

Midfrontal theta and pupil dilation parametrically track subjective conflict (but also surprise) during intertemporal choice

Hause Lin^a, Blair Saunders^a, Cendri A Hutcherson^a, & Michael Inzlicht^{a,b}

a. Department of Psychology, University of Toronto, Toronto, Canada

b. Rotman School of Management, Toronto, Canada

Corresponding author

Hause Lin

Department of Psychology, University of Toronto

1265 Military Trail

Toronto, ON, M1C 1A4, Canada

hause.lin@mail.utoronto.ca

Abstract

Many everyday choices are based on personal, subjective preferences. When choosing between two options, we often feel conflicted, especially when trading off costs and benefits occurring at different times (e.g., saving for later versus spending now).

Although previous work has investigated the neurophysiological basis of conflict during inhibitory control tasks, less is known about subjective conflict caused by competing subjective preferences. In this pre-registered study, we investigated subjective conflict during intertemporal choice, whereby participants chose between smaller immediate versus larger delayed rewards (e.g., \$15 today vs. \$22 in 30 days). We used economic modeling to parametrically vary eleven different levels of conflict, and recorded EEG data and pupil dilation. Midfrontal theta power, derived from EEG, correlated with pupil responses, and as predicted, these signals tracked even fine gradations of subjective conflict. Unexpectedly, both signals were also maximally enhanced when decisions were surprisingly easy. Therefore, these signals may track events requiring increased attention and adaptive shifts in behavioral responses, with conflict being only one type of such event. Our results suggest that the neural systems underlying midfrontal theta and pupil responses interact when weighing costs and benefits during intertemporal choice. Thus, understanding these interactions might elucidate how individuals resolve self-control conflicts.

Keywords: intertemporal choice; self-control; value-guided choice; conflict; theta oscillations; pupil dilation

1. Introduction

Many everyday decisions are value-guided. People have preferences—they value choice options to varying degrees—and then decide based on these subjective preferences (e.g., I prefer Android over iPhones, and savory over sweet foods). At the neural level, the brain assigns a subjective value to each available choice option and compares these values to arrive at a choice (Camerer 2013; Kable and Glimcher 2009; Konovalov and Krajbich 2016; Padoa-Schioppa 2011; Rangel et al., 2008). Because of the inherent cost-benefit trade-offs involved in choosing between options (e.g., save for later or spend money now; cookies or fruit for dessert), decision makers often feel conflicted when making value-guided decisions (Shenhav and Buckner 2014).

1.1. Objective versus subjective conflict

What we currently know about conflict during value-guided choice has largely been informed by studies using inhibitory control tasks (e.g., Stroop, go/no-go), whereby decisions are determined by objective states of the world (e.g., Botvinick et al., 2001). For example, on an incompatible (high-conflict) Stroop trial, reading the word would be incorrect but reading the color in which the word is printed in would be correct. Recent work, however, suggests that decisions based on objective states and subjective preferences involve slightly different processes (Polanía et al., 2014; Summerfield and Tsetsos 2012). Thus, drawing inferences about how people arbitrate between two closely valued options (e.g., Android vs. iPhone) from inhibitory control studies (e.g., is that word presented in red vs. green font) might be premature. Here, we examine the neurophysiological correlates of conflicts that arise from subjective preferences using

the classic intertemporal choice (delay discounting) task (Ainslie, 1975; Frederick et al., 2002; Thaler, 1981).

The intertemporal choice paradigm has been extensively used to investigate the psychological and neural underpinnings of self-control dilemmas and subjective value representation (Bernhardt et al., 2014; McClure et al., 2004; Zauberman and Urminsky 2016). Intertemporal preferences can be explained using formal economic models, and have been associated with many real-life behaviors requiring self-control, including pathological gambling, substance abuse, and social media usage (Dixon et al, 2003; Kollins, 2003; Shenhav et al., 2017). Crucially, this paradigm has often been used to investigate how different neural systems may contribute to competing valuations that give rise to self-control conflicts (Berns et al., 2007; McClure et al., 2007). Here, we investigate how different gradations of subjective conflict during intertemporal choice parametrically modulate two neurophysiological signals, midfrontal theta power and pupil dilation.

1.2. Midfrontal EEG conflict signals

Electroencephalography (EEG) is a temporally precise technique that is often used to investigate how conflict-related neural activity evolves over time (Cohen 2017; Yeung et al., 2004). Previous work suggests that conflict-related activity originates from the dorsal anterior cingulate cortex (dACC) and surrounding medial prefrontal cortical (mPFC) regions (Debener et al., 2005; Töllner et al., 2017; Ebitz and Platt 2015). Consistent with these findings, theta oscillations (~4–8 Hz) measured over midfrontal EEG electrode sites increase during high conflict trials (Cavanagh et al., 2012), and these theta dynamics are thought to implement adaptive control processes necessary

for resolving conflict (Cavanagh and Frank 2014; Cohen 2014b; Verguts 2017). In addition, theta oscillations have been proposed to underlie event-related components (ERPs) such as the N2 and error-related negativity that are observed when conflicting, mutually exclusive responses are activated simultaneously (e.g., Cavanagh et al., 2012; Yeung et al., 2004).

With a few exceptions (e.g., Nakao et al., 2010), however, most EEG studies of conflict have focused on objective response conflict during inhibitory control tasks. How these brain regions represent other forms of conflict, such as subjective conflict, remains less well-defined (Cohen 2014b). Further, to our knowledge, no EEG study has investigated midfrontal theta oscillations responses to fine gradations of conflict; instead, past work has relied on binary conflict, whereby conflict is either present or absent. Here, we assess theta power measured over midfrontal scalp electrodes while parametrically varying different levels of subjective conflict during intertemporal choice.

1.3. Conflict-related pupil dilation responses

Brain regions commonly implicated in value-guided choice include the orbitofrontal cortex and ACC, and these regions interconnect strongly with the brainstem nucleus locus coeruleus, which releases norepinephrine that is thought to modulate neural gain to optimize decision making (Aston-Jones and Cohen 2005a; Aston-Jones and Cohen 2005b; Aston-Jones and Waterhouse 2016; Berridge and Waterhouse 2003; Eldar et al., 2013). Although locus coeruleus-norepinephrine (LC-NE) gain-adjustment activity has been proposed to interact with EEG signals (Cavanagh and Frank 2014; Nieuwenhuis et al., 2005; Nieuwenhuis et al., 2011; Singer 2013; Verguts and Notebaert 2009; Womelsdorf et al., 2014), it remains a challenge to study these

proposed interactions because locus coeruleus activity can be difficult to measure in humans.

Pupil diameter, however, appears to be a promising noninvasive correlate of locus coeruleus activity and neural gain (Aston-Jones and Cohen 2005b; Murphy et al., 2011; Murphy et al., 2014; Rajkowski et al., 1994). For example, changes in pupil size have been associated with behaviors, such as exploit-explore trade-offs, that have been associated with LC-NE system activity and gain adjustment (Eldar et al., 2013; Eldar et al., 2016; Gilzenrat et al., 2010; Jepma and Nieuwenhuis 2011; Murphy et al., 2016; Warren et al., 2016). In addition, pupil responses are ideal for investigating conflict-related processes because they correlate with increased attention or mental effort during decision making (Kahneman & Beatty, 1966; Siegle et al., 2003; Simpson, 1969), autonomic arousal and ACC activity during inhibitory control task performance (Critchley et al., 2005; Laeng et al., 2011), and conflict during reinforcement learning (Cavanagh et al., 2014). Critically, recent studies have provided indirect evidence for LC-NE and EEG interactions by showing that pupil dilation correlates with EEG signals (e.g., theta oscillations) during perceptual and inhibitory control tasks (Dippel et al., 2017; Hong et al., 2014; Mückschel et al., 2016; Mückschel et al., 2017).

However, whether theta-pupil relationships are also present during value-guided choice remains untested. We therefore investigated how changes in pupil responses relate to parametric gradations in subjective conflict, and whether pupillary responses correlate with midfrontal theta power during intertemporal choice. We believe that showing such consilience—that similar basic processes are conserved across different types of decisions—will not only indicate that the theta-pupil associations generalize

across choice domains, but also that these correlations are robust and replicable, an issue of renewed importance in psychology and neuroscience (Button et al., 2013; Crandall and Sherman 2016; Open Science Collaboration 2015; Smaldino and McElreath 2016).

1.3. Present Study

Using a pre-registered economic modeling and parametric design (osf.io/7m9c2), we investigated whether even subtle gradations of subjective conflict during intertemporal choice parametrically modulate midfrontal theta and pupil responses. This work extends recent work showing theta-pupil correlations during inhibitory control tasks (Dippel et al., 2017).

Participants made intertemporal decisions several days before the main experiment. We then fitted the hyperbolic discounting model to each participant's data (Green and Myerson 2004), and parametrically varied intertemporal preferences and subjective choice conflict separately for each participant during a subsequent laboratory session (i.e., by using each participant's discount function to generate participant-specific delayed rewards). Previous work used this neurometric approach to show that specific brain regions encode the subjective value of delayed rewards during intertemporal decisions (Kable and Glimcher 2007; Peters and Büchel 2010). Here, we further show that economic modeling of the intertemporal choice task can provide insights into the neurophysiology of subjective conflict and self-control dilemmas involving cost-benefit trade-offs.

During the main task, we concurrently recorded EEG activity and pupil dilation as participants performed an intertemporal choice task with individually-tailored and model-

derived delayed rewards. Our results show that although theta power measured over midfrontal scalp electrodes and pupil dilation responses parametrically tracked even fine gradations of subjective conflict during intertemporal choice, both signals were, unexpectedly, enhanced when the decisions were surprisingly easy and involved little or no conflict. Thus, conflict itself may not be required to evoke midfrontal theta and pupil dilation responses. Our findings are consistent with past work suggesting that midfrontal theta is evoked by events that require increased attention and adaptive control, with conflict being just one type of such event (Cavanagh et al., 2012; Cavanagh and Frank 2014). Correlations between theta power and pupil responses suggest that these two signals might reflect activity in neural systems that jointly engage adaptive control processes (Verguts and Notebaert 2009), such as recruiting additional brain systems and adjusting neural gain that are necessary for optimizing decision making.

2. Methods

2.1. Participants

There were two sessions in this study. During session one, 219 participants (152 females, 64 males, 3 undisclosed; mean age 18.75 ± 1.87 SD) completed an intertemporal choice task online and we fitted the hyperbolic discount function to each participant's choices. We opted to use this discounting function because it has been shown to explain behavioral and neural data very well despite its simplicity (i.e., only one free parameter to be estimated) (Green and Myerson 2004; van den Bos and McClure 2013). As with previous work (Kable and Glimcher 2007), we then invited only participants who were clear hyperbolic discounters to complete session two, the main

laboratory experiment when neurophysiological activity was recorded as participants made intertemporal decisions.

68 participants (47 females, 21 males; mean age 18.47 ± 1.56 SD) completed session two, the main experiment. Before data collection, we pre-registered these procedures (osf.io/7m9c2), which were necessary because we planned to use each participant's hyperbolic function to parametrically vary intertemporal preferences and very fine gradations of subjective conflict (e.g., difference in subjective value between two intertemporal rewards = 0 or 1). All participants provided informed consent in accordance with policies of the university's institutional review board and had normal or correct-to-normal vision.

2.2. Experimental design and statistical analysis

The pre-registered design, data, and scripts can be found on Open Science Framework (osf.io/7m9c2). Minimum sample size for the main experiment was determined by running a power analysis in G*Power 3.1 (Faul et al., 2007): For 80% power ($\alpha = 0.05$), 33 participants were required, assuming small-to-medium effects ($f = 0.15$), and correlation among repeated measures = .50. We aimed instead for at least 60 participants, which gave us 95% power, assuming this effect size.

Statistical analyses were performed in R (R Core Team 2016). The design was entirely within-subjects; unless stated otherwise, all estimates and statistics were obtained by fitting two-level multilevel regression models (all factors and neurophysiological responses for each condition were nested within participants) with random intercepts (unstructured covariance matrix) using the R package lme4 (Bates et al., 2015). Probability values and degrees of freedom associated with each statistic

were determined using the Satterthwaite approximation, using the package `lmerTest` (Kuznetsova et al., 2016), and an r effect size was reported for fixed effects in each model. Bayes factors (BF) were computed by fitting Bayesian multilevel models using the R package `brms` (Bürkner 2016).

2.3. Stimuli and tasks

During session one, participants completed an online intertemporal choice task where they made 144 decisions. The immediate reward was always \$15 today and the delayed reward was \$15.50, \$24, \$42, \$71, \$107, or \$139, offered at a delay of 1, 10, 21, 50, 90, or 180 days (36 unique choice pairs). These values and delays were chosen such that they approximated those used in previous neuroimaging intertemporal choice studies (Kable and Glimcher 2007; Kable and Glimcher 2010). Each choice pair (e.g., \$15 in 0 days vs. \$139 in 10 days) was presented four times. Participants were told that there is no correct answer and they only have to choose the option they prefer. For each participant, we used logistic regression to estimate the indifference point at each delay and non-linear regression to fit the hyperbolic discount function $SV = A / (1 + kD)$, where SV is subjective value (expressed as the fraction of immediate reward), A is delayed reward amount, D is delay (in days), and k is a participant-specific constant, the only free parameter to be estimated in this model (Green and Myerson 2004). Each participant has a unique k parameter that describes the steepness of the discounting curve, with larger values reflecting steeper slopes. This parameter also captures individual differences in impulsivity, with larger values indicating greater impulsivity or temporal discounting. The hyperbolic discount function for each participant describes how any given delayed reward is translated into a subjective value for that participant.

As such, the function provides a principled way of quantifying the subjective value of any delayed reward.

