A Replication of the Ego-Depletion Effect: Control of Effort Engagement during the Depleting Task with Electroencephalography and Heart-Rate Variability

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Abstract

The ego-depletion effect has been interpreted as a temporary failure of self-control exertion after a first effortful task (Baumeister et al., 2007). Although the existence of this effect was previously challenged (Vohs et al., 2021), it was successfully replicated in a recent study applying an adequate experimental protocol (Mangin et al., 2021). In the present experiment, we applied a similar protocol while assessing the electrophysiological changes in effort engagement through mid-frontal theta and cardiac reactivity (Cavanagh & Frank, 2014; Mukherjee et al., 2011). A total of 32 participants in a between-subjects design performed the following task sequence: handgrip task at 13% of maximal voluntary contraction, a 30-min mental task (depleting or control task) and the handgrip task again (dependent task). The experimental group (N = 16) performed a modified Stroop task, while the control group (N = 16) watched an emotionally neutral documentary. EEG and ECG were recorded on a continuous basis. We assumed to observe an increase in the electrophysiological correlates of mental effort during the depleting task and a performance decrement in the subsequent dependent task. For the depleting condition, the behavioral results showed worse performance in the subsequent dependent task and the EEG results showed higher mid-frontal theta power. Heart-rate variability results showed an increase in parasympathetic activity over time during the depleting task. Therefore, the ego-depletion effect was once again successfully replicated. The depleting task required more mental effort than the control task, but a slight decrease in effort engagement over time was also observed.

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Impact statement: Our findings add a new perspective on replicating the ego-depletion effect by controlling the engagement of effort during the depleting and control tasks. Higher midfrontal theta power, an index of mental effort, was observed during the depleting task compared to the control task, and the ego-depletion effect was successfully replicated.

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The ego-depletion effect has been interpreted as a temporary failure of self-control exertion after a first effortful task (Baumeister et al., 2007). Although the existence of this effect was previously challenged (Vohs et al., 2021), it was successfully replicated in a recent study applying an adequate experimental protocol (Mangin et al., 2021). In the present experiment, we applied a similar protocol while assessing the electrophysiological changes in effort engagement through mid-frontal theta and cardiac reactivity (Cavanagh & Frank, 2014; Mukherjee et al., 2011). A total of 32 participants in a between-subjects design performed the following task sequence: handgrip task at 13% of maximal voluntary contraction, a 30-min mental task

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Key words: Ego-depletion, Mental effort, Mid-frontal theta, Cardiac reactivity

Introduction

Every day, we engage in cognitive and physical activities that challenge us to move beyond our habits and require greater effort, such as learning a new language, solving a complex mathematical equation, running a marathon, manipulating information in working memory, and managing multiple priorities. Such effortful tasks require higher-order executive functions, such as self-control, inhibitory control of our thoughts, emotions, impulses, and behaviors, to reach desired goals (Baumeister et al., 2007). When self-control is weakened by a first effortful task, a drop in a subsequent effortful task is generally observed. This phenomenon is known as the "ego-depletion effect" (Baumeister et al., 1998).

However, over the past decades, the existence of the ego-depletion effect has been challenged by meta-analytic studies and faced a replication crisis (Carter et al., 2015; Dang, 2018). For example, a worldwide replication study from 12 different laboratories (N = 1,775) showed a small effect size (d = 0.16) for the ego-depletion phenomenon (Dang et al., 2021). Another recent multilaboratory project (k = 36; N = 3,531) reported no evidence for the ego-depletion effect (d = 0.06) (Vohs et al., 2021). The ego depletion effect was first evidenced in social psychology with the sequential task protocol (Hagger et al., 2010). Then, sport sciences used the same protocol to examine the effects of mental fatigue induced by an effortful task on a subsequent physical task (Brown et al., 2020; Giboin & Wolff, 2019; Hunte et al., 2021; Van Cutsem et al., 2017).

Three theoretical approaches mainly explained the subsequent task performance decrease observed in the sequential task protocol. Based on the strength model of self-control, the first approach assumes that the ego-depletion effect occurs as the result of resource depletion, such as brain glucose (Baumeister et al., 2007). According to the second model, the ego-depletion effect is caused by the switching of motivation and/or attention toward a more pleasant task (Inzlicht et al., 2014). The third approach refers to the cost-benefit model and suggests that, when the costs to achieve the task goal are higher than the benefits associated with the achievement of the task goal, participants decrease their engagement in effortful control or drop out (Kurzban et al., 2013; Shenhav et al., 2017). In this regard, mental or cognitive fatigue can be viewed as a cost (Boksem & Tops, 2008), which has also been considered the cause of the ego-depletion effect experienced in prolonged cognitive activities (Muraven & Baumeister, 2000).

In a more recent model, the main cause of the decrease in the functional capacity to exert effortful control observed after a long and effortful task is explained by a weakening of the connectivity within and between large-scale neuronal networks underpinning effortful control, such as the salience network and the executive control network, and an accumulation of metabolites in brain regions involved in effortful control, such as the anterior cingulate cortex (André et al., 2019). Three possible metabolites have been proposed to be byproducts of neuronal activity that could decrease the capacity to exert effortful control: (1) the adenosine that operates in a negative feedback loop on neuronal activity and then decreases it (André et al., 2019; Cunha, 2001; Martin et al., 2018; Smith et al., 2019); (2) the glutamate, the neurotransmitter released by pyramidal neurons in cortical columns involved in cognitive control (Wiehler et al., 2022); (3) the amyloid- β (A β) peptides continuously secreted into the interstitial fluid by active neurons (Holroyd & Umemoto, 2016).

The integrative model of effortful control reconciles the three models cited in a previous paragraph: (1) in accordance with the strength model of self-control (Baumeister et al., 2007), it predicts that exerting effortful control leads to a progressive weakening of the capacity to exert effortful control; (2) in accordance with the process model of self-control depletion (Inzlicht et al., 2014), it conceives that ego depletion and mental fatigue can be accompanied by a decrease in motivation to exert effortful control; (3) in accordance with the cost-benefit models of effort-based decision-making (e.g., Shenhav et al., 2017), it views effortful control as costly and mental fatigue as an intrinsic cost generated by the sustained deployment of mental effort.

However, the integrative model of effortful control differs from these three models in different ways: (1) contrary to the strength model of self-control, it assumes that the duration of the effortful task and the executive control required to perform this task are two critical parameters to observe ego depletion (i.e., only long and demanding tasks induce ego depletion and mental fatigue); (2) contrary to the process model of self-control depletion, it assumes that the shift in motivation to exert effortful control is not the cause but a possible consequence of ego depletion and mental fatigue; (3) contrary to the cost-benefit models, it assumes that exerting effortful control is not intrinsically aversive.

According to the integrative model of effortful control, we assume that the replication studies aiming to examine the ego depletion effect did not use adequate protocols and that the ego-depletion effect can be replicated by considering some methodological precautions. First, according to the previous literature (Mangin et al., 2021), the depleting task must be sufficiently effortful to observe the ego-depletion effect. In general, tasks that involve core executive functions, including cognitive flexibility, updating of working memory, and inhibitory control, are good candidates for generating effortful control costs (André et al., 2019; Hofmann et al., 2012) and inducing the ego-depletion effect (Dang et al., 2021). For instance, while the choice of the letter-crossing task as a depleting task was not successful (Etherton et al., 2018; Wimmer et al., 2019; Xu et al., 2014), a modified Stroop task tapping two executive functions, cognitive flexibility and inhibitory control, was effective at inducing the ego depletion effect (Dang, 2018; Hagger et al., 2010; Mangin et al., 2021, 2022).

