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# Preparing for hard times: Scalp and intracranial physiological signatures of proactive cognitive control

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## Funding information

Ghent University Research Council (to C.J.); Ghent University grant (BOF17-GOA-004) (to T.V.)

## Abstract

Based on reward and difficulty information, people can strategically adjust proactive cognitive control. fMRI research shows that motivated proactive control is implemented through fronto-parietal control networks that are triggered by reward and difficulty cues. Here, we investigate electrophysiological signatures of proactive control. Previously, the contingent negative variation (CNV) in the ERPs and oscillatory power in the theta (4–8 Hz) and alpha band (8–14 Hz) have been suggested as signatures of control implementation. However, experimental designs did not always separate control implementation from motor preparation. Critically, we used a mental calculation task to investigate effects of proactive control implementation on the CNV and on theta and alpha power, in absence of motor preparation. In the period leading up to task onset, we found a more negative CNV, increased theta power, and decreased alpha power for hard versus easy calculations, showing increased proactive control implementation when a difficult task was expected. These three measures also correlated with behavioral performance, both across trials and across subjects. In addition to scalp EEG in healthy participants, we collected intracranial local field potential recordings in an epilepsy patient. We observed a slow-drift component that was more pronounced for hard trials in a hippocampal location, possibly reflecting task-specific preparation for hard mental calculations. The current study thus shows that difficulty information triggers proactive control in absence of motor preparation and elucidates its neurophysiological signatures.

## KEYWORDS

alpha rhythm, attention, cognitive control, EEG, motivation, oscillation/time frequency analyses

## 1 | INTRODUCTION

When faced with an important or difficult task, humans can shift to a higher gear to perform to the best of their abilities. When warned about an upcoming task, proactive cognitive control is used to regulate more basic cognitive processes (Braver, 2012). Control sharpens task performance but also

carries a cost (Kool, McGuire, Rosen, & Botvinick, 2010). This cost has to be weighed alongside possible benefits in the decision to enhance control (Shenhav, Botvinick, & Cohen, 2013; Westbrook & Braver, 2015). Whether or not cognitive control should be implemented is decided based on information about potential reward and task difficulty: Control is expedient when reward is likely or a task is difficult. It

has been shown in numerous studies that reward improves task performance (Aarts et al., 2014; Bijleveld, Custers, & Aarts, 2010; Botvinick & Braver, 2015; Janssens, De Loof, Pourtois, & Verguts, 2016; Padmala & Pessoa, 2010, 2011; Seitz, Kim, & Watanabe, 2009). It is also well established that the experience (Gratton, Coles, & Donchin, 1992) or expectation (Aarts & Roelofs, 2011) of task difficulty enhances control. This influence of reward and difficulty information on control was emphasized in theoretical accounts (Brehm & Self, 1989) and formalized in computational reinforcement learning (RL) models (Lieder, Shenhav, Musslick, & Griffiths, 2018; Silvetti, Vassena, Abrahamse, & Verguts, 2018; Verguts, Vassena, & Silvetti, 2015). Specifically, recent RL models assume that cognitive agents calculate and optimize not just expected reward (i.e., value) but a (linear) combination of reward and difficulty cost (e.g., reward – difficulty cost) in order to decide on whether to invest control or not. If the potential reward for exerting control is sufficiently large (relative to its cost), control is exerted.

This view on control is supported by fMRI studies showing that the anticipation of both reward and difficulty activate an overlapping brain network, consisting of several cortical and subcortical regions (Boehler et al., 2011; Krebs, Boehler, Roberts, Song, & Woldorff, 2012; Padmala & Pessoa, 2011; Vassena et al., 2014). This network closely matches the fronto-parietal control network, including also subcortical areas such as the dorsal striatum (Corbetta & Shulman, 2002; Dosenbach et al., 2007; Gitelman et al., 1999; Hopfinger, Buonocore, & Mangun, 2000; Kastner & Ungerleider, 2000; Padmala & Pessoa, 2011) and potentially also task-specific areas, depending on the task that the agent is confronted with.

Several studies have looked for electrophysiological signatures of proactive control. One possible signature reported in the literature is the contingent negative variation (CNV), a slow negative deflection in the ERP, observed in the interval between a cue and an imperative stimulus requiring a speeded response (Brunia & van Boxtel, 2001; Walter, Cooper, Aldridge, McCallum, & Winter, 1964). Several studies show that reward information influences the CNV: The amplitude of the CNV is more negative when a rewarding task is expected (Schevernels, Krebs, Santens, Woldorff, & Boehler, 2013; van den Berg, Krebs, Lorist, & Woldorff, 2014). The influence of task difficulty on the CNV has also been investigated (Tecce, 1972). Just like a reward cue, a difficulty cue increases the CNV amplitude (Schevernels et al., 2013; Vanlessen, De Raedt, Mueller, Rossi, & Pourtois, 2015). Interestingly, the CNV amplitude correlates with activation in the fronto-parietal network (Grent-’t-Jong & Woldorff, 2007). The CNV may result from proactive depolarization of neurons in task-relevant areas so that they can be quickly recruited on task onset (Rockstroh, Mi, Wagner, Cohen, & Elbert, 1993).

However, the CNV studies discussed above do not provide a clear electrophysiological signature of proactive control

implementation. Indeed, the CNV has been implicated in several cognitive processes. Besides proactive control (as studied here), it has also been implicated in timing (Macar & Vidal, 2003), response threshold setting (Boehm, van Maanen, Forstmann, & van Rijn, 2014), and motor preparation for an upcoming task (Brunia & van Boxtel, 2001). This renders it difficult to assign variations in CNV amplitude to changes specifically in activation of brain areas involved in proactive control. Some studies have separated motor and nonmotor parts of the CNV, either by timing and topography or by applying experimental paradigms postponing the motor response. However, these were mostly simple discrimination studies that did not focus on proactive cognitive control as the current study does (Frost, Neill, & Fenelon, 1988; Rohrbaugh, Syndulko, & Lindsley, 1976; Ruchkin, Sutton, Mahaffey, & Glaser, 1986).

The CNV (and the ERP approach in general) provides only one electrophysiological signature of control, namely, phase-locked effects in the EEG (Kappenman & Luck, 2011). To provide a more complete picture of cognitive processes, including phase-locked and nonphase-locked parts of the EEG signal, time-frequency decomposition of the signal can be used (Cohen, 2014). Two frequency bands in particular have been associated with proactive cognitive control. First, activity in the theta band is typically observed when there is a need for cognitive control (Cavanagh & Frank, 2014). It is thought that (slow, 4–8 Hz) theta waves originating from cognitive control areas are used to synchronize (fast, 30–80 Hz) gamma waves in task-relevant processing areas (Jensen, Bonnefond, & VanRullen, 2012; Verguts, 2017; Womelsdorf, Ardid, Everling, & Valiante, 2014). As a result, the areas from where those gamma waves originate would communicate more efficiently. Such control recruitment is usually studied in reactive control situations (e.g., in response to an error, punishment, a novel stimulus, and so on) but has also been observed proactively. For example, Womelsdorf, Johnston, Vinck, and Everling (2010) recorded activity in macaque anterior cingulate cortex, a key hub for cognitive control, and observed increased theta power while subjects were preparing for task onset. Recording EEG from the (human) scalp, van Noordt, Desjardins, Gogo, Tekokilic, and Segalowitz (2017) observed increased theta power while subjects were preparing for a difficult (antisaccade) task, relative to an easier (saccade) task. Other evidence for a role of theta in proactive cognitive control was reported by Cooper, Wong, Mckewen, Michie, and Karayanidis (2017). These authors found increased theta power (and theta synchrony across trials) while subjects prepared a task switch, relative to a task repetition. Second, power in the alpha band (8–14 Hz) may be relevant for proactive cognitive control. One computational explanation of the role of alpha (called gating by inhibition; Jensen & Mazaheri, 2010) is that alpha disrupts the gamma rhythms and theta-gamma coordination necessary for task processing (Vолох, Valiante, Everling,

