

Cognitive effort exertion enhances electrophysiological responses to rewarding outcomes

Mario Bogdanov*¹, H el ena Renault*¹, Sophia LoParco², Anna Weinberg¹, A. Ross Otto¹

¹ Department of Psychology, McGill University, Canada;

² Integrated Program in Neuroscience, McGill University, Canada

* These authors contributed equally to the study

Running title: Cognitive effort increases reward valuation

Word count: Abstract – 174

Main text – 9.521

Figures: 7

Tables: 3

Corresponding author:

Mario Bogdanov, PhD

Department of Psychology

McGill University

2001 McGill College Avenue

Montreal, QC H3A 1G1

Canada

Email: Mario.Bogdanov@mail.mcgill.ca

Abstract

Recent work has highlighted neural mechanisms underlying cognitive effort-related discounting of anticipated rewards. However, findings on whether effort exertion alters the subjective value of obtained rewards are inconsistent. Here, we provide a more nuanced account of how cognitive effort affects subsequent reward processing in a novel task designed to assess effort-induced modulations of the Reward Positivity (RewP), an event-related potential indexing reward-related neural activity. We found that neural responses to both gains and losses were significantly elevated in trials requiring more versus less cognitive effort. Moreover, time-frequency analysis revealed that these effects were mirrored in gain-related delta, but not in loss-related theta band activity, suggesting that people ascribed more value to high-effort outcomes. In addition, we also explored whether individual differences in behavioral effort discounting rates and reward sensitivity in absence of effort may affect the relationship between effort exertion and subsequent reward processing. Together, our findings provide evidence that cognitive effort exertion can increase the subjective value of subsequent outcomes, and that this effect may primarily rely on modulations of delta band activity.

Keywords: Mental Effort, Effort Discounting, Reward Positivity, Value-based Decision-making, Reward Processing

Owing to the limited-capacity nature of human information-processing, we tend only to engage in cognitively demanding activity when, all else being equal, it is worthwhile (Kool and Botvinick 2018). To this point, recent influential theoretical accounts of effort-based decision-making posit that the degree to which individuals choose to engage in demanding behavior in a given situation is determined by a cost-benefit analysis that weighs the potential rewards conferred by effort exertion against its costs (Shenhav et al. 2013, 2017; Westbrook and Braver 2015; Otto and Daw 2019). A critical assumption of this neuroeconomic framework is the notion that exertion—or intensification—of cognitive control, much like exerting physical force, is subjectively effortful and inherently aversive to the individual (Kool et al. 2013; Kool and Botvinick 2018; Vogel et al. 2020). Demonstrating this point, a recent and growing literature suggests that individuals are strongly motivated to avoid spending cognitive effort when given the choice (Kool et al. 2010), especially in circumstances when cognitive resources are sparse, for example in healthy aging or under stress (Westbrook et al. 2013; Bogdanov et al. 2021).

While it is well known that larger reward incentives can increase effort investment, consequently improving performance in a range of cognitive tasks (Small et al. 2005; Botvinick and Braver 2015; Otto and Vassena 2021), a key prediction of the cost-benefit account of cognitive control allocation is that motivating effects of rewards can be offset by task demands, that is, for a fixed level of reward incentives, a higher level of control demand reduces the net utility of effort exertion (Shenhav et al. 2013). More specifically, it is thought that, when deciding whether to exert effort or not, anticipated rewards requiring large amounts of cognitive effort to obtain are *discounted* and thus less attractive than smaller rewards that require less effort (Westbrook and Braver 2015). In support of this hypothesis, several studies have found that individuals will forego higher payouts to reduce demand across different cognitive task domains, including working memory and attention (Westbrook et al. 2013; Chong et al. 2017; McGuigan et al. 2019).

At the same time, a separate line of work suggests that the level of cognitive effort invested may augment—rather than discount—the subjective value of a reward conferred by effort exertion. For example, people appear to value outcomes more positively when they are received after having (actually or hypothetically) invested more work in a given task, compared to outcomes obtained with less effort (Arkes and Blumer 1985; Muehlbacher and Kirchler 2009; Norton et al. 2012; Sweis et al. 2018; Yan and Otto 2020). In other words, under different circumstances, effort appears to differentially affect distinct phases of reward processing: it reduces the value of anticipated rewards but also might (retrospectively) increase the value of obtained rewards (Berridge et al. 2009; Inzlicht et al. 2018).

Neuroscientific studies in humans and animals have further elucidated the interplay between effort and reward, suggesting that effort-based decision-making critically depends on striatal and mesolimbic dopaminergic projections to a large network of cortical and subcortical regions frequently implicated in executive control and reward processing (Botvinick and Braver 2015; Massar et al. 2015; Chong et al. 2017; Soutschek and Tobler 2018; Westbrook et al. 2019, 2020). Most notably, a body of fMRI work reveals that reward-related cognitive effort modulations, as well as effort-related discounting of anticipated rewards are linked to activity in the dorsal anterior cingulate cortex (dACC), which is thought to play a crucial role in detecting task demand and integrating effort and reward information by computing an “expected value of control” that ultimately determines whether a goal is worth pursuing and how much cognitive control should be applied to achieve it (Shenhav et al. 2017). Similarly, other fMRI studies find that activity in the ventral striatum as well as in the ventromedial prefrontal cortex (vmPFC), which is thought to reflect the subjective value of a chosen option, decreases with task demand and increases with reward on offer (Crosson et al. 2009; Vassena et al. 2014; Chong et al. 2017; Westbrook et al. 2019). Furthermore, studies using non-invasive brain stimulation techniques demonstrate that individual effort discounting behavior can be up- or down-regulated by increasing the neural excitability of the

frontopolar cortex (FPC) or decreasing neural excitability in the dorsolateral prefrontal cortex (dlPFC), respectively (Soutschek et al. 2018; Soutschek and Tobler 2020).

Importantly, while this body of work has focused on effort-reward computations at the anticipatory stage of effort-based decision-making—that is, at the time of choice, prior to reward outcomes—the effects of prior effort exertion on reward valuation at the time of outcome delivery are less consistent. For example, an fMRI study by Botvinick and colleagues (2009) found reduced BOLD-activity in the nucleus accumbens (NAcc) accompanying monetary rewards that followed high versus low levels of mental effort expenditure, suggesting that participants valued rewards less when they had to work harder for them. In contrast, more recent studies reported increased activity in the NAcc in response to rewards following high degrees of effort exertion (Hernandez Lallement et al. 2014; Dobryakova et al. 2017). Relatedly, a line of electroencephalogram (EEG) work has investigated how effort exertion modulates the Reward Positivity (RewP), a fronto-centrally distributed event-related potential (ERP) component that peaks between 250-350ms after outcome presentation and that is larger (i.e., more positive) following feedback indicating gains—e.g., monetary rewards or positive performance feedback—compared to feedback indicating losses (Foti et al. 2015; Proudfit 2015; Ethridge and Weinberg 2018). In one study, Ma and colleagues (2014) found larger RewPs toward monetary gains after completing more demanding versus simpler mental arithmetic problems but not toward neutral (no-win) feedback, suggesting that rewards received after exerting more effort were considered more valuable. Similarly, studies employing an effortful task-switching paradigm found that self-reported effort exertion and participants' level of perceived control over outcomes were associated with larger differences in ERP amplitudes between gain versus loss feedback in the time-window of the RewP (Harmon-Jones, Clarke, et al. 2020; Harmon-Jones, Willoughby, et al. 2020; Yi et al. 2020). Finally, echoing the imaging results of Botvinick et al. (2009), a

recent study found evidence for an attenuated, rather than potentiated, RewP responses after increased (physical) effort exertion (Bowyer et al. 2021).

In light of these inconsistent findings, here we consider what might give rise to these disparities in the observed effects of effort exertion on reward evaluation—specifically, the RewP. Putting aside more obvious differences between studies—such as the effort domain of interest (i.e., cognitive or physical), previous investigations vary considerably in the nuances of their experimental designs, such as the type of reward (monetary versus non-monetary), whether gains were contrasted with losses or simply with omitted rewards, the timing with which reward feedback information is delivered, and whether reward feedback is separated from performance feedback or is delivered concurrently. Accordingly, the primary aim of this study was to investigate whether the level of cognitive effort spent—on a well-characterized task which parametrically manipulates effort expenditure, mirroring paradigms used in cognitive effort and RewP research—increases or decreases the RewP magnitude in response to subsequent rewards resulting from effort outlay.

Further, recent work demonstrates that the magnitude of the RewP is associated with power in two frequency bands—the delta (1 – 4Hz) and theta frequency ranges (4 – 8Hz), potentially reflecting distinct cognitive processes (Weinberg et al. 2021). Specifically, time-frequency decompositions have previously uncovered increases in delta power following positive (gains) compared to negative outcomes (losses), and increases in theta power following negative compared to positive outcomes (Bernat et al. 2015; Foti et al. 2015). Therefore, we also sought to examine how previous effort expenditure affects spectral power in these two frequency bands, affording a more detailed examination of the mechanisms involved in the hypothesized effort-RewP relationship.

Finally, we considered the possibility that variability in earlier studies of effort-related RewP modulations might stem from individual differences in general reward responsivity and/or the degree of aversion toward engaging in demanding cognitive activities (Treadway,

Bossaller, et al. 2012; Treadway, Buckholtz, et al. 2012; Sandra and Otto 2018; Yan and Otto 2020; da Silva Castanheira et al. 2021). Using a cross-task individual differences approach, we sought to further explore how 1) baseline reward responsivity (that is, the RewP magnitude in absence of effort manipulations), and 2) individuals' tendency to discount anticipated rewards by task demands might predict RewPs, and— as gain-related delta activity has been found to be a stronger predictor of individual differences in reward sensitivity than the standard RewP (Foti et al. 2015; Ethridge et al. 2020, 2021; Weinberg et al. 2021)— spectral power following low versus high levels of cognitive effort exertion.

To do this, we first measured participants' baseline RewP responses— in the absence of any cognitive effort outlay—in the Doors task, a simple guessing game (Figure 1), commonly used to evoke the RewP (Weinberg et al. 2012, 2014; Proudfit 2015; Ethridge et al. 2021). Here, we expected to find larger ERP amplitudes following monetary gain compared to loss trials. We then measured behavioral indices of individuals' effort valuation using an established cognitive effort discounting task (EDT; Figure 2), in which participants were required to monitor rapid serial visual presentation (RSVP) letter streams for a target stimulus (McGuigan et al. 2019). In the RSVP, effort level is operationalized as the number of concurrent streams of stimuli that participants need to pay attention to. After familiarization with each demand level (*reinforcement phase*), participants made choices to perform low-effort/low-reward trials versus high-effort/high-reward trials, which permitted measurement of participants' effort discounting rates (*choice phase*). Finally, we used EEG to examine how effort outlay tied to reward receipt affects the RewP. Here we introduce a novel *effort-reward phase* to the EDT, in which participants were instructed to complete either low- or high-effort RSVP trials (i.e., monitoring a single stream versus four concurrent streams) and successful performance of each RSVP trial led to feedback corresponding to either a monetary gain or a loss with chance (50%) probability.