Second, the duration of the depleting task also plays an important role in the occurrence of the ego-depletion effect. In most of the previous ego-depletion studies, the duration of the depleting tasks was short: an average of 6.27 min (SD = 3.22 min) (Hagger et al., 2010). However, healthy subjects must exert their self-control long enough to be depleted (Blain et al., 2016). Recently, Boat et al (2020) showed that the longer the duration of the depleting task (4, 8, and 16 min), the greater the effects of deterioration on a subsequent physical task. In the same way, sport science studies using the sequential task protocol have observed that the performance of a physical task is generally degraded after a long (> 30 min) and continuous effortful cognitive activity (Van Cutsem et al., 2017). In this regard, assessing the engagement of the participants in the depleting task as a function of time on task can be helpful to examine if the task is sufficiently depleting.

Third, a recent study showed that the choice of the control task is also an essential factor in replicating the ego-depletion effect (Mangin et al., 2021). This study emphasized that the use of a boring control task, such as a congruent Stroop task, can prevent the observation of the ego-depletion effect. Performing a boring task seems as costly as a task involving executive functions and requires a certain amount of effortful control to be completed.

According to the three aforementioned points, an adequate protocol to replicate the ego-depletion effect would be a sequential task protocol that uses a 30-min effortful modified Stroop task tapping inhibitory control and cognitive flexibility as the depleting task, a time-to-exhaustion handgrip task as the dependent task, and a not boring 30-min documentary video-watching task requiring little effort as the control task.

The integrative model of effortful control also assumes that an increase in mid-frontal theta wavebands (4–7 Hz), a control signal generated by the salience network, more specifically the anterior cingulate cortex (ACC), one of its central nodes, is an indicator of effort engagement and compensatory effort. André et al. (2019) also claimed that the decrease in the capacity to exert effortful control induced by ego-depletion and mental fatigue can be observed in changes in the density of mid-frontal theta waves and performance

drop throughout the depleting task. In this respect, two patterns of results induced by ego-depletion and mental fatigue can be expected during a long effortful task: (1) a decrease of performance associated with a disengagement of effortful control; (2) a stability of performance associated with an increase of effortful control (i.e., compensatory effort). These changes in theta activity throughout the depleting task should be observed with electroencephalography (EEG).

In this respect, Umemoto et al (2019) assumed that the ACC is responsible for regulating control levels by balancing the reward-related benefits of control in contrast to its effort-related costs. These authors measured reward valuation and cognitive effort with two electrophysiological indices of ACC function during a 2-hour time estimation task (i.e., participants had to estimate 1 second on every trial), respectively the reward positivity (RewP) and frontal midline theta. Reward positivity (RewP) is an event-related potential (ERP) component produced by fast, phasic midbrain dopamine reward prediction and error signals that are modulated by ACC activity (Holroyd & Coles, 2002), and it is aroused by feedback stimuli with negative versus positive valence (Miltner et al., 1997). The authors observed the participants' performance throughout the time estimation task, giving them error and reward feedback based on their performance while their neural activities were assessed with EEG. The results showed a decrease in the reward positivity (RewP) amplitude with time on task in contrast to an increase in frontal midline theta power throughout the effortful task. According to their findings, when a long cognitively-demanding task is performed, two different phases can be distinguished. During the first phase of the task, high control levels are associated with strong reward valuation, which both contribute to significant improvements in task performance. In the later phase of the task, high control levels counteract the decrease in reward valuation, thereby helping to maintain stable task performance.

In addition, other EEG studies have also shown an increase in theta power during tasks requiring mental effort (e.g., Smit et al., 2005). Cavanagh and Frank (2014) also argued that the mid-frontal theta signal reflects diverse cognitive operations, including those involved in cognitive control. In a later study, they proposed that frontal-midline theta reflects midcingulate cortex (MCC) activity, which is involved in cognitive control and anxiety (Cavanagh & Shackman, 2015). An association of mid-frontal theta activity with different cognitive or motor sustained attention tasks is assumed to originate from the ACC (Kao et al., 2013; Onton et al., 2005; Sauseng et al., 2007). Evidence from a recent systematic review with a meta-analysis of 21 EEG studies performed on healthy individuals reported that frontal-midline theta is a robust biomarker of mental fatigue, with significant increases in theta activity in frontal, central, and posterior areas mainly observed (Tran et al., 2020). Another literature review also showed an increase (Borghini et al., 2014). We can conclude from the two reviews mentioned above that the increase in theta during a long effortful task is an index of compensatory effort to maintain the level of performance instead of mental fatigue.

In addition to mid-frontal theta assessed by EEG, other psychophysiological indices, such as pupil diameter, contraction of specific muscles, and sympathetic arousal (e.g., cardiac reactivity), can also be considered different indices of effort engagement (Shenhav et al., 2017). Heart rate variability (HRV), or the analysis of beat-to-beat intervals, is one of the most common and reliable physiological measurements used to assess mental effort (Aasman et al., 1987; Mukherjee et al., 2011; Mulder & Mulder, 1981; Veltman & Gaillard, 1993). The sympathetic and parasympathetic nervous systems influence HRV, which can vary depending on the subject's physiological and psychological state (Ernst, 2017). During the performance of a task that requires mental effort, the previous literature has mainly reported a decrease in heart rate variability (Capa et al., 2008; De Rivecourt et al., 2008; Wang et al., 2005; Weippert et al., 2009).

Accordingly, the principal aim of this study was to replicate the ego-depletion effect while controlling for the engagement of effort during the depleting and control task and using a similar sequential task protocol as in a previous study that successfully replicated this effect (Mangin et al., 2021). The electrophysiological changes in effort engagement throughout the depleting task will be assessed through mid-frontal theta density and cardiac reactivity. We expected higher mid-frontal theta density during the depleting task than during the control task. We also predicted a progressive increase in mid-frontal theta power as a function of time on task

(TOT) during the depleting task. Finally, we assumed that we would observe a decrease in HRV throughout the depleting task compared to the control task. Along with these physiological measures, we hypothesized that the participants might report a higher level of subjective fatigue and a lower motivation to perform the handgrip task after performing the mentally demanding task.

Methods

Participants

Thirty-two undergraduate students in their third year studying sport sciences at the University of Poitiers participated in this study. The participants were randomly assigned into two groups: a control group and an experimental group. Their characteristics can be found in Table 1. All of the participants were native French speakers and right-handed except one in the experimental group who was left-handed. All participants had normal to corrected-to-normal vision with no reports of color blindness. None of the participants revealed a history of language difficulties, learning impairments, or severe neurological, metabolic and/or psychiatric disorders. For the sake of our handgrip endurance-dependent task, we did not recruit individuals who had been engaged in a muscle reinforcement activity for more than 6 months or anyone who had injuries or functional problems with the dominant hand. The experimental procedure was explained to the participants via a written information sheet. Then, they signed a consent form to indicate their agreement. Finally, the participants received course credit in exchange for their participation. This experiment was conducted in accordance with the Declaration of Helsinki and with the approval of the University of Tours-Poitiers ethics committee (serial number 2019-01-02).

