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International Journal of Psychophysiology

journal homepage: www.elsevier.com



Opportunities to sit and stand trigger equivalent reward-related brain activity

Boris Cheval ^{a, b, 1}, Matthieu P. Boisgontier ^{c, d, 1}, Mariane F.B. Bacelar ^e, Robyn Feiss ^e, Matthew W. Miller ^{e, f, *}

- ^a Swiss Center for Affective Sciences, University of Geneva, Campus Biotech, Chemin des mines 9, 1202 Genève, Switzerland
- b Laboratory for the Study of Emotion Elicitation and Expression (E3Lab), Department of Psychology, University of Geneva, Geneva, Switzerland
- ^c Department of Physical Therapy, University of British Columbia, Canada
- ^d Department of Movement Sciences, KU, Leuven, Belgium
- ^e School of Kinesiology, Auburn University, 301 Wire Road, Kinesiology Building, Auburn, AL 36849, USA
- ^f Center for Neuroscience, Auburn University, USA

ARTICLE INFO

Keywords: Behaviors minimizing energetic costs Physical activity Physical inactivity Exercise Reward FFG

ABSTRACT

A recent theory contends that behaviors minimizing energetic cost are rewarding (Cheval et al., 2018). However, direct experimental evidence supporting this theory is lacking. To fill this knowledge gap, we investigated the effect of energy expenditure on reward-related brain activity in a pre-registered study. This preregistered study included thirty-one participants who were equipped with an electroencephalography (EEG) cap and performed a monetary incentive delay task. After attempting to quickly respond to a target, participants were given feedback instructing them to retrieve a token (reward condition) or to wait (no reward condition). In half of the rewarding trials, participants stood up to retrieve a token, thereby increasing energy expenditure. In the other half, participants just had to extend their arm to retrieve a token, thereby minimizing energy expenditure. The contingent negative variation event-related potential (ERP) component preceding the motor response was used as an indicator of reward pursuit. The reward positivity ERP component time-locked to feedback onset was used to determine reward valuation. Results showed that response time, contingent negative variation, and the reward positivity were not influenced by energy expenditure (remaining seated vs. standing up). This null effect of conditions was confirmed using equivalence tests. These results do not support the theory of energetic cost minimization but the equivalent effect of sitting and standing on reward-related brain activity is new knowledge that could contribute to shed light on the neural processes underlying the pandemic of physical inactivity.

1. Introduction

The adverse effects of physical inactivity on health and its economic burden have now been widely demonstrated (Chenoweth and Leutzinger, 2003; Lee et al., 2012). However, despite the intensification of actions promoting physical activity worldwide, the number of inactive adults keeps increasing (Kohl III et al., 2012). This inefficiency of public policies reflects an inability to fully understand the processes underlying this pandemic. Recently, we developed the theory of energetic cost minimization (TECM; Cheval et al., 2018), which contends that the prevalence of physical inactivity could be explained by the potential rewarding value of behaviors that minimize energetic cost, such as sitting instead of standing. TECM suggests that energetic mini-

mization has acquired a rewarding value across evolution because efficient actions provided an advantage for survival (Lee et al., 2016; Lieberman, 2015). Yet, while indirect evidence of this rewarding value has been provided (Cheval, Tipura et al., 2018), direct experimental evidence is lacking.

The indirect evidence stems from recent findings suggesting that additional brain resources are required to resist an automatic attraction to sedentary behaviors (Cheval, Tipura et al., 2018). In this study, participants' electroencephalographic (EEG) activity was examined while they performed a computerized approach-avoidance task using physical-activity (images of stick figures engaging in physical activity) and sedentary stimuli (images of stick figures engaging in sedentary behaviors) (Cheval et al., 2015; Cheval et al., 2014; Krieglmeyer and

Corresponding author at: School of Kinesiology, Auburn University, 301 Wire Road, Kinesiology Building, Auburn, AL 36849, USA.
 Email addresses: boris.cheval@unige.ch (B. Cheval); matthieu.boisgontier@ubc.ca (M.P. Boisgontier); mzf0029@auburn.edu (M.F.B. Bacelar); rsf0012@auburn.edu (R. Feiss); mwm0024@auburn.edu (M.W. Miller)

¹ BC and MPB contributed equally to this work.