Following previous findings (Westbrook et al. 2013; Chong et al. 2018; McGuigan et al. 2019; Hofmans et al. 2020), we hypothesized that we would observe substantial effort discounting in the choice phase of the EDT, such that participants would exhibit a decreased preference for the high-effort/high-reward task as the effort level on offer increased, and a greater preference for the high-effort/high-reward task as the reward on offer increased. On the basis of the limited existing behavioral and electrophysiological evidence in the domain of cognitive effort (Ma et al. 2014; Harmon-Jones, Clarke, et al. 2020; Harmon-Jones, Willoughby, et al. 2020; Yi et al. 2020), we expected larger RewP amplitudes in the effort-reward phase of the EDT in high- versus low-effort trials. This effect may be specific for gain compared to loss trials (Ma et al. 2014). As outlined above, recent findings argue for specific contributions of delta and theta band activity to processing gain and loss feedback, respectively (Bernat et al. 2011; Foti et al. 2015; Weinberg et al. 2021), which led us to predict that effort exertion may specifically affect gain-related delta but not theta activity. Finally, we reasoned that individual differences in both behavioral effort discounting and baseline reward responsiveness—vis-à-vis the magnitude of the canonical RewP assessed in the Doors task—might predict the magnitude of effort-induced RewP modulations in the effort-reward phase of the EDT, however, as these analyses were exploratory we did not have specific directional predictions for these relationships.

Materials and Methods

Participants and Experimental Design

We recruited 54 young, healthy participants recruited from the McGill University community. Two participants were excluded because they did not complete all tasks due to technical difficulties. The final sample consisted of 52 participants who underwent all experimental tasks in a fully within-subject design. Of the 50 participants who reported their age and gender, 62% were female, with ages ranging between 18 and 31 years old ($M = 22.85$, $SD = 3.04$). Each participant received \$25 CAD as compensation and an additional

fixed reward of \$5 for their performance in the Doors and effort discounting tasks (i.e., \$2.50 per task). Written informed consent was obtained from every participant at the beginning of the experiment. All procedures were in accordance with the Declaration of Helsinki and were approved by McGill University's Research Ethics Board.

Questionnaires

Participants completed a series of online questionnaires one day prior to their scheduled testing session, including the Mood and Anxiety Questionnaire (MASQ; Wardenaar et al. 2010), the Temporal Experience of Pleasure Scale (TEPS; Gard et al. 2006), the Ruminative Response Scale (RRS; Treynor et al. 2003), the Perceived Stress Scale (PSS, Cohen et al. 1994) and the Need for Cognition scale (NFC; Cacioppo et al. 1984). Correlational results of these measures and our main dependent variables are reported in the supplementary material.

Procedure

Upon arriving at the lab, participants gave informed consent and completed the reinforcement and choice phases of an effort discounting task (EDT; see below) on a computer. EEG was then recorded during the subsequent Doors Task (see below) and the effort-reward phase of the EDT. Finally, participants were asked to rate on a scale from 1 to 10 how effortful they perceived each demand level in the EDT to be. The Doors task was programmed in Presentation software (version 18.1, Neurobehavioral Systems, Inc., Berkeley, CA), the EDT was programmed using PsychoPy (Peirce 2007). Each testing session lasted for approximately two hours.

Experimental tasks

Doors Task

The Doors task, a forced-choice guessing task in which participants win or lose money, was used to elicit a baseline measurement of the individual's RewP, independent of effort manipulations (Weinberg et al. 2014; Foti et al. 2015; Proudfit 2015). In each trial,

participants were presented with an image of two identical doors and were asked to choose either the left or right door by clicking the corresponding mouse button (Figure 1).

Participants were instructed to guess which door was hiding a prize behind it, and that they would win money (50 cents) for each trial on which they guessed correctly but would lose money (25 cents) for each trial on which they guessed incorrectly. In reality, each door provided a win (versus loss) outcome 50% of the time. Following previous work using the Doors task (Proudfit 2015; Ethridge et al. 2021), reward amounts were asymmetric (i.e., monetary gains were twice as large as losses), since losses have been demonstrated to be (subjectively) valued twice as much as a corresponding gain of the same amount (Tversky and Kahneman 1992). After choosing a door, participants were presented with a fixation mark (+) for 1000ms, followed by feedback indicating whether they won or lost money, which took the form of a green arrow pointing up (“↑”) for a win and a red arrow pointing down (“↓”) for a loss, presented for 2000ms. Following feedback, a fixation mark appeared for 1500ms, and participants were then instructed to “Click for the next round”. There was a total of 40 trials, comprised of 20 gain trials and 20 loss trials, presented in random order. Upon completion of the task, all participants received a fixed payment of \$2.50.

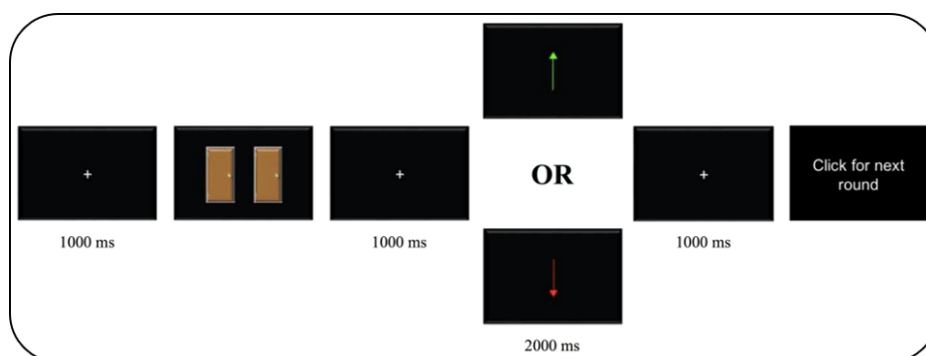


Figure 1. Doors task. In each trial, participants chose between two door images. In 50% of all trials, choices were followed by a green arrow, indicating a gain of 50 cents. In the other half, choices were followed by a red arrow, indicating a loss of 25 cents.

Effort Discounting Task (EDT)

The EDT used in this experiment consisted of three phases: A reinforcement phase, a choice phase, and an effort-reward phase. The first two phases were closely modeled after the task described by McGuigan and colleagues (2019), while the third phase was added to investigate the RewP response elicited by rewards conferred by exerting different levels of cognitive effort (Figure 2). In each of the 60 trials of the initial reinforcement phase, participants were presented with a ten-second rapid serial visual presentation (RSVP) stream of letters consisting of 24 individual letter-displays lasting for 416ms each. Participants were instructed to press the spacebar every time they saw the target letter “T”. Task demand (i.e., effort) was operationalized as the number of letter streams participants had to monitor concurrently (1 – 6) and was signaled by a discriminative cue at the beginning of each trial. Participants could earn a point in each trial by achieving at least one hit (i.e., pressing the spacebar while a “T” was present on screen) and less than three false alarms (i.e., pressing the spacebar in the absence of a “T”). Once a trial was finished, participants received performance feedback (i.e., whether they gained a point or not) for two seconds and then could initialize the next trial by a button press.

The subsequent choice phase consisted of 105 trials in which participants chose whether they would prefer to play a low-effort trial (i.e., monitoring a single letter stream for one point) or a higher effort trial for larger rewards (i.e., 2, 3, 4, 5, or 6 six letter streams for 2, 4, 6, 8 or 10 points). The low-effort/low-reward offer served as a baseline and was identical across all trials, while demand and reward levels in the high-effort/high-reward options were varied independently. All possible 25 high-effort/high-reward combinations were presented four times, for a total of 100 trials. In addition, we included five ‘catch’ trials to verify participants attended to the offered reward levels. In these trials, both choice options signaled low effort (i.e., monitoring one letter stream) but displayed different reward levels (i.e., 1 point vs. 2, 4, 6, 8, or 10 points). To ensure that the choice phase was incentives-compatible,

participants were required to play ten randomly selected effort-level/reward-level choices, with the understanding that points gained in these trials would translate to monetary reward at the end of the experiment. This phase allowed us to estimate individual levels of effort discounting—that is, how much potential reward a participant was willing to forgo in order to avoid expending additional cognitive effort.

The third and final part of the EDT, the novel effort-reward phase, measured effort-related modulations of the RewP response. This phase resembled the overall structure of the Doors task (see above), including feedback indicating monetary gains and losses for each trial. However, instead of choosing between two stimuli, participants were asked to once again complete a single RSVP trial with a given effort level: low effort (i.e., monitor one single letter stream) or high effort (i.e., monitor four concurrent letter streams). The level for the high-effort condition was chosen based on prior observations in our lab, suggesting that four concurrent letter streams represent a significant increase in effort while affording a reasonable accuracy level. Participants were informed that if they completed a trial successfully (i.e., above the threshold of at least one hit, less than three false alarms), they would sometimes win 50 cents and sometimes lose 25 cents. As in the standard Doors task, the true probability for each outcome was .5. Following a fixation mark presented for 1500ms, reward feedback was displayed as a green circle (signaling successful completion of the trial) and a white arrow either pointing up (“↑”), indicating a win, or pointing down (“↓”), indicating a loss, displayed for 2000ms. To obtain a sufficient number of trials for each effort/feedback combination (i.e., low-effort/win, low-effort/loss, high-effort/win and high-effort/loss), the task ended after participants had successfully completed 100 trials (25 per effort/outcome pairing). If participants failed to perform above the threshold in a given trial, they were presented with a red cross as feedback to signal an error. These trials were excluded from analysis and were replayed by participants until they met threshold performance. Overall, participants had relatively few failed trials ($M = 12.67$, $SD = 13.87$).