Procedures

This experiment occurred during a single session, and the participants in both groups underwent the exact same procedures. The session started with asking the participants to complete a sociodemographic questionnaire (height, weight and age) and a hand laterality scale (Oldfield, 1971) to determine their dominant hand. The participants were also tested for color blindness (Ishihara, 1918) to determine whether they were able to perform the Stroop task. Then, the participants answered questions regarding their general state and health. Certain experimental precautions related to any parameters that could have an effect on mental strain and fatigue were considered, such as not consuming alcohol, caffeine, nicotine or psychostimulant substances; avoiding stressful events and/or intense physical activity several hours before the session; and having a sufficient amount of sleep the night before the experiment. Later, the participants underwent a familiarization period to understand the flow and instructions of the mental and physical tasks. In the familiarization phase, the participants performed 48 trials of the incongruent Stroop task and tried out the handgrip device. Afterward, they were equipped with EEG and ECG electrodes. Next, they underwent the sequential stages of the experimental protocol while their electrophysiological data were recorded on a continuous basis, as shown in Figure 1. First, the participants were asked to perform a time-to-exhaustion handgrip task to determine their physical performance baseline, while their maximal voluntary contraction (MVC) was assessed before and after this task. Second, they performed a 30-min mental task that differed in each of the two groups. The experimental group performed a 30-min modified incongruent Stroop task tapping two executive functions: inhibitory control and cognitive flexibility. The control group watched a 30-minute documentary video. After the completion of the mental task, the participants repeated the time-to-exhaustion handgrip task and the MVC measurements before and after this physical task. Every 30 seconds during each handgrip task, the participants were asked to announce the amount of effort that they invested in the task, as well as the level of pain that they experienced in their dominant forearm and hand. Several other subjective measurements were made throughout the session at four different times: T1 = Baseline, T2 = Pre-MentalTask, T3 = Post-Mental Task, T4 = Post-Handgrip Task. We used a computerized visual analog scale (VAS) with an adapted scale (0% to 100%) to rate the level of their perceived fatigue (T1 to T4), the motivation

to perform the physical task (T1 and T3), the perceived difficulty of the mental task (T3) and finally the level of boredom experienced during the mental tasks (T3). The motivation to perform the dependent task and subjective mental fatigue were already assessed with a similar VAS (Brown & Bray, 2017), and this type of VAS was validated by Wewers and Lowe (1990). Finally, a computerized version of the Brief Self-Control Scale (Tangney et al., 2004) was used to assess the participants' trait self-control due to the probable influence of this trait on the ego-depletion effect. Previously, it has been argued that individuals with a high self-control trait tend to demonstrate a lower ego-depletion effect than individuals with a low self-control trait (DeWall et al., 2007).

Insert Figure 1 about here

Materials

Time-to-exhaustion task

To measure the isometric handgrip force of the individuals' dominant hand, we used a dynamometer (TSD121C, BIOPAC). AcqKnowledge software, version 4.2 (BIOPAC Systems Inc., Goleta, CA, USA), as well as an MP160WSW data acquisition unit, was used to record the force signal. Data were recorded online at a sampling rate of 2000 Hz and later stored and analyzed offline. The participants were asked to sit on a fixed chair with an arm support allowing for the imposition of an angle of ~90 degrees with their elbow and forearm, as shown in Figure 2. The participants were asked to remain in this anatomically neutral position throughout the handgrip task.

Insert Figure 2 about here

The participants started the physical task by performing an MVC to measure their true maximal force. For this measurement, they had to squeeze the dynamometer as strongly as possible for a duration of 3 seconds. This process was repeated until the time that the participants could not score higher in contraction peak force compared to their previous performances. Between each MVC measurement, there was a 30-s rest. The highest MVC measured before the first time-to-exhaustion task was used throughout the session as the reference for force feedback to calibrate the target zone for the time-to-exhaustion handgrip task (see the gauge on Figure 2). The target zone area was defined as a green arc representing 12% to 14% of the MVC. The participants were asked to maintain the contraction of their forearm in this area until exhaustion. Time to exhaustion was evaluated offline and considered the duration of the isometric contraction from the onset of the force signal to the exhaustion time (considered as staying out of the zone for more than 2 s). To assess the extent of muscle fatigue and to ensure that the participants performed the handgrip task as much as they could, we compared the difference between the MVC peak force measured before and after the timeto-exhaustion task. During the time-to-exhaustion task, every 30 s, we asked the participants to rate their perception of effort, which is referred to as the effort intensity necessary to squeeze the dynamometer while breathing and remaining in the green zone (Mangin et al., 2021) on the CR100 scale (Borg & Kaijser, 2006), as well as their perception of muscle pain, defined as the perceived pain intensity in their forearm muscles during the endurance task performance (Mangin et al., 2021) on the Cook scale (O'Connor & Cook, 2001). The "individual isotime" method (Nicolo et al., 2019) was used to analyze the participants' perceptions of muscle pain and effort. This method considers the shortest performance record of the participant on the handgrip task as his or her 100% individual isotime. Subsequently, the corresponding isotime points to 0%. 33%, and 66% of the individuals were calculated for their shortest performance. According to the calculated isotime points, their level of muscle pain and effort was assessed as a function of time on task.

Mental tasks

We used a computerized version of a modified Stroop task on a computer equipped with an S-R response box and E-prime software, version 2.0 (Psychological Software Tools, Pittsburgh, PA, USA). The participants sat in front of a screen and responded orally to the visual stimuli that appeared at the middle of the screen while their voices were recorded via two microphones, one to record the oral response of the participant (headset) and the other to measure his or her response time (fixed microphone). The participants underwent 888 trials of 2 seconds each. Every single trial started with a fixation point in the form of a cross that lasted 400 ms. The fixation point could be enclosed in a circle or a square for a duration of 50 ms, and then the cross remained on the screen alone. Immediately thereafter, a color name (green, red, yellow or blue) written in another ink color (e.g., "yellow" written in red) was displayed on the screen. The participants had to read the word if they saw a square (reading trials) or name the color of the ink if they saw a circle (naming ink color trials). The color word lasted on the screen until the participant's response. If the participants did not answer (omission) or had a reaction time longer than 1250 ms, the color word lasted 1250 ms and was followed by a fixation cross lasting 300 ms. When the participant answered before 1250 ms had elapsed, the fixation cross remained in the middle of the screen for the same amount of time (1250 ms + 300 ms) to have a duration of 2 s for each trial. The presentation order of the two categories of trials was completely random. The block of trials included 50% trials in which the participants had to read the color word and 50% of trials in which they had to name the font color for the sake of increasing the task difficulty by engaging cognitive flexibility and inhibitory control (Mangin et al., 2021) and limiting the learning effect (Dulaney & Rogers, 1994). Concerning the modified Stroop task, we were interested in analyzing performance as a function of time on task. Consequently, data were divided into 4 consecutive periods of 222 trials lasting 7 minutes and 30 seconds. For each time period, we calculated different performance parameters, such as the mean reaction time for correct responses (RT) and the error rates. For the video task, we chose a documentary movie named Earth by Fothergill and Linfield (2009). Later, the participants were asked to complete a multiple-choice questionnaire related to the content of the documentary to verify whether they were actively watching the movie or not. They did not know in advance that they will have to complete this questionnaire.