& Womelsdorf, 2015). Alpha waves may thus inhibit task-irrelevant information; conversely, alpha suppression would occur in task-relevant processing regions (Roux & Uhlhaas, 2014). Empirically, occipital alpha suppression has been observed when attention is increased in a visual attention paradigm (Janssens, De Loof, Boehler, Pourtois, & Verguts, 2018; Kelly, Lalor, Reilly, & Foxe, 2006; Worden, Foxe, Wang, & Simpson, 2000) and while subjects prepare an antisaccade (relative to saccade) task (van Noordt et al., 2017). Further, increased alpha power has been linked to inhibition of external stimuli, whereas alpha suppression has been linked to increased attention for such external stimuli (Benedek, Schickel, Jauk, Fink, & Neubauer, 2014). In a cued speeded response task, the influence of reward expectation on control implementation is also reflected in alpha power, with expectation of reward eliciting alpha suppression as well (van den Berg et al., 2014). However, alpha power measured in this study does not reflect pure cognitive preparation but is likely also influenced by motor preparation. Crucially, the effect of difficulty information on alpha power in a purely cognitive task has, to our knowledge, not been investigated thus far.

In this study, we investigated the CNV, theta, and alpha power as indexes of proactive cognitive control, while carefully controlling for motor preparation. In particular, we used a mental calculation task adapted from earlier fMRI research. Here, difficulty information activated the anticipatory fronto-parietal network, in absence of motor preparation (Vassena et al., 2014).

The first aim of the current study was to reveal a detailed electrophysiological signature of proactive cognitive control implementation in response to cued task difficulty. By studying both the CNV amplitude and spectral (theta and alpha) power changes, we captured both phase-locked and non-phase-locked attentional preparation in the EEG. Participants performed a (purely cognitive) calculation task that required no motor response until the calculation was finished, several seconds after CNV and power calculation. Hence any effects of difficulty information on pre-task activity can be assigned to changes in cognitive preparation. Based on theoretical models of proactive attentional control (Braver, 2012; Verguts et al., 2015) and previous fMRI research (Aarts & Roelofs, 2011; Aben et al., 2019; Krebs et al., 2012; Vassena et al., 2014), it is plausible that task difficulty information would influence control via activation of the fronto-parietal control network and subcortical areas, typically involved in proactive cognitive control. Based on the studies reviewed above, we thus hypothesized that such control would be reflected in increased CNV amplitude, increased theta power, and decreased alpha power, for hard trials compared to easy trials in the period leading up to the task.

The second aim of the current study was to directly link the observations at the scalp level to their putative source, the fronto-parietal control network. fMRI-seeded source

modeling has revealed lateral, prefrontal, frontal, and parietal areas as well as visual-sensory occipital areas contributing to the CNV signal measured at the scalp (Grent-'t-Jong & Woldorff, 2007). This suggests the involvement of the fronto-parietal network in generating the slow-drift attentional CNV component. In the current study, we used a more direct measure of electrical brain activity, namely, intracranial local field potential recordings of a patient diagnosed with epilepsy. EEG source modeling techniques such as dipole fitting and sLORETA are not suited to investigate deep sources due to volume conduction, so intracranial recordings provide an excellent opportunity to investigate deep subcortical sources more reliably. In this study, the resulting high spatial-resolution measurements in the parietal cortex, dorsal striatum (putamen), insula, and hippocampus were investigated and compared to the scalp measures of the control subjects, linking the scalp CNV and power changes to activity in these areas and to the proactive control network in general.

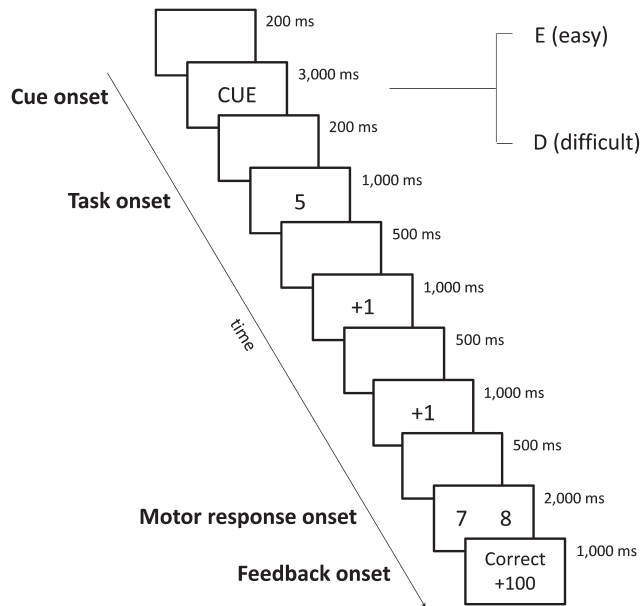
## 2 | METHOD

### 2.1 | Experimental design

Nineteen healthy, paid subjects (7 male, 12 female; aged 19–24) participated in this experiment. All participants filled in an informed consent form at the start of the experiment. Ethical approval was obtained from Ghent University Ethical Committee (Faculty of Psychology and Educational Sciences).

The participants performed 256 trials of a cued serial mental calculation task. Self-paced breaks occurred every 16 trials. Participants performed serial mental calculation trials that could be either easy or difficult (both 50% of trials). For an overview of trial events, see Figure 1. On each trial, a cue was presented for 3,000 ms, informing participants of the difficulty of the upcoming calculation (*E* for easy or *D* for difficult). The cue was followed by a blank screen (200 ms) and by the first number (1,000 ms), marking task onset. Two operations followed sequentially, each of them requiring addition or subtraction of a certain number (1,000 ms each, interspersed by blank screens for 500 ms, e.g.,  $5 + 7 - 9$ ) for hard trials; for easy trials, only +1 additions were used. Subsequently, two possible results were presented on the screen (2,000 ms), and participants selected the result they thought to be correct. A response had to be given within 2,000 ms from result onset. The correct and an incorrect outcome were presented left and right on the screen; location of the correct outcome was randomly determined on each trial. Subjects selected an outcome by pressing a left or right button, corresponding to the location on the screen. Following the response, feedback was presented (correct or incorrect, presented for 1,000 ms). For correct responses, participants received 100 points, which was also shown in the feedback (+100 points; +0 points for incorrect responses). Trials were interspersed by a 200-ms blank screen. The participants were





**FIGURE 1** Overview of a trial in the serial mental calculation task. At cue onset, a cue (letter *E* for easy or *D* for difficult) was presented, reliably predicting task difficulty. At task onset, a number was presented. This was followed by two operations to be performed on this number (presented sequentially). The CNV amplitude and power in the theta and alpha bands were studied in the interval between the cue onset and task onset

informed that the points would result in a proportional monetary reward at the end of the experiment; in practice, all participants received 35 euro for their participation.