Deutsch, 2010). On each trial, a manikin was presented above or below a stimulus, and participants were instructed to make a keyboard response to quickly move the manikin away from or toward the stimulus. In one condition, participants moved the manikin toward physical activity stimuli and away from sedentary stimuli. In the other condition, participants did the opposite. This EEG study assessed, for the first time, the brain processes underlying the automatic approach and avoidance reactions to these two types of stimuli. Event-related potentials (ERPs) time-locked to stimuli were extracted for analysis and showed larger N2amplitude when participants moved away from sedentary versus physical activity stimuli. As N2 is linked to inhibitory control, this result suggested that higher inhibitory activity was required to avoid sedentary stimuli (Folstein and Van Petten, 2008). Avoiding a rewarding stimulus such as high-calorie food has been shown to increase the inhibition-related N2 amplitude (Carbine et al., 2017). Therefore, the results of Cheval et al. (2018) suggested that sedentary stimuli, representing the lowest level of energy expenditure, could be rewarding. Yet, brain processes observed in participants using a keyboard in a sitting position may lack ecological validity and may not apply to daily activities involving actual variations of energy expenditure. To test whether energetic cost modifies reward-related brain activity, as suggested by TECM, this activity should be measured in tasks involving lower versus higher en-

In the current study, EEG activity was recorded when participants performed a monetary incentive delay task (Meadows et al., 2016a), which is known to activate the reward system (Knutson et al., 2000). In this task, participants attempted to quickly respond to a target, and then received a reward feedback and retrieved a token or did not receive a reward feedback and did not retrieve a token. Half of the trials required participants to increase energetic cost by standing up to retrieve the token, whereas the other half required participants to minimize energetic cost by remaining seated to retrieve the token. This manipulation of the physical position to retrieve the token (sitting or standing) was chosen because it represents an ecologically-valid mode of decreasing versus increasing energetic cost (Mansoubi et al., 2015). Response times to the target were examined to assess reward pursuit. Previous studies showed, for example, that response times are shorter when a reward versus no reward is at stake in a monetary incentive delay task (Novak and Foti, 2015; Novak et al., 2016; Threadgill and Gable, 2016) and that the magnitude of the reward is negatively correlated with the response time (i.e., the greater the reward, the shorter the response time; Meadows et al., 2016b).

Two ERP components were examined to assess reward-related brain activity. The contingent negative variation (CNV) was examined to assess reward pursuit. The CNV was obtained from the EEG signal collected while participants were preparing to respond to the target. The CNV is a negative deflection in the EEG between a warning stimulus and a target stimulus, reflecting response preparation (Brunia et al., 2012). The component is maximal at the midline electrode sites and those sites contralateral to the responding limb. The component is thought to be generated by brain areas required for response execution. The CNV is enhanced when individuals are preparing to make a response that may result in a monetary reward. For example, previous studies (Novak and Foti, 2015; Novak et al., 2016) showed that the CNV was larger for trials with rather than without financial incentives at stake, thereby suggesting that CNV is sensitive to the desirability of the reward being pursued.

The reward positivity (RewP) was examined to assess reward valuation. The RewP was extracted from the EEG signal collected during exposure to feedback. The RewP is a positive deflection in the EEG 250–350 ms following feedback presentation, and is maximal at the midline frontocentral electrode sites (Krigolson, 2018; Proudfit, 2015; Sambrook and Goslin, 2015). This component is believed to be generated by the anterior cingulate cortex, to reflect reward valuation, and

to be specifically related to positive reward-prediction errors (i.e., how much more rewarding feedback was than predicted) (Sambrook and Goslin, 2015). As the ACC is thought to control effortful behavior (Holroyd and McClure, 2015), if a behavior minimizes energetic cost and minimizing energetic cost leads to a positive reward-prediction error, consistent with TECM, then the anterior cingulate cortex should guide the organism to undertake such behaviors. The RewP is most commonly extracted from a difference wave derived by subtracting the average of no reward feedback trials from the average of reward feedback trials. Of interest in our study, RewP amplitude scales with the magnitude of the reward associated with the feedback (Meadows et al., 2016a; Novak and Foti, 2015; Novak et al., 2016; Sambrook and Goslin, 2015; Threadgill and Gable, 2016). For example, Sambrook and Goslin (2015) conducted a meta-analysis and observed that the RewP derived from reward feedback minus no reward feedback difference waves was larger when the reward associated with the feedback was greater. In a single-trial analysis, Meadows et al. (2016a) examined the RewP from each reward feedback trial wherein each trial was associated with a reward ranging in magnitude from \$0.00 USD to \$4.96 USD. Results showed that RewP amplitude was correlated with reward magnitude, thereby suggesting that the RewP is sensitive to the value of the reward that is received.

Based on the TECM (Cheval et al., 2018), we hypothesized that rewards that could be retrieved with lower energetic expenditure (i.e., remain seated vs. standing up) are associated with quicker response times (H1) and larger CNVs (H2), two outcomes that are indicative of greater reward pursuit. We also hypothesized that rewards that could be retrieved with lower energetic expenditure elicit larger RewPs, indicative of greater reward valuation (H3).