EEG Acquisition and Pre-Processing Pipeline

The EEG data were collected from a 64-channel Biosemi EEG headset with the electrode distribution based on the international 10-20 system. For the sake of better eye movement artifact detection, the participants' ocular activities were recorded via three electrooculogram (EOG) electrodes (two on the outer canthus of each eye and one on the infraorbital region of the right eye). The EEG and EOG signals were continuously recorded online throughout the whole experiment using the ActiView Biosemi version 6.05 acquisition system at a frequency of 2000 Hz referenced online to the average of the right and left mastoids. The MATLAB R2020b programming platform (MathWorks Inc., Natick, MA, USA), together with the open source EEGLAB 2021.0 toolbox (Delorme & Makeig, 2004), was used for offline data analysis. Data preprocessing steps and artifact rejection methods were adopted from a very recent reproducible workflow by Pernet and colleagues (2021). First, data were down sampled to 250 Hz, and a basic low-pass FIR filter to the higher edge of 40 Hz was applied to avoid 50-Hz line noise. Then, the clean_rawdata plugin in EEGLAB (version 2.2) was used to highpass filter the data at 0.5 Hz (transition band $[0.25 \ 0.75]$), as well as remove the bad channels (any channel with at least a 5-s flat line and/or with less than 0.8 robust estimate correlation to the other channels were considered bad channels). Next, the data were rereferenced to the average of the existing channels. Afterward, the data were decomposed into independent components using the ICA algorithm (runica algorithm with rank reduction based on the number of channels = -1, considering the average reference). An automatic algorithm was applied to label the components using ICLabel (Pion-Tonachini et al., 2019), and components labeled as muscle activities and eye movements with greater than 80% probability were omitted from the data. Then, the residual artifacts were removed using the artifact subspace reconstruction (ASR) algorithm parametrized to a 20-burst detection criteria threshold (Chang et al., 2018, 2020). Finally, we inspected the data visually and rejected any nonbrain components or artifactual portions of the data that were not detected hitherto by the automatic algorithm. No more than half of the components in each data point were rejected (the maximum number of component rejections was 32 of 64). A power spectral analysis was applied to observe the differences in the power of theta wavebands (4-7 Hz) during the Stroop task performance as opposed to the video task. The "spectopo" function in EEGLAB was used to perform the power spectral analysis and to compute each component power spectrum using the fast Fourier transform (FFT) with the following parameters: a window size of 1 second with a 50% overlap. We were also interested in the effect of time on task during the Stroop task on the theta waveband power; therefore, we also studied the data by dividing the 30 minutes corresponding to the Stroop task into 4 consecutive task periods of 7.5 minutes.

Task-related theta activity

According to the methodology used by Arnau et al. (2021), we conducted an analysis of stimulus-locked theta power during the Stroop task. Throughout the Stroop task, when the color word was displayed on the screen, a marker was sent to ActiView Biosemi with the help of the Eprime program indicating that the ongoing trial is either a 'naming ink color' trial or a 'reading' trial. Later, during the EEG offline analysis, the data were analyzed in the following time window: from 100 ms before the stimulus onset to 2000 ms after this onset. After removing the baseline recorded during the time window from 100 ms before the stimulus to the onset of the stimulus, we separated the 444 trials belonging to the 'naming ink color' condition from the 444 trials belonging to the 'reading' condition for further analyses. Then, the power spectral analysis was applied to observe the changes in theta wave band by comparing these two types of trial (reading vs. naming ink color) as the function of TOT.

Source localization technique

The DIPFIT plugin (Oostenveld & Oostendorp, 2002) in the EEGLAB 2021.0 toolbox (Delorme & Makeig, 2004) was used to calculate an equivalent current dipole model for each independent component through a four-shell spherical head model. A bilaterally symmetric dual dipole model was fitted for the components with bilaterally distributed scalp maps. Only components located inside the model of brain volume, for which their best-fitting single or dual equivalent dipole showed less than 15% residual variance from the spherical forward-model scalp projection, were contemplated for further analysis.

ECG

Heart rate variability (HRV) was continuously recorded using the Electrocardiograph (BIOPAC Systems Inc., Goleta, USA) and Acqknowledge 4.2 software (BIOPAC Systems Inc., Goleta, CA, USA) at a frequency of 2000 Hz by placing three EL503 electrodes on the participant's thorax as recommended by the American Heart Association (Kligfield et al., 2007). The Kubios HRV Premium software, version 3.5.0 (Tarvainen et al., 2014), was used to analyze the data. After applying the medium automatic artifact correction algorithm available in Kubios, the residual artifacts were rejected via manual inspection. One subject in the control group was excluded from further analysis due to the low quality of his or her ECG data. We studied the changes in HRV on the temporal basis of four equal time windows of 7 minutes and 30 seconds. We analyzed the data by examining the time and frequency domain parameters of HRV. For the time domain analysis, we chose the SDNN (standard deviation of NN intervals), and for the frequency domain analysis, the LF power (log power of the low-frequency band from 0.04 to 0.15 Hz), as well as HF (log power of the highfrequency band from 0.15 to 0.4 Hz), was assessed (Shaffer & Ginsberg, 2017). The SDNN demonstrates the components that are responsible for the variability in the recording period (Malik, 1996). High frequency can be considered the cardiac parasympathetic tone index (Reyes del Paso et al., 2013) since it reflects vagal tone (Laborde et al., 2017; Malik, 1996). Low frequencies are assumed to be markers of cardiac outflow, which is under the influence of both the sympathetic and parasympathetic autonomic nervous systems (Laborde et al., 2017; Malik, 1996).

Statistical analysis

The statistical analyses were performed with Jamovi software, version 2.2.5, and Jasp software, version 0.16.3.0. The statistical analysis of EEG data was performed in EEGLAB using EEGLAB Study parametric statistics. We set the alpha level for statistical significance to $\alpha = .05$. When the results were significant and marginal, the effect sizes were calculated: Cohen's d for the t test (only Student's t test was used in this study), rank biserial correlation for its equivalent nonparametric Mann-Whitney U test and partial eta square (η_p^2) for analysis of variance (ANOVA). When testing an effect involving a repeated-measures factor with more than two levels (e.g., time on task), we applied a Greenhouse-Geisser correction to consider any violation of the sphericity assumption. For EEG data, the FDR multiple comparison correction available in EEGLAB statistics was considered.

Results

Principal characteristics of the two groups of participants were compared to check whether they were homogenous or not (see Table 1). ANOVA with Group (Experimental vs. Control) as the between-subjects factor was performed on age, body mass index (BMI), trait self-control, maximal voluntary contraction (MVC), and average time to exhaustion (TTE) on the handgrip task performed at the beginning of the session (TTE-1). Table 1 shows that the two groups significantly differed in BMI and TTE-1 only. The control group had significantly lower BMI and TTE-1 than the experimental group. In addition, BMI and TTE1 significantly correlated (r = .330; p = .033). Consequently, BMI was used as a covariate in ANOVA leading to a significant effect and including the factor Group as a between-subjects factor. In the same way, the difference between TTE-1 and TTE-2 was used as the main outcome to test the ego-depletion effect, instead of TTE-2 only. The chi-square statistic on the percentage of men and women showed no significant difference between the groups.

