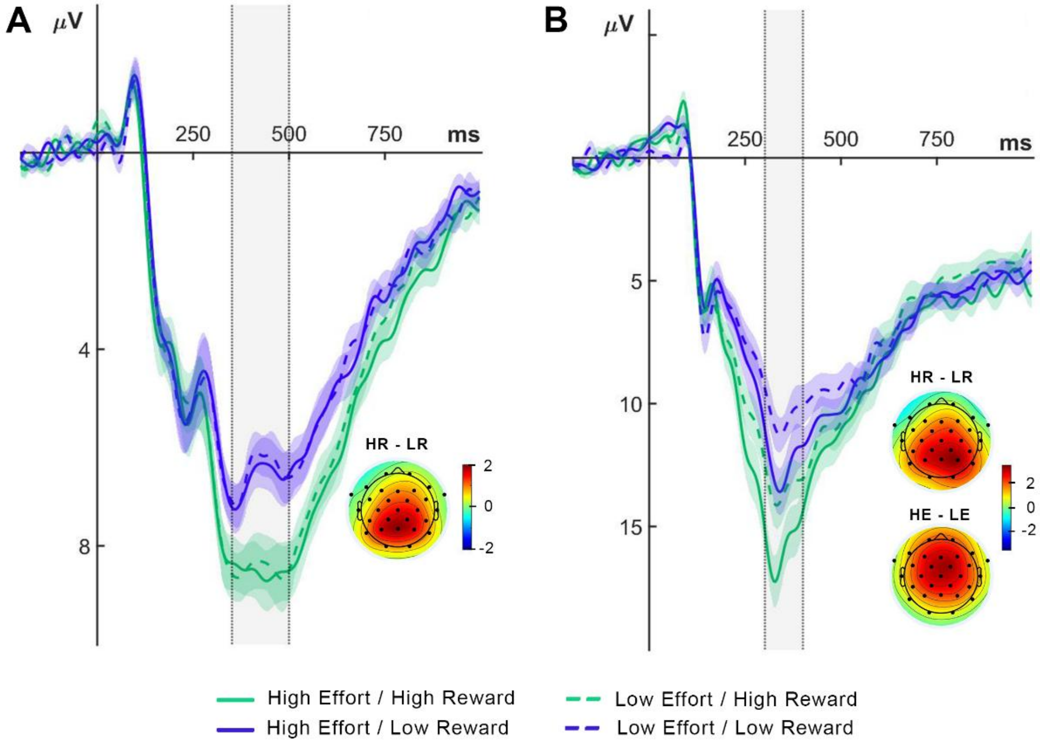

Figure 4. P3 during cue evaluation and feedback phases of the Effort Valuation task. A*) Time course of grand averages of P3 amplitudes from sensor Fz in each of the four conditions during the cue evaluation phase.* ***B)*** *Time course of grand averages of P3 amplitudes from sensor Fz in each of the four conditions during the feedback phase. Cue and feedback onset occurred at 0 ms. Shaded regions about the line reflect 95% confidence intervals using between-subjects standard error. Gray shaded regions in the ERP plots indicate the time window used for analysis. Topographic plots reflect the difference in grand averages between conditions in said time regions.* ***HR=****High Reward****, LR=****Low Reward,* ***HE=****High Effort,* ***LE=****Low Effort,* ***HR-LR=*** *Difference between High Reward and Low Reward conditions,* ***HE-LE=*** *Difference between High Effort and Low Effort conditions.*

3.2. Study 2

3.2.1. Behavioral and Self-Report Data

As in Study 1, we were interested in making sure that success rates were similar between high and low effort trials. In Study 2 however, we also needed to make sure that success rates were significantly higher for high compared to low probability trials. LMM revealed no significant effect of Effort (*b*=0.16, *p*=0.869) or Effort and Block interaction (*b*= -0.30, *p*=0.658) on success rates

(Supplementary Table 1). As shown in Figure 5a, we found a significant positive effect of Probability (*b*=36.28, *p*<0.000), such that, on average, participants correctly completed 86.8% (SD=7.2%) of high probability trials and 50.5% (SD=11.1%) of the low probability trials. Thus, we concluded that 1) the extended practice phase stabilized reward probabilities early in the Probabilistic Effort Valuation Task, thus eliminating the need to exclude trials from the EEG analyses, and 2) that success rates were substantially different between low and high probability trials, regardless of effort type.