Before the start of the experiment, the participants completed the need for cognition questionnaire (Cacioppo, Petty, & Feng Kao, 1984). They also performed a training block of 16 trials. In this block, they rated each calculation on how difficult and how enjoyable it was on a 7-point Likert scale. No EEG was recorded during this training block. At the end of the experiment, participants again rated how difficult and enjoyable they found the easy versus hard trials.

To assess effects of the difficulty manipulation on performance, a linear mixed effects model (LME) for reaction times (RTs) and a generalized (logistic) linear mixed effects model (GLME) for binary responses (i.e., for accuracy, 0 or 1) were fitted, with a random intercept per subject and centered predictors. Effects in the fitted models were tested by analysis of variance (ANOVA) Type III tests, and  $\chi^2$  statistics are reported. The RT analyses were performed only on the trials with a correct response.

## 2.2 | EEG data acquisition, processing, and analysis

Continuous EEG activity was acquired at 512 Hz using a 64-channel (pin type) BioSemi Active Two system (<http://www.biosemi.com>) referenced to the CMS-DRL ground and

positioned according to the extended 10-20 International EEG system. Six additional electrodes were attached to the head: left and right mastoids, two electrodes for vertical and horizontal electro-oculogram. Data for two participants were removed due to excessive noise and technical difficulties.

EEG data were analyzed with EEGLAB (Delorme & Makeig, 2004), ERPLAB (<http://erpinfo.org/erplab>), and FieldTrip software (Oostenveld, Fries, Maris, & Schoffelen, 2011), running on MATLAB. The data were rereferenced offline to linked mastoids. Independent component analysis was applied to continuous data to identify and remove components associated with eyeblinks. Epochs of  $-1,000$  to  $+3,000$  ms locked to cue onset were selected. Epochs were visually inspected, and epochs containing artifacts were removed.

For the ERP analysis, the selected epochs were baseline corrected to the precue period ( $-1,000$  to  $0$  ms locked to cue onset). Next, the epochs were averaged per condition, electrode, and participant. The data were further downsampled to 256 Hz to speed up the clustering analysis. For each of the 64 electrodes and time points from  $-200$  to  $3,000$  ms relative to cue onset (819 time points), a paired  $t$  test across participants was performed on the difference between the ERP potential (henceforth, also called activation) for the easy and hard condition. These  $t$  statistics were then entered into a cluster-based permutation analysis to correct for multiple comparisons (Maris & Oostenveld, 2007). Because of the temporally extended nature of the CNV, 20% of the highest  $t$  statistics were clustered. For the ERPs, clustering occurred in the spatiotemporal domain ( $t$  value threshold = 1.38). We considered electrodes to be (spatial) neighbors if their distance was less than 4 cm. The cluster statistic was calculated as the maximal  $t$  statistic within a cluster multiplied by the size of that cluster. The empirical  $p$  value was obtained by performing 1,000 random permutations of the clustering analysis. For each permutation, the condition labels (easy vs. hard trials) were randomized per subject and electrode. A familywise significance threshold of 5% was applied to the empirical  $p$  values to detect significant clusters. The significant clusters are visualized in a grand average, displaying the average ERP across the significant channels, for the easy and hard trials separately. Their topography is illustrated with topoplots. For each electrode, the difference in average cluster activation between the easy and hard trials is displayed; large black dots indicate the cluster electrodes. In addition, to relate the cluster activation to the behavioral performance, the average cluster activation (across significant electrodes and time points) was extracted per subject for the between-subjects analysis, and per trial for the within-subject analysis.

For the time-frequency analysis, fast Fourier transform was applied to the selected epochs in a moving window (width: 250 time points/488 ms, with Hann tapering), resulting in power estimates centered at time points ranging from  $-750$  ms to  $2,750$  ms (50-ms steps) locked to cue onset.

Event-related spectral perturbation (ERSP; i.e., power) estimates were acquired using the *newtimef* function from EEGLAB. Estimates were obtained for seven uniformly distributed frequencies from the theta to alpha band (3.34–13.34 Hz). The power estimates were baselined to the average power estimates centered between –750 and –250 ms relative to cue onset and converted to the decibel scale. For each of the 64 electrodes, seven frequencies, and power estimates centered at –200 to 2,750 ms relative to cue onset (60 time points), a paired *t* test across participants was performed on the difference between the power estimates for the easy and hard condition. Twenty percent of the highest and 20% of the lowest *t* statistics were clustered in a cluster-based permutation analysis to correct for multiple comparisons. This was done separately for the theta ( $3 < \theta < 8$ ; three frequencies; lower and upper *t*-value thresholds –0.18 and 1.30, respectively) and alpha ( $8 < \alpha < 15$ ; four frequencies; lower and upper *t*-value thresholds –1.30 and 0.34, respectively) bands. For the significant clusters, a time-frequency plot illustrates the difference between the averaged power estimates for easy and hard trials, summed across the significant electrodes. The topography of the significant clusters is visualized with topoplots for the theta and alpha frequency bands separately. For each electrode, the difference in average cluster power estimates between the easy and hard trials is displayed; large black dots indicate the electrodes in the cluster. To relate the cluster activation to the behavioral performance, the average cluster activation in each frequency band (across significant electrodes, frequencies, and time points) was extracted per subject for the between-subjects analysis and per trial for the within-subject analysis.

### 2.3 | Patient experimental design and analysis

We also collected intracranial recordings (iEEG) from a patient suffering from epilepsy (left-handed woman with normal IQ, age 29). Informed consent and ethical approval were obtained for this study as well (Human Ethical Committee, University Hospital Ghent).

Electrodes were implanted on several sites, including one depth electrode in hippocampus, parahippocampal areas, and fusiform cortex (10 contact points, henceforth called the hippocampal electrode); one depth electrode in insula, dorsal striatum (putamen), and pulvinar (10 contact points; referred to as the striatal electrode), and a right subdural temporo-parietal grid ( $5 \times 8$  contact points). The exact locations of these contact points (MNI coordinates) were determined by two independent researchers based on a structural MRI scan taken after implantation (see Figure 2); the absolute mean deviation between their estimated coordinates was 0.4 mm. Data were collected at 1,024 Hz and downsampled offline to 256 Hz.

For these recordings, the same experimental design was used as for the healthy EEG subjects, but due to time constraints, only 128 trials were performed. Also, the cue-task interval was extended to 4,000 ms (resulting in epochs of –1,000 to 4,000 ms relative to cue onset). Epochs were visually inspected, and epochs containing epileptic activity or other artifacts were removed (25.8% of the hippocampal electrode, 31.3% of the striatal electrode, and 36.7% of the temporo-parietal grid data). The selected epochs were baseline corrected to the precue period (–1,000 to 0 ms). No rating data at all were collected in the patient.

For the behavioral data of the iEEG patient, a linear effects model (LM) for the RTs and a generalized linear effects model (GLM) for the accuracy responses were fitted. An ANOVA Type III test was performed, and *F* statistics are reported. The RT analyses were again performed only on the trials with a correct response.

As in the ERP analysis on the EEG data, two sample *t* tests across trials were performed on time points from –200 to 4,000 ms relative to cue onset (1,075 time points) to detect activation differences between easy and hard trials. The *t* statistics were entered into three separate cluster-based permutation analyses: one for each depth electrode and one for the electrode grid. The 20% highest *t* statistics were clustered. For the ERPs, clustering occurred in the spatiotemporal domain; adjacent electrodes were considered to be neighbors. The resulting cluster statistics were compared to 1,000 random samples from the distribution where the condition labels were randomized before clustering.