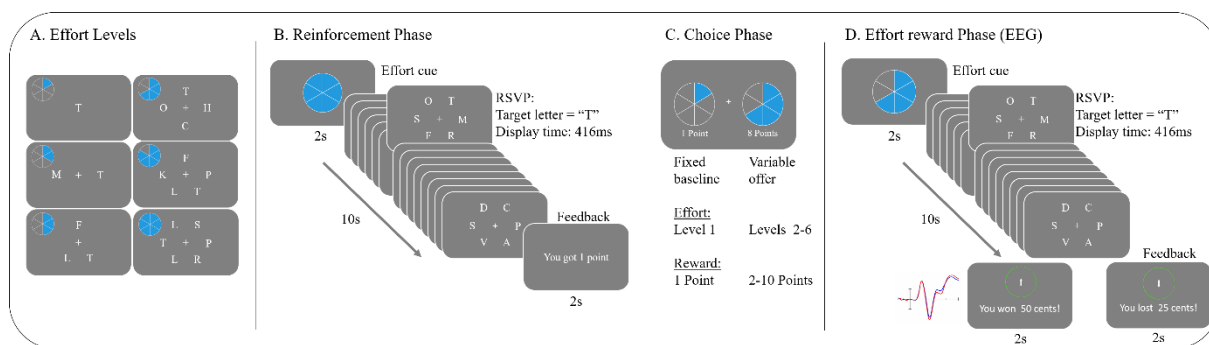


Figure 2. Effort discounting task (EDT). In this task, participants are asked to observe RSVP letter streams and to respond with a button press whenever they detect the target (“T”). Effort was operationalized as the number of concurrent RSVP streams (A). The EDT consisted of three phases (B-D). In the reinforcement phase, participants completed 10 trials of each effort level. After an initial cue stimulus signalling task demand, letter stimuli were presented rapidly on the screen for 10 seconds. Feedback then indicated whether participants completed the trial successfully (B). In the choice phase, participants chose between two options, indicating whether they would prefer to play a low-effort/low-reward trial (fixed: one RSVP stream for one point) or a high-effort/high-reward trial (variable: 2 – 6 streams for 2 – 10 points). Ten percent of all choices were randomly selected to be played out (C). In the effort-reward phase, we collected EEG data while participants completed either low-effort (one RSVP stream) or high-effort trials (four RSVP streams). If participants completed the trials successfully, they received either gain (+ 50 cents) or loss (- 25 cents) feedback. Failed trials were repeated (D).

Electroencephalographic Recording and Data Processing

Continuous EEG during the Doors task and the effort-reward phase of the EDT was recorded using a BrainVision actiCHamp system (Brain Products, Munich, Germany). Recordings were taken from 32 scalp electrodes based on the 10/20 system and a ground electrode at Fpz. A sampling rate of 1000 Hz was used to record data with electrode impedance set below 10 k Ω .

BrainVision Analyzer software (Brain Products, Munich, Germany) was used to conduct offline analyses. All unsegmented data were band-pass filtered with cut-offs of 0.1 and 30 Hz and a roll-off slope of 24 dB/octave, then segmented as described below and referenced to the average of TP9 and TP10. Each trial was corrected for blinks and eye

movements using FT9 as the horizontal electrooculogram (HEOG) channel and FP1 as the vertical electrooculogram (VEOG) channel per an adaptation of the algorithm published by Gratton et al. (1983).

For all analyses, the data were segmented into 2500ms epochs beginning 1000ms before feedback onset and continuing for 1500ms following feedback onset. Following this, an automatic method was used to detect and reject artifacts, whereby intervals were rejected from individual channels in each trial if they contained a voltage step of more than $30.0 \mu\text{V}$ between sample points, a voltage difference of $150.0 \mu\text{V}$ within a trial, an amplitude of less than $-125 \mu\text{V}$ or more than $125 \mu\text{V}$, or a maximum voltage difference of less than $0.50 \mu\text{V}$ within 100ms intervals. Following a visual inspection of the data, a manual artifact rejection was applied over the automatic artifact rejection if artifacts still remained in the processed data.

Time-Window Analyses

For time-window analyses, RewP was scored as the average activity at sensors Cz, FC1, and FC2 (FC_{avg}) between 250ms and 350ms following feedback, given evidence that the RewP is maximal at frontocentral sites on the head during this time-window following reward feedback and based on visual inspection of the grand-averaged data from this sample (Proudfit 2015). Our choices for both the time-window and the electrode positions used for all analyses were based on a hypothesis- and data-independent collapsed localizer approach (Luck and Gaspelin 2017). Separate averages were then created for gain and loss feedback in the Doors task, and for gain and loss feedback with respect to low-or high-effort trials in the effort-reward phase of the EDT. In each task, the time from -200ms to 0ms prior to feedback served as baseline (Ethridge and Weinberg 2018; Ethridge et al. 2020).

Time-Frequency Analyses

As we were primarily interested in identifying dissociable sources of activity that contribute to the observed RewP waveform, time-frequency analyses in each task were

performed on the grand average for each condition (i.e., gain or loss), with the time from -500ms to -300ms prior to feedback onset used as a baseline. We then performed a continuous wavelet transform using the Morlet complex with a minimal frequency of 0.01 Hz and a maximum frequency of 20 Hz, 40 frequency steps, Morlet parameter c of 3.5, and Gabor Normalization. For each feedback type, layers were then extracted corresponding to the delta and theta frequency bands. The layer extracted for delta had a central frequency of 2.894 (Gauss. Low = 2.067, Gauss. High = 3.721) and the layer extracted for theta had a central frequency of 5.878 (Gauss. Low = 4.199, Gauss. High = 7.557). Finally, for each response type in each task (i.e., gain or loss in the Doors task, high effort-gain, high effort-loss, low effort-win, and low effort-loss in the effort-reward phase of the EDT), power in the delta and theta frequencies were scored as the average activity at Cz, FC1, and FC2 (FC_{avg}) between 200ms and 400ms following feedback onset (Bernat et al. 2011; Foti et al. 2015; Ethridge et al. 2020).

Inferential Statistics

Our key inferential statistics were based upon mixed-effects regression models, implemented with the lme4 package for R (Bates and Maechler 2009). First, to assess participants' baseline RewP response to rewards in the Doors task, we calculated separate regression models to predict ERP amplitude as well as delta and theta power (see Time-Window and Time-Frequency analysis above) as a function of reward outcome (gains vs. losses).

In the EDT, we estimated a model predicting participants' subjective effort rating scores as a function of effort level encountered in the initial reinforcement phase of the task. Participants' choice behavior in the subsequent choice phase of the EDT was analyzed using a logistic regression predicting acceptance of high-effort/high-reward offers (0 = low demand choice, 1 = high demand choice) as a function of effort level (level 2 – 6), reward (2 – 10 points), and their interaction. All predictors were entered into the model as both fixed effects

and participant-level random slopes, with random intercepts. Finally, for the regression analysis of the critical effort-reward phase of the EDT, participants' discrimination performance was quantified as d' (z-standardized hit rate – z-standardized false alarm rate) which was predicted by effort level (low versus high), reward (gains versus losses), and the interaction term, again both as fixed and random effects in addition to a random intercept. Analogous to the Doors task, we calculated separate regression analyses to predict RewP amplitude and frequency band power (for both delta and theta bands) by effort level (high versus low) and reward (gains versus losses) and their interaction term as fixed effect and included a random intercept and random slopes for effort and reward levels. To explore the effect of individual differences in effort discounting on the RewP measures, we included the z-standardized model parameter k (derived from modeling choice behavior in the choice phase; see below) as an additional fixed effect predictor and allowed it to interact with all other predictors. All individual difference measures were z-scored prior to being entered in the analyses. Finally, we explored potential relationships between our task-based measures: the effort discounting parameter k (see below), the difference in ERP amplitudes to gains versus losses in the standard Doors task (i.e., a Δ RewP), and the differences in ERP amplitudes in high- and low-effort trials in the effort-reward phase of the EDT, and participants' scores in the questionnaires testing using Pearson correlations (reported in table S1 in the supplement).

Computational Model of Effort Discounting

Following previous work (Klein-Flügge et al. 2015; Chong et al. 2017; Massar et al. 2019, 2020; Vogel et al. 2020), we used a computational model of choice to quantify individuals participants' levels of effort discounting in the choice phase of the EDT. First, we compared the goodness of fit of the following three subjective value (SV) functions, which prescribes the functional form with which a given reward on offer amount is discounted by a given effort level:

$$\text{Linear: } SV_{(high\ effort)} = R_{high\ Effort} - k \times E_{high\ effort}$$

$$\text{Parabolic: } SV_{(high\ effort)} = R_{high\ Effort} - k \times (E_{high\ effort})^2$$

$$\text{Hyperbolic: } SV_{(high\ effort)} = R_{high\ Effort} \times \frac{1}{1 + k \times E_{high\ effort}}$$

where SV is the subjective value of the high-effort/high-reward offer in the current trial, R is the amount of reward (i.e., 2, 4, 6, 8 or 10 points) on offer, E is the effort level (i.e., 2, 3, 4, 5 or 6 concurrent letter streams) on display and k is a free parameter governing the subject-specific level of effort discounting. Intuitively, higher k -values correspond to steeper discounting of rewards due to effort levels, and thus indicate that a given participant is less likely to choose high-effort/high-reward offer in the choice phase of the EDT. The probability of choosing the high-effort/high-reward offer ($P_{high\ effort}$) was determined by a softmax choice rule:

$$P_{high\ effort} = \frac{e^{\beta * SV_{high\ effort}}}{e^{\beta * SV_{low\ effort}} + e^{\beta * SV_{high\ effort}}}$$

where P depends on the SV of the high-effort option in relation to the SV s of both options.

Here, β represents the inverse temperature parameter of the softmax function, where larger β -values indicate that choices are more sensitive to SV differences between options.

The models were then fit to the each participant's choice data with maximum likelihood estimation using the 'fmin' optimization function in SciPy package for Python (Virtanen et al. 2020). We then calculated both the Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC) for each model to compare fits (Akaike 1974; Schwarz 1978). Both goodness-of-fit measures indicate that choices were best described by a model that assumed linear effort discounting (Table 1), mirroring the findings reported by McGuigan et al. (2019), which employed the same EDT paradigm and choice model.

Table 1. AIC and BIC values for all compared computational models.

Model	AIC	BIC
Linear	3487.12	3491.27
Parabolic	4860.00	4864.15
Hyperbolic	4503.10	4507.26

Note. AIC = Akaike Information Criterion, BIC = Bayesian Information Criterion

For the linear model, the best-fitting parameters were as follows: k : $Mean \pm SE = 1.60 \pm 0.59$; β : $Mean \pm SE = 11.72 \pm 3.50$. One participant showed particularly strong aversion against effort (proportion of high-effort/high-reward offer chosen $\sim 21\%$), resulting in a particularly high k -value. This person was labeled as an outlier and was excluded from analyses using this parameter. For the remaining sample, the estimates were: k : $Mean \pm SE = 1.02 \pm 0.11$; β : $Mean \pm SE = 11.95 \pm 3.56$.