We also detected a significant effect of effort type on number of decisions and response time, so that participants in Study 2 made more decisions (*b*=-3.43, *p*<0.000) and decided more quickly (*b*=0.27, *p*<0.000) in low compared to high effort trials (Figures 5b and c; Supplementary Tables 2 and 3). LMMs also revealed significant Block effects such that participants chose more quickly (*b*=-0.03, *p*<0.000) and made more decisions in the 8-second time window (*b*=0.27, *p*<0.000) across trial types as the task went on. However, there was a significant effect of Probability (*b*=-0.13, *p*=0.04) on number of decisions, such that lower probability of succeeding actually invigorated effortful responding instead of diminishing it.

The high effort task was also rated as more difficult than the low effort task (*b*=2.42, *p*<0.000; see Figure 5d and Supplementary Table 4). Probability of success also impacted subjective ratings of difficulty, such that low probability tasks were rated as more difficult than high probability tasks (*b*=-1.53, *p*=<0.000). We also detected a significant Probability and Block interaction (*b*= -0.23, *p*=0.001), such that high and low probability trials were rated as equally difficult at baseline (before participants experienced the differential success rates), but low probability trials were reported as increasingly effortful throughout the task. We were also interested in knowing if participants were accurately perceiving their probability of success. As expected, participants also reported feeling more likely to succeed in high vs low probability trials (*b*= 1.45, *p*<0.000), but only after the baseline period as there were no differences in success probability during the calibration (see Figure 5e). Despite having equal success rates across both levels of effort, LMM revealed that participants reported feeling less likely to successfully complete high effort trials than low effort trials (*b*=-1.43, *p*<0.000; see Supplementary Table 7). Subjective ratings of probability of success also significantly decreased with time on task (*b*=-0.18, *p*<0.000). This decrease was steeper for low probability (*b*=0.28, *p*<0.000) and low effort trials (*b*=0.12, *p*=0.011).

As in Study 1, participants reported feeling more fatigued with time on task (*b*=0.69, *p*<0.000; see Figure 5f and Supplementary Table 5), but no relationship between fatigue ratings and average block accuracy was detected (*b*=-0.004, *p*=0.06). Thus, taken together, these findings suggest that our paradigm successfully manipulated effort demand while keeping reward probability constant throughout the task.