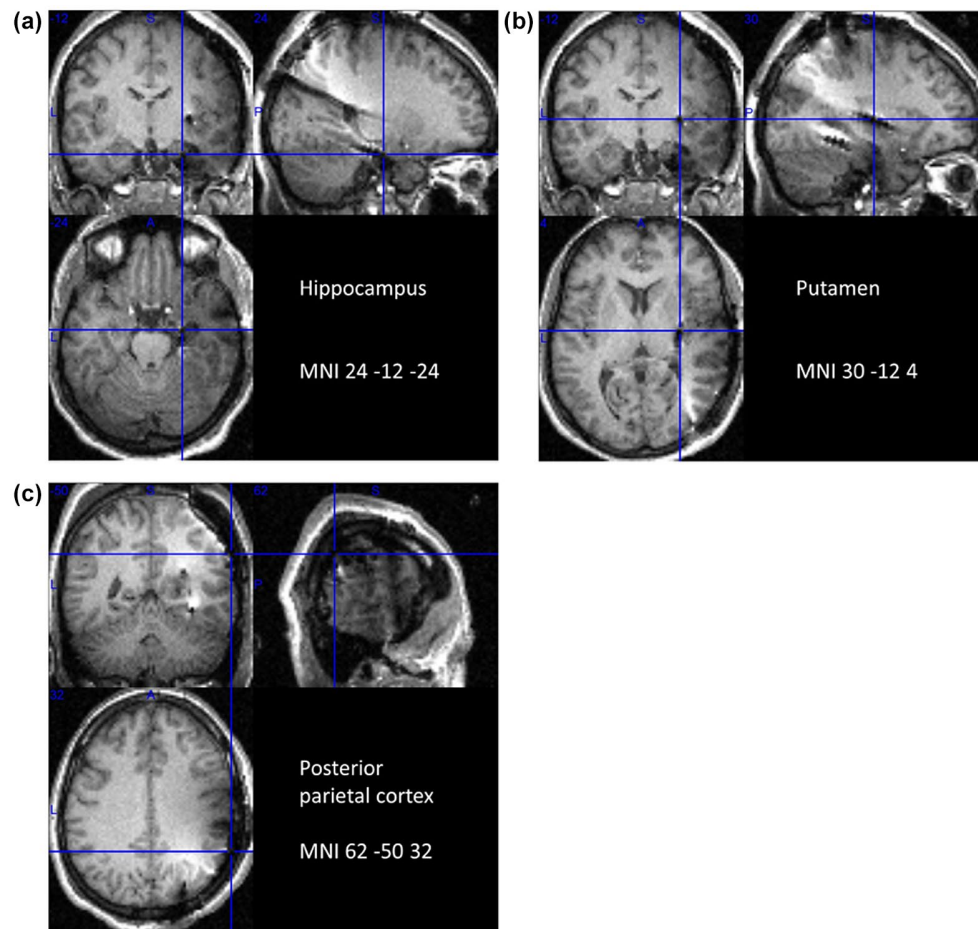
The time-frequency analysis of the iEEG data also paralleled that of the EEG data, but this time resulting in trial-level power estimates centered at time points ranging from –750 ms to 3,750 ms (50-ms steps) locked to cue onset. Two-sample *t* tests were performed to detect differences between the easy and hard trials. The same cluster-based permutation analysis was performed as on the EEG data: one for each depth electrode and one for the electrode grid.

The trial-level average activity was extracted from the significant clusters from the ERP as well as the power analyses. This trial-level activity was used as a centered predictor in the (G) LM analysis on the behavioral data (accuracies as well as RTs).

## 3 | RESULTS

### 3.1 | Behavioral results

LME analyses revealed a significant effect of difficulty on both error rates,  $\beta = -1.96$ ,  $\chi^2(1, N = 19) = 73.98$ ,  $p < 0.001$ , and RTs,  $\beta = 33.5$ ,  $\chi^2(1, N = 19) = 140.89$ ,  $p < 0.001$ , with more errors and slower responses for hard than for easy trials (error rate: 1%, RT: 425 ms for easy vs. error rate: 6%, RT: 492 ms for hard). These results show that the difficulty manipulation was effective and performance was worse for hard trials.



**FIGURE 2** MRI images displaying implantation of intracranial contact points in the patient. Three contact points of interest are marked with crosshairs. Two independent researchers determined reliable MNI coordinates for these sites based on visual inspection of the MRI images. Locations and coordinates for sites in the (a) hippocampus, (b) putamen, and (c) posterior parietal cortex are shown

Participants also judged the hard trials as more difficult than the easy trials, both during the training phase,  $t(18) = 7.84$ ,  $p < 0.001$ ,  $d = 1.80$ , and after the experiment,  $t(18) = 6.64$ ,  $p < 0.001$ ,  $d = 1.52$ . Nevertheless, whereas participants did not differentially enjoy the hard or easy trials during the training phase,  $t(18) = 0.56$ ,  $p = 0.59$ ,  $d = 0.13$ , they significantly enjoyed the hard trials more at the end of the experiment,  $t(18) = 3.44$ ,  $p = 0.0029$ ,  $d = 0.79$ . Their enjoyment of hard trials remained approximately constant,  $t(18) = -0.79$ ,  $p = 0.44$ ,  $d = 0.18$ , but the easy trials were enjoyed less across time,  $t(18) = -5.04$ ,  $p < 0.001$ ,  $d = 1.16$ .

### 3.2 | CNV

The cluster-based permutation test revealed a significant difference between CNV activation for easy and hard trials in a cluster spanning from 640 to 3,000 ms postcue onset (50 electrodes;  $p < 0.001$ ). Figure 3 illustrates the more pronounced CNV component for hard trials compared to easy trials.

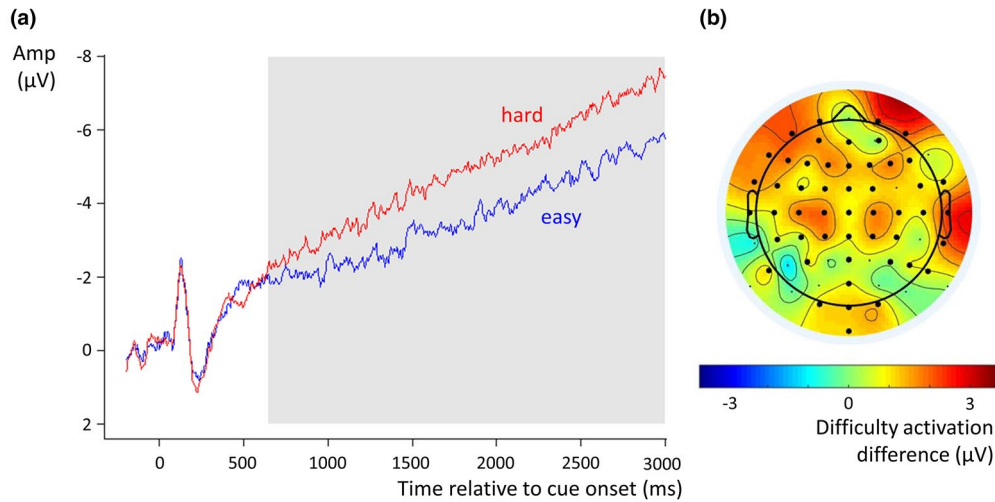
Across subjects, a larger difference between the activation for easy and hard trials in the CNV cluster correlated

with a larger accuracy benefit for easy trials over hard trials,  $r(15) = -0.38$ ,  $p = 0.0016$ . Likewise, the RT benefit for easy over hard trials showed a trend toward a correlation with a larger easy versus hard difference in CNV, but this trend was not significant,  $r(15) = 0.67$ ,  $p = 0.064$ . The trial-level CNV activation was not predictive for the behavioral performance.