Insert Table 1 about here

Maximal voluntary contraction

ANOVA with Moment (before the mental task vs. after the mental task) and Repetition (HG1 vs. HG2) as within-subjects factors and Group (Experimental vs. Control) as a between-subjects factor was performed on MVC performance. The results of this test showed that the interaction Moment X Repetition X Group did not reach significance: F(1, 30) = .004, p = .946, $\eta^2_p = .000$. In the same way, the interactions Moment X Repetition, Moment X Group and Repetition X Group were not significant: F(1, 30) = 1.791, p = .191, $\eta^2_p = .056$; F(1, 30) = .037, p = .849, $\eta^2_p = .001$; F(1, 30) = 2.925, p = .098, $\eta^2_p = .089$, respectively. Simple main effect analysis showed that the effect of Moment was significant: F(1, 30) = 83.254, p < .001, $\eta^2_p = .735$. The mean value of MVC was significantly lower after the time-to-exhaustion handgrip task (M = 13.3 kg, SE = .738) than before it (M = 17.5 kg, SE = .862). In addition, we observed a significant effect of Repetition: F(1, 30) = 4.948, p = .034, $\eta^2_p = .142$. The mean value of MVC was significantly higher during the first handgrip task (M = 15.7 kg, SE = .826) compared to the second handgrip task (M = 15.0 kg, SE = .745). On average, the participants' MVC was reduced by 23.33% after the time-to-exhaustion handgrip task. This decrease in MVC reflects a lower capacity to produce a muscular force. Finally, we did not observe a significant effect of Group: F(1, 30) = .321, p = .575, $\eta^2_p = .011$.

Ego depletion effect

Since the initial performance of the two groups in the handgrip task was not homogeneous, the time-to-exhaustion (TTE) was calculated separately for each subject as follows: TTE Delta (min) = time-to-exhaustion in the second handgrip task minus time-to-exhaustion in the first handgrip task. Finally, to highlight the ego-depletion effect, the TTE delta of the two groups was compared with the two-sample t test.

The results indicated that the TTE delta was significantly lower for the experimental group (M = -3.45 min, SD = 3.17) than for the control group (M = -1.47 min, SD = 1.31): t(30) = 2.31, p = .028, d = 0.818. However, the results of the Shapiro-Wilk test for the TTE delta also showed a violation of the assumption of normality: W = .933, p = .046. Therefore, we used the nonparametric Mann-Whitney U test to avoid any violation of normality, and the results showed a significant difference as well: U (N_{Video} = 16, N_{Stroop} = 16) = 71, p = .032, r = .455; (see Figure 3). The decrease in performance in the experimental group (M = 33.5%, SD = 30.2%) was larger than the decrease in performance observed in the control group (M = 18.2%, SD = 25.2%).

Because the replication of the ego depletion effect is the main objective of this paper, we also conducted ANCOVA with Group as a between-subjects factor and BMI as a covariate. In this case, the effect of Group no longer reached the significance level: F(1, 29) = 3.939, p = .057, $\eta^{2}_{\pi} = .120$. We also performed the analyses while excluding participants who had a decrease or an increase more than 2 standard deviations from the mean. One participant was removed (point 26 on Figure 4). The results of the t test without the outlier showed a significantly lower TTE delta for the experimental group (M = -2.92 min, SD = 2.44) compared to the control group (M = -1.47 min, SD = 1.31): t(29) = 2.08, p = .046, d = 0.749. While conducting ANCOVA with BMI as a covariate and removing the outlier, the effect of Group reached significance: F(1, 28) = 4.464, p = .044, $\eta^{2}_{\pi} = .137$.

Insert Figure 3 about here

Perceptions of effort and muscle pain during the handgrip endurance task

We conducted ANOVA with Group (Experimental vs. Control) as the between-subjects factor and Time of measurement (before the mental task vs. after the mental task) and Individual isotime (0%, 33%, 66% and 100%) as within-subjects factors on the subjective effort perception during the two time-to-exhaustion handgrip tasks. When testing an effect involving individual isotime, we applied a Greenhouse-Geisser correction to consider any violation of the sphericity assumption. The interaction Group X Time of measurement X Individual isotime did not reach significance: $F(2.11, 63.30) = 1.364, p = .263, \eta^2_p = .043$. In the same way, the interactions Group X Time of measurement and Group X Individual isotime did not reach significance: $F(1, 30) = 2.081, p = .160, \eta^2_p = .065)$ and $F(2.21, 66.41) = .887; p = .426, \eta^2_p = .029$, respectively. In contrast, the interaction between Time of measurement and Individual isotime reached significance: $F(2.11, 63.30) = 11.825, p < .001, \eta^2_p = .283$ (see Figure 4). The perception of effort increased more sharply during the second time-to-exhaustion task (TTE-2) than during the first time-to-exhaustion task (TTE-1). The effect of Group was not significant: $F(1, 30) = .321, p = .575, \eta^2_p = .011.$

The same ANOVA was conducted on the subjective perception of muscle pain during the two time-toexhaustion handgrip tasks. The second-order interaction between among Group, Time of measurement and Individual isotime did not reach significance: $F(1.696, 50.869) = .793, p = .439, \eta^2_p = .026$. In the same way, the interactions Group X Time of measurement and Group X Individual isotime did not reach significance: $F(1, 30) = 1.195, p = .283, \eta^2_p = .038$ and $F(2.053, 61.601) = .303, p = .745, \eta^2_p = .010$, respectively. In contrast, the interaction between Time of measurement and Individual isotime reached significance: $F(1.696, 50.869) = 6.302, p = .005, \eta^2_p = .174$ (see Figure 4). The perception of pain increased more sharply during the second time-to-exhaustion task. Finally, the effect of Group was not significant: F(1, 30) = 1.54, p = .224, $\eta^2_{\rm p} = .049$.

Insert Figure 4 about here

Performance in the mental tasks

To assess the performance in the Stroop task, two separate ANOVA with Time on task (TOT; T1, T2, T3 & T4) and Type of trial (reading vs. naming ink color) as within-subjects factors were conducted on the mean reaction time (RT) and the error rate. A Greenhouse-Geisser correction was applied to the degrees of freedom to avoid any problem of sphericity. The interaction Time on task X Type of trial reached significance for mean RT (see Figure 5): F (2.282, 34.227) = 4.881; p < .05; $\eta^2_{\rm p}$ = .245. This interaction is explained by the difference between 'reading' trials and 'naming ink color' trials that increased with time on task. The interaction Time on task X Type of trial and the simple effect of Time on task did not reach significance for error rate: F (2.344, 35.154) = 0.125; p = .910; $\eta^2_{\rm p}$ = .000 and F (1.024, 15.367) = 1.102; p = .312; $\eta^2_{\rm p}$ = .053, respectively.

In addition, the simple effect of Type of trial is significant for mean RT and error rate: F (1, 15) = 155.904; p < .0001; $\eta^2_{\rm p} = .912$ and F (1, 15) = 156.565; p < .0001; $\eta^2_{\rm p} = .913$, respectively. As expected, reading trials leaded to shorter mean RT (629.44 ms vs. 741.19 ms) and smaller error rate (6.66% vs. 15.42%) than 'naming ink color' trials.

Insert Figure 5 about here

To verify whether the participants paid attention to the content of the documentary, the percentage of their correct responses was compared to the level of chance (i.e., 50%) via the one-sample t test. According to the results, the participants answered significantly better than chance (M = 78.1%, SD = 9.11%): t (16) = 12.4, p < .001, d = 3.09.