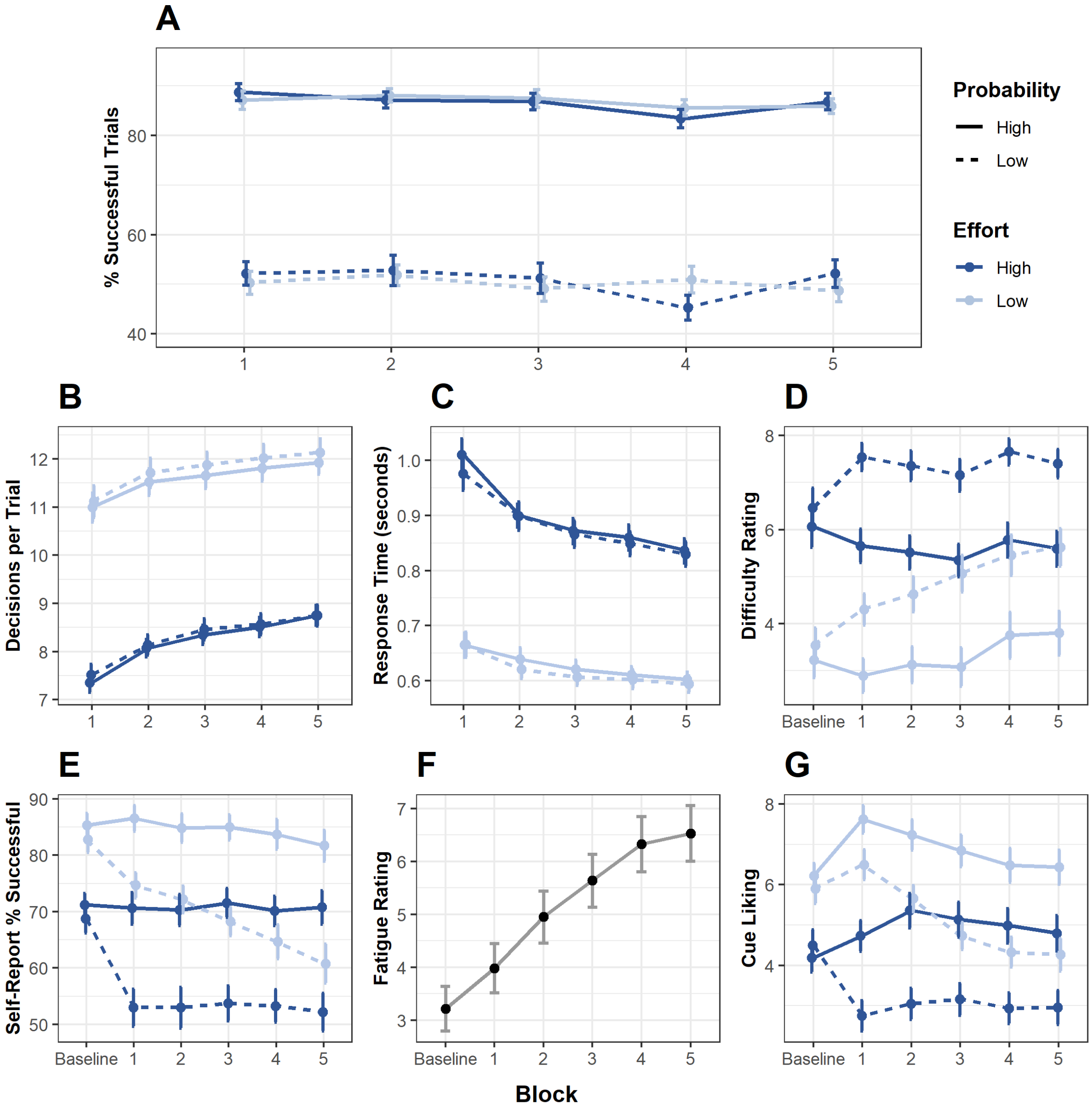

Figure 5. Probabilistic Effort Valuation Task adequately manipulates mental effort, but probability of success modulates subjective ratings of difficulty and liking. A) *Mean percentage of successful trials between high and low probability trials across the task.* ***B)*** *Average number of decisions made in the 8-second time window for the different trial types across the task. Participants made more decisions in the high vs low effort trials, and slightly more decisions in low vs high probability trials.* ***C)*** *Effect of effort on average response time (in seconds) for each decision made in the different trial types.* ***D)*** *Effect of effort and probability of success on subjective reports of task difficulty; larger values indicate increased self-report difficulty.* ***E)*** *Effect of effort and probability of success on subjective estimates of the percentage of trials (based on each EffortXProbability condition) that were successfully completed in a given block.* ***F)*** *Average self-report ratings of fatigue at each block; larger values indicate increased self-report ratings of fatigue.* ***G)*** *Effect of probability and effort on subjective ratings of cue liking; higher values indicate higher appetitive responses to cue. Error bars represent the standard error of the mean.*

However, unlike Study 1, cue liking ratings in Study 2 generally decreased with time on task (*b*=-0.16, *p*=0.000; see Supplementary Table 6). Probability of successfully completing the task also modulated cue liking, so that high probability cues were generally liked more than low probability cues (*b*=1.61, *p*=.137). We also detected a significant Probability and Block interaction (*b*=0.34, *p*<0.000). Figure 5f illustrates how, despite being explicitly told which cues indicated lower vs higher probabilities of success before baseline measurement, participants initially based cue liking on effort demands alone. With more time on task however, liking for cues indicating lower success ratings began to decline. Finally, 100% of participants correctly identified which cues were associated with high and low effort trials in the end of session questionnaire.