We used each participant's hyperbolic discount function to generate idiosyncratic, participant-specific delayed rewards that allowed us to parametrically vary value difference for session two based on value difference between the immediate and delayed rewards. As with session one, the immediate reward for session two was always \$15 today. The participant-specific delayed rewards (e.g., \$24.14 in 10 days) had pre-determined subjective values of 4, 7, 10, 12, 14, 15, 16, 18, 20, 23, and 26 at three different delays (10, 30, and 60 days). We also included three no-brainer, 'catch', delayed rewards that served as control conditions and attention checks, one at each delay: \$15 in 10 days, \$15 in 30 days, and \$15 in 60 days. We expected these no-brainer trials to be the easiest or least conflicting choices. In total, there were 36 unique choice pairs, and each choice pair—including no-brainer choices—was presented with equal probability: three times per block for seven blocks (756 trials in total). On each trial during the EEG and eye tracking session, participants chose between a fixed immediate reward of \$15 today and a model-derived participant-specific delayed reward.

During session two, EEG, eye tracking, and corrugator supercilii facial electromyography (EMG) data were collected while participants made intertemporal decisions. EMG data were recorded for other analyses that are unrelated to this study and will not be reported here. Participants were told that they are taking part in a decision-making study and that there are no correct or wrong answers, and that they should simply state their preference in a series of choices. They were also told that at

the end of the experiment, they might receive one of their choices, which was randomly selected by the computer from the set of all their choices. At the end of the experiment, during debriefing, the experimenter presented each participant with 10 lottery tickets (two are winning tickets). If the participant selected the winning ticket, they received that randomly selected choice, which was paid in the form of an Amazon gift voucher that was emailed to them after the appropriate delay. Given this payment scheme, participants were told at the beginning of the experiment that they should make each choice as though it were the one they are actually going to receive.

Participants completed the task in a dimly-lit room and rested their heads on a chinrest. All stimuli were presented using PsychoPy (Peirce 2007; Peirce 2009) and since the immediate reward was \$15 for all trials, the display was simplified to minimize eye movement by presenting only the delayed reward at the center of the screen with a black background (Fig. 1). At a viewing distance of 93 cm, the stimulus (delayed reward) subtended approximately 2.15° horizontally and 0.93° vertically. Participants had up to three seconds to decide whether to choose the immediate reward (\$15) or the model-derived delayed reward by pressing either the F or J key (counterbalanced across participants) with their left or right index finger. On each trial, a red central fixation cross appeared for 150 ms. The delayed reward was then displayed in white at the center and remained on screen until the participant responded or until a maximum of 3000 ms had passed. Once the delayed reward had been removed from the screen, a blank black screen appeared for a random interval that varied randomly from 300 to 700 ms. Participants first completed 15 practice trials with feedback showing them what they had chosen (\$15 in 0 days or a model-derived delayed reward). They then completed 7

actual blocks of 108 trials each. Each choice pair was presented three times per block and thus 21 times over 7 blocks. After each block, participants were given the opportunity to rest. They were also told to try to avoid blinking and movement excessively during the experiment. The intertemporal choice task took about 30 minutes to complete.

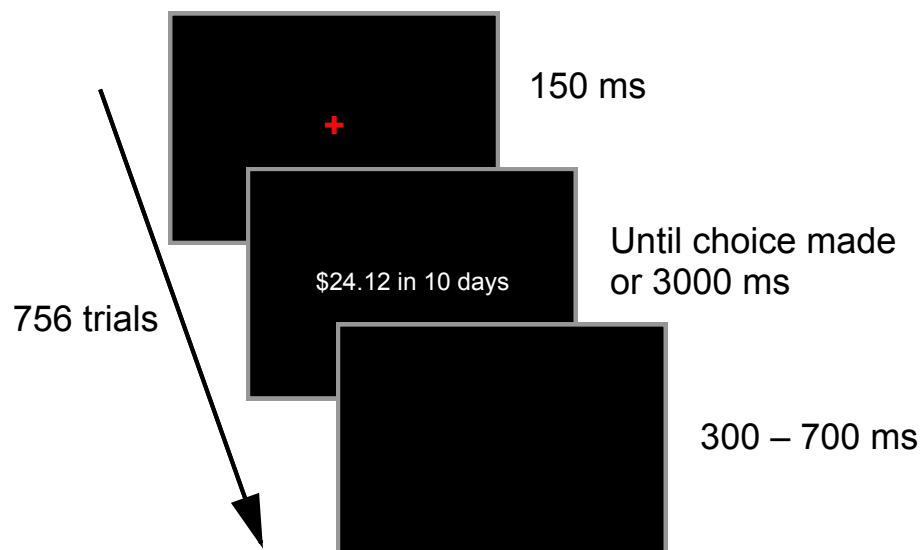


Fig. 1. Intertemporal choice task trial sequence. The sequence of events within a trial is shown. On each of 756 trials, participants pressed either the F or J key (counterbalanced across participants) to choose between an immediate (\$15 today) and a participant-specific model-derived delayed reward (e.g., \$24.14 in 10 days). Participants were told at the beginning of the experiment that the immediate reward was always \$15 today and would never be presented visually. Participants had up to 3 s to decide. The inter-trial interval varied randomly from 300 to 700 ms. Seven blocks of 108 choices each were presented. Each of 36 unique choice pairs (including no-brainer choices) was presented three times per block.

2.4. Identifying choice outliers

To identify choice outliers, we analyzed behavioral responses for no-brainer catch choices (\$15 in 0 days vs. \$15 in 10, 30, or 60 days) where we expected participants to always prefer the immediate reward of \$15 today. For each participant, we calculated the percentage of no-brainer trials whereby they made the 'wrong' choice (chose \$15 in 10, 30, or 60 days rather than \$15 today). We then used a robust median absolute deviation outlier detection method to identify participants whose error percentage was three or more median absolute deviations from the median error percentage (Leys et al., 2013). Nine participants made the 'wrong' choice (chose delayed reward) too frequently on no-brainer choices (mean 61.33%; range 26.90–95.00%), and were excluded from all analyses. The remaining 59 participants made 5.50% (range 0–23.81%) 'wrong' choices.

2.5. Adjusting subjective values of delayed rewards

Based on the hyperbolic function modeling, we expected participants to experience maximum decision conflict (i.e., theoretical indifference point) when the immediate and delayed rewards have the same subjective values. Theoretically, when both intertemporal options have the same subjective value, participants should choose either intertemporal reward 50% of the time and should also respond slowest. However, previous value-based decision-making studies have shown that it is common to observe discrepancies between theoretical (i.e., based on modeling) and empirical (i.e., actual behavior) indifference points (Kolling et al., 2012; Kolling et al., 2016; Shenhav et al.,

2014). Such discrepancies could lead to incorrect conclusions (Shenhav et al., 2014), especially when the study requires fine differences in subjective values.

We found that our theoretical and empirical indifference points did not perfectly coincide, in that participants had a slight preference for the delayed reward at the theoretical point of indifference (Fig. 2A), suggesting that the subjective value of the delayed rewards were imprecise. Following previous work (Shenhav et al., 2014; Shenhav et al., 2016), we fitted three logistic regressions (one for each intertemporal delay) to each participant's behavioral choices to determine three empirical indifference points at each intertemporal delay, which allowed us to infer from participant's choices the subjective value of each delayed reward. We used the difference between theoretical and empirical difference points to adjust the subjective value of the delayed rewards. The adjusted subjective values would provide more accurate estimates of value difference and decision conflict, and was used as a regressor for all analyses.

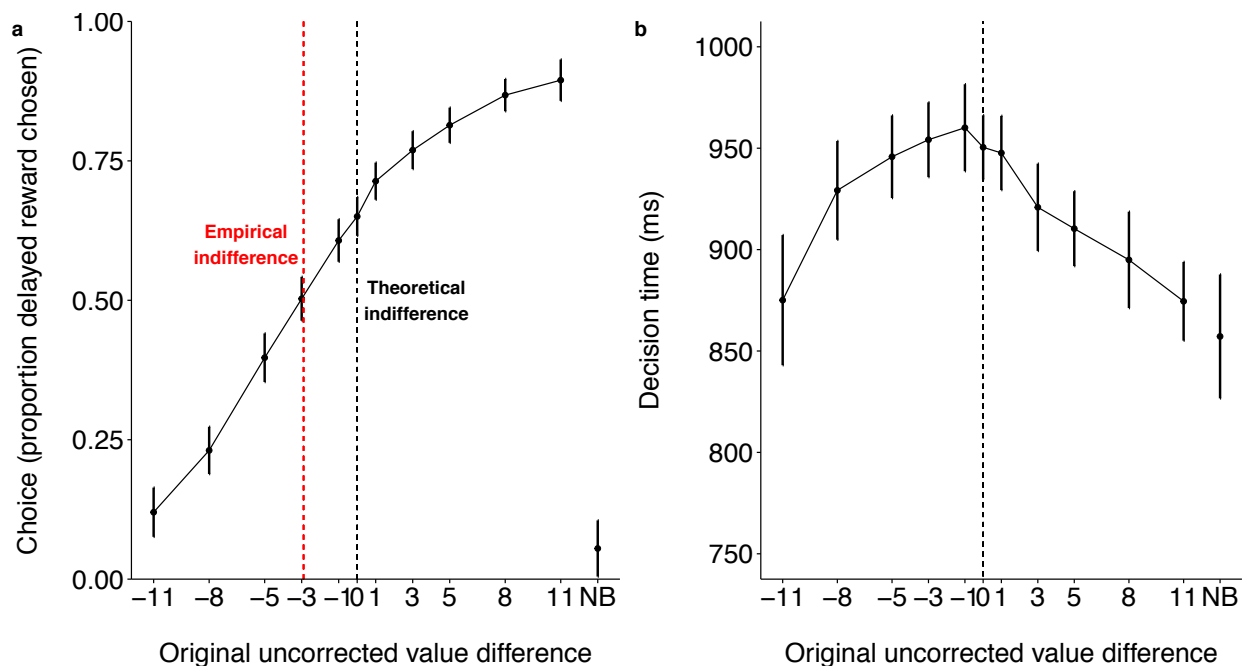


Fig. 2. Uncorrected choice proportion and decision time. (A) Sigmoid function for proportion of delayed reward chosen. When difference value < 0 , the immediate reward should be chosen more frequently. When difference value > 0 , the delayed reward should be preferred. (B) Inverted-U relationship between difference value and decision time. Black dashed line is the theoretical indifference point (model-derived value difference is 0) where participants were expected to be most conflicted. Red dashed line is the empirical indifference point where participants were choosing as though they were experiencing the most decision conflict. Note the leftward shift of the indifference point. NB refers to no-brainer choice. Error bars indicate 95% confidence intervals.

2.6. EEG recording and preprocessing

Electrophysiological signals were measured via EEG and facial electromyography (EMG) and sampled at 1024 Hz. Impedances were ≤ 5 k Ω during recording. Continuous EEG activity was measured over seven cortical midline sites (Fpz, Fz, FCz, Cz, CPz, Pz, Oz) using Ag/AgCl electrodes embedded in a stretched Lycra cap (Electro-Cap International, Eaton, OH). Because we had not intended to localize neural sources when designing the study and were primarily interested in conflict-related responses, we recorded only from midline electrodes and focused primarily on midfrontal sites (i.e., FCz) where conflict activity has typically been observed (Cavanagh et al., 2012; Nakao et al., 2010; Yeung et al., 2004). Vertical electrooculography (VEOG) was recorded around the right eye with two electrodes. Signals were amplified using ANT TMSi Refa8 device (Advanced Neuro Technology, Enschede, The Netherlands), grounded to the forehead, and referenced online to the

average of all electrodes. Offline, EEG signals were re-referenced to the average of electrodes placed on the two earlobes. During pre-processing, data were high-pass filtered at 0.1 Hz (12 dB/oct, zero phase-shift Butterworth filter) and eye blinks were removed using independent component analysis in EEGLAB (Delorme et al., 2007; Delorme and Makeig 2004).

Time-frequency calculations were computed using custom MATLAB (MathWorks) scripts (Cavanagh et al., 2012; Cohen 2014a). EEG data were segmented into long epochs of 5000 ms (–2500 to 2500 ms relative to event onset) to avoid potential time-frequency decomposition edge artifacts. Time-frequency measures were computed by multiplying the fast Fourier transformed (FFT) power spectrum of single-trial EEG data with the FFT power spectrum of a set of complex Morlet wavelets, and taking the inverse FFT. The wavelet family is defined as a set of Gaussian-windowed complex sine waves, $e^{-i2\pi t f} e^{-t^2/(2\sigma^2)}$, where t is time, f is frequency (increased from 1 to 30 Hz in 40 linearly spaced steps) and σ defines the width (decreased from 0.318 to 0.053) or number of cycles (increased from 4 to 10 in logarithmically spaced steps) of each frequency band. The end result of this process is identical to time-domain signal convolution. Time-frequency power was defined as $Z(t)$ (power time series: $p(t) = \text{real}[z(t)]^2 + \text{imag}[z(t)]^2$), and was normalized by conversion to a decibel scale, $10 \log_{10} [\text{power}(t) / \text{power}(\text{baseline})]$, allowing a direct comparison of effects across frequency bands. For stimulus-locked time-frequency power, epochs were baseline normalized for each frequency by the average power from –500 to –200 ms before stimulus onset. Values for statistical analysis were summed over time and frequency (340 to 840 ms, 3.2 to 7.7 Hz), and were based on inspection of the grand average time-frequency

power plots (collapsed localizer approach) (Luck and Gaspelin 2017). For peri-response time-frequency power, epochs were baseline normalized for each frequency by the same pre-stimulus average baseline power described above. Values for statistical analysis were summed over time and frequency (−160 to 40 ms, 3.2–7.7 Hz), and were based on inspection of the grand average time-frequency power plots. To visualize theta power time course for each experimental condition, we also computed theta power over time by computing and plotting mean theta power (3.2–7.7 Hz) at each time point.