Subjective measurements using visual analog scales

Subjective feeling of fatigue

ANOVA with Group (Experimental vs. Control) as the between-subjects factor and Time of measurement (T1 = Baseline, T2 = Pre-Mental Task, T3 = Post-Mental Task, T4 = Post-Handgrip Task) as the within-subjects factor was performed on the subjective feeling of fatigue. We applied a Greenhouse-Geisser correction to consider any violation of the sphericity assumption. The results showed that the interaction between Group and Time of measurement did not reach significance: $F(2.774, 83.212) = 2.24, p = .095, \eta^2_p = .069$. In the same way, the effect of Group was not significant: $F(1, 30) = 2.629, p = .115, \eta^2_p = .081$. In contrast, the effect of Time of measurement reached significance: $F(2.774, 83.212) = 22.299, p < .001, \eta^2_p = .426$. According to a planned comparison conducted to explain the effect of time of measurement, we observed a significant, linear increase in fatigue level as time progressed, regardless of the first Mental task: t(90) = 7.637, p < .001.

Motivation

Repeated-measures ANOVA with Group (Experimental vs. Control) as a between-subjects factor and Time of measurement (T1 = Pre-Mental Task, T2 = Post-Mental Task) as a within-subjects factor was conducted

on the motivation to perform the time-to exhaustion handgrip task. According to the results, the interaction between Group and Time of measurement did not reach significance: F(1, 30) = 0.030, p = .862, $\eta^2_{\rm p} = .001$. The effects of Time of measurement and Group did not reach significance either: F(2.57, 77.12) = 3.216, p = .083, $\eta^2_{\rm p} = .097$ and F(1, 30) = 2.14, p = .154, $\eta^2_{\rm p} = .067$, respectively.

Task difficulty

The results of the two-sample t test demonstrated that the participants in the experimental group perceived the Stroop task (M = 74.9, SD = 19.7) to be more difficult than the control group did for the documentary viewing task (M = 20.1, SD = 22.2):t (30) = -7.39, p < .001, d = -2.61.

Boredom

The two-sample t test was performed to compare perceived boredom during the depleting versus control tasks. The effect of Group (Experimental vs. Control) did not reach significance: t (39) = - 1.11, p = .274, d = -0.394. Unexpectedly, the Stroop task performed by the experimental group was not perceived as boring more than the documentary viewing task performed by the control group.

EEG indices

Power spectral analysis

We used the unpaired t test with FDR correction for multiple comparisons to compare the theta wave band power spectral density during the Stroop task compared to the documentary viewing task. A statistically significant higher theta power spectral density was observed mainly in the frontal, prefrontal and central areas during the Stroop task compared to the documentary viewing task, more specifically in the AF7, AF3, FC5, FC3, AF4, AF8, F8, F6, FC6, C6, C4, C2 and P4 electrodes. However, we also detected significantly higher theta power during the documentary viewing task, mainly in occipital areas, more precisely the POz, O1, Iz, Oz, PO7 and PO8 electrodes (see Figure 6).

Insert Figure 6 about here

Later, to assess the effect of time on task on the stimulus-locked theta power density recorded during the modified Stroop task, the EEG recording was divided into 4 equal time periods of 7 min and 30 s. Then, we performed a repeated-measures ANOVA with Time on task (T1, T2, T3 & T4) and Type of trial (reading vs naming ink color) as within-subjects factors on the 64 electrodes. The results showed that the effect of Time on task on the stimulus-locked theta power density reached significance only for 4 electrodes: FC1, P2, CP2, P4. The effect is identical for the 4 electrodes: stimulus-locked theta power decreased with time on task. We reported hereafter the results of the ANOVA only for FC1: $F(2.684, 40.258) = 11.008, p < .001, \eta^2_p = .423$ (see Figure 7). The effect of Type of trial did not reach significance for the 4 electrodes. For the electrode FC1, we obtained the following results: $F(1, 15) = 0.004, p = .952, \eta^2_p = .000$.

Insert Figure 7 about here

Source localization analysis

A K-means clustering (K = 33) algorithm using EEGLAB Study Statistics was performed only on the components that represented higher theta power during the Stroop task in the same regions, as previously observed based on the results of our power spectral analysis. To identify the best clusters, first, the outlier

clusters recognized automatically by EEGLAB were excluded, and then the clusters including sufficient numbers of participants and components (i.e., at least 8 participants representing more than 50% of the data) were considered. From the results of kmean clustering, 6 of 35 clusters were identified and contained more than 50% of the data. As shown in Figure 9, the sources of cerebral activation originated from the prefrontal, frontal and central areas, more precisely regions close to the ACC, thalamus and posterior cingulate cortex.

Insert Figure 8 about here

ECG indices

We conducted 3 separate repeated-measures ANOVAs with Time on task (T1, T2, T3 and T4) as the withinsubjects factor and Group as the between-subjects factor on the HRV parameters (SDNN, HF & LF). When testing an effect involving Time on task as a repeated-measure factor, we applied a Greenhouse-Geisser correction to consider any violation of the sphericity assumption.

The results for the SDNN index showed a significant interaction of Time on task X Group: F (2.073, 60.130) = 3.889, p = .025, ${}^2_{\rm p} = .118$ (see Figure 9, panel A). This interaction disappeared when conducting ANCOVA with BMI as a covariate: F (2.09, 58.62) = 2.198; p = 0.118; ${}^2_{\rm p} = .073$.

For the HF, the interaction of Time on task X Group and the simple effect of Group did not reach significance: $F(2.746, 79.639) = .589, p = .609, {}^{2}{}_{p} = .020$ and $F(1\ 29) = .516, p = .478, {}^{2}{}_{p} = .017$, respectively. However, the effect of Time on task was significant: $F(2.746, 79.639) = 2.964, p = .041, {}^{2}{}_{p} = .093$. HF increased throughout the mental task, regardless of the task.

Finally, concerning the results for LF, the interaction of Time on task X Group reached significance: F (2.477, 70.959) = 5.104, p= .005, ^{2}p = .150 (see Figure 9, panel B). This interaction was still significant when conducting ANOVA with BMI as a covariate: F (2.58, 72.24) = 3.40; p = .028; ^{2}p = .108. A breakdown of this interaction showed that LF for the control group decreased, whereas LF for the experimental group increased between T1 and T2:F (1, 29) = 5.915; p = .021; ^{2}p = .169.

Insert Figure 9 about here

Discussion

The principal aim of this study was to replicate the ego-depletion effect while controlling for effort engagement in depleting and control tasks with the use of psychophysiological measurements, such as electrophysiological changes in mid-frontal theta and cardiac reactivity. The ego-depletion effect did not escape the replication crisis (Alós-Ferrer et al., 2019; Hagger et al., 2016; Lurquin et al., 2016; Vohs et al., 2021; Xu et al., 2014), and testing one more time its reproducibility in more favorable conditions seems pertinent for the advancement of the discipline. Consequently, we used a protocol that already successfully obtained the ego-depletion effect (Mangin et al., 2021). This protocol included a long and effortful depleting task (i.e., a modified computerized incongruent Stroop task), a nonboring control task (i.e., a documentary viewing task) and an effortful physically dependent task (i.e., time-to-exhaustion handgrip task at 13% of MVC).

Overall, the participants in each group followed the instructions during the mental task. On the one hand, the participants who performed the Stroop task had a percentage of errors less than 12% for the reading

trials and 20% for the 'naming ink color' trials throughout the cognitively demanding task. On the other hand, the participants who performed the documentary viewing task had a percentage of correct responses significantly greater than the chance level. In addition, the participants' MVC significantly decreased after the time-to-exhaustion handgrip task compared to beforehand, regardless of the group and the moment of the session (before or after the mental task). This decrease in MVC reflects muscular fatigue and suggests that the participants truly contracted their forearm muscles until exhaustion. This inference is confirmed by the significant increase in the perception of pain and effort throughout the time-to-exhaustion handgrip task. It is also interesting to note that the motivation to perform the time-to-exhaustion handgrip task did not change regardless of the group and the moment of the session. Several theoretical models predict a decrease in motivation to perform an effortful task after the completion of a first effortful task (Inzlicht et al., 2014; Kurzban et al., 2013). Our experiment did not support this hypothesis.