3.2.2. Cue Evaluation Phase

ERP and oscillatory patterns in Study 2 are qualitatively similar to those in Study 1. With respect to cue-related theta, repeated measures ANOVA detected a significant effect of sensor at F(1.35, 41.85)=24.85, *p*<0.000, η_p^2=0.42), but again no effects related to Effort (F(1, 31)= 0.007, *p*=0.933, η_p^2<0.00), Probability (F(1, 31)=0.68, *p*=0.417, ηp^2=0.02), or their interactions (Supplementary Table 12). Figure 6a shows cue-related theta power activation. Bayesian methods were again used to quantify the evidence in favor of these null effects. Bayesian rmANOVA confirmed that the data best supports a model with only a main effect of Sensor (BF_{10}= 38828.24). Averaging across all models there is strong evidence in favor of including Sensor (BF_{incl}= 413136.71) and weak evidence of including Effort, Reward Magnitude, and their interactions (all BF_{incl}<0.169). Bayesian pairwise t-tests revealed strong evidence in favor of a null effect of Effort (BF_{01}= 12.35) and moderate evidence in favor of a null effect of Probability (BF_{01}= 5.13). Thus, we conclude that although FMT was generally present during the cue evaluation phase, it was not modulated by our task manipulations.

Cue-P3 however showed a significant effect of Probability (F(1, 30)= 17.40, *p*=0.001, η_p^2=0.37), such that cue-P3 amplitudes were significantly greater for Low Probability (M=2.47, SD=2.67) compared to High Probability cues (M=1.82, SD=2.26; see Figure 7a and Supplementary Table 13). We also detected significant effects of Sensor (F(1.23, 36.78)= 136.51, *p*<0.000, η_p^2=0.82), and a significant Probability and Sensor interaction (F(1.27, 38.21)= 11.81, *p*<0.001, η_p^2=0.28). Post-hoc Wilcoxon signed-rank tests and pairwise t-tests indicated that cue-P3 amplitudes were significantly larger for Low compared to High Probability cues in Pz (Pz: *Z*= -4.31, *p*<0.000, *p-adj.*<0.001, *r*=0.76), but that this difference diminished in more frontal sensors (Fz: t(31)=-2.51, *p*=0.017, *p-adj.*=0.73; Cz:

Z= -3.12, *p*=0.002, *p-adj.*=0.053, *r*=0.55). Cue-P3 was not modulated by Effort (F(1,30)=0.44, *p*=0.51, ηp^2=0.01) or effort-related interactions (EffortXProbability: F(1, 30)=0.02, *p*=0.90, η_p^2<0.00, EffortXSensor: F(1.22, 36.63)=0.12, *p*=0.79, η_p^2=0.28), replicating previous results from Study 1.