Results

Effort Discounting Task (EDT) Behavior

First, we observed that participants' ratings of effort levels encountered in the reinforcement phase of the EDT indicated that the effort manipulation successfully induced changes in subjective effort, as higher effort levels were consistently perceived as increasingly more difficult ($\beta \pm SE = 1.25 \pm 0.03$, $t = 36.99$, $p < .001$; Figure 3A).

Following previous work (McGuigan et al. 2019), we observed that participants' choices to engage in high-effort/high-reward trials in the choice phase of the EDT (Figure 3B-D) were informed by the amount of both effort and reward on offer: willingness to choose the high-effort/high-reward offer decreased with increasing effort levels (Figure 3C; effort level $\beta \pm SE = -1.39 \pm 0.14$, $z = -9.78$, $p < .001$) and increased with larger rewards (Figure 3D; reward effect $\beta \pm SE = 0.69 \pm 0.18$, $z = 3.91$, $p < .001$; Figure 3). Furthermore, we found a significant effort \times reward interaction ($\beta \pm SE = 0.22 \pm 0.06$, $z = 3.36$, $p < .001$), indicating that

participants were willing to exert more cognitive effort when the reward was high and, conversely, showed steeper effort discounting when rewards were low (Figure 3B).

To investigate whether individual differences in effort discounting are related to the subjective evaluation of task demand, we added participants' k -value (the individual effort discounting parameter obtained by computational modeling of choice behavior) as an individual difference variable to the regression predicting subjective effort ratings. As before, effort level significantly predicted subjective ratings ($\beta \pm SE = 1.05 \pm 0.05, p < .001$). While the main effect of k -value was not significant ($\beta \pm SE = 0.01 \pm 0.22, p = .989$), we found an interaction effect between effort level \times k -value ($\beta \pm SE = 0.18 \pm 0.04, p < .001$), indicating that subjective effort ratings of participants with higher k -values (i.e., steeper discounters) appeared subjectively more sensitive to increases in task demands.

Finally, in the effort-reward phase of the EDT, we found that participants' discrimination performance was worse in high-effort trials compared to low-effort trials (main effect effort: $\beta \pm SE = -0.48 \pm 0.02, t = -26.35, p < .001$), indicating that high-effort trials were indeed more difficult. Critically, the performance was comparable between gain and loss trials (main effect reward: $\beta \pm SE = -0.01 \pm 0.02, p = .831$; interaction effect effort \times reward: $\beta \pm SE = -0.02 \pm 0.02, p = .398$).

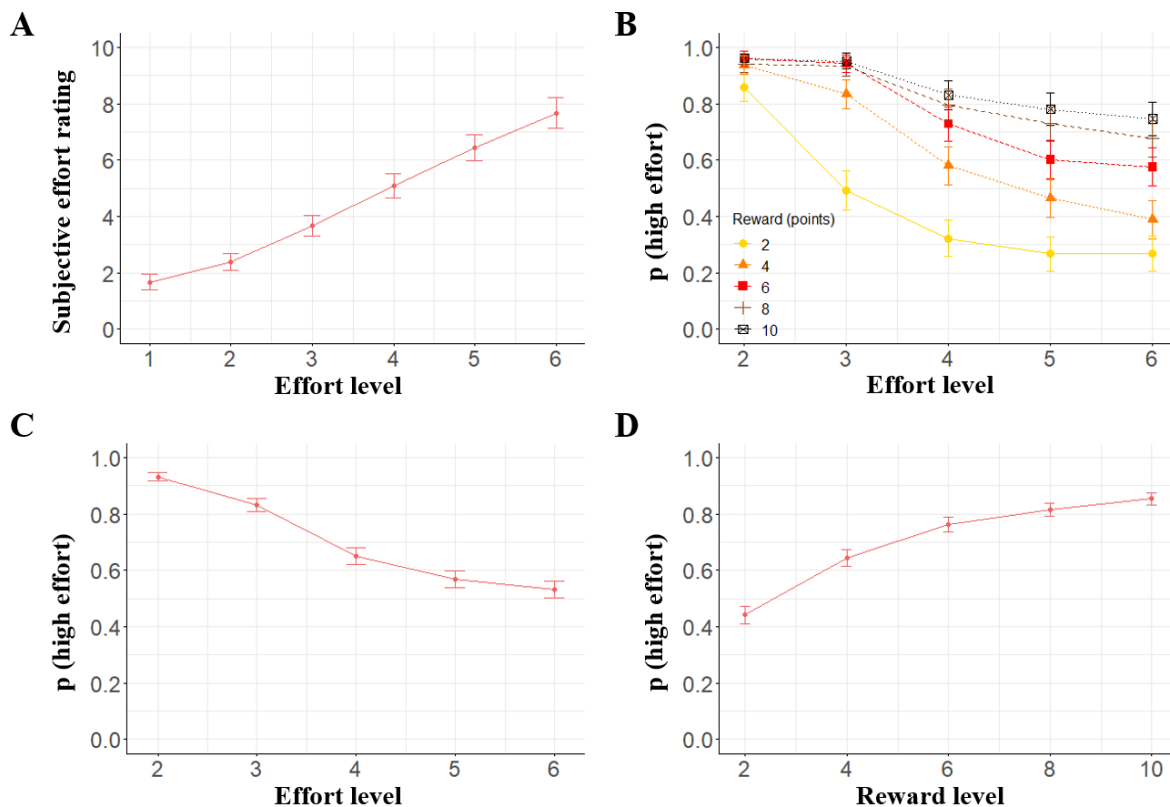


Figure 3. Effort ratings and choice behavior in the EDT. Participants' subjective effort ratings increased with task demand (A). Their choices in the second phase of the EDT were markedly affected by both effort and reward on offer (B-D). Willingness to choose the high-effort/high-reward option fell with rising task demand (C) but increased when rewards got larger (D). Steepness of effort discounting depended on the associated rewards. Specifically, the proportion of high-effort choices sank more rapidly for lower compared to larger rewards (B).

Baseline EEG Measures of Reward Responsiveness

Turning to the EEG analysis, we first sought to confirm participants exhibited a canonical RewP in the Doors task, which provided probabilistic reward feedback delivered after each choice but was not tied to effort exertion. Corroborating previous RewP studies (Foti et al. 2015; Proudfit 2015; Ethridge et al. 2020), we found that gains, compared to losses, led to larger positive deflections of the ERP between 250ms and 350ms after feedback presentation (Figure 4A, D), which was statistically confirmed by a linear regression of feedback type on the RewP amplitude during this time window ($\beta \pm SE = 1.58 \pm 0.34$, $t = 4.70$, $p < .001$; Figure 5A). A time-frequency decomposition (Figure 4D, G) revealed the same effect to be present in the delta band, where gains led to higher power compared to

losses ($\beta \pm SE = 0.30 \pm 0.11$, $t = 2.79$, $p = .007$) but not in the theta band, where greater power was elicited by losses compared to gains ($\beta \pm SE = -0.48 \pm 0.12$, $t = -4.15$, $p < .001$; see Figure 5B, C).

Cognitive effort exertion increases EEG responses to reward outcomes

The primary interest of this study was to investigate how the exertion of cognitive effort would modulate RewP magnitude in the effort-reward phase of the EDT. Figure 4 depicts ERP waveforms (B, C), scalp topographies (E, F), and spectral power for differences in gain and loss trials (H, J) separately for the low- and high-effort conditions. Similar to our findings in the Doors task, we observed more positive ERP deflections between 250ms and 350ms following gains versus losses (main effect reward feedback: $\beta \pm SE = 1.04 \pm 0.17$, $p < .001$), confirming the predicted RewP response in the effort-reward phase of the EDT. Importantly, we also found a main effect of effort level ($\beta \pm SE = 1.82 \pm 0.24$, $p < .001$), indicating a more positive RewP in high-effort compared to low-effort trials. The effort \times reward interaction effect was non-significant ($\beta \pm SE = -0.06 \pm 0.13$, $p = .656$), suggesting that effort exertion generally increased the amplitude of neural responses in the time-window of the RewP for both gains and losses without affecting the relation between outcome types (Figure 5D).

Time-frequency decompositions revealed that the effects observed for ERP amplitudes were mirrored in delta but not theta band activity (Figure 5 E-F). More specifically, delta power was significantly higher following gain versus loss outcomes (main effect reward: $\beta \pm SE = 0.25 \pm 0.06$, $p < .001$), and following high compared to low-effort levels (main effect effort: $\beta \pm SE = 0.76 \pm 0.09$, $p < .001$). There was again no significant interaction between outcome and effort level ($\beta \pm SE = 0.05 \pm 0.05$, $p = .345$) for delta power. On the other hand, theta power was significantly higher for losses compared to gains (main effect reward: $\beta \pm SE = -0.14 \pm 0.05$, $p = .012$) but was unaffected by effort level (main effect effort: $\beta \pm SE = 0.07 \pm 0.06$, $p = .219$; effort \times reward interaction: $\beta \pm SE = -0.01 \pm 0.05$, $p = .822$).

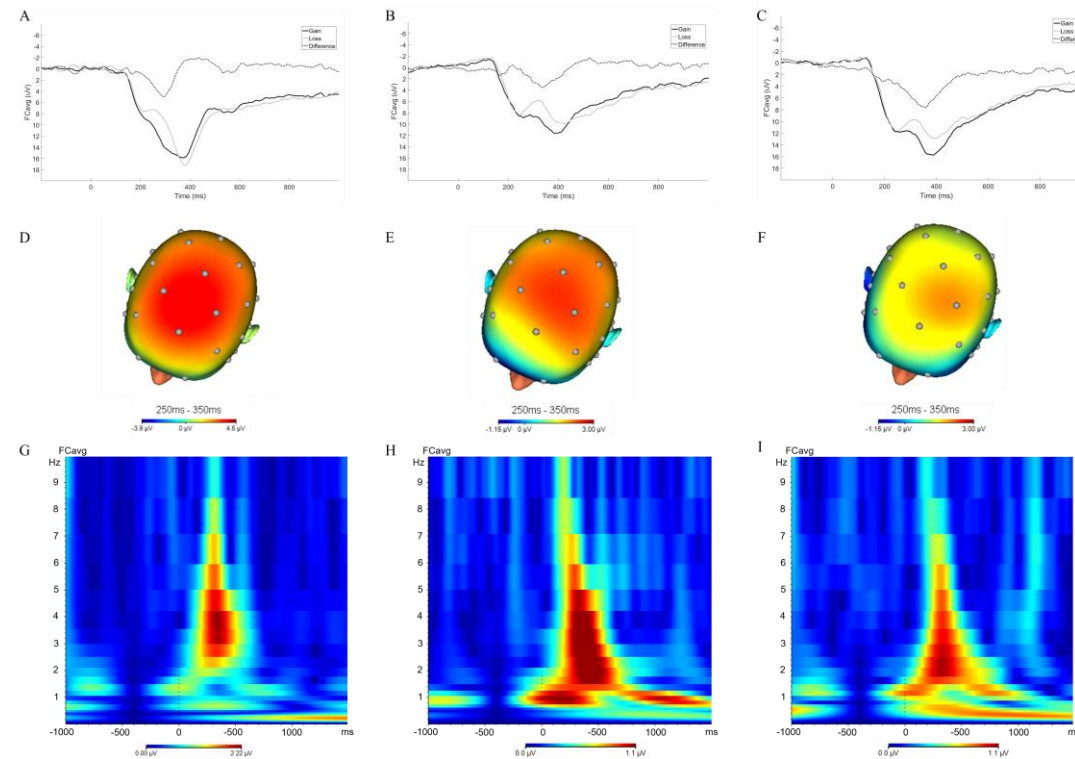


Figure 4. ERP responses, scalp topographies, and spectral power during reward feedback in the Doors task and the EDT. ERP waveforms represent an average across electrode positions Cz, FC1, and FC2 (FCavg), depicting neural response to reward and loss feedback in the Doors task (A), low-effort trials in the EDT (B), and high-effort trials in the EDT (C). “Difference” represents the gain minus loss difference. Scalp topographies show gain minus loss difference between 250-350 ms following feedback onset (D-F). Time-frequency plots depict the difference in power between gain and loss trials at FCavg in the Doors task (G), low effort-low effort trials in the EDT (H), and high-effort trials in the EDT (J).