To compute event-related potentials (ERPs), pre-processed (0.1 Hz high-pass filtered) EEG signals were then digitally low-pass filtered at 20 Hz (12 dB/oct, zero phase-shift Butterworth filter). Epochs were checked for artifacts and automatically rejected using the following criteria: voltage steps of more than 15 μV between sample points, a voltage difference of 150 μV within 150 ms intervals, voltages above 85 μV and below −85 μV , moving window peak-to-peak voltages exceeding 150 μV (150 ms window with 50 ms step size), and spectra estimates that deviated from baseline by ± 50 dB in the 0–2 Hz frequency window (to detect eye movements) and +25 or −100 dB in the 20–40 Hz frequency window (to detect muscle activity). Mean amplitudes within a selected time window were reported for all ERPs. For stimulus-locked ERPs, epochs were baseline-corrected by the average power from −200 to 0 ms relative to stimulus onset. For response-locked ERPs, epochs were baseline-corrected by the average power from −200 to −100 ms relative to response onset. Time windows for statistical analysis for stimulus- (500 to 800 ms) and response-locked (0 to 100 ms) ERPs were determined based on inspection of the grand-average ERP waveforms (Luck and Gaspelin 2017). Because the stimulus-locked N2 component has typically been

associated with response conflict during inhibitory control tasks (Yeung et al., 2004), we also visually inspected the grand-average ERP waveform to localize the second negativity after stimulus onset (i.e., 340 to 440 ms).

2.7. Eye tracking and pupil dilation preprocessing

Pupillometric data were recorded using the EyeLink 1000 Desktop Mount eye tracker (SR Research, Mississauga, Ontario, CA). The EyeLink system was configured using a 35-mm lens, 5-point gaze location calibration, monocular right-eye sampling at a rate of 1000 Hz, and centroid fitting for pupil area recordings. Pupil measures reflected pupil area. All data processing were performed using custom R scripts. Blink artifacts detected using the EyeLink blink detection algorithm were removed using linear interpolation from 100 ms prior to and 200 ms post blink onset (Cavanagh et al., 2014). Because blinks usually do not last longer than 500 ms, any time window where pupil data were missing for ≥ 500 ms was not interpolated and instead treated as missing data.

Continuous data were epoched (-500 to 4000 ms) surrounding the onset of stimulus. Trials with decision times ≤ 250 ms or above the decision time deadline of 3000 ms were excluded. Pupil responses were calculated as the percent change from the trial-specific pre-fixation baseline mean (-500 to -300 ms: only a black blank screen was shown). Stimulus-induced pupil dilation responses begin with a light-induced constriction and recovery that last for about 1000 ms, and pupil dilations are very slow and thus are lagged in time to eliciting events, often peaking about 1000 ms (Cavanagh et al., 2014; van Steenbergen and Band 2013).

To determine the time window where changes in mean pupil dilation response were curvilinearly associated with value difference (statistically significant quadratic coefficient), we fitted a quadratic model at each millisecond from 1001 to 3000 ms after stimulus presentation and controlled for error rates with false discovery rate (FDR) correction (Benjamini and Hochberg 1995). We used this data-driven mass univariate approach because pupil dilation responses are much more protracted than neural responses and it can be difficult to visually determine the temporal dynamics of an effect. The first 1000 ms was excluded from this analysis because stimulus-induced pupil dilation responses begin with a light-induced constriction and recovery that last for about 1000 ms, and pupil responses are slow and thus are lagged in time to eliciting events, often peaking after about 1000 ms (Cavanagh et al., 2014; van Steenbergen and Band 2013). The time window from 1110 to 3000 ms survived FDR correction ($p < .05$) and was used to calculate the mean pupil dilation response associated with each experimental condition.

2.8. Theta-pupil correlations over time

To integrate midfrontal theta and pupil data, we first used the region-of-interest method by correlating across all participants mean theta power (3.2–7.7 Hz from 340 to 840 ms) with mean pupil data (1001 to 3000 ms) associated with each experimental condition computed for each participant separately. To further probe theta-pupil relationships over time, we explored correlations across the entire time series (rather than just region-of-interest) for EEG and pupil data (Chmielewski et al., 2017). We downsampled both the EEG and pupil data to 50 Hz (each time point is 20 ms), and then computed the correlation coefficient across all participants, using each time point

from the entire EEG theta series (–500 to 1500 ms) with each time point from the entire pupil time series (–500 to 3000 ms). 17776 correlations were performed, and we used FDR correction to control for error rates, and visualized only correlations that survived FDR correction ($p < .05$).

3. Results

3.1. Choice and reaction time reflect subjective value comparison and conflict

Choice and decision time patterns suggest that participants had compared the subjective values of the immediate and delayed rewards and experienced subjective decision conflict (Fig. 3). When the immediate and delayed rewards were equally desirable (value difference = 0), participants chose the delayed reward 51% of the time (Fig. 3A). A logistic regression indicated that choice was predicted by value difference, in that participants were more likely to choose the delayed over the immediate reward (coded as 1 and 0 respectively) as value difference increased from –11 to +11 ($b = 0.28$, $z = 91.08$, $p < .001$). As predicted, the relationship between value difference and decision time was curvilinear (quadratic $b = -0.13$, $SE = 0.01$, $t(1178) = -14.71$, $p < .001$, $r = .39$), suggesting that participants could discern even fine differences in subjective value (Fig. 3B): Decision time was slowest (mean = 1067 ms; $SD = 139$ ms) when the immediate and delayed rewards had the same subjective value (value difference = 0); they were much faster when the immediate reward was clearly better than the delayed reward (value difference = –11; mean = 963 ms; $SD = 145$ ms) or vice versa (value difference = +11; mean = 843 ms; $SD = 67$ ms). Decision times for no-brainer choices were also relatively fast (mean = 857 ms; $SD = 112$ ms; Fig. 3B), suggesting little subjective conflict.

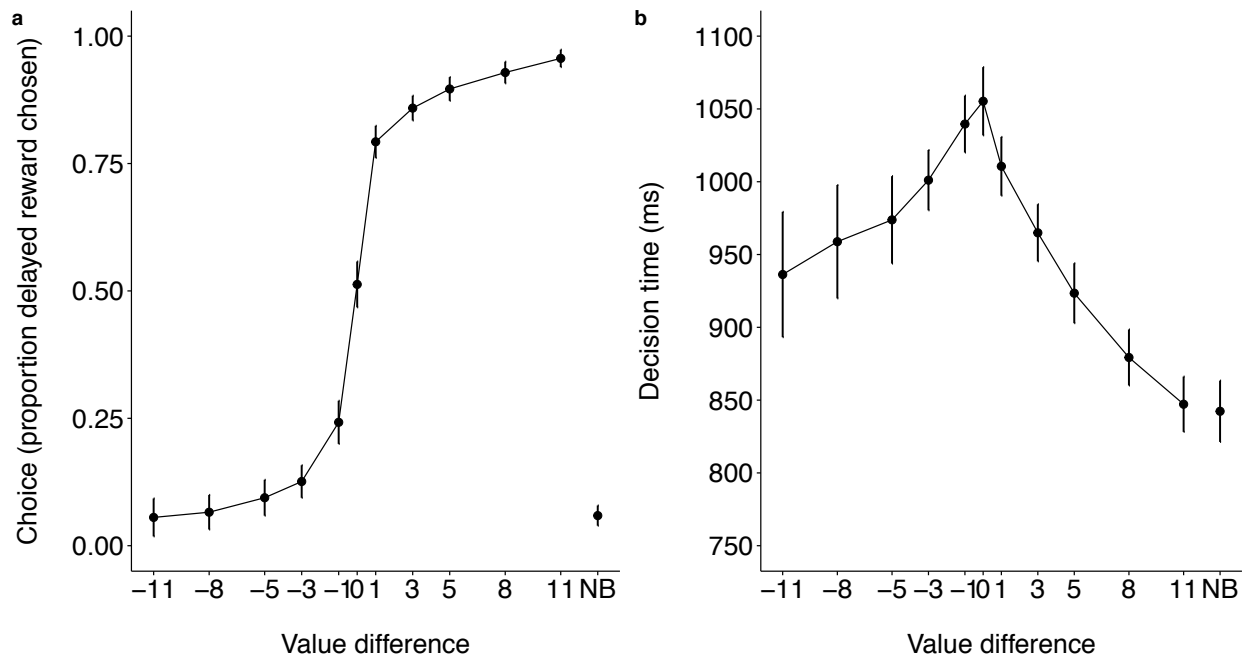


Fig. 3. Choice proportion and decision time based on adjusted value difference. Logistic regression was used to adjust subjective values for each participant based on observed choice. (A) Sigmoid function for proportion of delayed reward chosen. When value difference was 0, the immediate and delayed rewards had the same subjective value of 15. When difference values were negative, the delayed rewards had smaller subjective values relative to the immediate reward and were chosen less frequently. When difference values were positive, delayed rewards had larger subjective values and were chosen more frequently. (B) Inverted-U relationship between value difference and decision time. NB refers to the no-brainer choice. Error bars indicate 95% confidence intervals.

3.2. EEG dynamics: Midfrontal theta power and event-related potentials (ERPs)

We observed a robust increase in stimulus-locked theta power (3.2–7.7 Hz) over midfrontal scalp electrodes after choice presentation. Because previous studies have observed strongest conflict effects on electrode FCz (e.g., Cavanagh et al., 2012), we also focus our analyses on this electrode. Theta power (340 to 840 ms after choice onset) was enhanced when the immediate and delayed rewards had similar subjective values (Fig. 4A). As predicted, value difference was curvilinearly related to theta power (quadratic $b = -0.26$, $SE = 0.05$, $t(1181) = -5.60$, $p < .001$, $r = .16$), indicating that theta power decreased as it became increasingly clearer that one reward had a higher subjective value than the other (Fig. 4C). Additional analyses suggested that this effect was maximal at electrode FCz: Although the non-significant interaction between electrode (FPz, Fz, FCz, Cz, CPz, Pz, Oz) and quadratic coefficient suggests that the quadratic effect was observed across all electrode sites, ($F(6, 12126) = 0.32$, $p = .927$), the effect was strongest at FCz ($r = .16$), and weaker at frontopolar (FPz: $p = .003$, $r = .07$), posterior (Pz: $p < .001$, $r = .10$) and occipital (Oz: $p = .007$, $r = .07$) sites.

Although the inverted-U relationship between value difference and theta power appears to suggest that midfrontal theta parametrically tracks fine gradations of subjective conflict (Fig. 4), three additional findings indicate that theta power reflects more than just variation in decision conflict. First, a conflict account would predict that no-brainer choices should be the least conflicting of all choices and should therefore evoke minimal theta power. However, unexpectedly, theta power for no-brainer choices was significantly and robustly higher than the mean theta power of all other choices combined ($b = 0.35$, $SE = 0.06$, $t(1348) = 6.11$, $p < .001$, $r = .16$; Fig. 4). Moreover, theta power for no-brainer choices was not significantly different from that associated with the

most conflicting choices whereby value difference is 0 ($b = -0.14$, $SE = 0.09$, $t(292) = -1.55$, $p = .122$, $r = .09$). To supplement this null finding, we computed a Bayes Factor (BF) to test two hypotheses ($H_0: \theta_{\text{no-brainer}} = \theta_{\text{most-conflict}}$; $H_1: \theta_{\text{no-brainer}} < \theta_{\text{most-conflict}}$), and found moderate evidence favoring the hypothesis that theta power for no-brainer and the most conflicting choices were in fact equal ($BF_{01} = 4.39$), despite no-brainer choices being an easy decision. Second, theta power for all choices was stronger when delayed rewards were presented sooner (10 days) rather than later (30 or 60 days) ($b = -0.002$, $SE = 0.001$, $t(1196) = -2.38$, $p = .017$, $r = .07$), suggesting that theta power also tracks the immediacy or saliency of the delayed reward. Third, we included decision time in the model but it did not predict theta power ($b = -0.04$, $SE = 0.13$, $t(480) = -0.33$, $p = .741$, $r = .02$), and all results were similar after controlling for decision time, suggesting that theta power reflected more than just decision time or choice difficulty. Taken together, these three findings suggest that midfrontal theta might indicate the need to increase attention and engage adaptive control, rather than track conflict *per se*.