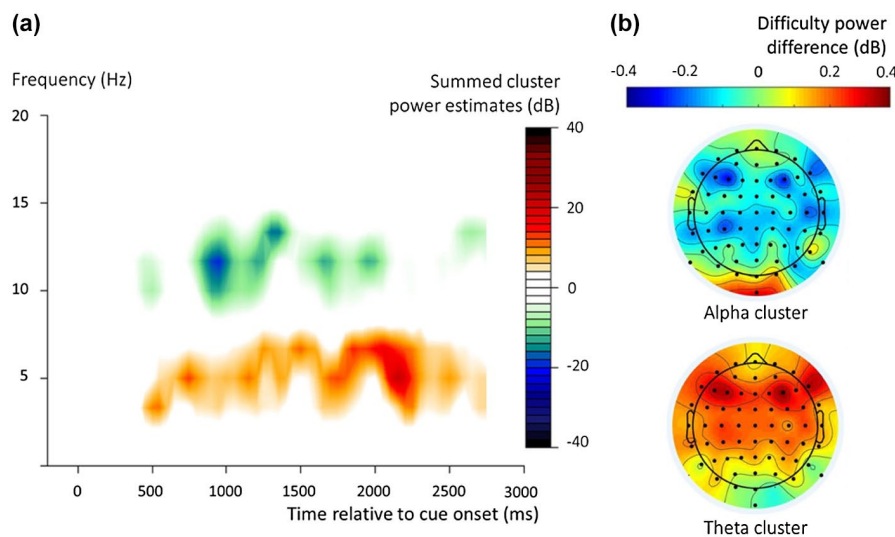
### 3.3 | Time-frequency analysis

The cluster-based permutation analysis resulted in two significant clusters ( $p < 0.001$ ); see Figure 4. Power estimates were significantly higher for hard trials compared to easy trials in a theta band cluster between 450 and 2,750 ms relative to cue onset. Conversely, power estimates in the alpha band between 400 and 2,750 ms were significantly more suppressed (i.e., alpha suppression) on the hard relative to easy trials.

Across subjects, a larger difference in power estimates between the easy and hard trials was not predictive for better behavioral performance; this holds for both clusters. Accuracy was not significantly predicted by power estimates



**FIGURE 3** (a) Grand average, and (b) topoplot for the CNV cluster. The CNV component leading up to task onset is significantly more negative for hard trials (depicted in red) compared to easy trials (depicted in blue), from 640 to 3,000 ms postcue onset (indicated by a gray box on the grand average; the topoplot represents the average activation difference in this time period). This reflects increased proactive control for hard trials across a wide area (significant electrodes are indicated with large black dots on the topoplot)



**FIGURE 4** (a) Time-frequency plot, and (b) topoplot for the power estimate clusters that differentiate between easy and hard trials. The time-frequency plot displays the summed power estimates for the theta (450 to 2,750 ms relative to cue onset), and alpha (400 to 2,750 ms) band. The topoplots represent the difference in the average power estimates between the easy and hard trials; cluster electrodes are indicated with large black dots in (b)

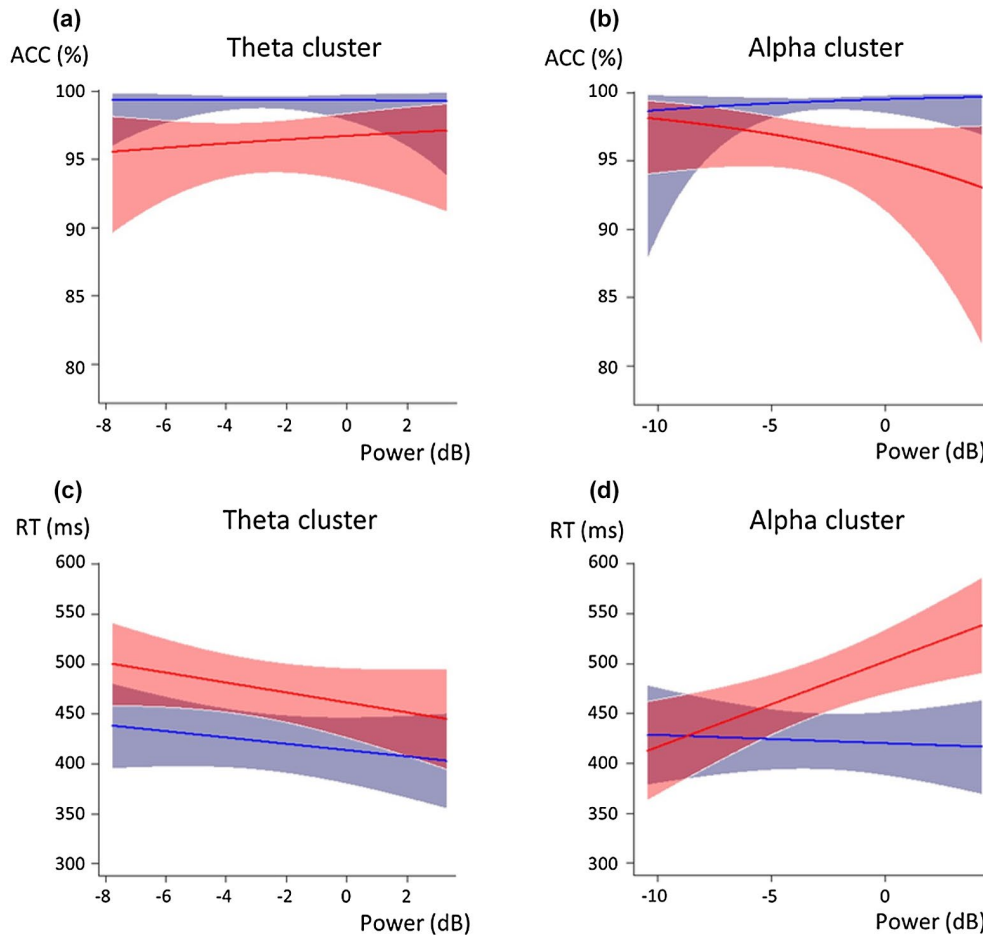
in either the theta cluster or the alpha cluster; there were also no significant interactions with the trial type (all  $ps > 0.17$ ).

On a trial-by-trial basis, theta or alpha power did not predict accuracy (Figure 5a,b). However, higher activity in the theta cluster significantly predicts lower RTs,  $\beta = 6.60$ ,  $\chi^2(1, N = 17) = 7.95$ ,  $p = 0.0048$ , without a significant interaction with trial type,  $\beta = 1.82$ ,  $\chi^2(1, N = 17) = 0.16$ ,  $p = 0.69$  (Figure 5c). Alpha suppression significantly interacted with trial type,  $\beta = -9.39$ ,  $\chi^2(1, N = 17) = 6.41$ ,  $p = 0.011$  (Figure 5d). Follow-up analyses revealed that, while stronger alpha

suppression numerically leads to lower RTs on hard trials, this effect was not significant,  $\beta = -5.61$ ,  $\chi^2(1, N = 17) = 2.40$ ,  $p = 0.12$ .