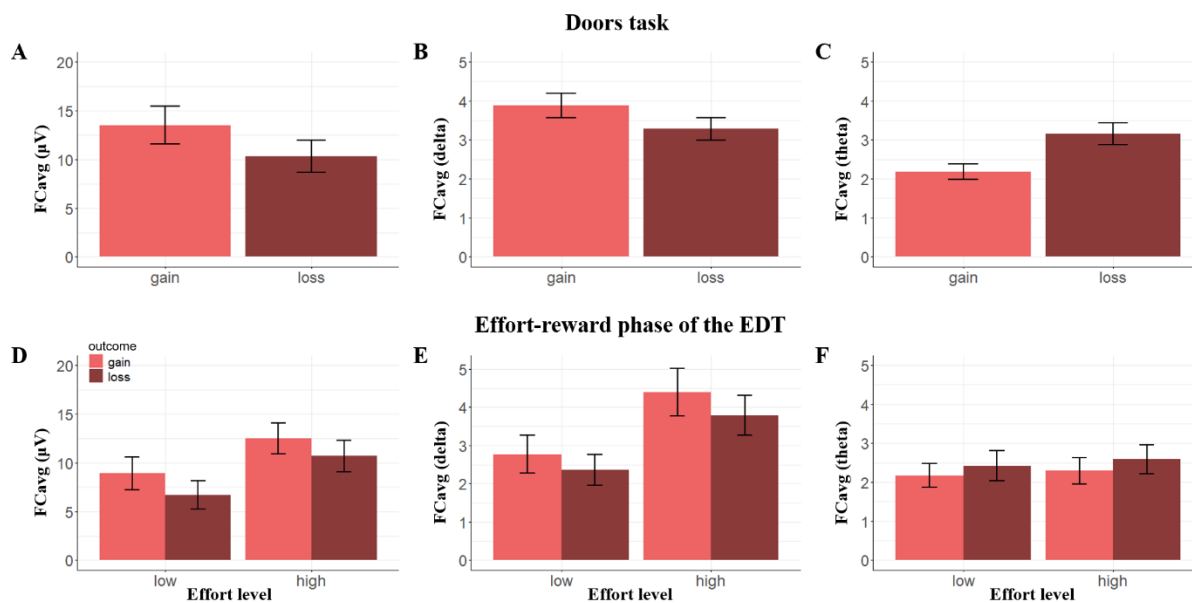


Figure 5. RewP measures in the Doors task and the effort-reward phase in the EDT. Electrophysiological responses to outcome feedback were averaged across electrodes Cz, FC1, and FC2 (FCavg). In the Doors task, we saw larger ERP amplitudes and higher activity in the delta band in gain compared to loss trials (A-B). Activity in the theta band, on the other hand, was higher for losses than for gains (C). We saw the same overall pattern of activity in the effort-reward phase of the EDT. However, ERP amplitudes and delta power were markedly increased for both gain and loss outcomes in high-effort compared to low-effort trials (D-E). Theta power was unaffected by the effort manipulation (F).

Individual Differences in Effort Discounting may modulate gain-related Delta Power in the EDT

In an exploratory analysis, we also considered whether individual differences in behavioral effort discounting, quantified by the individual discounting parameter k estimated from choices in the EDT, were related to RewP magnitude as well as delta and theta power—our main electrophysiological measures of reward sensitivity—following high- and low-effort exertion.

To test this statistically, we added participants' k -values to the above-described regression models used to predict response to feedback (i.e., time-domain-scored RewP magnitude, and power in the delta and theta bands) in the effort-reward phase of the EDT.

The full coefficient estimates for the three resultant models are provided in Table 2. With respect to delta band activity, we observed a significant effort \times reward \times k -value interaction ($p = .006$), indicating that shallow-discounting participants exhibit smaller differences in delta power in response to gains versus losses, especially following low-effort versus high-effort trials. These data suggest that participants with smaller cognitive effort costs (i.e., shallow effort discounters) may experience rewards conferred by low-demand (or easy) tasks as less valuable. In contrast, we observed no significant predictive effects of participants' k -values upon RewP amplitudes or theta power, nor interactions with reward and effort level (all $p > .227$). Figure 6A depicts the relationship between individual differences in effort discounting and reward-dependent delta band activity separately for participants displaying steep (high k value estimate) versus shallow (low k) effort discounting rates (determined by a median split for visualization purposes). As can be seen, activity in the delta band for steep effort discounters resembles the overall RewP pattern (Figure 5E), with stronger activity following gains versus losses and in high-effort trials versus low-effort trials. Shallow discounters, on the other hand, only appeared to manifest the expected gain-loss differentiation following high-effort, but not low-effort trials (Figure 6B).

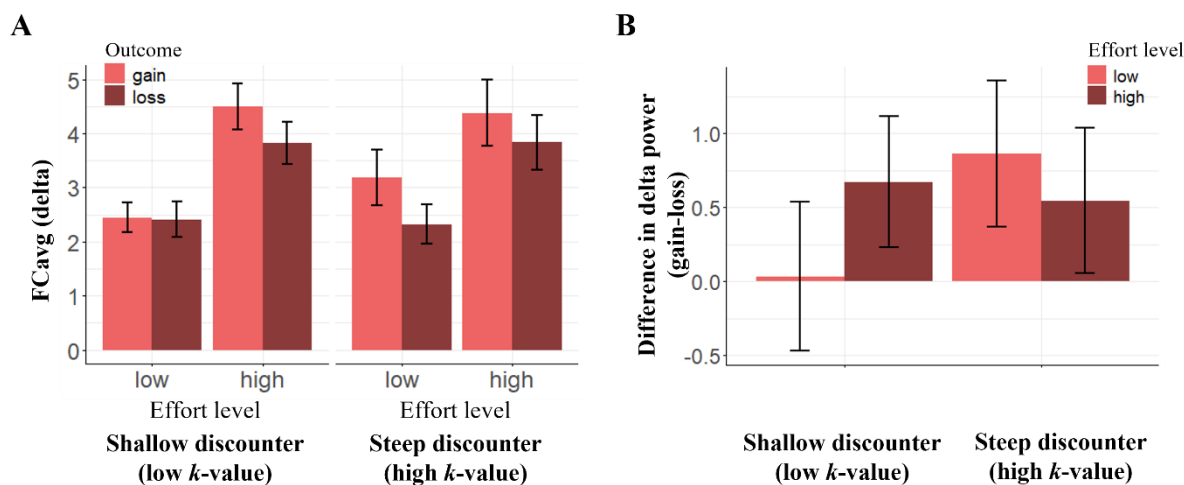


Figure 6. Effects of individual differences in effort discounting on delta power in response to outcome feedback. Participants whose choice behavior indicated steep discounting (i.e., a high sensitivity to effort costs)

displayed higher delta power toward gains compared to losses in both high and low-effort trials (A). In shallow discounters, this difference is only apparent in high-effort but not in low-effort trials (B).

Table 2. Mixed-effects regression coefficients indicating the effects of effort, reward, and discounting behavior on RewP measures in the EDT.

Coefficient	RewP Amplitude			Delta			Theta	
	β (SE)	p -value		β (SE)	p -value		β (SE)	p -value
Intercept	0.11 (0.15)	0.44		3.28 (0.37)	<.001	***	0.01 (0.12)	.918
Effort	0.33 (0.04)	<.001	***	0.69 (0.15)	<.001	***	0.05 (0.05)	.315
Reward	0.18 (0.04)	<.001	***	0.13 (0.10)	.205		-0.11 (0.04)	.014 *
k -value	0.76 (0.63)	.227		0.08 (0.29)	.782		0.08 (0.12)	.519
Effort \times reward	-0.02 (0.04)	.631		0.23 (0.08)	.007	**	-0.01 (0.04)	.744
Effort \times k -value	0.11 (0.17)	.520		0.09 (0.12)	.469		0.01 (0.05)	.920
Reward \times k -value	0.03 (0.17)	.845		0.13 (0.08)	.130		-0.04 (0.04)	.335
Effort \times reward \times k -value	-0.05 (0.17)	.785		-0.18 (0.06)	.006	**	0.05 (0.04)	.227

Note. k -values were z-scored. Effort refers to effort level (high vs. low). Reward refers to outcome identity (gain vs. loss). k -value refers to the model-derived effort discounting parameter of each participant.

Individual Differences in Reward Responsiveness (baseline RewPs) may predict Effort

Discounting in the EDT

We were also interested in whether individual differences in baseline reward processing—assessed by RewP magnitude in the standard Doors task—might predict effort-based decision-making in the EDT. For an exploratory analysis, we thus added the time-domain-scored ERP responses to gains and losses in the Doors task as predictors to the logistic regression used to predict choices in phase 2 of the EDT (full results are reported in Table 3). As before, we found that choices were driven by the interplay of effort level (main effect effort: $p < .001$) and reward magnitude (main effect reward: $p < .001$; effort \times reward interaction: $p = .001$) on offer. Interestingly, we also saw a significant effort \times gains

interaction ($p = .003$), suggesting that participants with a larger RewP in response to gain trials in the Doors task were more likely to choose high-effort/high-reward offers in the EDT, especially when the effort level was intermediate (level 4 and 5, see Figure 7). In addition, we found an unexpected main effect of ERP responses to loss trials in the Doors task on choice behavior ($p < .001$), suggesting that smaller loss responses (i.e., more negative deflections of the ERP in the time-window of the RewP) were associated with higher acceptance rates of high-effort/high-reward trials.