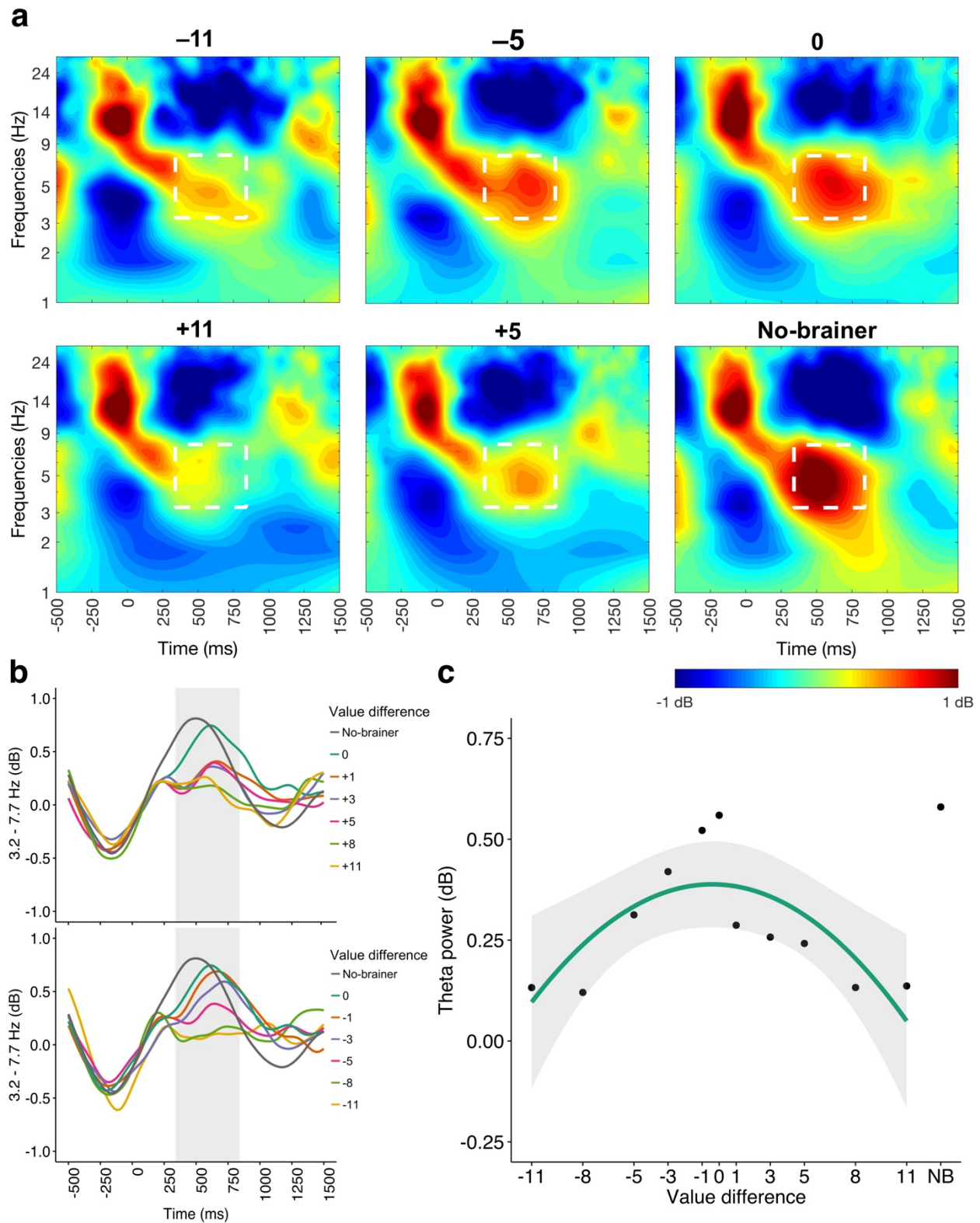


Fig. 4. Theta power enhancement after stimulus presentation over midfrontal scalp electrode (FCz), collapsed over different intertemporal delays (10, 30, and 60 days).

Increased power (3.2–7.7 Hz) was observed between 340 to 840 ms. (A) Theta power for selected value differences of –11, –5, 0, +5, +11, and no-brainer choice. White-dashed box shows region of interest used to compute mean theta power. (B) Theta power (3.2–7.7 Hz) time course. Top and bottom rows show positive and negative value differences respectively. (C) Curvilinear relationship between value difference and theta power. NB refers to no-brainer choice. Error bars indicate 95% confidence intervals.

Given the midfrontal theta power findings and previous studies on conflict-related ERPs, we also expected to subjective conflict to modulate stimulus-locked ERPs at midfrontal regions, specifically the N2. However, unlike previous studies on objective response conflict using inhibitory control tasks (Yeung et al., 2004), subjective conflict in our study did not modulate the N2 component (340 to 440 ms; quadratic $b = 0.12$, $SE = 0.20$, $t(1179) = 0.62$, $p = .538$, $r = .02$), but instead modulated a positive-polarity ERP over the FCz electrode from 500 to 800 ms after choice onset (Fig. 5A). Value difference was curvilinearly related to the amplitude of this ERP (Fig. 5B; quadratic $b = -0.51$, $SE = 0.20$, $t(1220) = -2.50$, $p = .013$, $r = .07$), suggesting that this ERP also tracked fine gradations of subjective conflict during intertemporal choice, though the effect was only modest in size. The amplitude of this ERP was associated with decision time ($b = -1.23$, $SE = 0.56$, $t(856) = -2.20$, $p = .028$, $r = .07$), but not whether delayed rewards were presented sooner or earlier ($b = -0.004$, $SE = 0.004$, $t(1192) = -1.22$, $p = .222$, $r = .04$). As with theta power, this ERP also appeared to track more than just conflict. The amplitude of this ERP for no-brainer choices was larger than that associated with all the other choices combined ($b = 1.17$, $SE = 0.23$, $t(1349) = 5.10$, $p < .001$, $r = .14$; Fig. 5B).

The amplitude for no-brainer choices did not significantly differ from that associated with the most conflicting choices ($b = 0.31$, $SE = 0.35$, $t(288) = 0.87$, $p = .386$, $r = .05$), and a Bayesian analysis found strong evidence favoring the hypothesis that ERP amplitudes for these two types of choices were in fact equal ($BF_{01} = 30.77$).

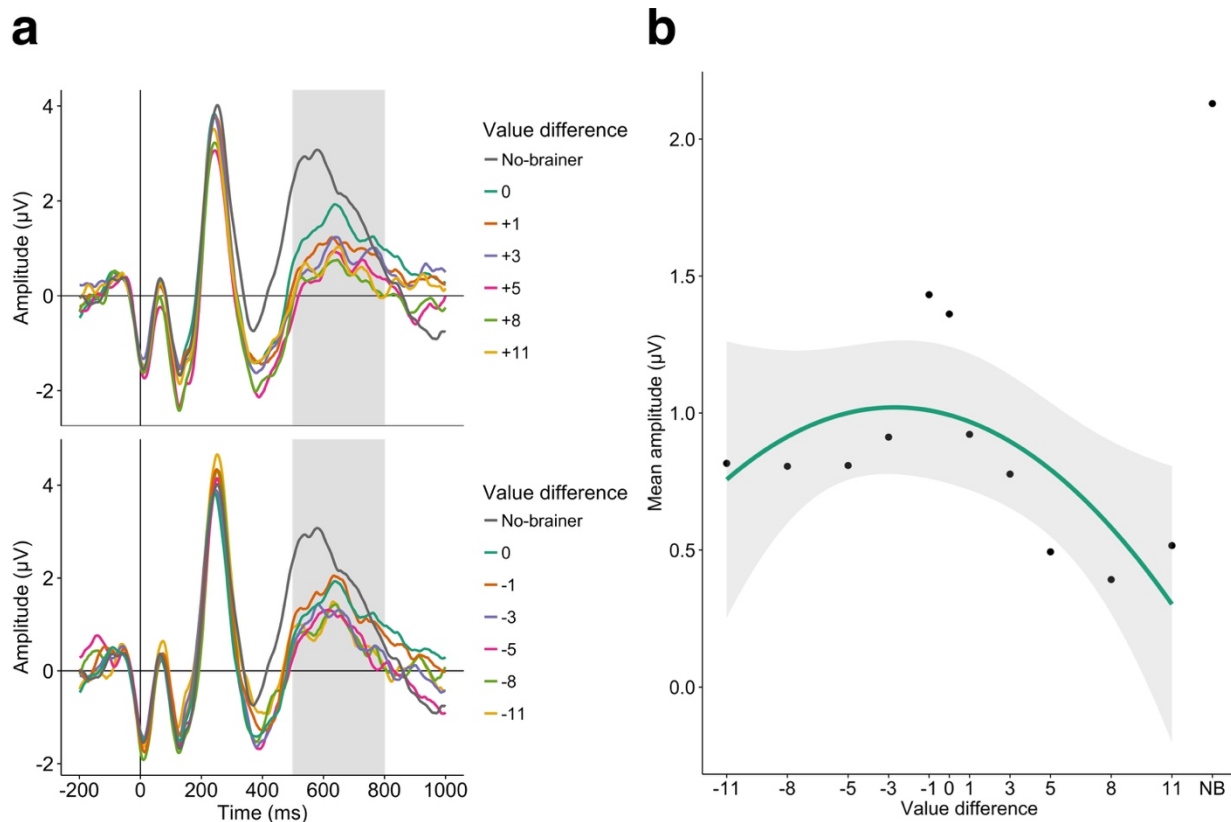


Fig. 5. Event-related potential after stimulus presentation at FCz electrode. (A) A positivity was observed around 500–800 ms. (B) Mean amplitude of positivity for each value difference and no-brainer choice. NB refers to no-brainer choice. Error bars indicate 95% confidence intervals.

Because previous work on conflict using inhibitory control tasks found that response-locked midfrontal signals tracked binary high versus low conflict (e.g., Cavanagh et al., 2012), we therefore predicted in our pre-registration that these response-locked conflict signals would track different levels of subjective conflict. Indeed, as with previous work, peri-response (−360 to 140 ms relative to response onset) theta power (3.2–7.7 Hz) parametrically tracked fine gradations of subjective conflict during intertemporal decisions (Fig. 6A). Value difference was curvilinearly related with theta power ($b = -0.22$, $SE = 0.05$, $t(1183) = -4.54$, $p < .001$, $r = .13$; Fig. 6C). As with stimulus-locked theta power, peri-response theta power was stronger when delayed rewards were presented sooner (10 days) rather than later (30 or 60 days) ($b = -0.002$, $SE = 0.001$, $t(1204) = -2.22$, $p = .027$, $r = .06$), suggesting that theta power might track the immediacy or saliency of the delayed reward. After including decision time in the model, the curvilinear relationship between theta power and value difference remained significant ($b = -0.18$, $SE = 0.05$, $t(1228) = -3.51$, $p < .001$, $r = .10$), suggesting that theta power reflected more than just decision time or choice difficulty. Peri-response theta power for no-brainer choices was significantly and robustly higher than the mean theta power of all other choices combined ($b = 0.36$, $SE = 0.06$, $t(1351) = 6.35$, $p < .001$, $r = .17$; Fig. 6C), suggesting that midfrontal theta tracks more than just conflict. Moreover, theta power for no-brainer choices was not significantly different from that associated with the most conflicted choices whereby value difference is 0 ($b = -0.03$, $SE = 0.09$, $t(293) = -0.36$, $p = .718$, $r = .02$); a Bayesian analysis also found strong evidence favoring the hypothesis that theta power for no-brainer and the most conflicting choices were equal ($BF_{01} = 11.84$). Taken together, these findings suggest

that variations in intertemporal preferences and conflict modulate midfrontal theta power.

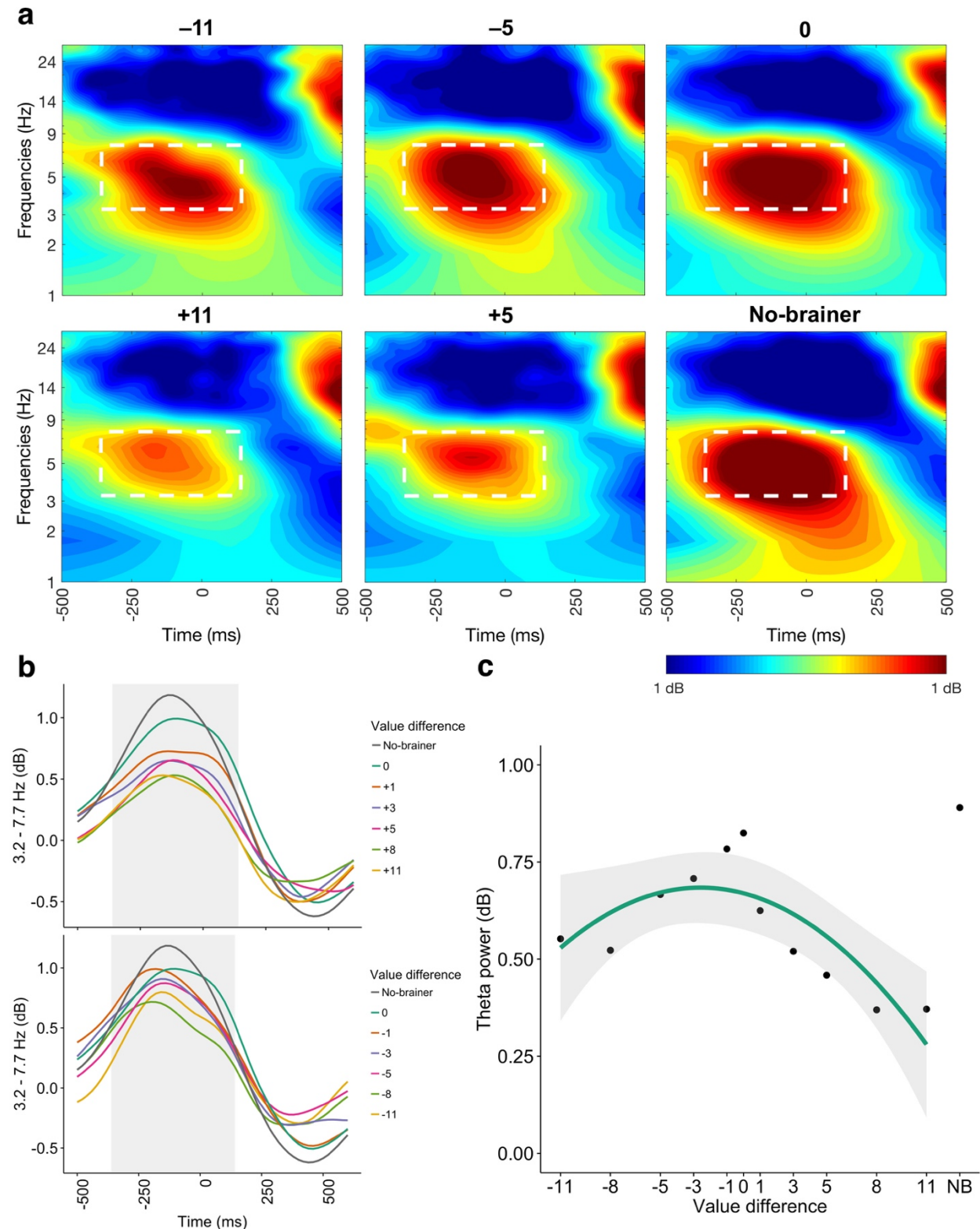


Fig. 6. Theta power enhancement after around response over midfrontal scalp electrode (FCz), collapsed over different intertemporal delays (10, 30, and 60 days). Increased power (3.2–7.7 Hz) was observed between –360 to 140 ms around response onset. (A) Theta power for selected value differences of –11, –5, 0, +5, +11, and no-brainer choice. White-dashed box shows region of interest used to compute mean theta power. (B) Theta power (3.2–7.7 Hz) time course. Top and bottom rows show positive and negative value differences respectively. (C) Curvilinear relationship between value difference and theta power. NB refers to no-brainer choice. Error bars indicate 95% confidence intervals.