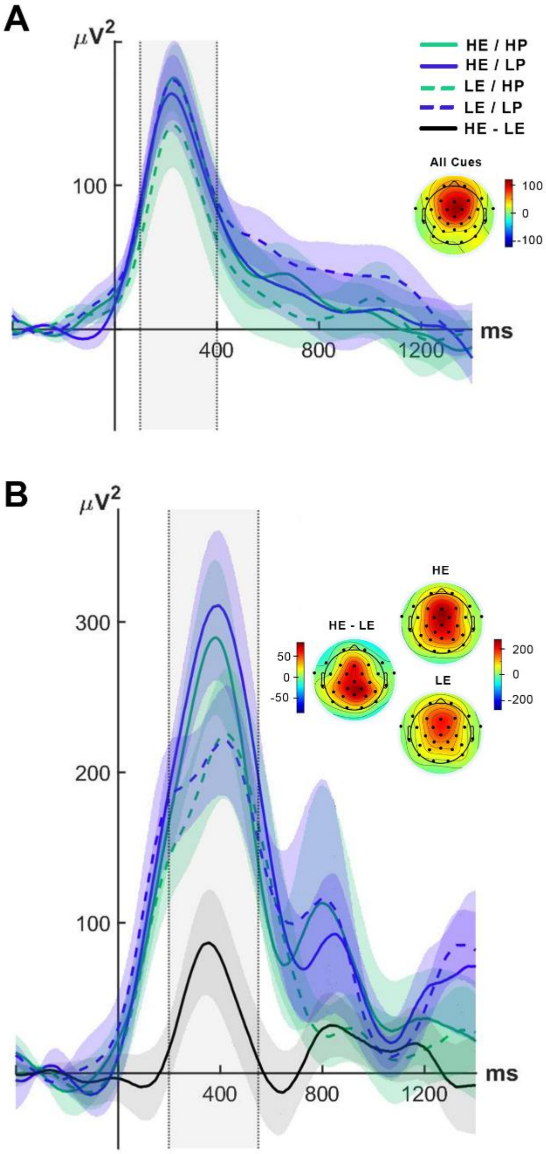

Figure 6. FMT during cue evaluation and feedback phases of the Probabilistic Effort Valuation Task. A) *Time course (in milliseconds) of theta power (µV2) during cue presentation. Shaded regions about the lines represent 95% confidence intervals while the shaded panel represents the time window selected for analysis. Inset shows the topographic distribution of theta power across all cues 100 to 400ms after cue onset.* ***B)*** *Time course (in milliseconds) of theta power (µV2) during correct feedback. Shaded regions about the lines represent 95% confidence intervals while the shaded panel represents the time window selected for analysis. Insets show the topographic distribution of theta power 200 to 300ms after correct feedback onset****. HP=****High Probability,* ***LP=****Low Probability,* ***HE=****High Effort,* ***LE=****Low Effort,* ***HE-LE=*** *Difference between High Effort and Low Effort conditions.*

3.2.3. Feedback Phase

In Study 2, repeated measures ANOVA revealed a main effect of Sensor (F(1, 31)=11.59, p=0.001, η_p^2=0.27) and Effort in FMT (F(1, 31)=11.594*,* p=0.003, η_p^2=0.272), such that FMT was significantly more enhanced across all electrodes for rewards received after exerting High (M=228.03, SD=194.66) compared to Low Effort (M=159.65, SD=156.45). Figure 6b displays the effect of effort on FMT power at feedback (see Supplementary Table 14).