In light of the exploratory approach to our individual difference analyses, we aimed to evaluate the plausibility of our findings by computing a sensitivity analysis for each effect of interest that allowed us to compare our regression weights with the smallest effect we would have been able to detect in our sample with a power of 80%. Overall, these sensitivity analyses indicated that our findings are reliable. For a detailed overview of the results, please refer to table S2 in the supplement.

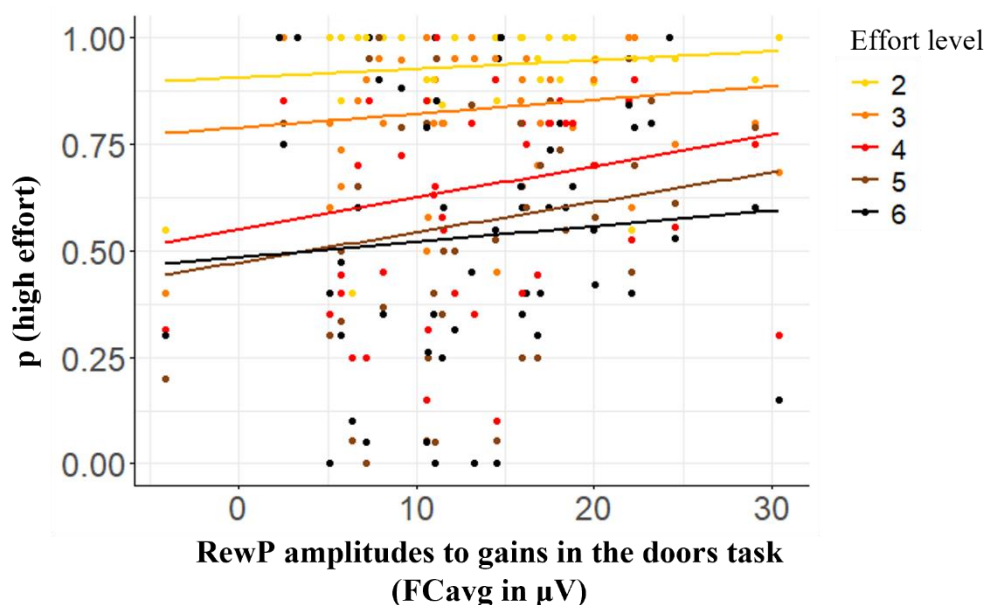


Figure 7. Relationship between RewP responses to gain feedback in the Doors task and choice behavior in the EDT. Participants with larger ERP amplitudes towards gains in the Doors task were more willing to accept high-effort/high-reward offers for intermediate effort levels 4 and 5. This relationship was not present in low or very high-effort levels.

Table 3. Mixed-effects regression coefficients indicating the effects of effort, reward, and ERP responses to gains and losses in the standard Doors task on participants' choice behavior in the EDT.

Coefficient	β (<i>SE</i>)	<i>z</i> -value	<i>p</i> -value	
Intercept	2.72 (0.38)	7.01	<.001	***
Effort	-1.48 (0.14)	-10.57	<.001	***
Reward	0.73 (0.15)	5.03	<.001	***
Doors gains	0.10 (0.47)	0.20	.839	
Doors losses	-1.08 (0.29)	-3.79	<.001	***
Effort \times reward	0.18 (0.06)	3.23	.001	**
Effort \times Doors gains	0.39 (0.11)	3.01	.003	**
Reward \times Doors losses	0.08 (0.10)	0.82	.413	
Doors gains \times Doors losses	0.01 (0.28)	0.01	.990	
Effort \times reward \times Doors gains	0.01 (0.05)	0.05	.959	

Note. ERP responses were *z*-scored. Effort refers to effort level (high vs. low). Reward refers to outcome identity (gain vs. loss). Doors gains and Doors losses refer to participants' baseline RewP amplitudes measured for gain and loss trials in the Doors task.

Discussion

The last decade has seen a surge of interest in the neurocognitive mechanisms underlying cost-benefit decision-making about effort expenditure as well as effort-related effects on reward processing (Shenhav et al. 2013; Botvinick and Braver 2015; Chong et al. 2017). While there is substantial evidence suggesting that the prospect of effort may reduce the value of anticipated rewards tied to effort exertion—and, in turn, the willingness to engage in cognitively demanding behavior (Westbrook and Braver 2015; Kool and Botvinick 2018), it remains unclear whether prior effort exertion enhances—versus attenuates—neural and/or psychophysiological indices of the subjective value of ensuing outcomes (Botvinick et al. 2009; Hernandez Lallement et al. 2014; Ma et al. 2014; Dobryakova et al. 2017; Harmon-Jones, Clarke, et al. 2020; Yi et al. 2020; Bowyer et al. 2021).

Here, we provide evidence in support of the idea that cognitive effort exertion may in fact increase participants' response to reward feedback as measured by the RewP, an ERP component specifically associated with reward valuation (Bernat et al. 2015; Foti et al. 2015; Proudfit 2015). In accordance with our hypothesis, we found that exerting more cognitive effort amplified the magnitude of the RewP in response to gains conferred by this effort. However, while some previous work implied that effort might selectively enhance RewP amplitudes toward gains but not to losses (Ma et al. 2014), we also found larger positive deflections of the ERP responses to losses following high- compared low-effort trials, indicating a weaker neural response to losses (i.e., smaller loss-related negative deflections of the ERP) in these trials.

In order to better understand this result, we used time frequency decompositions to isolate activity related to delta and theta frequency bands that have previously shown to differentially contribute to the RewP (Bernat et al. 2015; Weinberg et al. 2021). This analysis revealed that high-effort trials resulted in increased power in the gain-related delta band for both gain and loss feedback. In contrast, power in the loss-related theta band was *only* sensitive to outcome type (gain vs. loss), and not effort level. In other words, it appears as if the effects of cognitive effort exertion on the RewP, i.e., the enhanced positive deflections of the ERP, specifically depend on effort-related modulations of activity in the reward-sensitive delta band, independent of outcome type. Such specific increases in delta but not theta power in high- vs. low-effort trials have previously been related to changes in the participants' processing of higher order characteristics of the task. More precisely, prior research has shown that while both delta and theta band activity are sensitive to outcome type, delta power can also be modulated by more complex task features such as experimental context or participants' expectations toward reward-related feedback (Bernat et al. 2015; Watts et al. 2017; Watts and Bernat 2018), as well as more external manipulations such as psychosocial stress induction, that have been argued to affect the motivational saliency of reward feedback

(Ethrige et al. 2020). As such, it is possible that increases in cognitive effort exertion in our task might have enhanced the perceived value of both outcome types similarly.

Alternatively, the fact that effort increased RewP amplitude and delta power similarly for gain and loss trials may be, in part, a result of coupling task success with reward versus loss receipt in our task paradigm. More specifically, to ensure an equal trial count in all conditions of the effort-reward phase of the EDT and to dismiss trials in which participants had not exerted a minimum amount of effort, only trials for which the participant succeeded on the effortful task provided gain/loss feedback, while failed trials were replayed. Thus, it is possible even after loss feedback that a participant derived value simply from the fact that they managed to complete a high-effort trial successfully (which would be conferred by either gain or loss feedback). Another possibility to consider here is that participants knew they had to replay failed trials. As such, completing a trial successfully and thus avoiding a replay might have led to a feeling of relief, even in loss trials, which has been shown to modulate the RewP and that might have been greater for high-effort compared to low-effort trials (Gheza et al. 2018). Relatedly, failing a trial might carry an additional cost, as it would have prolonged the experimental session, and accordingly, performing well could have further increased the subjective value of a gain or loss outcome. While the present design is not suited to disentangle these possibilities, systematically varying the coupling between performance and reward feedback may be a fruitful avenue for future investigations. Still, we should note that while this feature of our task design could conceivably explain the effort-related increase in RewP amplitude and delta power in loss trials, we do not think it explains why we did not observe a stronger effort modulation of the RewP in gain versus loss trials, a pattern that has been previously observed in studies employing similar designs (in which only successful trials led to reward feedback; (Ma et al. 2014; Yi et al. 2020). Moreover, if we had observed a specific effect of effort on gain trials, it should have still been detectable above and beyond

the contributions of performance feedback, given that the potential reward for successfully finishing a trial would have been constant across gain and loss feedback.

Our results contribute to the small but growing literature examining the interplay between effort exertion and reward valuation indexed by the RewP (Ma et al. 2014; Krigolson et al. 2015; Gheza et al. 2018; Umemoto et al. 2019; Harmon-Jones, Clarke, et al. 2020; Yi et al. 2020; Bowyer et al. 2021). Given the nascent state of this line of research, it is not surprising that findings so far have been inconsistent, with some studies reporting larger, others smaller RewPs in response to reward outcomes following effort exertion. This heterogeneity of results might stem in part from substantive differences in study design across these experiments, including the type of effort manipulated, operationalization of task demand levels, or outcomes used to elicit RewP responses. In addition, some tasks include an inherent time-on-trial difference between effort conditions (i.e., low-effort trials might take less time to complete than high-effort trials), present performance feedback and reward feedback sequentially, or introduce a considerable delay between task completion and feedback presentation (Ma et al. 2014; Bowyer et al. 2021), which has been shown to affect RewP responses (Weinberg et al. 2012). To avoid most of these pitfalls, the critical effort-reward phase in our paradigm was specifically designed to closely resemble established tasks in the RewP as well as the cognitive effort discounting literature, namely the Doors task and the EDT (Foti et al. 2015; McGuigan et al. 2019).

Another potential explanation for the inconsistent effects of effort exertion on RewP magnitudes previously observed are the well-documented individual differences in reward responsiveness to rewarding feedback (Ethridge and Weinberg 2018) as well as subjective cognitive effort costs (Westbrook et al. 2013; Chong et al. 2017). For example, recent work finds that individuals low in intrinsic motivation to exert effort—operationalized by the Need for Cognition (Cacioppo et al. 1984)—exhibit more pronounced effort discounting and are more likely to increase cognitive effort exertion for incentives (Westbrook et al. 2013; Sandra

and Otto 2018). As such, intrinsic motivation to exert effort might bear upon the valuation of reward conferred by effort, possibly observable in modulations of the RewP (Harmon-Jones, Willoughby, et al. 2020). Here, we examined individual differences in effort discounting rates of anticipated rewards relate to reward valuation using the same cognitive task (i.e., the EDT). We observed that choice behavior in the EDT closely mirrored previous findings on effort-based choice (Chong et al. 2017; McGuigan et al. 2019; Massar et al. 2020) and that choices were consistent with a cost-benefit trade-off between effort and anticipated rewards (Shenhav et al. 2013; Westbrook and Braver 2015; Kool and Botvinick 2018). Further, computational modelling revealed that participants' choice behavior was best captured by a linear effort discounting function, which follows the results of McGuigan et al. (2019), who employed a very similar version of the EDT.