2. Methods

2.1. Participants

Sample size was determined with an a priori power calculation conducted with G*Power 3.1.9.2 (Faul et al., 2007). The experiment was powered to detect medium size effects (dz = 0.5) in one-tailed paired-sample *t*-tests, with $\alpha = 0.05$ and $\beta = 0.8$. The calculation yielded N = 27, but we aimed for N = 31 to account for lost data (e.g., due to poor EEG recording). Participants provided informed written consent to the protocol approved by the Auburn University Institutional Review Board (Protocol #18-318 EP 1808) and in compliance with the Declaration of Helsinki regarding human experimentation. Thirty-one young healthy right-handed participants completed the experiment. One participant's data were removed because of an experimenter error during data collection, and one participant's data were removed because the task was not performed as instructed, leaving a final N=29 (age: 22 ± 2 years; body mass index: 24 ± 4 kg/m²; 16 females). Of this final sample, two participants' EEG data were unusable due to excessive artifact and three participants' EEG data were missing for one block of the experiment due to experimenter error.

2.2. Procedures

2.2.1. Monetary incentive delay task

Participants were seated in a 90-cm wide \times 73-cm deep \times 93-cm high foldup butterfly chair (Mainstays soft faux-leather butterfly chair; Fig. 1). Adjacent to the right side of the chair and 60 cm above the floor was a tabletop (45-cm wide \times 60-cm long) on which rested a computer mouse. Adjacent to the left side of the chair and 63 cm above the floor was a tabletop (45-cm wide \times 61-cm long) on which rested one red and one blue plastic container. Participants were instructed to sit back in the chair such that their back, neck, and head were supported by the chair. They were told to rest their right arm on the table

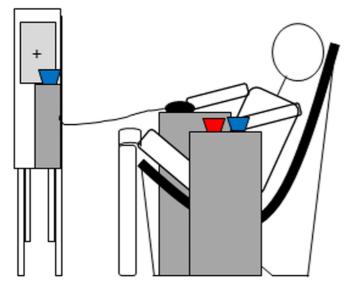


Fig. 1. Set-up. The participant was seated in a butterfly chair with a table on both sides of the chair. The right arm rested on the table and used a computer mouse to respond to stimuli during the monetary incentive delay task. The left arm rested on the table that held a blue container filled with plastic coins and a red container to place the coins earned during the task. A table was positioned in front of the participant with a computer monitor resting upon it (the monitor is depicting a fixation cross). A computer tower was positioned to the left of the monitor (from the participant's perspective) with a blue container filled with plastic coins on it. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

to their right and their left arm on the table to their left, to start each trial in this position and maintain it throughout the experiment unless the task required them to move (i.e., to stand up). A 72-cm high table was 36 cm from the front of the chair. A computer monitor with a 48-cm screen was 21 cm away from the front of the table and 17 cm above the table. To the left of the computer monitor was a 40.5-cm high computer tower, on which rested a blue plastic container identical to the one to the left of the chair. Both of these blue containers held plastic coins. The containers were positioned such that participants had to extend their elbow approximately 180° and flex their shoulder in the sagittal plane to reach into the container. Participants could reach into the (lower) container on the table to their left by extending their elbow and remaining seated. Participants had to stand up and extend their elbow to reach into the (upper) container on the computer tower.

After positioning the participant, the experimenter read the following instructions related to the task procedures:

"You will be completing a task to try to earn money by earning plastic coins. Each coin is like a ticket that you enter into a raffle for \$10. So, the more coins you earn, the more likely you are to win \$10. You will earn coins largely based on your reaction time in the task, which will consist of four blocks of trials with a 1-minute break between each block. Each trial will begin by presenting you with an image indicating from which container you will retrieve the coin you earn from that trial, if you earn a coin. If the container is on the lower line, then you will retrieve that coin from the container on the table next to you. If the container is on the upper line, then you will retrieve that coin from the container on top of the computer tower. Next, on the screen, you will be presented with a cross on which you should fixate. Sometime after being presented with the cross, you will see a target square. Your objective is to press the left mouse button while the target is present. This means that you should press the button as quickly as you can after the target appears, trying to press the button before the target disappears. If you succeed in pressing the button while the target is present, then you are

more likely to earn a reward for the trial. Before learning whether you earned the reward, you will once again fixate on a cross. Then, you will receive feedback indicating whether you earned the reward or not. If you see a checkmark, then you earned the reward. If you see an X, then you did not. Although whether you earn the reward is largely based on whether you pressed the button while the target is present, it is not the sole criterion. Rather, your success in pressing the button while the target is present is entered into an algorithm that determines whether you earn the reward: if you succeed, the algorithm is more likely to determine that you earn the reward. However, you may earn a reward for a slow response or even if you fail to make a response, and you may fail to earn a reward for a quick response. Nonetheless, it is crucial that you try to press the button while the target is present in order to maximize your likelihood of earning the reward and, thus, winning the raffle. If you see a checkmark indicating that you earned the reward, do not immediately retrieve the coin. Rather, follow the instructions on the screen. Specifically, do not move while the word "WAIT" is on the screen. When the word "SET" appears on the screen, you should position your hand above the appropriate container. If the appropriate container is the one on top of the computer tower, then you should stand up before positioning your hand. When the word "GO" appears on the screen, you should pick one coin out of the appropriate container, return to your start position, sitting back in the chair, and then place the coin in your red collection container. Next, you will be prompted to start the next trial."