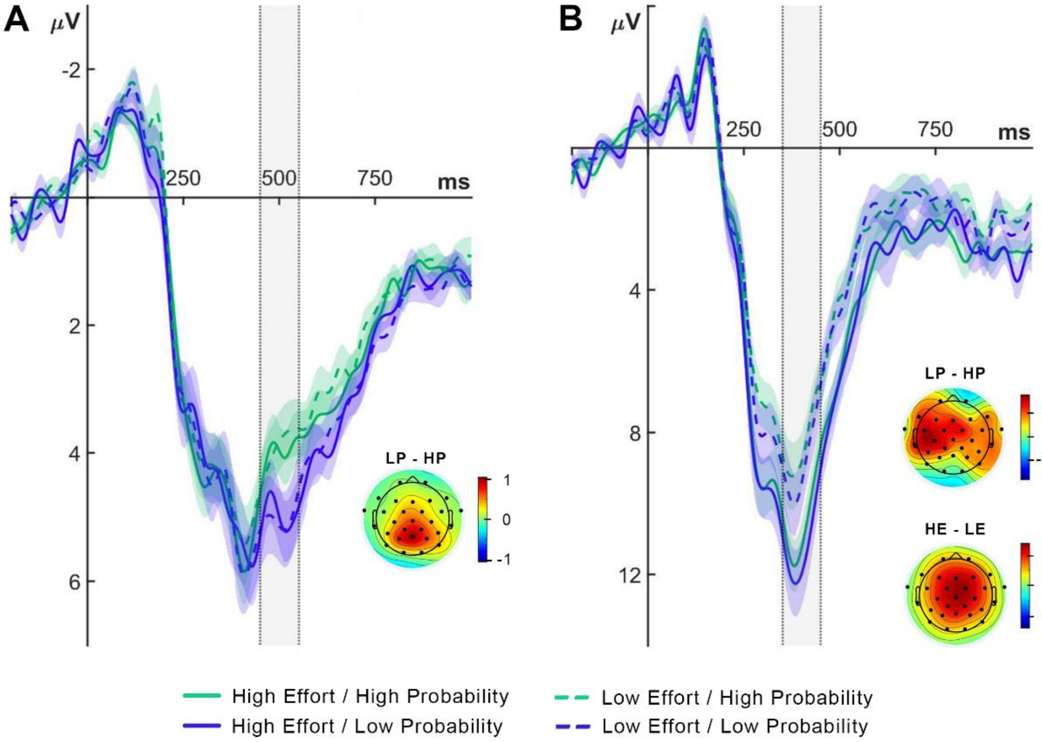

Figure 7. P3 during cue evaluation and feedback phases of the Probabilistic Effort Valuation task. A) *Time course of grand averages of P3 amplitudes from sensor Fz in each of the four conditions during the cue evaluation phase.* ***B)*** *Time course of grand averages of P3 amplitudes from sensor Fz in each of the four conditions during the feedback phase. Cue and feedback onset occurred at 0 ms. Shaded regions about the line reflect 95% confidence intervals using between-subjects standard error. Gray shaded regions in the ERP plots indicate the time window used for analysis. Topographic plots reflect the difference in grand averages between conditions in said time regions.* ***HP=****High Probability,* ***LR=****Low Probability,* ***HE=****High Effort,* ***LE=****Low Effort,* ***LP-HP=*** *Difference between Low Probability and High Probability conditions,* ***HE-LE=*** *Difference between High Effort and Low Effort conditions.*

Similarly, repeated-measures ANOVA detected a significant main effect of Effort (F(1, 31)=73.96, p<0.000, η_p^2=0.71), such that fb-P3 amplitudes were significantly greater for rewards after completing High Effort (M=10.89, SD=4.30) compared to a Low Effort trials (M=8. 31, SD=4.25; see

Figure 7b and Supplementary Table 15). The data also revealed a significant main effect of Probability (F(1, 31)=4.78, p=0.036, η_p^2=0.13) and Sensor (F(1.37, 42.33)=8.95, p<0.000, η_p^2=0.22). Fb-P3 amplitudes were larger when receiving rewards from Low Probability (M=8. 92, SD=4.49) compared to High Probability trials (M=9.59, SD=4.62).

4. Discussion

Most goal-directed behavior is mentally costly. While previous studies have elucidated the neural correlates and temporal dynamics of effort-based reward valuation, many relied on paradigms that did not control for unequal reward probabilities between effort conditions and focused their analyses on either early or late phases of reward processing. The current studies aimed to explore the role of the temporal dynamics of effort-based reward in the absence of probability discounting. To this end, we explored the response patterns of EEG indices of cognitive control and reward processing in the mPFC (FMT) and of incentive salience (P3). Across two studies, we were able to show that our novel paradigm experimentally isolated effort demands from reward probability. EEG data revealed that FMT power was generally enhanced during cue evaluation but did not selectively track upcoming effort demands, reward magnitude or reward probability. At feedback, however, FMT power was sensitive to expended effort, but did not track other reward features. By contrast, during cue presentation, P3 was sensitive to reward magnitude and reward probability, but not effort. At feedback however, P3 amplitudes scaled positively with effort demands, suggesting that expended effort demands increased the salience of reward, but only during the consummatory phase. These findings suggest that when reward probabilities are equal between high and low effort conditions, the mPFC does not track net value of prospective effort-based rewards and that expended effort enhances, instead of discounts, the salience of reward at feedback.