While individual participants' discounting rates in the choice phase were not related to RewP amplitude or theta band activity in the effort-reward phase of the EDT, we did find that individual differences in behavioral effort discounting modulated activity in the reward-sensitive delta band. Specifically, the otherwise apparent higher delta power for gains compared to losses disappeared in low-effort trials for shallow discounters, i.e., participants who were more inclined to engage in high-effort trials in the choice phase of the EDT. This implies that participants who were less sensitive to the costs of effort may have ascribed less value to gain feedback than steeper discounters when it was received without much effort. In addition, we also examined how the baseline RewP response measured in the standard Doors task was related to the RewPs elicited after effort exertion. We found that the relative difference between RewP amplitudes toward gains and losses (i.e., the Δ RewP) in the Doors task was predictive of the same difference in low- but not high-effort trials, indicating that having to exert large amounts of effort induces stronger individual variability in the evaluation of positive and negative reward feedback. Interestingly, we saw that participants who displayed larger RewP amplitudes in gain trials in the Doors task were more likely to

accept high-effort/high-reward offers in the choice phase of the EDT, suggesting that individuals who were more responsive to positive reward feedback were also more willing to acquire larger rewards despite the required effort. This was especially apparent in trials with intermediate task demand (Figure 7), possibly suggesting that participants were less certain about their choices in these trials compared to trials with very low or very high effort demands, increasing the influence of individual differences in reward sensitivity to affect decision-making. Taken together, these results highlight the importance of examining individual difference measures of both reward and effort sensitivity in understanding how cognitive effort exertion modulates reward responsiveness. At the same time, it is important to note that our individual differences analyses were exploratory in nature, and that, owing to our study's sample size, may not be sufficiently powered to make conclusive statements about the predictive effects of RewP magnitudes or effort discounting. Consequently, our results speak to the need for independent, high-powered replication studies to better understand these individual differences.

Interestingly—and in contrast to the relatively nascent discussion in the EEG literature—the notion that past effort may retrospectively increase the value of outcomes tied to effort exertion finds support across a number of lines of work in psychology. For example, people are willing to pay more money for furniture they build themselves compared to off-the-shelf products (the so-called “IKEA effect”; Norton et al. 2012), more willing to follow courses of action they have already put effort in, even if the outcome is objectively less desirable (e.g., “sunk cost” effects; Arkes and Blumer 1985; Yan and Otto 2020), and less willing to share money earned by effortful behavior compared to money earned without effort (Muehlbacher and Kirchler 2009). Proposed explanations for such effects emphasize differences in emotional states between aversive effort exertion and more positive reward consumption (“contrast effect” or “state-dependent valuation”) as well as cognitive processes to rationalize prior effort investments—for instance, through an effort justification

mechanism (Festinger 1957; Bem 1967; Alessandri et al. 2008; Pompilio and Kacelnik 2010; Harmon-Jones, Clarke, et al. 2020). Indeed, the observation that effort exertion enhances reward responsivity are, conceptually, in line with these past behavioral findings.

Finally, although this study aimed to investigate the effects of cognitive effort exertion on subsequent reward processing in young, healthy adults, our findings might have useful implications for clinical research. More specifically, changes in the neurocomputational mechanisms supporting effort-based decision-making have been recently proposed to underlie motivational deficits and syndromes like apathy and anhedonia that are prevalent in many psychiatric and neurological conditions, including Major Depression, Schizophrenia, and Parkinson's Disease (Chong et al. 2015; Park et al. 2017; Husain and Roiser 2018; Le Heron et al. 2018). While blunted RewP responses, and specifically reductions in gain-related delta band activity, have been shown to be associated with (and predictive of the development of) depressive symptoms (Bress et al. 2013; Weinberg et al. 2015), it has yet to be shown whether previously exerted effort differentially affects reward valuation at outcome delivery in people with depression. An improved understanding of how effort and reward information are integrated at different stages of reward processing in health and disease may help to develop new or more specific treatment options for individuals suffering from amotivational symptoms.

In conclusion, we provide evidence that the exertion of cognitive effort increases electrophysiological correlates of reward processing during subsequent outcome delivery. Specifically, participants exhibited larger ERP amplitudes to both gain and loss feedback in high-effort compared to low-effort trials. Time-frequency decomposition revealed that this effect was primarily driven by oscillations in the gain-related delta frequency, whereas loss-related theta power was unaffected by our effort manipulation. Cognitive effort exertion thus may have increased the motivational value of both outcome types. Finally, we observed that individual differences in effort discounting for anticipated rewards may modulate the

canonical gain-loss differentiation in delta power, implying that participants who are more sensitive to cognitive effort evaluate ensuing rewards differently from less effort-sensitive individuals. Although more work is still necessary to fully understand the inconsistent observations in the literature, our findings provide new insights into the cognitive and neural mechanisms underlying the modulating effects of effort exertion on reward valuation.

Funding

This work was supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant; a New Researchers Grant from the Fonds de Recherche du Québec – Nature et Technologies (FRQ-NT); a Canada Foundation for Innovation (CFI) Infrastructure Grant; a short-term Postdoc Fellowship by the German Academic Exchange Service (DAAD); and a Research Fellowship by the German Research Foundation (DFG).

Acknowledgments

We gratefully acknowledge the assistance of Claire Punturieri during data collection.

References

- Akaike H. 1974. A new look at the statistical model identification. *IEEE transactions on automatic control*. 19:716–723.
- Alessandri J, Darcheville J-C, Zentall TR. 2008. Cognitive dissonance in children: Justification of effort or contrast? *Psychonomic Bulletin & Review*. 15:673–677.
- Arkes HR, Blumer C. 1985. The psychology of sunk cost. *Organizational Behavior and Human Decision Processes*. 35:124–140.
- Bates D, Maechler M. 2009. Package ‘lme4’ (Version 0.999375-32): linear mixed-effects models using S4 classes. Available (April 2011) at <http://cran.r-project.org/web/packages/lme4/lme4.pdf>.
- Bem DJ. 1967. Self-perception: An alternative interpretation of cognitive dissonance phenomena. *Psychological review*. 74:183.
- Bernat EM, Nelson LD, Baskin-Sommers AR. 2015. Time-frequency theta and delta measures index separable components of feedback processing in a gambling task. *Psychophysiology*. 52:626–637.
- Bernat EM, Nelson LD, Steele VR, Gehring WJ, Patrick CJ. 2011. Externalizing psychopathology and gain–loss feedback in a simulated gambling task: Dissociable components of brain response revealed by time-frequency analysis. *Journal of abnormal psychology*. 120:352.
- Berridge KC, Robinson TE, Aldridge JW. 2009. Dissecting components of reward: ‘liking’, ‘wanting’, and learning. *Current opinion in pharmacology*. 9:65–73.
- Bogdanov M, Nitschke JP, LoParco S, Bartz JA, Otto AR. 2021. Acute Psychosocial Stress Increases Cognitive-Effort Avoidance. *Psychological Science*. 09567976211005465.
- Botvinick MM, Braver T. 2015. Motivation and cognitive control: from behavior to neural mechanism. *Annual review of psychology*. 66:83–113.
- Botvinick MM, Huffstetler S, McGuire JT. 2009. Effort discounting in human nucleus accumbens. *Cognitive, Affective, & Behavioral Neuroscience*. 9:16–27.
- Bowyer C, Brush C, Threadgill H, Harmon-Jones E, Treadway M, Patrick CJ, Hajcak G. 2021. The effort-doors task: Examining the temporal dynamics of effort-based reward processing using ERPs. *NeuroImage*. 228:117656.
- Bress JN, Foti D, Kotov R, Klein DN, Hajcak G. 2013. Blunted neural response to rewards prospectively predicts depression in adolescent girls. *Psychophysiology*. 50:74–81.
- Cacioppo JT, Petty RE, Feng Kao C. 1984. The efficient assessment of need for cognition. *Journal of personality assessment*. 48:306–307.
- Chong TT-J, Apps M, Giehl K, Sillence A, Grima LL, Husain M. 2017. Neurocomputational mechanisms underlying subjective valuation of effort costs. *PLoS biology*. 15:e1002598.
- Chong TT-J, Apps MA, Giehl K, Hall S, Clifton CH, Husain M. 2018. Computational modelling reveals distinct patterns of cognitive and physical motivation in elite athletes. *Scientific reports*. 8:1–11.
- Chong TT-J, Bonnelle V, Manohar S, Veromann K-R, Muhammed K, Tofaris GK, Hu M, Husain M. 2015. Dopamine enhances willingness to exert effort for reward in Parkinson’s disease. *cortex*. 69:40–46.
- Cohen S, Kamarck T, Mermelstein R. 1994. Perceived stress scale. *Measuring stress: A guide for health and social scientists*. 10.

- Crosson PL, Walton ME, O'Reilly JX, Behrens TE, Rushworth MF. 2009. Effort-based cost-benefit valuation and the human brain. *Journal of Neuroscience*. 29:4531–4541.
- da Silva Castanheira K, LoParco S, Otto AR. 2021. Task-evoked pupillary responses track effort exertion: evidence from task-switching. *Cognitive, Affective, & Behavioral Neuroscience*. 21:592–606.
- Dobryakova E, Jessup RK, Tricomi E. 2017. Modulation of ventral striatal activity by cognitive effort. *Neuroimage*. 147:330–338.
- Ethridge P, Ali N, Racine SE, Pruessner JC, Weinberg A. 2020. Risk and resilience in an acute stress paradigm: Evidence from salivary cortisol and time-frequency analysis of the reward positivity. *Clinical Psychological Science*. 8:872–889.
- Ethridge P, Freeman C, Sandre A, Banica I, Dirks MA, Weinberg A. 2021. Intergenerational transmission of depression risk: Mothers' neural response to reward and history of depression are associated with daughters' neural response to reward across adolescence. *Journal of Abnormal Psychology*.
- Ethridge P, Weinberg A. 2018. Psychometric properties of neural responses to monetary and social rewards across development. *International Journal of Psychophysiology*. 132:311–322.
- Festinger L. 1957. *A theory of cognitive dissonance*. Stanford university press.
- Foti D, Weinberg A, Bernat EM, Proudfit GH. 2015. Anterior cingulate activity to monetary loss and basal ganglia activity to monetary gain uniquely contribute to the feedback negativity. *Clinical Neurophysiology*. 126:1338–1347.
- Gard DE, Gard MG, Kring AM, John OP. 2006. Anticipatory and consummatory components of the experience of pleasure: a scale development study. *Journal of research in personality*. 40:1086–1102.
- 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.
- Gratton G, Coles MG, Donchin E. 1983. A new method for off-line removal of ocular artifact. *Electroencephalography and clinical neurophysiology*. 55:468–484.
- 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.
- 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.
- Hernandez Lallement J, Kuss K, Trautner P, Weber B, Falk A, Fliessbach K. 2014. Effort increases sensitivity to reward and loss magnitude in the human brain. *Social cognitive and affective neuroscience*. 9:342–349.
- Hofmans L, Papadopetraki D, van den Bosch R, Määttä JI, Froböse MI, Zandbelt BB, Westbrook A, Verkes R-J, Cools R. 2020. Methylphenidate boosts choices of mental labor over leisure depending on striatal dopamine synthesis capacity. *Neuropsychopharmacology*. 45:2170–2179.
- Husain M, Roiser JP. 2018. Neuroscience of apathy and anhedonia: a transdiagnostic approach. *Nature Reviews Neuroscience*. 19:470.
- Inzlicht M, Shenhav A, Olivola CY. 2018. The effort paradox: Effort is both costly and valued. *Trends in cognitive sciences*. 22:337–349.