Finally, in a similar peri-response window (0 to 50 ms), we also observed a peri-response ERP that was parametrically modulated by subjective conflict during intertemporal choice (Fig. 7A). This ERP resembled neural responses typically observed following correct responses during inhibitory control tasks (Vidal et al., 2000), as well as the conflict negativity that has been shown to track binary high versus low subjective conflict (Di Domenico et al., 2016; Nakao et al., 2010). Value difference was curvilinearly associated with the amplitude of this ERP (quadratic $b = 0.76$, $SE = 0.21$, $t(1182) = 3.58$, $p < .001$, $r = .10$), but whether delayed rewards were presented sooner or earlier was not associated with amplitude, ($b = -0.001$, $SE = 0.004$, $t(1197) = -0.30$, $p = .766$, $r = .10$). After including decision time in the model, the quadratic relationship remained significant (quadratic $b = 0.63$, $SE = 0.23$, $t(1227) = 2.82$, $p = .005$, $r = .08$). Unlike the other EEG responses reported earlier, the amplitude of this ERP for no-brainer choices was not larger than that associated with all the other choices combined ($b = -0.42$, $SE =$

0.26, $t(1356) = -1.63$, $p = .102$, $r = .04$; Fig. 7). Taken together, these findings suggest that subjective conflict induced by competing subjective preferences parametrically modulates this peri-response negativity.

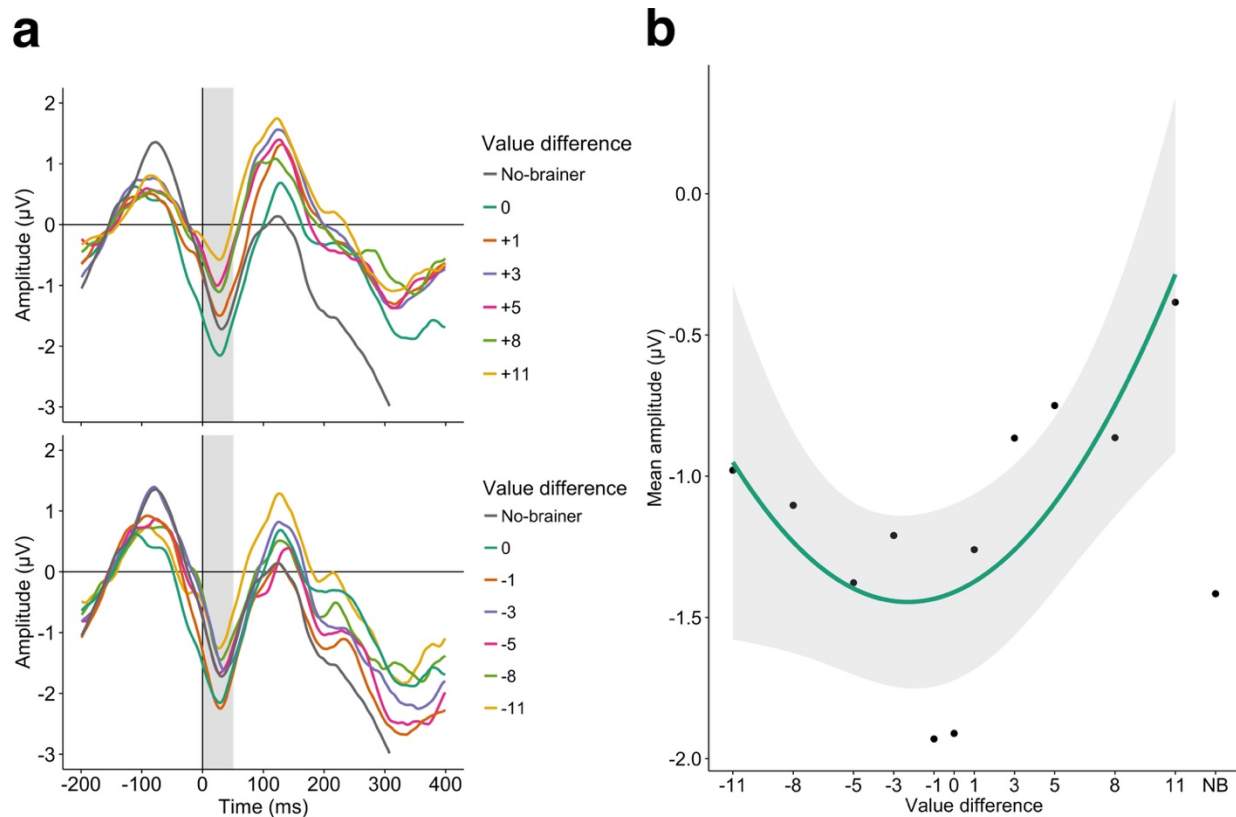


Fig. 7. Event-related potential around response onset at FCz electrode. (A) The conflict negativity was observed around 0–50 ms. (B) Mean amplitude of conflict negativity for each value difference and no-brainer choice. NB refers to no-brainer choice. Error bars indicate 95% confidence intervals.

In summary, we found that having competing subjective preferences for different intertemporal rewards induces subjective conflict, which parametrically modulated stimulus- and response-locked theta power (3.2–7.7 Hz) and ERPs measured over

midfrontal scalp electrodes (FCz). However, the surprisingly easy no-brainer choices also evoked enhanced midfrontal theta, and theta power was also enhanced when delayed rewards were presented sooner rather than later. These findings suggest that midfrontal theta power do not track conflict *per se*, but might track motivationally relevant events that require attending to, such as high conflict or surprisingly easy no-brainer choices. Interestingly, our subjective conflict in our value-guided choice paradigm did not modulate the N2 component that is usually associated with conflict effects (Yeung et al., 2004). Instead, subjective conflict in our intertemporal choice task modulated a stimulus-locked positivity (Fig. 5) that resembled the early P3 component, which has been associated with decisions processes that reflect phasic LC-NE system activity (Nieuwenhuis et al., 2005; Nieuwenhuis et al., 2011). In addition, the response-locked conflict negativity was the only signal that tracked just subjective conflict but not the immediacy of the delayed reward or the surprising no-brainer choices. Thus, along with previous studies, our findings suggest much consilience across different types of decisions (e.g., inhibitory control, value-guided decisions) and EEG signals (e.g., theta power, ERPs), but more work has to be done to address the details such as how the time courses different decision types differ and why no-brainer choices also enhance theta power.

3.3. Pupil dilation responses

We found that subjective conflict parametrically modulated post-stimulus pupil dilation responses (Fig. 8). Value difference was curvilinearly related to pupil dilation responses (quadratic $b = -0.64$, $SE = 0.14$, $t(1137) = -4.47$, $p < .001$, $r = .13$), indicating that pupil responses decreased as one reward became more desirable than the other.

Pupil responses were not influenced by whether delayed rewards were presented sooner or later ($b = -0.005$, $SE = 0.003$, $t(1158) = -1.58$, $p = .114$, $r = .05$). All the above effects were similar when decision time was included in the model (quadratic $b = -0.54$, $SE = 0.15$, $t(1179) = -3.58$, $p < .001$, $r = .10$).

As with EEG signals, pupil responses seem to track more than just conflict. Pupil responses for no-brainer choices were larger than that associated with all the other choices combined (quadratic $b = 0.67$, $SE = 0.17$, $t(1296) = 3.93$, $p < .001$, $r = .11$). Pupil responses for no-brainer choices and the most conflicting choices did not significantly differ ($b = -0.051$, $SE = 0.25$, $t(280) = -0.20$, $p = .842$, $r = .01$), and there is strong evidence favoring the hypothesis that pupil responses for these two types of choices were equal ($BF_{01} = 30.57$).

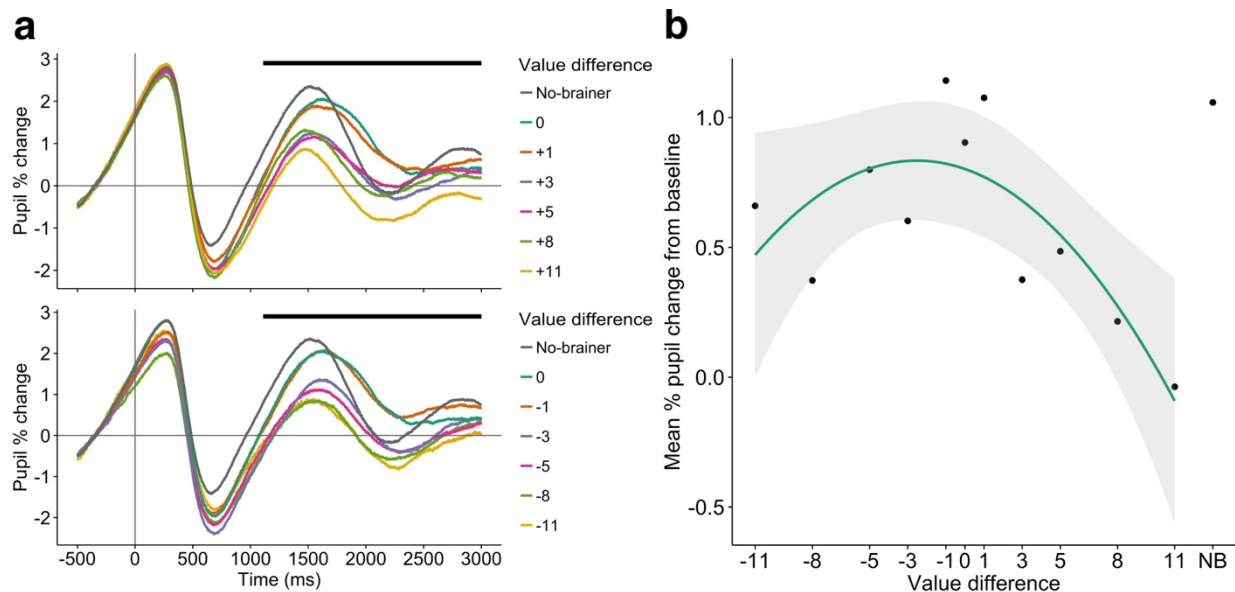


Fig. 8. Pupil dilation response after stimulus presentation. (A) Pupil dilation responses tracked value difference. Black horizontal line shows time points (1110 to 3000 ms) that survived FDR correction ($p < .05$). (B) Mean pupil dilation response (1110 to 3000 ms)

for each value difference and no-brainer choice. NB refers to no-brainer choice. Error bars indicate 95% confidence intervals.

3. 4. Pupil responses associated with EEG dynamics

We performed within-person multi-level model analysis to integrate midfrontal and pupil data. We correlated theta power (mean power: 3.2–7.7 Hz, 340 to 840 ms) with pupil dilation (mean pupil size: 1001 to 3000 ms) associated with each experimental condition computed for each participant separately. Midfrontal theta power correlated with pupil dilation responses, ($b = 0.03$, $SE = 0.01$, $t(1330) = 3.76$, $p < .001$, $r = .10$, $BIC = 2870$). Although this effect was small, it was robust and remained significant after controlling for decision time and subjective conflict, ($b = 0.03$, $SE = 0.009$, $t(1333) = 3.22$, $p = .001$, $r = .09$, $BIC = 2880$), suggesting that the theta-pupil relationship was not driven by subjective conflict or decision time. Pupil responses also correlated with the positive-polarity stimulus-locked ERP ($b = 0.11$, $SE = 0.04$, $t(1313) = 3.07$, $p = .002$, $r = .08$, $BIC = 6591$), but the effect became non-significant after including subjective conflict (value difference) in the model ($p = .301$, $r = .03$, $BIC = 5837$), suggesting that it might be subjective conflict that is driving the relationship between pupil responses and this ERP.

To further explore the theta-pupil relationship, we correlated 20 ms time bins from the mean theta power (3.2–7.7 Hz) and pupil responses time series (Fig. 9). Soon after choice onset, theta power at 250 to 750 ms significantly correlated with pupil responses from 750 to 1500 ms. These correlations suggest that during value-guided choice, the

neural systems thought to underlie midfrontal theta power and pupil dilation responses might interact soon after choice onset.