Although the mPFC has been repeatedly implicated in the signaling of effort-based rewards, we did not find any relationship between mPFC function – putatively measured by FMT – and prospective effort demands during the cue evaluation phase. One plausible explanation for this is that the mPFC is only recruited when the environment requires a comparison between more than one option. Previous studies have observed that BOLD in the mPFC/ACC scales positively with effort demands and negatively with the subjective value of effort-based rewards (Chong et al., 2017; Klein-Flügge et al., 2016; Massar et al., 2015; Prévost et al., 2010; Skvortsova et al., 2014). However, these studies used paradigms that required participants to decide between two effort-based rewards, making it difficult to disentangle whether the ACC was signaling net value or exerting cognitive control to facilitate decision-making and action selection. Notably, studies that have experimentally isolated decision difficulty have shown that mPFC/ACC activity scales positively with decision difficulty and single offer net value (Westbrook et al., 2019), but not effort demand (Hogan et al., 2019) or foraging value (Shenhav et al., 2014). Similarly, increased phasic FMT was associated with greater probability of selecting the high-effort choice in physical effort-based reward task, but only in difficult decision trials (Umemoto et al., 2022). The two studies that used paradigms without choice reported mixed results: only one reported that ACC activity scaled with net value (Croxson et al., 2009) and neither detected a relationship between ACC BOLD and prospective effort (Croxson et al., 2009; Stoppel et al., 2011). In our studies, FMT was enhanced during cue evaluation, but was not sensitive to net value or any of the features of prospective effortful reward. The absence of a net value signal in cue-FMT, however, cannot be attributed to a lack of saliency in our effort or reward manipulations. In fact, across both of our studies, increased effort demands attenuated self-report cue liking, suggesting that prospective effort was indeed integrated into estimates of subjective value. Nevertheless, in the absence of alternative options and the need for action selection, FMT did not signal subjective value. Thus, our findings indirectly lend support to a growing body of evidence that suggests that the mPFC/ACC tracks cognitive control requirements of weighing options (Kolling et al., 2016) or guiding action selection (Holroyd & McClure, 2015) rather than net value per se.

At feedback, however, FMT selectively tracked expended effort, but not reward magnitude or probability. Our findings are at odds with previous studies that have shown that FRN/RewP – ERPs which are also produced in the ACC (Holroyd & Umemoto, 2016; Walsh & Anderson, 2012) – are sensitive to reward magnitude and that this effect is potentiated by effort expenditure (Bogdanov et al., 2022; Wang et al., 2017; Yi et al., 2020). However, it is unclear to what degree FRN/RewP findings are generalizable to FMT activity, since reward magnitude and expectancy have been shown to affect FRN/RewP and FMT differently (Paul et al., 2020), which suggests they track partially separable neurocognitive processes. Conversely, our present results are consistent with previous findings that report augmented BOLD activity in the ACC for increased attentional and cognitive effort demands, but not integrated net value, at reward feedback (Hernandez Lallement et al., 2014; Stoppel et al., 2011). Our findings are also in line with proposals that the mPFC/dACC responds selectively to the value of events that are specifically relevant to the allocation of control (Shenhav et al., 2013). In our paradigm, the difficulty of the effort demands was continuously calibrated through the task. Because reward magnitude and probability of successful outcome were fixed, feedback was only informative about the degree to which previously expended effortful control adequately met the effort demand for that specific trial. Thus, FMT power in positive feedback could feasibly reflect performance monitoring or action value updating, both functions that have been previously attributed to theta band oscillations generated in the ACC (Luft, 2014; Ullsperger et al., 2014). Alternatively, self-report ratings in Study 2 suggest that despite equal reward probabilities across effort conditions, participants generally perceived having a higher probability of success on low compared to high effort trials. Since FMT has been shown to index unsigned prediction errors and unexpected outcomes (Cavanagh et al., 2012; Mas-Herrero & Marco-Pallarés, 2014; Rawls et al., 2020), one possible explanation for enhanced FMT at high effort feedback could be that rewards obtained through more effort are perceived as less likely and therefore unexpected. However, if this were the case, we would expect theta power to have been potentiated for reward feedback in low probability trials as well. To conclusively test the role of theta in prediction error and performance monitoring, future experiments should use paradigms that manipulate reward likelihood independently of success rate and designs that are adequately powered to analyze responses to unsuccessful trials.