- Klein-Flügge MC, Kennerley SW, Saraiva AC, Penny WD, Bestmann S. 2015. Behavioral modeling of human choices reveals dissociable effects of physical effort and temporal delay on reward devaluation. *PLoS Comput Biol.* 11:e1004116.
- Kool W, Botvinick M. 2018. Mental labour. *Nature human behaviour.* 2:899–908.
- Kool W, McGuire JT, Rosen ZB, Botvinick MM. 2010. Decision making and the avoidance of cognitive demand. *Journal of Experimental Psychology: General.* 139:665.
- Kool W, McGuire JT, Wang GJ, Botvinick MM. 2013. Neural and behavioral evidence for an intrinsic cost of self-control. *PloS one.* 8:e72626.
- Krigolson OE, Hassall CD, Satel J, Klein RM. 2015. The impact of cognitive load on reward evaluation. *brain research.* 1627:225–232.
- Le Heron C, Apps M, Husain M. 2018. The anatomy of apathy: A neurocognitive framework for amotivated behaviour. *Neuropsychologia.* 118:54–67.
- Luck SJ, Gaspelin N. 2017. How to get statistically significant effects in any ERP experiment (and why you shouldn't). *Psychophysiology.* 54:146–157.
- 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.
- Massar SA, Libedinsky C, Weiyang C, Huettel SA, Chee MW. 2015. Separate and overlapping brain areas encode subjective value during delay and effort discounting. *Neuroimage.* 120:104–113.
- Massar SA, Lim J, Sasmita K, Chee MW. 2019. Sleep deprivation increases the costs of attentional effort: Performance, preference and pupil size. *Neuropsychologia.* 123:169–177.
- Massar SA, Pu Z, Chen C, Chee MW. 2020. Losses Motivate Cognitive Effort More Than Gains in Effort-Based Decision Making and Performance. *Frontiers in human neuroscience.* 14:287.
- McGuigan S, Zhou S-H, Brosnan MB, Thyagarajan D, Bellgrove MA, Chong TT. 2019. Dopamine restores cognitive motivation in Parkinson's disease. *Brain.* 142:719–732.
- Muehlbacher S, Kirchler E. 2009. Origin of endowments in public good games: The impact of effort on contributions. *Journal of Neuroscience, Psychology, and Economics.* 2:59.
- Norton MI, Mochon D, Ariely D. 2012. The IKEA effect: When labor leads to love. *Journal of consumer psychology.* 22:453–460.
- Otto AR, Daw ND. 2019. The opportunity cost of time modulates cognitive effort. *Neuropsychologia.* 123:92–105.
- Otto AR, Vassena E. 2021. It's all relative: Reward-induced cognitive control modulation depends on context. *Journal of Experimental Psychology: General.* 150:306–313.
- Park IH, Lee BC, Kim J-J, Kim JI, Koo M-S. 2017. Effort-based reinforcement processing and functional connectivity underlying amotivation in medicated patients with depression and schizophrenia. *Journal of Neuroscience.* 37:4370–4380.
- Peirce JW. 2007. PsychoPy—psychophysics software in Python. *Journal of neuroscience methods.* 162:8–13.
- Pompilio L, Kacelnik A. 2010. Context-dependent utility overrides absolute memory as a determinant of choice. *Proceedings of the National Academy of Sciences.* 107:508–512.
- Proudfit GH. 2015. The reward positivity: From basic research on reward to a biomarker for depression. *Psychophysiology.* 52:449–459.

- Sandra DA, Otto AR. 2018. Cognitive capacity limitations and Need for Cognition differentially predict reward-induced cognitive effort expenditure. *Cognition*. 172:101–106.
- Schwarz G. 1978. Estimating the dimension of a model. *Annals of statistics*. 6:461–464.
- Shenhav A, Botvinick MM, Cohen JD. 2013. The expected value of control: an integrative theory of anterior cingulate cortex function. *Neuron*. 79:217–240.
- Shenhav A, Musslick S, Lieder F, Kool W, Griffiths TL, Cohen JD, Botvinick MM. 2017. Toward a rational and mechanistic account of mental effort. *Annual review of neuroscience*. 40:99–124.
- Small DM, Gitelman D, Simmons K, Bloise SM, Parrish T, Mesulam M-M. 2005. Monetary incentives enhance processing in brain regions mediating top-down control of attention. *Cerebral Cortex*. 15:1855–1865.
- Soutschek A, Kang P, Ruff CC, Hare TA, Tobler PN. 2018. Brain stimulation over the frontopolar cortex enhances motivation to exert effort for reward. *Biological psychiatry*. 84:38–45.
- Soutschek A, Tobler PN. 2018. Motivation for the greater good: neural mechanisms of overcoming costs. *Current Opinion in Behavioral Sciences*. 22:96–105.
- Soutschek A, Tobler PN. 2020. Causal role of lateral prefrontal cortex in mental effort and fatigue. *Human Brain Mapping*. 41:4630–4640.
- Sweis BM, Abram SV, Schmidt BJ, Seeland KD, MacDonald AW, Thomas MJ, Redish AD. 2018. Sensitivity to “sunk costs” in mice, rats, and humans. *Science*. 361:178–181.
- Treadway MT, Bossaller NA, Shelton RC, Zald DH. 2012. Effort-based decision-making in major depressive disorder: a translational model of motivational anhedonia. *Journal of abnormal psychology*. 121:553.
- Treadway MT, Buckholtz JW, Cowan RL, Woodward ND, Li R, Ansari MS, Baldwin RM, Schwartzman AN, Kessler RM, Zald DH. 2012. Dopaminergic mechanisms of individual differences in human effort-based decision-making. *Journal of Neuroscience*. 32:6170–6176.
- Treynor W, Gonzalez R, Nolen-Hoeksema S. 2003. Rumination reconsidered: A psychometric analysis. *Cognitive therapy research*. 27:247–259.
- Tversky A, Kahneman D. 1992. Advances in prospect theory: Cumulative representation of uncertainty. *Journal of Risk and uncertainty*. 5:297–323.
- Umemoto A, Inzlicht M, Holroyd CB. 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.
- Vassena E, Silvetti M, Boehler CN, Achten E, Fias W, Verguts T. 2014. Overlapping neural systems represent cognitive effort and reward anticipation. *PLoS One*. 9:e91008.
- Virtanen P, Gommers R, Oliphant TE, Haberland M, Reddy T, Cournapeau D, Burovski E, Peterson P, Weckesser W, Bright J. 2020. SciPy 1.0: fundamental algorithms for scientific computing in Python. *Nature methods*. 17:261–272.
- Vogel TA, Savelson ZM, Otto AR, Roy M. 2020. Forced choices reveal a trade-off between cognitive effort and physical pain. *Elife*. 9:e59410.
- Wardenaar KJ, van Veen T, Giltay EJ, de Beurs E, Penninx BW, Zitman FG. 2010. Development and validation of a 30-item short adaptation of the Mood and Anxiety Symptoms Questionnaire (MASQ). *Psychiatry research*. 179:101–106.

- Watts AT, Bachman MD, Bernat EM. 2017. Expectancy effects in feedback processing are explained primarily by time-frequency delta not theta. *Biological psychology*. 129:242–252.
- Watts AT, Bernat EM. 2018. Effects of reward context on feedback processing as indexed by time-frequency analysis. *Psychophysiology*. 55:e13195.
- Weinberg A, Ethridge P, Ait Oumeziane B, Foti D. 2021. Time-frequency analyses in event-related potential methodologies. *Oxford Handbook of Human EEG Frequency Analysis* New York: Oxford University Press.
- Weinberg A, Liu H, Hajcak G, Shankman SA. 2015. Blunted neural response to rewards as a vulnerability factor for depression: Results from a family study. *Journal of abnormal psychology*. 124:878.
- Weinberg A, Luhmann CC, Bress JN, Hajcak G. 2012. Better late than never? The effect of feedback delay on ERP indices of reward processing. *Cognitive, Affective, & Behavioral Neuroscience*. 12:671–677.
- Weinberg A, Riesel A, Proudfit GH. 2014. Show me the money: the impact of actual rewards and losses on the feedback negativity. *Brain and cognition*. 87:134–139.
- Westbrook A, Braver TS. 2015. Cognitive effort: A neuroeconomic approach. *Cognitive, Affective, & Behavioral Neuroscience*. 15:395–415.
- Westbrook A, Kester D, Braver TS. 2013. What is the subjective cost of cognitive effort? Load, trait, and aging effects revealed by economic preference. *PloS one*. 8:e68210.
- Westbrook A, Lamichhane B, Braver T. 2019. The subjective value of cognitive effort is encoded by a domain-general valuation network. *Journal of Neuroscience*. 39:3934–3947.
- Westbrook A, van den Bosch R, Määttä J, Hofmans L, Papadopetraki D, Cools R, Frank M. 2020. Dopamine promotes cognitive effort by biasing the benefits versus costs of cognitive work. *Science*. 367:1362–1366.
- Yan X, Otto AR. 2020. Cognitive effort investment and opportunity costs in strategic decision-making: An individual differences examination. *Personality and Individual Differences*. 167:110283.
- Yi W, Mei S, Zhang M, Zheng Y. 2020. Decomposing the effort paradox in reward processing: Time matters. *Neuropsychologia*. 137:107311.