Finally, we correlated CNV and power effects. Across subjects, the average activity difference between the easy versus hard trials was not significantly correlated between the CNV, theta, and alpha clusters (all  $ps > 0.097$ ). On the trial level, activity in the CNV cluster significantly predicts the power estimates in the theta cluster,  $\beta = -0.0025$ ,  $\chi^2(1, N = 17) = 4.81$ ,  $p = 0.028$ , and in the alpha cluster,





**FIGURE 5** Trial-to-trial correlations between spectral power and behavioral performance for (a, b) accuracy, and (c, d) RTs. The regression lines and the 95% confidence intervals are depicted in blue for easy trials and in red for hard trials

$\beta = -0.0029$ ,  $\chi^2(1, N = 17) = 4.82$ ,  $p = 0.028$ . The power estimates in the theta cluster were highly predictive for the power estimates in the alpha,  $\beta = -0.42$ ,  $\chi^2(1, N = 17) = 595$ ,  $p < 0.001$  cluster.

### 3.4 | Patient data

Behaviorally, the patient's performance was in line with the performance of the healthy participants. Although the error rate was not significantly higher for the hard trials (error rate: 4.69% for easy vs. 12.50% for hard),  $F(1, 126) = 2.50$ ,  $p = 0.12$ , the responses were significantly slower (RT: 434 ms for easy vs. 555 ms for hard),  $F(1, 115) = 23.36$ ,  $p < 0.001$ .

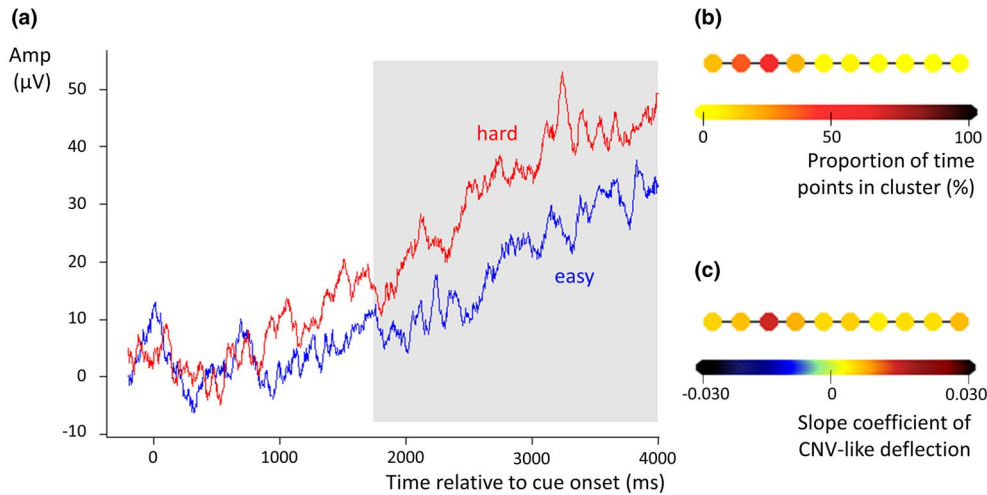
In the iEEG data, a cluster of contact points on the hippocampal depth electrode revealed a CNV-like deflection that was more pronounced for hard compared to easy trials ( $p = 0.041$ ). The cluster extended from 1,742 to 4,000 ms post-cue onset (Figure 6a) and involved mainly the third contact point (see Figure 6b), located in the hippocampus (MNI 24 –12 –24). This third contact point not only showed the most sustained difference between the easy and hard trials but was also the contact point with the most pronounced CNV-like

deflection (Figure 6c). The trial-level activity in the cluster was not predictive for the behavioral performance.

No sustained difference between the ERPs for easy and hard trials could be found in the striatal depth electrode or the temporo-parietal grid. The time-frequency analysis also revealed no significant clusters.

## 4 | DISCUSSION

In this study, we provide a detailed and reliable electrophysiological signature of proactive control in a cognitive task. Following a difficulty cue, we showed a more pronounced CNV (see Figure 3), more theta power, and more alpha power suppression (see Figure 4) when participants were preparing for hard versus easy trials, reflecting increased cognitive control. A CNV-like effect was also found in a hippocampal contact point measured intracranially. These electrophysiological markers show that precued task difficulty motivates proactive control long before motor involvement. The CNV, theta, and alpha power modulations likely reflect stronger activation in the fronto-parietal cognitive control



**FIGURE 6** (a) Grand average, and (b) topoplot for the iEEG CNV cluster on the hippocampal depth electrode. A CNV-like deflection leading up to task onset was significantly more pronounced for hard trials (depicted in red) compared to easy trials (depicted in blue), from 1,742 to 4,000 ms postcue onset (indicated by a gray box on the grand average). The third contact point (located in the hippocampus, MNI 24 –12 –24) displayed the most sustained difference between easy and hard trials (b) and showed the most pronounced CNV-like deflection (c)

network. Thus, the current study supports the notion that difficulty information influences proactive control through activation of cortical fronto-parietal brain areas. This is in line with predictions by computational reinforcement learning models (Silvetti et al., 2018; Verguts et al., 2015) and fMRI research (Boehler et al., 2011; Krebs et al., 2012; Vassena et al., 2014).

To allow straightforward attribution of the ERP slow-drift amplitude, theta power, and alpha power modulations solely to cognitive task preparation, we used a task that carefully excluded motor preparation from the period leading up to task onset. Our mental calculation task did not require a motor response until after the complete calculation was finished and two outcome options were presented (based on Vassena et al., 2014). It is therefore very unlikely that motor preparation occurred during the cue-task interval. We showed that task onsets in difficult trials were preceded by a more pronounced CNV, stronger theta power, and stronger alpha power suppression. This is in line with previous studies, reporting effects of difficulty on the CNV (Schevernels et al., 2013; Vanlessen et al., 2015), on proactive theta power (van Noordt et al., 2017), and on proactive alpha power (van den Berg et al., 2014). In the current study, we show very clear effects of cued difficulty on all three measures, in the absence of motor preparation. We thus confirm that difficulty information is an important cue motivating proactive cognitive control.

A potential alternative explanation to our findings is in terms of value-based expectancy effects; perhaps, the CNV was observed because subjects expected an upcoming reward. However, in such a view, the largest CNV would have been observed in the condition with the highest probability of reward, that is, in the easy condition. Since we observed the exact opposite, we consider such an explanation as unlikely.

A potential alternative explanation for the theta increase and alpha suppression is in terms of arousal; both effects have indeed been associated with arousal (Coull, 1998). However, the fact that we observe (across-subject and across-trial) correlations with behavioral performance clearly indicates a link between power changes and behavioral tasks performance. Arousal may therefore be a mediator, but alone it is not sufficient to account for the observed effects.

The attentional CNV component measured in the current study potentially corresponds to other ERPs reported in the literature, in particular, the pretarget negativity documented in task-switching studies (Karayanidis, Provost, Brown, Paton, & Heathcote, 2011). The CNV is in some respects also closely related to the stimulus-preceding negativity (SPN; Brunia & van Boxtel, 2001). Like the CNV, the SPN is a slow negative deflection in the ERP marking preparatory attentional processes. However, unlike the CNV, the SPN is typically defined as a preparatory component seen before a stimulus providing information on performance, typically a feedback or a reward stimulus.