The mentally demanding Stroop task, which requires repeated inhibitory control and cognitive flexibility, led to a faster performance drop in the subsequent dependent task. Furthermore, the subjective data showed that the Mental task performed by the experimental group was considered more difficult than that performed by the control group. In a previous study (Mangin et al., 2021), the ego-depletion effect was replicated in a within-subjects design with a large sample size (N = 55). In the current study, we observed the ego-depletion effect in a between-subjects design with a smaller sample size (N = 32; 16 in each condition). This outcome could be an argument to support the reproducibility of the ego-depletion effect when using the aforementioned experimental protocol, even with a small number of participants. In addition, a recent meta-analysis assessing the effect of mental fatigue on physical performance also indicated that between-subjects designs lead to larger effect sizes compared to within-subjects designs (Brown et al., 2020).

The results concerning mid-frontal theta confirmed that the Stroop task required more mental effort than the documentary viewing task. We observed higher theta waveband power mainly in the frontal, prefrontal and central areas, specifically at the AF7, AF3, FC5, FC3, FP2, AF4, AF8, F8, F6, FC6, C6, C4, C2 and P4 electrodes, during the Stroop task. These results were in accordance with the results that have been observed in previous studies as an index of mental effort investment during other mentally demanding tasks (Fairclough & Ewing, 2017; Puma et al., 2018).

The results of our source localization also showed that the sources of cerebral activation originated mainly from the prefrontal, frontal and central areas and, more precisely, regions close to the anterior cingulate cortex (ACC), thalamus and posterior cingulate cortex (PCC). Therefore, these results support one of the hypothesis of the integrative model of effortful control (André et al., 2019), according to which an increase in the mid-frontal theta waveband (4–7 Hz) generated by the ACC, one of the principal nodes of the salience network, is an indicator of effort engagement in a task requiring effortful control.

However, contrary to our expectations, but in agreement with the results observed by Arnau et al (2021), the results of time on task assessment of task-related theta power showed a decrease in theta power throughout the Stroop task, and regardless the type of trial (reading vs. naming ink color), suggesting a progressive disengagement of effort. In accordance with the EEG results, we also noted a gradual increase in HRV parameters (SDNN, HF & LF) toward the end of the task for the participants who performed the Stroop task. This observation suggested that parasympathetic activity was more dominant toward the end of the Stroop task, indicating that the participants were habituated to the process of the task and were performing the task more spontaneously. Surprisingly, we observed a negative correlation between the increase in reaction time for the trials that required more inhibitory control (i.e., the 'naming ink color' trials) and the increase in heart rate variability assessed with SDNN: the higher the increase in RT throughout the Stroop task, the lower the increase in SDNN (r = -.546; p < .05). This negative correlation suggests that participants who showed a higher decline in performance, also showed a lower decrease in parasympathetic activity. This result does not support the hypothesis of a progressive disengagement of effort throughout the Stroop task and is more compatible with the view that in parallel to the habituation to the Stroop task resulting in an increase in parasympathetic activity, participants who showed a higher decline in performance need to invest more effortful control to stay committed to the Stroop task.

The EEG results during the video condition showed a higher theta power mainly in the occipital areas, more precisely in the POz, O1, Iz, Oz, PO7 and PO8 electrodes. During this task, the participants were watching an emotionally neutral movie showing animals in their natural environment, and at the end of the task, they were asked to answer some simple questions about the content of the movie. Since this task was relatively easy and did not require much effort, the occipital areas were mainly activated to have a good perception of the visual scenes. Although other brain areas could also be activated to store pertinent information in long-term memory to answer the questions at the end of the movie, activation was not particularly observed in our analysis. The electrophysiological results of the video task mainly established less engagement of effort in the mid-frontal areas and more engagement in visual processing areas in the occipital regions. Our main focus was on the theta waveband as far as it is an index of effort, and we wanted to ensure that the control task required significantly less effort. On that account, we can confirm that the control task was less mentally demanding than the experimental task, as argued in our previous study (Mangin et al., 2021).

Overall, this study showed that it is crucial to control performance and effort engagement during depleting and control tasks to verify whether the depleting task requires more effort than the control task, and whether the participants stayed engaged throughout the whole depleting task. In the present study, although we observed a disengagement of effort during the Stroop task, we still observed the ego depletion effect.

Limits

As a limitation of this study, we first note the small sample size. Although, as mentioned earlier, we have successfully replicated the ego-depletion effect, it is difficult to generalize the results to the whole population with our limited sample size.

The dissimilarity between the experimental and control tasks can be mentioned as the second limitation of this study. In the documentary viewing task, the participants were more passive and confronted with a large variety of visual stimuli. In contrast, in the depleting Stroop task, they were more active (i.e., naming and reading aloud) and confronted with the repetition of a small number of different visual stimuli. However, it was shown in our previous study (Mangin et al., 2021) that the video task was an effective control task because it was not boring but was less effortful than the Stroop task. For instance, it has been shown that the congruent version of the Stroop task is highly boring and, in this way, taxing the self-control resources of the participants to continue the task. Finding a control task as similar as possible to the depleting task but requiring little effort and inducing little boredom is not easy.

According to the TOT results observed in the depleting task in the present study, we can view the disengagement of effort that occurred in the Stroop task as the third limitation of this study. The integrative model of effortful control (André et al., 2019) predicts that the higher and the longer the engagement in effort during the depleting task, the larger the size of the ego depletion effect. According to this prediction, if the participants of our experiments had maintained their effort throughout the depleting task, the egodepletion effect would have been larger. Previous studies showed that knowledge of results (Sanders, 1983) and rewards (Herlambang et al., 2019) allows participants to maintain effort throughout long effortful task. Manipulating knowledge of results and/or rewards during the depleting task could be an interesting way to test this prediction.

Future perspectives

The increase in parasympathetic activity observed during the depleting task can also be interpreted as a habituation and/or automatization of the Mental task. For future studies aiming to induce an ego-depletion effect, it would be crucial to use a depleting task that is as little automatable as possible to observe a TOT effect throughout the depleting task. The beneficial effect of practice and automatization can reduce or nullify the detrimental effect of mental fatigue. During the computerized Stroop task, certain participants with short reaction times were able to rest between two trials for a few hundred milliseconds. Throughout the task, these participants could have learned to benefit from these microbreaks to invest less effort and

save energy. A task constraining the participants to maintain information in working memory between two trials, such as a dual 2-back task requiring the encoding of two characteristics of each stimulus – for instance, its color and spatial location in a 4x4 matrix – could be a strategy to force participants to maintain a high level of concentration throughout the task and then reduce task automatization.