Our findings also show that FMT signals are distinct and separable from signals of incentive salience (cue-P3). Unlike FMT, cue-P3 amplitudes were sensitive to prospective reward magnitude and probability. This is in line with a vast literature showing a robust relationship between cue-P3 and cued incentives and event likelihood, leading some to propose that cue-P3 reflects motivated attention towards salient stimuli (see Glazer et al., 2018 for an extensive review). From this perspective, we can conclude that more motivational salience is attributed to high magnitude and low probability rewards, but when reward rate does not vary as a function of effort demand, this salience signal was not modulated as a function of prospective effort. At feedback, however, increased effort demand enhanced P3 responses for positive outcomes, suggesting that expended effort increased the incentive salience of received rewards. These findings are in line with a growing body of work that suggests that exerted effort amplifies reward saliency signals in human (Ma et al., 2014; Schevernels et al., 2014, 2016; Wang et al., 2017; M. Zhang & Zheng, 2022) and non-human primates (Tanaka et al., 2019) and provide further support to the perspective that more value is assigned to rewards that are earned through higher effort costs (for a full review see Inzlicht et al., 2018). Furthermore, unlike previous studies, the tasks used in the current experiments equalized performance outcomes and reward likelihood between effort conditions. Therefore, we can conclude that effort-related differences in fb-P3 were driven primarily by expended effort and not by other factors, such as reward expectancy or likelihood, which modulate P3 amplitudes (Hajcak et al., 2005, 2007; Wu & Zhou, 2009).

Despite the strengths of our paradigm, there were some limitations to the design. As stated earlier, analyses were limited to successful trials due to the relatively high success rate (achieved via the calibration), thus we could not explore the role of FMT in tracking performance in the context of failure or non-reward. Second, the mPFC is a highly heterogenous region that has been linked to a variety of cognitive control and outcome-processing functions (Clithero & Rangel, 2014; Domenech & Koechlin, 2015; Vassena et al., 2017). Although the high temporal resolution of EEG was useful for the purposes of our study, combined fMRI-EEG or magnetoencephalography would be well-suited for exploring how the specific subregions of the mPFC contribute to effort-based reward processing.

In summary, in two studies we showed that in the absence of alternative options/choice and different reward probability rates, the FMT did not track features of prospective effort-based reward. Instead, FMT power was only enhanced for successful high effort outcomes, which suggests that the mPFC plays a more general performance-monitoring role as opposed to tracking pure cognitive control demands or integrated net value representations. Further, we showed that P3 amplitudes were sensitive to reward magnitude and probability, but not effort, during cue evaluation and that effort enhanced P3 amplitudes to reward at feedback, again suggesting that effort increased the incentive salience of a reward. Understanding how effort-based reward is processed is crucial for understanding psychopathological conditions marked by altered reward motivation, such as Parkinson's disease (Chong et al., 2015; McGuigan et al., 2019), depression (Hammar et al., 2011; Treadway et al., 2012), schizophrenia (Barch et al., 2014; Cooper et al., 2019), substance use disorders (Leventhal et al., 2008), and attention-deficit/hyperactivity disorder (Egeland et al., 2010). However, these states of amotivation can be caused by deficits in one or several components of effort-based reward processing, such as reduced salience of prospective and obtained rewards, dysfunctional weighing of prospective cognitive control demands, misallocation of control, and/or deficits in performance monitoring. Thus, novel paradigms are needed to reduce the influence of confounds when investigating the key processing stages effort-based reward. This study paves the way towards that goal.

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Declarations of interest:

None.

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