Source localization studies using dipole fitting (Böcker, Brunia, & van den Berg-Lenssen, 1994) and positron emission tomography (PET; Brunia, de Jong, van den Berg-Lenssen, & Paans, 2000) have proposed several areas as contributing sources to the SPN, including the frontal and parietal cortex. The fronto-parietal network has also been identified as an important contributor to the CNV, in addition to motor areas (Gómez, Flores, & Ledesma, 2007; Gómez, Flores, & Ledesma, 2007). Slow-drift components measured at the scalp, such as the SPN and CNV, are thought to result from summed postsynaptic potentials in pyramidal neurons from cortical areas involved in the upcoming task (Birbaumer, Roberts, Lutzenberger, Rockstroh, & Elbert,

1992; Elbert, 1993). The SPN and CNV may derive from underlying source neurons in an up state, a state of increased neural excitability due to elevation of the membrane potential (Hernández-López, Bargas, Surmeier, Reyes, & Galarraaga, 1997; Nicola, Surmeier, & Malenka, 2000). This may lower the threshold for firing in task-relevant areas, thus leading to fast engagement of these neurons at task onset (Elbert, 1993; McAdam, 1969). The SPN and CNV are therefore excellent markers of cortical priming (Walter et al., 1964). In sum, SPN and CNV may both index preparatory processes but measured at different stages of the task and, therefore, involving different areas.

As a second neural marker of control, we observed increased theta power during the cue-target period. As mentioned above, a putative computational role for theta power in (proactive) cognitive control is that it can synchronize gamma-band rhythms in posterior processing areas. In particular, this is thought to occur via phase-amplitude coupling (phase from theta and amplitude from gamma band; Fries, 2015; Verguts, 2017). Such theta-gamma coupling has been observed using intracranial recordings while monkeys performed cognitive tasks (Vолоh et al., 2015) and in humans using magneto-encephalogram (MEG; Landau, Schreyer, Van Pelt, & Fries, 2015). Consistently, Daitch et al., 2016, recorded iEEG in patients performing mental arithmetic tasks and observed phase-amplitude coupling between two cortical regions that have since long been implicated in mental arithmetic (Dehaene, 1992), namely, parietal cortex (which provided theta phase) and ventro-temporal cortex (which provided gamma amplitude). Thus, we suggest that proactive control is implemented in mental arithmetic, as in other tasks, by phase-amplitude coupling of control areas with task-specific processing areas, such that the task is processed efficiently at stimulus onset. It would be interesting to test this in future iEEG studies with electrodes at both proactive-control-relevant and arithmetic-relevant locations.

As a third neural marker of control, we also observed alpha suppression during the cue-target period. This decrease in alpha power was larger for hard trials than for easy trials, between 1,500 and 2,250 ms following the difficulty cue. This alpha power decrease very likely reflects increased control for processing upcoming stimuli, since alpha oscillations are a well-established mechanism for attentional suppression (Jensen & Mazaheri, 2010). The gating by inhibition framework states that alpha oscillations reflect inhibition of irrelevant (gamma-band) input and can be strategically adjusted to admit relevant information into processing. Also, alpha power is negatively correlated with BOLD activity measured by fMRI (Laufs et al., 2003; Ritter, Moosmann, & Villringer, 2009), and neural firing in monkeys is negatively correlated with alpha oscillations (Haegens, Nacher, Luna, Romo, & Jensen, 2011). Based on this, we hypothesized that

alpha oscillations would play a role in proactive control. In visual attention tasks, decreases in alpha power have been shown in occipital regions that are actively involved in task performance (Kelly et al., 2006; Thut, Nietzel, Brandt, & Pascual-Leone, 2006; Worden et al., 2000). Similar proactive alpha power modulations in somatosensory areas also show that alpha mechanisms are not limited to visual areas but act in different areas depending on the task (Haegens, Händel, & Jensen, 2011). Alpha modulations are also actively used to shield working memory from irrelevant distracting input (Bonnefond & Jensen, 2012, 2013). For cognitive tasks, alpha power before task onset predicts performance and can be strategically adjusted (e.g., following errors) to increase cognitive control (Mazaheri, Nieuwenhuis, Van Dijk, & Jensen, 2009). Our findings are in line with the findings above and show that alpha suppression can be triggered by a difficulty cue and marks proactive control.

Intracranial recordings in the hippocampal electrode showed a slow-drift component following cue onset. Activation in the hippocampus leading up to task onset likely reflects task-specific preparation rather than general proactive control. Mental calculation relies on extensive brain networks, and some research has implicated the hippocampus in these networks. It has been shown that the hippocampus is activated more strongly in addition operations with carrying (as in the hard condition in the current experiment) compared to additions without carrying (as in the easy condition in the current experiment; Kong et al., 2005). Also, the hippocampus is involved in retrieval but not in counting strategies (Cho, Ryali, Geary, & Menon, 2011). In children, the hippocampus plays a role specifically in addition problems and is activated in problems where a retrieval strategy is used (De Smedt, Holloway, & Ansari, 2011). In the current study, easy mental calculations consisted solely of “+1” operations, strongly promoting a counting strategy, whereas hard calculations likely promoted different strategies, such as retrieval. These studies thus support the idea that the hippocampus plays a role specifically in the currently used mental calculation task, especially in the hard condition.

Taken together, the CNV, theta power, alpha power, and intracranial hippocampal recordings suggest that preparation for a difficult task relies on general control networks as well as task-specific areas. This is in line with control models and fMRI research that predict control to be implemented by the fronto-parietal network in specific (sensory) areas involved in task execution (Egner & Hirsch, 2005; Gómez, Flores, & Ledesma, 2007; Hopfinger et al., 2000; Weissman, Warner, & Woldorff, 2004). It also corresponds to the idea that slow preparatory scalp components reflect activation in control areas as well as task-specific areas (Birbaumer et al., 1992). However, future research will be necessary to test which effects are task (arithmetic) specific or not.

Computational models predict that both reward and difficulty information can motivate proactive control. In this study, cues indicating difficult trials were followed by an increased CNV, increased theta power, and decreased alpha power. Similarly, van den Berg et al. (2014) showed an increased CNV amplitude and decreased alpha power following reward cues. Although the paradigms used in the two studies differ substantially, these similar CNV and alpha modulations suggest comparable effects of reward and difficulty on motivating proactive control. Additionally, models predict that reward and difficulty could have interacting effects on control implementation: difficulty might influence task preparation only when reward is likely (Shenhav et al., 2013; Verguts et al., 2015). In a study by Schevernels et al. (2013), difficulty and reward information were combined in a cue leading up to a speeded response task. Here, reward information influenced the early CNV. Later in the trial, difficulty information also influenced the CNV but only for rewarded trials, showing an interaction of reward and difficulty information. This interaction in the context of non-motor, mental preparation remains to be studied in future research.

Computational models further predict that proactive control implementation (as seen in CNV, theta, and alpha power) will drop due to lack of motivation when the task becomes so difficult that reward becomes very unlikely, even when control is implemented (Verguts et al., 2015). The calculation difficulty in the current study was very low, with excellent performance also for difficult trials (mean error rate 6% for hard trials, 1% for easy trials). Consequently, more control was implemented for hard trials, reflected in a higher CNV amplitude. Contrary to the current study, Silveti, Nuñez Castellar, Roger, and Verguts (2014) showed a lower CNV amplitude for hard compared to easy trials. In their study, a very difficult task was used, leading to a 60% error rate (chance level) for hard trials and a 20% error rate for easy trials. This suggests that indeed control implementation is not recruited when task difficulty becomes too high. Future research should systematically manipulate task difficulty in order to investigate its hypothesized inverted-U relation with control implementation.