Participants completed 1 block of 8 practice trials followed by 1 block of 24 trials, then 3 blocks of 28 trials each (Fig. 2). Unbeknownst to the participants, 50% of trials in each block were pre-determined to result in reward feedback and 50% to result in no reward feedback. Further, in each block, half of the time, reward feedback occurred on trials that began with the lower container stimulus (sit trials), and the other half of the time, reward feedback occurred on trials that began with the upper container stimulus (stand trials). Thus, each block was equally comprised of sit-reward, sit-no reward, stand-reward, and stand-no reward trials, which were randomly ordered within each block. Following the task, participants were debriefed about the experiment and were asked three questions. First, they were asked whether they suspected their performance on the task did not influence their likelihood of winning the raffle. Second, they were asked to indicate how much they believed their responses in the task influenced the feedback they received. Third, they were asked whether it felt more rewarding when they earned a coin they stood up to retrieve or a coin they remained seated to retrieve. Data related to these questions is provided in Appendix A. The monetary incentive delay task was scripted and delivered with Presentation software. The script and stimuli can be found at https://doi.org/10.17605/OSF.IO/8MKTH.

2.2.2. EEG recording and initial processing

Scalp EEG was collected from 22 channels of an EEG cap housing a 64 channel BrainVision actiCAP system (Brain Products GmbH, Munich, Germany) labeled in accord with an extended international 10–20 system (Oostenveld and Praamstra, 2001) and sampled at 250 Hz. EEG data were online-referenced to the left earlobe and a common ground was employed at the FPz electrode site. Electrode impedances were maintained below 25 k Ω throughout the study and a high-pass filter was set at 0.016 Hz. The EEG signal was amplified and digitized with a BrainAmp DC amplifier (Brain Products GmbH) linked to BrainVision Recorder software (Brain Products GmbH). EEG data processing was conducted with BrainVision Analyzer 2.1 software. Data were re-referenced to an averaged ears montage, band-passed filtered between 0.1 and 30 Hz with 4th order rolloffs with a 60 Hz notch employing a zero-

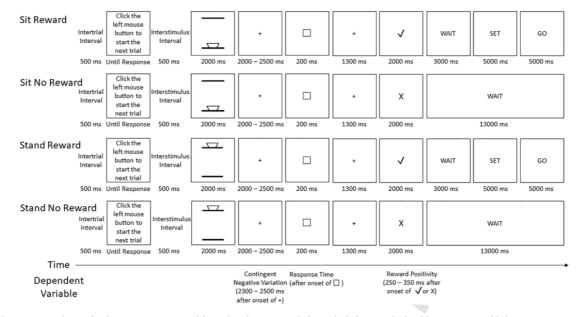


Fig. 2. Study design. Four trial types for the monetary incentive delay task and time intervals from which the reward-related brain activity and behavior measures were derived. Each trial was preceded by an inter-trial interval followed by a prompt for the participant to initiate a response. After the response, an inter-stimulus interval occurred and the trial type (sit vs. stand) stimulus was presented. Next, a fixation cross was presented for a random time interval and the contingent negative variation (CNV) ERP component was extracted from the EEG. After the offset of the cross, the target appeared, and the participant's response time was recorded. After the target disappeared, a fixation cross appeared followed by a feedback was displayed. On reward feedback trials, participants were presented with a prompt to wait, followed by a prompt to set their hand over the appropriate blue container with the coins, standing up to do so for the stand trials. Then, the set prompt was replaced by a go prompt, which instructed the participant to take a coin from the container and place it in the red collection container while returning to their starting position in the chair.

phase shift Butterworth filter. Next, a researcher with expertise in EEG processing visually inspected the data and marked obvious non-ocular artifacts. Then, ocular artifacts were reduced employing the ICA-based ocular artifact rejection function within the BrainVision Analyzer software (electrode FP2 served as the VEOG/HEOG channel; BrainProducts, 2013). This function searches for an ocular artifact template in channel FP2 and then, finds ICA-derived components that account for a user specified (70%) amount of variance in the template-matched portion of the signal from FP2. These components were removed from the EEG signal, which was then reconstructed for further processing.

2.2.3. Demographics

We collected data about demographic variables that could be related to the reward associated with energetic cost minimization, such as body mass index, typical exercise behavior, and recent physical activity (Cheval et al., 2018). After providing informed consent and before performing the monetary incentive delay task, participants self-reported their age, sex, height, weight, and handedness (Oldfield, 1971). After completing the task, participants filled out three versions of the International Physical Activity Questionnaire (IPAQ) (Craig et al., 2003) that asked about physical activity behavior and sedentary behavior during (1) a typical week; (2) the last 3 days; and (3) the current day. After completing the IPAQs, participants filled out the Situated Decisions to Exercise Questionnaire (SDEQ), which indexes contextual decisions about exercise behavior (Brand and Schweizer, 2015). Specifically, the SDEQ describes a situation (e.g., "You're leaving class/work and you are just about to go to the gym. Now you hear that your friends plan to go for a drink. They invite you.") and asks, "Do you exercise or not?" Responses are made on a 5-point scale, anchored by "By All Means/Definitely Yes", "By No Means/Definitely No". The internal consistency of the SDEQ was assessed with Chronbach's a, which yielded a value of 0.641, indicating marginal reliability. Demographics data are available in Appendix B.