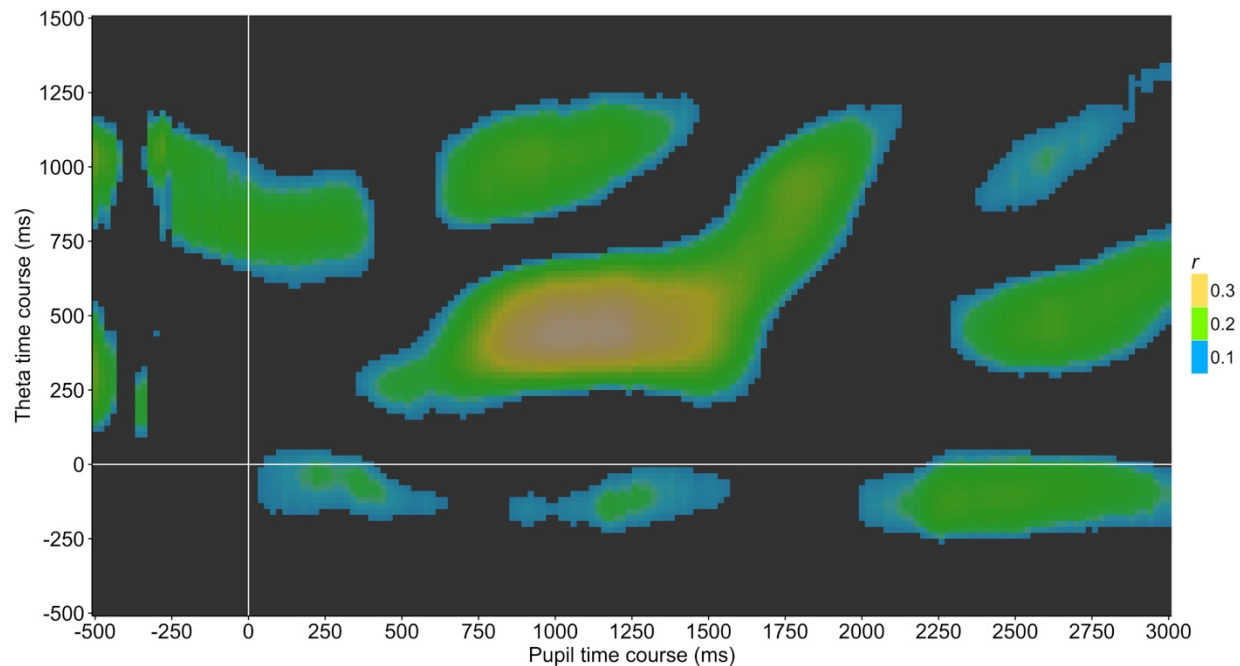


Fig. 9. Theta-pupil correlations across entire time series. The x-axis reflects time points (in 20 ms bins) across pupil dilation time series (–500 to 3000 ms), whereas the y-axis reflects time points (in 20 ms bins) across theta power (3.2–7.7 Hz) time series (–500 to 1500 ms). Intertemporal choices were presented at 0 ms. Each time point in each series was correlated with time points in the other series, and the strength of the relationship at each time point is reflected in the heatmap. Colored (non-black) regions survived FDR correction ($p < .05$), with brighter colors indicating stronger correlations between midfrontal theta power and pupil dilation responses. Strongest correlations were observed during these periods: midfrontal theta (250 to 750 ms) and pupil responses (750 to 1500 ms).

4. Discussion

We recorded EEG signals over midfrontal scalp electrodes and pupil dilation responses while participants made intertemporal decisions. Extending recent work on theta-pupil relationships during inhibitory control tasks (Dippel et al., 2017; Mückschel et al., 2017), we show that midfrontal theta power and pupil dilation track not only objective conflict during inhibitory control tasks, but also subjective conflict produced by value-guided choice involving trade-offs between costs and benefits occurring at different times. Even though participants were simply expressing their preferences for different intertemporal rewards and had little or no prepotent responses to inhibit, subjective conflict modulated midfrontal theta power and pupil responses. What is more, theta power and pupillary responses did not track conflict in a binary, all-or-none fashion, as might be concluded by recent work. Instead, fine gradations of subjective conflict *parametrically* modulated midfrontal theta power and pupil responses, with the neurophysiological responses discriminating even small changes in subjective conflict.

Both midfrontal theta and pupil responses track subjective intertemporal preferences, or how similar the subjective values of the immediate and delayed rewards were. These signals increased in magnitude when the two rewards had the same subjective value (high choice conflict); when the subjective value of one reward became higher than the other (less choice conflict), the magnitude of both signals decreased. Unexpectedly, however, midfrontal theta and pupil responses were also enhanced when decisions were surprisingly easy (e.g., \$15 today or \$15 in 10 days), suggesting that these signals might track more than just conflict between two choices or responses. Instead, and consistent with past theorizing (e.g., Alexander and Brown 2011;

Cavanagh and Frank 2014), these neurophysiological responses may signal events (e.g., surprising or conflicting) requiring increased attention and adaptive control, regardless of their valence (e.g., Hauser et al., 2014; Jahn et al., 2014; Sallet et al., 2013; Talmi et al., 2013).

When faced with a no-brainer choice, participants might realize that unlike other choices, it was unnecessary to consider the relevant costs (delay) and benefits (reward magnitude). They could instead rely on heuristics (e.g., always take the immediate reward), and this switch from value- to heuristics-guided decision strategy may be driven by adaptive control processes (Cohen 2016; Holroyd and Coles 2002; Karlsson et al., 2012; Shenhav et al., 2013; Tervo et al., 2014). Enhanced midfrontal theta and pupil responses might therefore reflect dynamic switching between brain networks (Cocchi et al., 2013; Uddin 2015). Further, past work suggests that pupil responses correlate strongly with LC-NE system activity (Aston-Jones and Cohen 2005b; Murphy et al., 2014; Rajkowski et al., 1994), and this neuromodulatory system may be involved in resetting networks and optimizing behavior (Bouret and Sara 2005; Nieuwenhuis et al., 2005; Sara and Bouret 2012; Urai et al., 2017; Usher et al., 1999; Warren et al., 2016). Therefore, consistent with these proposals and findings, our results also provide some evidence that midfrontal theta oscillations and norepinephrine help implement adaptive control and optimize behavioral responses (e.g., Verguts and Notebaert 2009).

Crucially, our findings provide evidence of convergence across qualitatively different sorts of stimuli—that midfrontal theta is involved in not only cognitive control during inhibitory control tasks (e.g., Stroop, go/no-go) but also value-guided choice. Although our EEG electrode array preclude us from localizing midfrontal theta sources,

previous work suggests that midfrontal theta oscillations are generated in the ACC and surrounding mPFC (Asada et al., 1999; Debener et al., 2005; Töllner et al., 2017). Thus, future work should not only investigate whether common neural sources generate midfrontal theta dynamics in value-guided choice and inhibitory control tasks, but also use value-guided choice paradigms to gain further insights into the functional significance of midfrontal theta dynamics. The latter is especially important, given that we are the first to investigate midfrontal theta during intertemporal choice and there is no one-to-one mapping between neural oscillatory frequencies and cognitive function. Instead, the theta dynamics we have observed may reflect memory load, mental effort, or binding of widely distributed cortical assemblies (Sammer et al., 2007; Wascher et al., 2014; Zakrzewska and Brzezicka 2014). Moreover, such studies will help elucidate how midfrontal theta dynamics underlie good everyday self-regulation and decision making (e.g., Ertl et al., 2013; Knyazev 2007).

As for changes in pupil size, some have described these as reflecting changes in neural gain mediated by LC-NE system activity (Aston-Jones and Cohen 2005b; Eldar et al., 2013; Murphy et al., 2014). For example, changes in pupil responses correspond to changes in locus coeruleus firing rate (Joshi et al., 2016; Murphy et al., 2014; Varazzani et al., 2015), as well as norepinephrine concentrations (Phillips et al., 2000; Warren et al., 2016). Extending recent work (Chmielewski et al., 2017; Dippel et al., 2017; Mückschel et al., 2017), we found that midfrontal theta correlated with pupil dilation responses, suggesting that the mPFC and LC-NE might interact to resolve conflict and respond to surprising events even during choices based on personal

preferences. However, given that we did not directly measure mPFC and locus coeruleus activity, such suggestions remain speculative.

Future research using pharmacological interventions will be necessary to show that changes in pupil dilation and midfrontal theta during value-guided choice are indeed mediated by changes in norepinephrine concentrations. Such studies will help rule out other contributors to pupil responses, such as the colliculi (super and inferior) and other neurotransmission systems (dopamine and acetylcholine) (Sara 2009; Wang and Munoz 2015). Interestingly, previous studies have found changes in neurophysiological activity (e.g., error-related negativity) but not behavioral responses or choices after manipulating norepinephrine concentrations (Jepma et al., 2010; Riba et al., 2005), indicating that more work needs to be done to understand the specific interactions between the LC-NE system and adaptive control processes such as theta oscillatory dynamics during decision making (Verguts and Notebaert 2009).

Because the intertemporal choice paradigm has generally been used to model and study self-control conflicts (e.g., Berns et al., 2007), our results suggest that overlapping processes may subserve inhibition processes and value-guided decision making, as well as self-control (Berkman, 2017; Berkman et al., in press; Shenhav, in press). For example, changes in midfrontal theta oscillations and pupil responses when faced with self-control conflicts involving cost-benefit trade-offs might reflect differential recruitment of the underlying adaptive control systems. As such, understanding how these systems are recruited and interact may explain why certain people are more successful than others at self-regulation.

In summary, we used economic modeling to show that subjective conflict during intertemporal choice parametrically modulated midfrontal theta power and pupil dilation responses. Unexpectedly, however, these signals also increased when intertemporal decisions were surprisingly easy, suggesting that these signals may instead reflect the need to increase attention and adaptive control to resolve conflicting or surprising events. Our results suggest that exerting self-control and making good decisions in everyday life may depend on interactions between neural systems that generate midfrontal theta oscillations and pupil dilation responses. Finally, our approach highlights the benefits of integrating cognitive neuroscience and neuroeconomics, which can provide insights into how inhibitory and adaptive control processes underlie value-guided choice. Conversely, neuroeconomic approaches offer paradigms that can inform and constrain cognitive neuroscience theories.

References

- Ainslie, G., 1975. Specious reward: A behavioral theory of impulsiveness and impulse control. *Psychol. Bull.* 82(4), 463-496. <http://dx.doi.org/10.1037/h0076860>
- Alexander, W.H., Brown, J.W., 2011. Medial prefrontal cortex as an action-outcome predictor. *Nat. Neurosci.* 14(10), 1338-1344. <http://dx.doi.org/10.1038/nn.2921>
- Asada, H., Fukuda, Y., Tsunoda, S., Yamaguchi, M., Tonoike, M., 1999. Frontal midline theta rhythms reflect alternative activation of prefrontal cortex and anterior cingulate cortex in humans. *Neurosci. Lett.* 274(1), 29-32. [http://dx.doi.org/10.1016/s0304-3940\(99\)00679-5](http://dx.doi.org/10.1016/s0304-3940(99)00679-5)
- Aston-Jones, G., Waterhouse, B., 2016. Locus coeruleus: From global projection system to adaptive regulation of behavior. *Brain Res.* 1645, 75-78. <http://dx.doi.org/10.1016/j.brainres.2016.03.001>
- Aston-Jones, G., Cohen, J.D., 2005a. Adaptive gain and the role of the locus coeruleus-norepinephrine system in optimal performance. *J. Comp. Neurol.* 493(1), 99-110. <http://dx.doi.org/10.1002/cne.20723>
- Aston-Jones, G., Cohen, J.D., 2005b. An integrative theory of locus coeruleus-norepinephrine function: Adaptive gain and optimal performance. *Anu. Rev. Psychol.* 28, 403-450. <http://dx.doi.org/10.1146/annurev.neuro.28.061604.135709>
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Statist. Softw.* 67(1), 1-48. <http://dx.doi.org/10.18637/jss.v067.i01>.
- Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate: A practical and powerful approach to multiple testing. *J. Roy. Stat. Soc. B. Met.*, 289-300.

Berkman, E.T., 2017. Value-based choice: An integrative, neuroscience-informed model of health goals. *Psychol. Health*. 1-18.

<http://dx.doi.org/10.1080/08870446.2017.1316847>

Berkman, E.T., Hutcherson, C., Livingston, J.L., Kahn, L.E., Inzlicht, M., in press. Self-control as value-based choice. *Curr. Dir. Psychol. Sci.*

Bernhardt, B.C., Smallwood, J., Tusche, A., Ruby, F.J., Engen, H.G., Steinbeis, N., Singer, T., 2014. Medial prefrontal and anterior cingulate cortical thickness predicts shared individual differences in self-generated thought and temporal discounting. *NeuroImage* 90, 290-297. <http://dx.doi.org/10.1016/j.neuroimage.2013.12.040>

Berns, G.S., Laibson, D., Loewenstein, G., 2007. Intertemporal choice—Toward an integrative framework. *Trends. Cogn. Sci* 11(11), 482-488.

<http://dx.doi.org/10.1016/j.tics.2007.08.011>

Berridge, C.W., Waterhouse, B.D., 2003. The locus coeruleus-noradrenergic system: Modulation of behavioral state and state-dependent cognitive processes. *Brain Res. Rev.* 42(1), 33-84. [http://dx.doi.org/10.1016/s0165-0173\(03\)00143-7](http://dx.doi.org/10.1016/s0165-0173(03)00143-7)

Botvinick, M.M., Braver, T.S., Barch, D.M., Carter, C.S., Cohen, J.D., 2001. Conflict monitoring and cognitive control. *Psychol. Rev.* 108(3), 624-652.

<http://dx.doi.org/10.1037/0033-295X.108.3.624>

Bouret, S., Sara, S.J., 2005. Network reset: A simplified overarching theory of locus coeruleus noradrenaline function. *Trends Neurosci.* 28(11), 574-582.