In the present study, we assessed the deployment of mental effort during a depleting task and a control task through three different indices of heart rate variability (HRV): one time-domain index (SDNN) and two frequency-domain indices (LF and HF). As a general rule, HRV indices decrease when the sympathetic nervous system is activated in response to stressors, such as performing a task that requires effortful control. In contrast, HRV indices increase when the parasympathetic nervous system is activated during resting periods (Appelhans & Luecken, 2006; Berntson et al., 1997). However, several authors have suggested that the low frequency component (LF), which highly correlates with SDNN and HF, is largely determined by the central autonomic outflow and, more particularly, the parasympathetic nervous system (Cooley et al., 1998; Reyes del Paso et al., 2013). Consequently, heart rate variability indices would be indirect, inversely related indices of sympathetic activity. More recent works have shown that another cardiac reactivity index would be a more direct index of sympathetic activation and therefore of mental effort engagement (Drost et al., 2022; Mallat et al., 2020): the pre-ejection period (PEP). This index corresponds to the time interval between the beginning of the depolarization of the ventricles (Q point on the ECG) and the ejection of blood into the aorta (B point on the impedance-cardiogram) (Brenner & Beauchaine, 2011). The shorter that the PEP is, the higher that the effort engaged in the Mental task is. Because Goedhart et al (2008) demonstrated that LF and HF did not show the expected negative correlation with PEP, it seems more appropriate to use PEP in future studies aiming to assess mental effort during the depleting, control and/or dependent task of the sequential task protocol.

Another point that can be addressed in future studies is the assessment of the event-related potential (ERP) components in addition to theta power density, such as the N2 component during a depleting task eliciting a stimulus-response conflict, which has been associated with dorsal ACC-related control processes (Cavanagh & Frank, 2014). From that perspective, variations in the amplitude of the N2 component could reflect variations in effortful control throughout the task.

In other respects, the integrative model of effortful control (André et al., 2019) assumes that the connectivity of the large-scale neuronal networks involved in effortful control, such as the salience network and the central executive network, can be weakened in long, depleting tasks. Therefore, in future studies, other brain imaging methods, such as resting-state functional magnetic resonance imaging (r-fMRI), can be used to assess the connectivity of brain networks involved in the ego-depletion effect. Several studies have used activation fMRI (e.g., Friese et al., 2013; Gergelyfi et al., 2021) to examine the pattern of activation in different brain regions during the dependent task of a sequential task protocol. However, to our knowledge, only one study has already used the sequential task protocol with the aim of examining the influence of mental fatigue on brain connectivity at rest (Esposito et al., 2014). This study reported a decrease in connectivity in the left and right frontoparietal executive attentional networks (bilateral middle frontal gyrus and right angular gyrus). These results must be confirmed by other studies varying the depleting and dependent tasks.

Finally, it could also be interesting to conduct studies with noninvasive brain stimulation methods, such as transcranial direct current stimulation (TDCs), that can assess the question of effort capacity amelioration by stimulating the ACC region of the brain. We can question whether, in the case of boosting the salience network capacity to generate the mid-frontal theta or the effort signal, it is possible to reduce the ego-depletion effect and mental fatigue. To this extent, since humans are frequently engaged in depleting Mental tasks, it would be interesting to find different countermeasures to reduce the cognitive fatigue caused by effortful tasks and then improve individuals' performance in their daily lives.

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Declaration of competing interest

The authors declare no conflicts of interest.

Open practices

The materials and the data of the experiment can be found online at https://osf.io/deyhn/?view_on-ly=7b00aa67e1cc437c8abedd258031b995

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Figure and Table Captions

Figure 1: Time course of the sequential task protocol. Mental tasks: Experimental group = Modified Incongruent Stroop task; Control group = Documentary viewing task. MVC: Maximal voluntary contraction. Handgrip task: Time-to-exhaustion task. HG1: Measurement of MVC before the time-to-exhaustion task. HG2: Measurement of MVC after the time-to-exhaustion task. TTE-1: Time-to-exhaustion handgrip task performed before the mental task. TTE-2: Time-to-exhaustion performed after the mental task.

Figure 2: Overview of the experimental setup. The participants equipped with a 64-channel Biosemi EEG headset while performing the handgrip task. The maximized version of the force gauge is displayed on the screen of the computer. The green arc defines the target zone (i.e., a range between 12% and 14% of MVC), which was visible throughout the duration of the task. The participants had to maintain the gauge indicator in this green area until exhaustion. The perimeter of the gauge represents 100% of the participant's maximal voluntary contraction (MVC).

Figure 3: Box and whisker plots illustrating the comparison of the decrease in time-to-exhaustion (time-to-exhaustion delta) between the experimental and control groups. The participants who performed the Stroop task as the depleting task (experimental group) showed a larger decrease in performance after this task than the decrease in performance observed in the group of participants who performed the documentary viewing task as the control task (control group). The black dot just above "Experimental" indicates the outlier data of participant 26.

Figure 4: Perception of effort (Panel A) and pain (Panel B) during the two time-to-exhaustion handgrip tasks as a function of individual isotime (0%, 33%, 66%, 100%). A significant, linear increase in the effort and pain level as a function of individual isotime was observed.

Figure 5: Mean reaction time as a function of time on task (T1-T4) and type of trials (reading vs. naming ink color).

Figure 6: Power spectral density analysis during the Mental tasks. The left topographic color plot shows the mean theta power spectral density for all 16 subjects in the experimental group during the 30 min of the Stroop task. The central topographic color plot shows the mean theta power spectral density for all 16 subjects in the control group during the 30 min of the documentary viewing task (Video). The right topographic color plot shows the p values found when using the unpaired t test with FDR multiple comparison correction to compare the theta power differences between the two groups. The color bar scale located in the middle of the figure shows the log power 10 (μ V²). The greater that the color tends toward dark red, the higher that the density of the theta waves is. The second color bar scale on the right shows the p value. The greater that the color tends toward dark red, the greater that the p value tends toward 0.001.

Figure 7: Task-related theta power density as a function of time on task (T1-T4) during the modified Stroop task in electrode FC1.

Figure 8: Scalp maps and dipole source locations of the 6 independent component clusters of the 16 participants in the experimental group, which performed the modified Stroop task. The first image on the top represents the scalp maps of each cluster, and the second image on the bottom shows the 3D dipole source locations and their projections onto the MNI brain template. For each set of three figures illustrating a cluster, there are top, coronal and sagittal views from left to right. The blue dots represent each of the bilaterally symmetric dual dipoles originating from the EEG signal sources, and the red dot is the mean of all these dipoles.

Figure 9: Heart rate variability indices (Panel A: standard deviation of NN intervals in ms – SDNN; Panel B: log power of the low-frequency band in $\log(ms^2)$ – LF power) as a function of time on task and group (experimental and control).

Table 1: Participant characteristics. The top value of each cell of the two "group" columns indicates the mean, and the bottom value in brackets of each cell of the same columns corresponds to the standard deviation.

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Variable	Experimental group	Control group	p value
Age (years)	21.73(2.14)	21.25(1.61)	.481
Sex (M/F)	8/8	7/9	.723
BMI (kg/m^2)	23.96(2.69)	21.50(2.01)	.006*
Trait self-control (13-65)	47.75 (6.19)	44.56 (4.56)	.108
MVC (kg)	18.68 (6.79)	17.00(3.56)	.390
TTE-1 (min)	8.32 (4.30)	5.31(1.53)	.012*

Note: * = p value <.05; M = Male; F = Female; BMI = Body mass index; MVC = Maximal voluntary contraction; TTE = Time to exhaustion. The means and standard deviations (in brackets) are reported for each group in the two central columns.



Continuous electrophysiological measurements



Figure 2



Figure 3

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Figure 6









Figure 9