2.3. Dependent variables

2.3.1. Response time

In the present experiment, participants' response times were computed as the difference in time between target appearance and participants' first response. If the participants made no response prior to feedback or if the participants anticipated and responded before the target appeared, the trial was excluded from subsequent analysis. This procedure resulted in the rejection of 11.0 ± 11.8 (mean \pm SD) trials per participant. The remaining trials were natural log transformed and averaged. The main results were presented using natural log-transformed response times as the dependent variable. However, models were also tested using the raw response times and these tests led to consistent results.

2.3.2. Contingent negative variation ERP component (CNV)

Here, the CNV was extracted from an epoch beginning 200 ms prior to the onset of the trial-type stimulus (image depicting a container on an upper or lower line; stand or sit trial, respectively) and ending 4500 ms after this stimulus. Then, the epoch was baseline-corrected with respect to the pre-stimulus interval (-200-0 ms). Next, epochs containing a change of $>50\,\mu\text{V}$ from one data point to the next, a change of $100\,\mu V$ within a moving 200-ms window, or a change of $<0.5\,\mu V$ within a moving 200-ms window in any of the electrodes of interest (FC1, FCz, C1, Cz) were excluded from subsequent analysis. Further, any epochs containing EEG that was marked as containing an obvious artifact during visual inspection and any epochs in which participants responded before 4000 ms were removed. This resulted in the rejection of 11.3 ± 11.0 epochs per participant. The remaining epochs were averaged within trial type (sit vs. stand). The CNV was quantified by taking the mean amplitude during the final 200 ms before the target could appear (3800-4000 ms after trial type stimulus onset) at FC1, FCz, C1, and Cz, then averaging across these electrodes (Novak and Foti, 2015; Novak et al., 2016).^{2,3}

2.3.3. Reward positivity ERP component (RewP)

In the present experiment, the RewP was extracted from an epoch beginning 200 ms prior to the onset of the feedback stimulus and ending 1000 ms after this stimulus. Then, the epoch was baseline corrected with respect to the pre-stimulus interval (–200–0 ms). Next, epochs containing a change of $> 50 \,\mu\text{V}$ from one data point to the next, a change of $100\,\mu\text{V}$ within a moving 200-ms window, or a change of $<0.5\,\mu\text{V}$ within a moving 200-ms window in any of the electrodes of interest (Fz, FCz, Cz) were excluded from subsequent analysis. Further, any epochs containing EEG that was marked as containing an obvious artifact during visual inspection were excluded from subsequent analysis. This resulted in the rejection of 2.85 ± 4.56 epochs per participant. Next, epochs time-locked to reward feedback were averaged separately for sit and stand trials, and the same was done for epochs time-locked to no reward feedback. Then, the average of the no reward feedback epochs was subtracted from the average of the reward feedback epochs separately for sit and stand trials to create a difference wave for sit trials and a difference wave for stand trials. To determine the time window for RewP quantification, the sit and stand difference waves were averaged together for each participant. Since difference waves exhibited substantial interindividual variability in RewP peak latency, we adapted each participant's RewP time window to their RewP peak latency at the electrode (Fz, FCz, or Cz) at which it peaked (Clayson et al., 2013).4 Specifically, we centered a 40-ms time window on each participants' positive peak amplitude at Fz, FCz, or Cz within 250-350 ms. We then computed mean amplitude in this time window for Fz, FCz, and Cz and then averaged across these electrodes. We did this separately for the sit and stand difference waves.

2.4. Statistical analysis

The confirmatory analyses were conducted with one-tailed paired sample *t*-tests (trial type: sit vs. stand) for the three dependent variables. Reward (reward vs. no reward) was not a factor because on each trial the reward manipulation occurred after the CNV and response time were measured, and the RewP was derived from a reward minus no reward difference wave. Non-significant results in a null-hypothesis significance test do not provide evidence for the absence of an effect (Harm and Lakens, 2018). Therefore, to draw informative conclusions in case of the null effect of condition (sit vs. stand), we planned to apply a two one-sided tests (TOST) procedure to test equivalence for a dependent *t*-test (Cohen's dz) using the TOSTER package, version 0.3.4 of the R software (Lakens, 2017).

3. Results

Means and standard deviations for response time, CNV amplitude, and RewP amplitude are shown in Table 1.

Table 1
Dependent variable descriptive data by condition.