<http://dx.doi.org/10.1016/j.tins.2005.09.002>

Bürkner, P.C., 2016. brms: An R package for Bayesian multilevel models using Stan. *J. Statist. Softw.*

- Button, K.S., Ioannidis, J.P., Mokrysz, C., Nosek, B.A., Flint, J., Robinson, E.S., Munafò, M.R., 2013. Power failure: Why small sample size undermines the reliability of neuroscience. *Nat. Rev. Neurosci.* 14(5), 365-376.
<http://dx.doi.org/10.1038/nrn3475>
- Camerer, C.F., 2013. Goals, methods, and progress in neuroeconomics. *Annu. Rev. Econ.* 5(1), 425-455. <http://dx.doi.org/10.1146/annurev-economics-082012-123040>
- Cavanagh, J.F., Frank, M.J., 2014. Frontal theta as a mechanism for cognitive control. *Trends. Cogn. Sci* 18(8), 414-421. <http://dx.doi.org/10.1016/j.tics.2014.04.012>
- Cavanagh, J.F., Wiecki, T.V., Kochar, A., Frank, M.J., 2014. Eye tracking and pupillometry are indicators of dissociable latent decision processes. *J. Exp. Psychol. Gen.* 143(4), 1476-1488. <http://dx.doi.org/10.1037/a0035813>
- Cavanagh, J.F., Zambrano-Vazquez, L., Allen, J.J., 2012. Theta lingua franca: A common mid-frontal substrate for action monitoring processes. *Psychophysiology* 49(2), 220-238. <http://dx.doi.org/10.1111/j.1469-8986.2011.01293.x>
- Chmielewski, W.X., Mückschel, M., Ziemssen, T., Beste, C., 2017. The norepinephrine system affects specific neurophysiological subprocesses in the modulation of inhibitory control by working memory demands. *Hum. Brain Mapp.* 38(1), 68-81.
<http://dx.doi.org/10.1002/hbm.23344>
- Cocchi, L., Zalesky, A., Fornito, A., Mattingley, J.B., 2013. Dynamic cooperation and competition between brain systems during cognitive control. *Trends. Cogn. Sci* 17(10), 493-501. <http://dx.doi.org/10.1016/j.tics.2013.08.006>
- Cohen, M.X., 2017. Where does EEG come from and what does it mean. *Trends Neurosci.* 40(4), 208-218. <http://dx.doi.org/10.1016/j.tins.2017.02.004>

Cohen, M.X., 2014a. Analyzing neural time series data: Theory and practice. MIT Press.

Cohen, M.X., 2014b. A neural microcircuit for cognitive conflict detection and signaling.

Trends Neurosci. 37(9), 480-490. <http://dx.doi.org/10.1016/j.tins.2014.06.004>

Cohen, M.X., 2016. Midfrontal theta tracks action monitoring over multiple interactive time scales. NeuroImage 141, 262-272.

<http://dx.doi.org/10.1016/j.neuroimage.2016.07.054>

Crandall, C.S., Sherman, J.W., 2016. On the scientific superiority of conceptual replications for scientific progress. J. Exp. Soc. Psychol.

<http://dx.doi.org/10.1016/j.jesp.2015.10.002>

Critchley, H.D., Tang, J., Glaser, D., Butterworth, B., Dolan, R.J., 2005. Anterior cingulate activity during error and autonomic response. NeuroImage 27(4), 885-

895. <http://dx.doi.org/10.1016/j.neuroimage.2005.05.047>

Debener, S., Ullsperger, M., Siegel, M., Fiehler, K., von Cramon, D.Y., Engel, A.K., 2005. Trial-by-trial coupling of concurrent electroencephalogram and functional magnetic resonance imaging identifies the dynamics of performance monitoring. J. Neurosci. 25(50), 11730-11737. <http://dx.doi.org/10.1523/JNEUROSCI.3286-05.2005>

Delorme, A., Sejnowski, T., Makeig, S., 2007. Enhanced detection of artifacts in EEG data using higher-order statistics and independent component analysis.

NeuroImage 34(4), 1443-1449. <http://dx.doi.org/10.1016/j.neuroimage.2006.11.004>

Delorme, A., Makeig, S., 2004. EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. J. Neurosci. Meth.

134(1), 9-21. <http://dx.doi.org/10.1016/j.jneumeth.2003.10.009>

- Di Domenico, S.I., Le, A., Liu, Y., Ayaz, H., Fournier, M.A., 2016. Basic psychological needs and neurophysiological responsiveness to decisional conflict: An event-related potential study of integrative self processes. *Cogn. Affect. Behav. Neurosci.* 16(5), 848-865. <http://dx.doi.org/10.3758/s13415-016-0436-1>
- Dippel, G., Mückschel, M., Ziemssen, T., Beste, C., 2017. Demands on response inhibition processes determine modulations of theta band activity in superior frontal areas and correlations with pupillometry - implications for the norepinephrine system during inhibitory control. *NeuroImage* 157, 575-585. <http://dx.doi.org/10.1016/j.neuroimage.2017.06.037>
- Dixon, M.R., Marley, J., Jacobs, E.A., 2003. Delay discounting by pathological gamblers. *J. Appl. Behav. Anal.* 36(4), 449-458. <http://dx.doi.org/10.1901/jaba.2003.36-449>
- Ebitz, R.B., Platt, M.L., 2015. Neuronal activity in primate dorsal anterior cingulate cortex signals task conflict and predicts adjustments in pupil-linked arousal. *Neuron* 85(3), 628-640. <http://dx.doi.org/10.1016/j.neuron.2014.12.053>
- Eldar, E., Niv, Y., Cohen, J.D., 2016. Do you see the forest or the tree? Neural gain and breadth versus focus in perceptual processing. *Psychol. Sci.* 27(12), 1632-1643. <http://dx.doi.org/10.1177/0956797616665578>
- Eldar, E., Cohen, J.D., Niv, Y., 2013. The effects of neural gain on attention and learning. *Nat. Neurosci.* 16(8), 1146-1153. <http://dx.doi.org/10.1038/nn.3428>
- Ertl, M., Hildebrandt, M., Ourina, K., Leicht, G., Mulert, C., 2013. Emotion regulation by cognitive reappraisal - the role of frontal theta oscillations. *NeuroImage* 81, 412-421. <http://dx.doi.org/10.1016/j.neuroimage.2013.05.044>
- Faul, F., Erdfelder, E., Lang, A.-G., Buchner, A., 2007. G* Power 3: A flexible statistical

power analysis program for the social, behavioral, and biomedical sciences. *Behav. Res. Meth.* 39(2), 175-191. <http://dx.doi.org/10.3758/bf03193146>

Frederick, S., Loewenstein, G., O'Donoghue, T., 2002. Time discounting and time preference: A critical review. *Journal of Economic Literature* 40(2), 351-401. <http://dx.doi.org/10.1257/002205102320161311>

Gilzenrat, M.S., Nieuwenhuis, S., Jepma, M., Cohen, J.D., 2010. Pupil diameter tracks changes in control state predicted by the adaptive gain theory of locus coeruleus function. *Cogn. Affect. Behav. Neurosci.* 10(2), 252-269. <http://dx.doi.org/10.3758/cabn.10.2.252>

Green, L., Myerson, J., 2004. A discounting framework for choice with delayed and probabilistic rewards. *Psychol. Bull.* 130(5), 769-792. <http://dx.doi.org/10.1037/0033-2909.130.5.769>

Hauser, T.U., Iannaccone, R., Stämpfli, P., Drechsler, R., Brandeis, D., Walitza, S., Brem, S., 2014. The feedback-related negativity (FRN) revisited: New insights into the localization, meaning and network organization. *NeuroImage* 84, 159-168. <http://dx.doi.org/10.1016/j.neuroimage.2013.08.028>

Holroyd, C.B., Coles, M.G.H., 2002. The neural basis of human error processing: Reinforcement learning, dopamine, and the error-related negativity. *Psychol. Rev.* 109(4), 679-709. <http://dx.doi.org/10.1037//0033-295X.109.4.679>

Hong, L., Walz, J.M., Sajda, P., 2014. Your eyes give you away: Prestimulus changes in pupil diameter correlate with poststimulus task-related EEG dynamics. *PLoS One* 9(3), e91321. <http://dx.doi.org/10.1371/journal.pone.0091321>

Jahn, A., Nee, D.E., Alexander, W.H., Brown, J.W., 2014. Distinct regions of anterior

cingulate cortex signal prediction and outcome evaluation. *NeuroImage* 95, 80-89.

<http://dx.doi.org/10.1016/j.neuroimage.2014.03.050>

Jepma, M., Te Beek, E.T., Wagenmakers, E.J., van Gerven, J.M., Nieuwenhuis, S.,
2010. The role of the noradrenergic system in the exploration-exploitation trade-off:
A psychopharmacological study. *Front. Hum. Neurosci.* 4, 170.

<http://dx.doi.org/10.3389/fnhum.2010.00170>

Jepma, M., Nieuwenhuis, S., 2011. Pupil diameter predicts changes in the exploration-
exploitation trade-off: Evidence for the adaptive gain theory. *J. Cog. Neuro.* 23(7),
1587-1596. <http://dx.doi.org/10.1162/jocn.2010.21548>

Joshi, S., Li, Y., Kalwani, R.M., Gold, J.I., 2016. Relationships between pupil diameter
and neuronal activity in the locus coeruleus, colliculi, and cingulate cortex. *Neuron*
89, 1-14. <http://dx.doi.org/10.1016/j.neuron.2015.11.028>

Kable, J.W., Glimcher, P.W., 2007. The neural correlates of subjective value during
intertemporal choice. *Nat. Neurosci.* 10(12), 1625-1633.

<http://dx.doi.org/10.1038/nn2007>

Kable, J.W., Glimcher, P.W., 2009. The neurobiology of decision: Consensus and
controversy. *Neuron* 63(6), 733-745.

<http://dx.doi.org/10.1016/j.neuron.2009.09.003>

Kable, J.W., Glimcher, P.W., 2010. An "as soon as possible" effect in human
intertemporal decision making: Behavioral evidence and neural mechanisms. *J.*
Neurophysiol. 103(5), 2513-2531. <http://dx.doi.org/10.1152/jn.00177.2009>

Kahneman, D., Beatty, J., 1966. Pupil diameter and load on memory. *Science*
154(3756), 1583-1585.

Karlsson, M.P., Tervo, D.G.R., Karpova, A.Y., 2012. Network resets in medial prefrontal cortex mark the onset of behavioral uncertainty. *Science* 338(6103), 135-139.

<http://dx.doi.org/10.1126/science.1226518>

Knyazev, G.G., 2007. Motivation, emotion, and their inhibitory control mirrored in brain oscillations. *Neurosci Biobehav Rev* 31(3), 377-395.

<http://dx.doi.org/10.1016/j.neubiorev.2006.10.004>

Kolling, N., Behrens, T.E.J., Wittmann, M.K., Rushworth, M.F.S., 2016. Multiple signals in anterior cingulate cortex. *Curr. Opin. Neurobiol.* 37, 36-43.

<http://dx.doi.org/10.1016/j.conb.2015.12.007>

Kolling, N., Behrens, T.E.J., Mars, R.B., Rushworth, M.F.S., 2012. Neural mechanisms of foraging. *Science* 336(6077), 95-98. <http://dx.doi.org/10.1126/science.1218004>

Kollins, S.H., 2003. Delay discounting is associated with substance use in college students. *Addict. Behav.* 28(6), 1167-1173. [http://dx.doi.org/10.1016/S0306-4603\(02\)00220-4](http://dx.doi.org/10.1016/S0306-4603(02)00220-4)

Kononov, A., Krajbich, I., 2016. Over a decade of neuroeconomics what have we learned. *Organ. Res. Methods*, 10-26.

<http://dx.doi.org/10.1177/1094428116644502>

Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2016. lmerTest: Tests in linear mixed effects models R package version 2.0-33.