Dependent variable	Sit (mean ± SD)	Stand (mean \pm SD)
Ln(Response Time) (ms)	7.76 ± 0.17	7.79 ± 0.13
Contingent negative variation (μ V)	-6.08 ± 5.75	-6.20 ± 5.35
Reward positivity (μ V)	6.18 ± 3.73	7.30 ± 5.71

3.1. Response time

Results of the equivalence test were in line with a non-significant effect of condition (sit vs. stand). Specifically, we tested the equivalence of log-transformed response time of the sit and stand condition, with correlation between observations of 0.821, using equivalence bounds of -0.095 and +0.095 (on a raw scale) (Novak et al., 2016), with an alpha of 0.05. The equivalence test was significant ($t_{(28)}=3.50,\ p<0.001)$ and the null hypothesis test was non-significant, $t_{(28)}=-1.60,\ p=0.060$ (one-tailed). Taken together, these results suggest the absence of a meaningful effect of condition (sit vs. stand) on response time. This absence of effect was confirmed by the results of the null hypothesis significance test based on raw reaction time (p = 0.13).

3.2. Contingent negative variation ERP

The grand average waveform and topoplot for the CNV are depicted in Fig. 3, Panels A and B, respectively. Results of the equivalence test were in line with a non-significant effect of condition (sit vs. stand). Specifically, we tested the equivalence of CNV of the sit and stand condition, with correlation between observations of 0.931, using equivalence bounds of -1.234 and +1.234 (on a raw scale) (Novak et al., 2016), with an alpha of 0.05. The equivalence test was significant, $t_{(26)} = -2.74$, p = 0.005 and the null hypothesis test was non-significant, $t_{(26)} = 0.297$, p = 0.616 (one-tailed). The result is visualized in Fig. 3, Panel C, where the 90% confidence interval is plotted and compared to the equivalence bounds. As the 90% confidence interval did not include the equivalence bounds, we can declare equivalence. In other words, based on the combined results of these two tests we can conclude that there was evidence for the absence of an effect of our conditions (sit vs. stand) on CNV.

3.3. Reward positivity ERP

The grand average waveform and topoplot for the RewP is depicted in Fig. 4, Panels A and B. Results of the equivalence test were in line with a non-significant effect of condition (sit vs. stand). Specifically, we tested the equivalence of RewP of the sit and stand condition, with correlation between observations of 0.645, using equivalence bounds of -3.926 and 3.926 (on a raw scale) (Meadows et al., 2016a), with an alpha of 0.05. The equivalence test was significant, $t_{(26)} = 3.38$, p = 0.001 and the null hypothesis test was non-significant, $t_{(26)} = -1.33$, p = 0.903 (one-tailed). The result is visualized in Fig. 4C, where the 90% confidence interval is plotted and compared to the equivalence bounds. As the 90% confidence interval did not include the equivalence bounds, we can declare equivalence. In other words, based on the combined results of these two tests we can conclude that there was evidence for the absence of an effect of our conditions (sit vs. stand) on RewP.

 $^{^2}$ In the pre-registration document, the epoch is incorrectly noted as ending 3500 ms after the stimulus onset, and CNV quantification is incorrectly noted to be mean amplitude between 2800 and 3000 ms after stimulus onset. However, the last 200 ms before the target could appear begin 3800 ms after the stimulus onset, which was the intended epoch of interest (Novak and Foti, 2015; Novak et al., 2016).

³ For both CNV and RewP, if one of the electrodes to be used for averaging had malfunctioned during recording, this electrode was excluded from the average. This was the case for only one participant.

⁴ We also confirmed that this peak corresponded to a negative deflection in the no reward feedback waveforms (Krigolson, 2018), which was the case for all but four participants. For these participants, the positive peak between 250 and 350 ms of the difference waveform that corresponded with a negative deflection in the no reward feedback waveforms was used to determine the RewP time window.

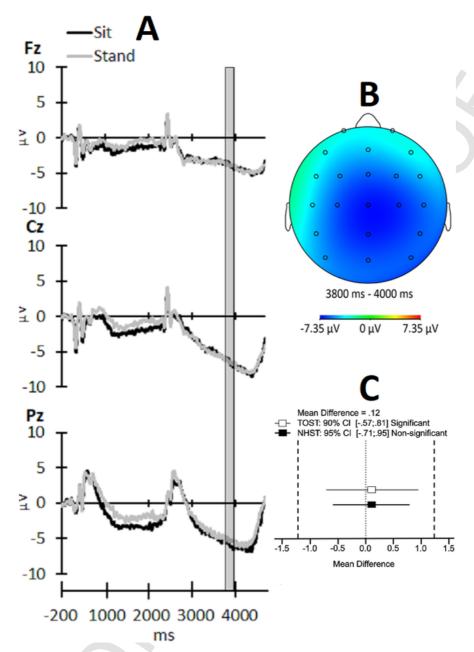


Fig. 3. Contingent negative variation. A: Grand average waveforms for the ERP time-locked to the onset of the trial type (sit or stand condition) stimulus at the Fz, Cz, and Pz electrodes. The highlighted area represents the final 200 ms before earliest target onset, and contingent negative variation ERP component (CNV) mean amplitude is computed for this epoch. B: Topography of the CNV averaged across condition. C: Equivalence test for CNV showing the 90% confidence interval in relation to the equivalence bounds of -1.234 and +1.234.

4. Discussion

This study was designed to investigate whether energetic cost modifies reward-related brain activity. The EEG activity of 27 participants was analyzed when they remained seated or stood up in response to monetary incentives. Based on the TECM (Cheval et al., 2018), we hypothesized that rewards that could be retrieved with lower energetic expenditure (i.e., remain seated vs. standing up) are associated with quicker response times (H1), greater brain activity linked to reward pursuit (H2), and greater brain activity linked to reward valuation (H3).

Results did not support the hypotheses derived from the TECM (Cheval et al., 2018). Response times were similar across conditions. CNV amplitude was not significantly larger for rewards that could be

retrieved with minimal energetic expenditure (remain seated vs. stand up). These results did not support the hypothesis that actions involving lower energy expenditure were associated with greater reward pursuit than actions involving higher energy expenditure (H1 and H2). RewP amplitude was not larger for actions involving lower energy expenditure either, thereby suggesting that these actions were not valued more than actions involving higher energy expenditure (H3). Moreover, equivalence tests confirmed the absence of effects of energy expenditure (sit vs. stand) on the three outcomes.

These results are inconsistent with previous functional magnetic resonance imaging (fMRI) research showing decreased activation of brain regions involved in reward processing, such as anterior cingulate cortex, when participants were informed that they would have to exert higher levels of physical effort to subsequently receive a reward (Croxson et al., 2009; Prévost et al., 2010). Results are also inconsistent

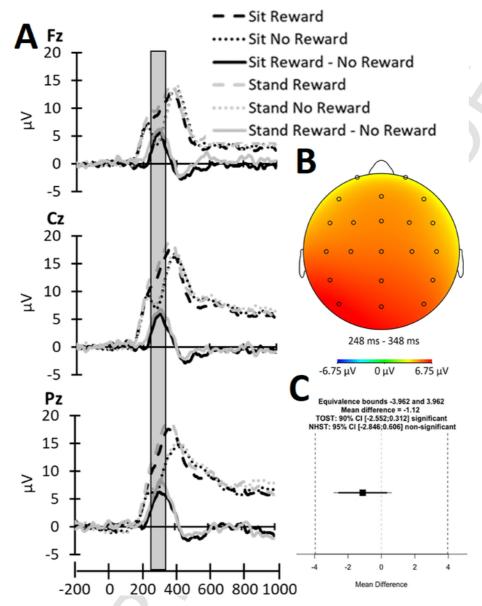


Fig. 4. Reward positivity. A: Grand average waveforms for the ERP time-locked to the onset of reward/no reward feedback at the Fz, Cz, and Pz electrodes. The solid lines represent the reward – no reward difference waves for each condition. The highlighted area represents the epoch in the difference wave used to compute mean amplitude in adaptive 40 ms time windows. B: Topography of the difference wave reward positivity ERP component (RewP) averaged across condition. C: Equivalence test for RewP showing the 90% confidence interval in relation to the equivalence bounds of –3.926 and +3.926.

with fMRI research demonstrating that participants use prediction errors to make decisions to minimize energy expenditure by employing a brain network that includes anterior cingulate cortex (Skvortsova et al., 2014). In the present experiment, the RewP reflected a reward-prediction error generated by anterior cingulate cortex, but the RewP was not enhanced for trials associated with low energy expenditure (sit trials). However, there are some notable differences between past research and the present experiment, besides the different method used to record brain activity. For example, the present research had participants increase energy expenditure by standing up, whereas past research had participants increase energetic cost in less ecologically-valid ways, such as by applying pressure to a force sensor or moving a trackball computer mouse. Second, the present experiment differed in that participants' brain activity associated with reward-prediction errors/reward valuation was measured at the time of reward consumption (i.e., receiving the feedback indicating that they had earned the reward; Novak et al., 2016), whereas the prior research measured reward valuation when participants were given a cue about subsequent energy expenditure. Future research could investigate the effects of opportunities to minimize energetic cost on different stages of reward processing, likely using EEG, given its exquisite temporal resolution (Novak and Foti, 2015; Novak et al., 2016).

Some explanations could account for the null results reported in the present study. First, the energetic cost difference between standing and remaining seated may be insufficient and could be associated with small effect sizes. Future studies should use paradigms with larger energetic expenditure differences. For example, participants could be instructed to stand up and sit back down several times (retrieving a coin each time) after each instance they earn a reward. This condition could be contrasted with another condition wherein participants remain seated and repeatedly reach into a container several times to retrieve coins. Second, participants may not have been sufficiently sensitive to the reduction of energetic cost. The TECM posits that energetic minimization is more rewarding for individuals who have recently ex-

pended energy and who are not physically fit. Here, participants generally came into the experiment having expended little energy on their testing day (relative to their typical weekly energy expenditure), but also reporting typical physical activity behavior and body mass indices associated with high levels of physical fitness (see Appendix B). Future studies should include an acute exercise before the rewarding task and select a sample of physically inactive participants. Third, the automatic neuro-behavioral adaptation favoring the optimization of energetic cost may not be mediated by the reward network and may rely on other processes such as purely biomechanical adaptation mechanisms.