Laeng, B., Ørbo, M., Holmlund, T., Miozzo, M., 2011. Pupillary Stroop effects. *Cogn. Process.* 12(1), 13-21. <http://dx.doi.org/10.1007/s10339-010-0370-z>

Leys, C., Ley, C., Klein, O., Bernard, P., Licata, L., 2013. Detecting outliers: Do not use standard deviation around the mean, use absolute deviation around the median. *J.*

- Exp. Soc. Psychol. 49(4), 764-766. <http://dx.doi.org/10.1016/j.jesp.2013.03.013>
- Luck, S.J., Gaspelin, N., 2017. How to get statistically significant effects in any ERP experiment (and why you shouldn't). *Psychophysiology* 54(1), 146-157.
<http://dx.doi.org/10.1111/psyp.12639>
- McClure, S.M., Laibson, D.I., Loewenstein, G., Cohen, J.D., 2004. Separate neural systems value immediate and delayed monetary rewards. *Science* 306(5695), 503-507. <http://dx.doi.org/10.1126/science.1094492>
- McClure, S.M., Ericson, K.M., Laibson, D.I., Loewenstein, G., Cohen, J.D., 2007. Time discounting for primary rewards. *J. Neurosci.* 27(21), 5796-5804.
<http://dx.doi.org/10.1523/JNEUROSCI.4246-06.2007>
- Mückschel, M., Chmielewski, W., Ziemssen, T., Beste, C., 2017. The norepinephrine system shows information-content specific properties during cognitive control - evidence from EEG and pupillary responses. *NeuroImage* 149, 44-52.
<http://dx.doi.org/10.1016/j.neuroimage.2017.01.036>
- Mückschel, M., Gohil, K., Ziemssen, T., Beste, C., 2016. The norepinephrine system and its relevance for multi-component behavior. *NeuroImage*.
<http://dx.doi.org/10.1016/j.neuroimage.2016.10.007>
- Murphy, P.R., Boonstra, E., Nieuwenhuis, S., 2016. Global gain modulation generates time-dependent urgency during perceptual choice in humans. *Nat. Commun.* 7, 13526. <http://dx.doi.org/10.1038/ncomms13526>
- Murphy, P.R., O'Connell, R.G., O'Sullivan, M., Robertson, I.H., Balsters, J.H., 2014. Pupil diameter covaries with BOLD activity in human locus coeruleus. *Hum. Brain Mapp.* 35(8), 4140-4154. <http://dx.doi.org/10.1002/hbm.22466>

- Murphy, P.R., Robertson, I.H., Balsters, J.H., O'Connell, R.G., 2011. Pupillometry and P3 index the locus coeruleus-noradrenergic arousal function in humans. *Psychophysiology* 48(11), 1532-1543. <http://dx.doi.org/10.1111/j.1469-8986.2011.01226.x>
- Nakao, T., Mitsumoto, M., Nashiwa, H., Takamura, M., Tokunaga, S., Miyatani, M., Ohira, H., Katayama, K., Okamoto, A., Watanabe, Y., 2010. Self-knowledge reduces conflict by biasing one of plural possible answers. *Pers. Soc. Psychol. B.* 36(4), 455-469. <http://dx.doi.org/10.1177/0146167210363403>
- Nieuwenhuis, S., Aston-Jones, G., Cohen, J.D., 2005. Decision making, the P3, and the locus coeruleus-norepinephrine system. *Psychol. Bull.* 131(4), 510-532. <http://dx.doi.org/10.1037/0033-2909.131.4.510>
- Nieuwenhuis, S., De Geus, E.J., Aston-Jones, G., 2011. The anatomical and functional relationship between the P3 and autonomic components of the orienting response: P3 and orienting response. *Psychophysiology* 48(2), 162-175. <http://dx.doi.org/10.1111/psyp.2011.48.issue-2>
- Open Science Collaboration, 2015. Estimating the reproducibility of psychological science. *Science* 349(6251). <http://dx.doi.org/10.1126/science.aac4716>
- Padoa-Schioppa, C., 2011. Neurobiology of economic choice: A good-based model. *Anu. Rev. Psychol.* 34, 333-359. <http://dx.doi.org/10.1146/annurev-neuro-061010-113648>
- Peirce, J.W., 2007. PsychoPy—Psychophysics software in Python. *J. Neurosci. Meth.* 162(1-2), 8-13. <http://dx.doi.org/10.1016/j.jneumeth.2006.11.017>
- Peirce, J.W., 2009. Generating stimuli for neuroscience using PsychoPy. *Front.*

Neuroinform. 2, 10. <http://dx.doi.org/10.3389/neuro.11.010.2008>

Peters, J., Büchel, C., 2010. Episodic future thinking reduces reward delay discounting through an enhancement of prefrontal-mediocortical interactions. *Neuron* 66(1), 138-148. <http://dx.doi.org/10.1016/j.neuron.2010.03.026>

Phillips, M.A., Szabadi, E., Bradshaw, C.M., 2000. Comparison of the effects of clonidine and yohimbine on spontaneous pupillary fluctuations in healthy human volunteers. *Psychopharmacology* 150(1), 85-89. <http://dx.doi.org/10.1007/s002130000398>

Polanía, R., Krajbich, I., Grueschow, M., Ruff, C.C., 2014. Neural oscillations and synchronization differentially support evidence accumulation in perceptual and value-based decision making. *Neuron* 82(3), 709-720. <http://dx.doi.org/10.1016/j.neuron.2014.03.014>

R Core Team, 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rajkowski, J., Kubiak, P., Aston-Jones, G., 1994. Locus coeruleus activity in monkey: Phasic and tonic changes are associated with altered vigilance. *Brain Res. Bull.* 35(5), 607-616. [http://dx.doi.org/10.1016/0361-9230\(94\)90175-9](http://dx.doi.org/10.1016/0361-9230(94)90175-9)

Rangel, A., Camerer, C., Montague, P.R., 2008. A framework for studying the neurobiology of value-based decision making. *Nat. Rev. Neurosci.* 9(7), 545-556. <http://dx.doi.org/10.1038/nrn2357>

Riba, J., Rodríguez-Fornells, A., Morte, A., Münte, T.F., Barbanoj, M.J., 2005. Noradrenergic stimulation enhances human action monitoring. *J. Neurosci.* 25(17), 4370-4374. <http://dx.doi.org/10.1523/JNEUROSCI.4437-04.2005>

- Sallet, J., Camille, N., Procyk, E., 2013. Modulation of feedback-related negativity during trial-and-error exploration and encoding of behavioral shifts. *Front. Neurosci.* 7. <http://dx.doi.org/10.3389/fnins.2013.00209>
- Sammer, G., Blecker, C., Gebhardt, H., Bischoff, M., Stark, R., Morgen, K., Vaitl, D., 2007. Relationship between regional hemodynamic activity and simultaneously recorded EEG-theta associated with mental arithmetic-induced workload. *Hum. Brain Mapp.* 28(8), 793-803. <http://dx.doi.org/10.1002/hbm.20309>
- Sara, S.J., 2009. The locus coeruleus and noradrenergic modulation of cognition. *Nat. Rev. Neurosci.* 10(3), 211-223. <http://dx.doi.org/10.1038/nrn2573>
- Sara, S.J., Bouret, S., 2012. Orienting and reorienting: The locus coeruleus mediates cognition through arousal. *Neuron* 76(1), 130-141. <http://dx.doi.org/10.1016/j.neuron.2012.09.011>
- Shenhav, A., in press. The perils of losing control: Why self-control is not just another value-based decision. *Psychol. Inq.*
- Shenhav, A., Botvinick, M.M., Cohen, J.D., 2013. The expected value of control: An integrative theory of anterior cingulate cortex function. *Neuron* 79(2), 217-240. <http://dx.doi.org/10.1016/j.neuron.2013.07.007>
- Shenhav, A., Buckner, R.L., 2014. Neural correlates of dueling affective reactions to win-win choices. *Proc. Natl. Acad. Sci. USA* 111(30), 10978-10983. <http://dx.doi.org/10.1073/pnas.1405725111>
- Shenhav, A., Straccia, M.A., Cohen, J.D., Botvinick, M.M., 2014. Anterior cingulate engagement in a foraging context reflects choice difficulty, not foraging value. *Nat. Neurosci.* 17(9), 1249-1254. <http://dx.doi.org/10.1038/nn.3771>

- Shenhav, A., Rand, D.G., Data, J.D.G., 2017. The relationship between intertemporal choice and following the path of least resistance across choices, preferences, and beliefs. *Judgm. Decis. Mak.* 12(1), 1. <http://dx.doi.org/10.2139/ssrn.2724547>
- Shenhav, A., Straccia, M.A., Botvinick, M.M., Cohen, J.D., 2016. Dorsal anterior cingulate and ventromedial prefrontal cortex have inverse roles in both foraging and economic choice. *Cogn. Affect. Behav. Neurosci.*
<http://dx.doi.org/10.3758/s13415-016-0458-8>
- Siegle, G.J., Steinhauer, S.R., Stenger, V.A., Konecky, R., Carter, C.S., 2003. Use of concurrent pupil dilation assessment to inform interpretation and analysis of fMRI data. *NeuroImage* 20(1), 114-124. [http://dx.doi.org/10.1016/S1053-8119\(03\)00298-2](http://dx.doi.org/10.1016/S1053-8119(03)00298-2)
- Simpson, H.M., 1969. Effects of a task-relevant response on pupil size. *Psychophysiology* 6(2), 115-121.
- Singer, W., 2013. Cortical dynamics revisited. *Trends. Cogn. Sci.* 17(12), 616-626.
<http://dx.doi.org/10.1016/j.tics.2013.09.006>
- Smaldino, P.E., McElreath, R., 2016. The natural selection of bad science. *R. Soc. Open Sci.* 3(9), 160384. <http://dx.doi.org/10.1098/rsos.160384>
- Summerfield, C., Tsetsos, K., 2012. Building bridges between perceptual and economic decision-making: Neural and computational mechanisms. *Front. Neurosci.* 6(70), 1-20. <http://dx.doi.org/10.3389/fnins.2012.00070>
- Talmi, D., Atkinson, R., El-Deredy, W., 2013. The feedback-related negativity signals salience prediction errors, not reward prediction errors. *J. Neurosci.* 33(19), 8264-8269. <http://dx.doi.org/10.1523/JNEUROSCI.5695-12.2013>

- Tervo, D.G.R., Proskurin, M., Manakov, M., Kabra, M., Vollmer, A., Branson, K., Karpova, A.Y., 2014. Behavioral variability through stochastic choice and its gating by anterior cingulate cortex. *Cell* 159(1), 21-32.
<http://dx.doi.org/10.1016/j.cell.2014.08.037>
- Thaler, R.H., 1981. Some empirical evidence on time inconsistency. *Rev. Econ. Stud.* 23, 165-180. [http://dx.doi.org/10.1016/0165-1765\(81\)90067-7](http://dx.doi.org/10.1016/0165-1765(81)90067-7)
- Töllner, T., Wang, Y., Makeig, S., Müller, H.J., Jung, T.-P., Gramann, K., 2017. Two independent frontal midline theta oscillations during conflict detection and adaptation in a simon-type manual reaching task. *J. Neurosci.* 37(9), 2504-2515.
<http://dx.doi.org/10.1523/jneurosci.1752-16.2017>
- Uddin, L.Q., 2015. Salience processing and insular cortical function and dysfunction. *Nat. Rev. Neurosci.* 16(1), 55-61. <http://dx.doi.org/10.1038/nrn3857>
- Urai, A.E., Braun, A., Donner, T.H., 2017. Pupil-linked arousal is driven by decision uncertainty and alters serial choice bias. *Nat. Commun.* 8, 14637.
<http://dx.doi.org/10.1038/ncomms14637>
- Usher, M., Cohen, J.D., Servan-Schreiber, D., Rajkowski, J., Aston-Jones, G., 1999. The role of locus coeruleus in the regulation of cognitive performance. *Science* 283(5401), 549-554. <http://dx.doi.org/10.1126/science.283.5401.549>
- van den Bos, W., McClure, S.M., 2013. Towards a general model of temporal discounting. *J. Exp. Anal. Behav.* 99(1), 58-73. <http://dx.doi.org/10.1002/jeab.6>
- van Steenbergen, H., Band, G.P.H., 2013. Pupil dilation in the Simon task as a marker of conflict processing. *Front. Hum. Neurosci.* 7.
<http://dx.doi.org/10.3389/fnhum.2013.00215>

- Varazzani, C., San-Galli, A., Gilardeau, S., Bouret, S., 2015. Noradrenaline and dopamine neurons in the reward/effort trade-off: A direct electrophysiological comparison in behaving monkeys. *J. Neurosci.* 35(20), 7866-7877.
<http://dx.doi.org/10.1523/JNEUROSCI.0454-15.2015>
- Verguts, T., Notebaert, W., 2009. Adaptation by binding: A learning account of cognitive control. *Trends. Cogn. Sci* 13(6), 252-257.
<http://dx.doi.org/10.1016/j.tics.2009.02.007>
- Verguts, T., 2017. Binding by random bursts: A computational model of cognitive control. *J. Cog. Neuro.* 29(6), 1103-1118. http://dx.doi.org/10.1162/jocn_a_01117
- Vidal, F., Hasbroucq, T., Grapperon, J., Bonnet, M., 2000. Is the 'error negativity' specific to errors? *Bio. Psych.* 51(2), 109-128.
- Wang, C.A., Munoz, D.P., 2015. A circuit for pupil orienting responses: Implications for cognitive modulation of pupil size. *Curr. Opin. Neurobiol.* 33, 134-140.
<http://dx.doi.org/10.1016/j.conb.2015.03.018>
- Warren, C.M., Eldar, E., van den Brink, R.L., Tona, K.D., van der Wee, N.J., Giltay, E.J., van Noorden, M.S., Bosch, J.A., Wilson, R.C., Cohen, J.D., Nieuwenhuis, S., 2016. Catecholamine-mediated increases in gain enhance the precision of cortical representations. *J. Neurosci.* 36(21), 5699-5708.
<http://dx.doi.org/10.1523/JNEUROSCI.3475-15.2016>
- Wascher, E., Rasch, B., Sanger, J., Hoffmann, S., Schneider, D., Rinkenauer, G., Heuer, H., Gutberlet, I., 2014. Frontal theta activity reflects distinct aspects of mental fatigue. *Biol. Psychol.* 96, 57-65.
<http://dx.doi.org/10.1016/j.biopsycho.2013.11.010>

- Womelsdorf, T., Valiante, T.A., Sahin, N.T., Miller, K.J., Tiesinga, P., 2014. Dynamic circuit motifs underlying rhythmic gain control, gating and integration. *Nat. Neurosci.* 17(8), 1031-1039. <http://dx.doi.org/10.1038/nn.3764>
- Yeung, N., Botvinick, M.M., Cohen, J.D., 2004. The neural basis of error detection: Conflict monitoring and the error-related negativity. *Psychol. Rev.* 111(4), 931-959. <http://dx.doi.org/10.1037/0033-295X.111.4.931>
- Zakrzewska, M.Z., Brzezicka, A., 2014. Working memory capacity as a moderator of load-related frontal midline theta variability in Sternberg task. *Front. Hum. Neurosci.* 8, 399. <http://dx.doi.org/10.3389/fnhum.2014.00399>
- Zauberman, G., Urminsky, O., 2016. Consumer intertemporal preferences. *Curr. Opin. Psychol.* 10, 136-141. <http://dx.doi.org/10.1016/j.copsyc.2016.01.005>