Among the strengths of the present study are the investigation of the effects of engaging in ecologically-valid behaviors involving lower versus higher energy expenditure on reward-related brain activity, the implementation of a paradigm known to elicit this brain activity (Knutson et al., 2000; Meadows et al., 2016a; Meadows et al., 2016b; Novak and Foti, 2015; Novak et al., 2016; Threadgill and Gable, 2016), and the assessment of the activity using a select couple of large ERP components, including one that was isolated with a difference wave (RewP; Luck, 2014). However, three potential limitations should be noted. First, as mentioned above, we used a homogenous sample of participants who may not have found energetic cost minimization particularly rewarding. Second, our paradigm elicited anticipatory responses (before the target appeared), which caused us to discard response time and CNV data from some trials. Future studies should consider monetary incentive delay paradigms that are less likely to elicit such responses (e.g., paradigms with more variability between the target cue and the target as well as paradigms without a specific response window; e.g., Meadows et al., 2016b). Finally, our paradigm instructed participants that their responses would influence their feedback, when in fact it was unrelated to their responses. Although this technique ensured equiprobable reward/ no reward feedback within sit and stand conditions (Meadows et al., 2016a), it may have not been ideal for investigating the effects of condition on the RewP. This follows because the RewP is believed to reflect a reward-prediction error, which is the difference between the actual reward associated with a feedback stimulus and the expected reward. Since participants were told their response times influenced whether they received reward feedback, they likely anticipated getting reward feedback for trials with faster response times. This anticipation effect could have masked an effect of condition on RewP results, but it is unlikely to have done so. This follows because response time did not meaningfully differ as a function of condition (see Section 3.1), and participants believed their responses partially influenced whether they received a reward (see Appendix A). Nonetheless, for future studies, we suggest using veridical feedback that is still equiprobable between conditions (e.g., Holroyd and Krigolson, 2007; Novak and Foti, 2015; Novak et al., 2016), or not having feedback linked to responses and not deceiving participants to think otherwise (e.g., Proudfit, 2015).

5. Conclusion

The present study directly tested, for the first time, whether opportunities to sit or stand trigger different reward-related brain activity, as contended by the theory of energetic cost minimization (Cheval et al., 2018). Results did not support this hypothesis as they showed that reward-related brain activity was equivalent at lower (remaining seated) and higher (standing up) level of energy expenditure. Yet, this null result is informative and future studies addressing some limitations of the current one, while leveraging its strengths, could contribute to shed light on the neural processes underlying the pandemic of physical inactivity.

Contributors

B.C., M.P.B., M.W.M. designed the analyses. M.F.B.B., R.F., M.W.M. collected the data. B.C., M.P.B., M.W.M. analyzed the data. B.C., M.P.B., M.W.M. drafted the manuscript. B.C., M.P.B., M.F.B.B., R.F., M.W.M. critically appraised and approved the final version of the manuscript.

Funding

B.C. is supported by an Ambizione grant (PZ00P1_180040) from the Swiss National Science Foundation (SNSF).

Competing interests

The authors declare no conflict of interests.

Ethical approval

This study was approved by the Auburn University Institutional Review Board (Protocol #18-318 EP 1808).

Pre-registration and data sharing

The methods were preregistered at https://aspredicted.org/hu54t. pdf. Questionnaires are available at https://doi.org/10.17605/OSF.IO/8MKTH. Data are available at https://doi.org/10.17605/OSF.IO/8MKTH. Scripts are available at https://doi.org/10.17605/OSF.IO/8MKTH.

Uncited reference

Cheval et al., n.d

Appendix A. Debriefing questions and responses

Indicate how much you believed your responses influenced whether you
earned a reward. One-hundred-point visual analog scale is anchored by "0,
not at all" and "100, completely".

M = 51.4 (SD = 25.3).

 Did you believe the number of coins you earned would influence your chances in the raffle?

Yes = 27

No = 1

- Which type of trial felt more rewarding to win?

Sit = 12

Stand = 5

No Difference = 8

Appendix B. Demographic data

Variable	Mean (SD)
METs ^a /week	6110 (4728)
METs/last 3 days	1987 (1718)
METs/present day	187 (282)
Sitting/week (min)	351 (217)
Sitting/last 3 days (min)	402 (268)
Sitting/present day (min)	140 (137)
$SDEQ^b$	2.33 (0.547)

^a METs refer to metabolic equivalents and express the energy cost of physical activities as a multiple of the resting metabolic rate. Here, METs refer to values obtained from the

International Physical Activity Questionnaires (Craig et al., 2003).

b Situated Decision to Exercise Questionnaire.

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