In conclusion, the current study provides a comprehensive electrophysiological signature of proactive control, unconfounded by motor preparation. We showed that proactive control is triggered by difficulty information, and this is reflected in the CNV, theta power, and alpha power. Also, we linked this scalp activity to underlying brain areas by intracranial recordings. Active (perhaps task-specific) preparation in the hippocampus was observed. The neural signatures of proactive cognitive control demonstrated in the current experiment provide an excellent tool for future research in cognitive control.

## ACKNOWLEDGMENTS

C.J. was a Ph.D. fellow supported by the Ghent University Research Council while conducting this research. TV was supported by grant BOF17-GOA-004 from Ghent University. We thank three reviewers, Anna Marzecova, and Gilles Pourtois for useful discussions and comments on the article.

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## REFERENCES

- Aarts, E., & Roelofs, A. (2011). Attentional control in anterior cingulate cortex based on probabilistic cueing. *Journal of Cognitive Neuroscience*, 23(3), 716–727. <https://doi.org/10.1162/jocn.2010.21435>
- Aarts, E., Wallace, D. L., Dang, L. C., Jagust, W. J., Cools, R., & D'Esposito, M. (2014). Dopamine and the cognitive downside of a promised bonus. *Psychological Science*, 25(4), 1003–1009. <https://doi.org/10.1177/0956797613517240>
- Aben, B., Calderon, C. B., Van der Cruyssen, L., Picksak, D., Van den Bussche, E., & Verguts, T. (2019). Context-dependent modulation of cognitive control involves different temporal profiles of fronto-parietal activity. *NeuroImage*, 189, 755–762. <https://doi.org/10.1016/j.neuroimage.2019.02.004>
- Benedek, M., Schickel, R. J., Jauk, E., Fink, A., & Neubauer, A. C. (2014). Alpha power increases in right parietal cortex reflects focused internal attention. *Neuropsychologia*, 56, 393–400. <https://doi.org/10.1016/j.neuropsychologia.2014.02.010>
- Bijleveld, E., Custers, R., & Aarts, H. (2010). Unconscious reward cues increase invested effort, but do not change speed-accuracy tradeoffs. *Cognition*, 115(2), 330–335. <https://doi.org/10.1016/j.cognition.2009.12.012>
- Birbaumer, N., Roberts, L. E., Lutzenberger, W., Rockstroh, B., & Elbert, T. (1992). Area-specific self-regulation of slow cortical potentials on the sagittal midline and its effects on behavior. *Electroencephalography and Clinical Neurophysiology/ Evoked Potentials Section*, 84(4), 353–361. [https://doi.org/10.1016/0168-5597\(92\)90088-S](https://doi.org/10.1016/0168-5597(92)90088-S)
- Böcker, K. B. E., Brunia, C. H. M., & van den Berg-Lenssen, M. M. C. (1994). A spatiotemporal dipole model of the stimulus preceding negativity (SPN) prior to feedback stimuli. *Brain Topography*, 7(1), 71–88. <https://doi.org/10.1007/BF01184839>
- Boehler, C. N., Hopf, J.-M., Krebs, R. M., Stoppel, C. M., Schoenfeld, M. A., Heinze, H.-J., & Noesselt, T. (2011). Task-load-dependent activation of dopaminergic midbrain areas in the absence of reward. *Journal of Neuroscience*, 31(13), 4955–4961. <https://doi.org/10.1523/JNEUROSCI.4845-10.2011>
- Boehm, U., van Maanen, L., Forstmann, B., & van Rijn, H. (2014). Neuroimage trial-by-trial fluctuations in CNV amplitude reflect anticipatory adjustment of response caution. *NeuroImage*, 96, 95–105. <https://doi.org/10.1016/j.neuroimage.2014.03.063>
- Bonnefond, M., & Jensen, O. (2012). Alpha oscillations serve to protect working memory maintenance against anticipated distracters. *Current Biology*, 22(20), 1969–1974. <https://doi.org/10.1016/j.cub.2012.08.029>





- Bonnefond, M., & Jensen, O. (2013). The role of gamma and alpha oscillations for blocking out distraction. *Communicative & Integrative Biology*, 6(1), e22702. <https://doi.org/10.4161/cib.22702>
- Botvinick, M. M., & Braver, T. S. (2015). Motivation and cognitive control: From behavior to neural mechanism. *Annual Review of Psychology*, 66, 83–113. <https://doi.org/10.1146/annurev-psych-010814-015044>
- Braver, T. S. (2012). The variable nature of cognitive control: A dual mechanisms framework. *Trends in Cognitive Sciences*, 16(2), 106–113. <https://doi.org/10.1016/j.tics.2011.12.010>
- Brehm, J. W., & Self, E. A. (1989). The intensity of motivation. *Annual Review of Psychology*, 40, 109–131. <https://doi.org/10.1146/annurev-ps.40.020189.000545>
- Brunia, C. H., de Jong, B. M., van den Berg-Lenssen, M. M., & Paans, A. M. (2000). Visual feedback about time estimation is related to a right hemisphere activation measured by PET. *Experimental Brain Research*, 130(3), 328–337. <https://doi.org/10.1007/s002219900293>
- Brunia, C. H. M., & van Boxtel, G. J. (2001). Wait and see. *International Journal of Psychophysiology*, 43(1), 59–75. [https://doi.org/10.1016/S0167-8760\(01\)00179-9](https://doi.org/10.1016/S0167-8760(01)00179-9)
- Cacioppo, J. T., Petty, R. E., & Feng Kao, C. (1984). The efficient assessment of need for cognition. *Journal of Personality Assessment*, 48(3), 306–307. [https://doi.org/10.1207/s15327752jpa4803\\_13](https://doi.org/10.1207/s15327752jpa4803_13)
- Cavanagh, J. F., & Frank, M. J. (2014). Frontal theta as a mechanism for cognitive control. *Trends in Cognitive Sciences*, 18(8), 414–421. <https://doi.org/10.1016/j.tics.2014.04.012>
- Cho, S., Ryali, S., Geary, D. C., & Menon, V. (2011). How does a child solve 7 + 8? Decoding brain activity patterns associated with counting and retrieval strategies. *Developmental Science*, 14(5), 989–1001. <https://doi.org/10.1111/j.1467-7687.2011.01055.x>
- Cohen, M. X. (2014). *Analyzing neural time series data: Theory and practice*. Cambridge, MA: MIT Press.
- Cooper, P. S., Wong, A. S. W., Mckewen, M., Michie, P. T., & Karayanidis, F. (2017). Frontoparietal theta oscillations during proactive control are associated with goal-updating and reduced behavioral variability. *Biological Psychology*, 129(Sept), 253–264. <https://doi.org/10.1016/j.biopsycho.2017.09.008>
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews. Neuroscience*, 3(3), 201–215. <https://doi.org/10.1038/nrn755>
- Coull, J. T. (1998). Neural correlates of attention and arousal: Insights from electrophysiology, functional neuroimaging and psychopharmacology. *Progress in Neurobiology*, 55(4), 343–361. [https://doi.org/10.1016/S0301-0082\(98\)00011-2](https://doi.org/10.1016/S0301-0082(98)00011-2)
- Daitch, A. L., Foster, B. L., Schrouff, J., Rangarajan, V., Kaşikçi, I., Gattas, S., & Parvizi, J. (2016). Mapping human temporal and parietal neuronal population activity and functional coupling during mathematical cognition. *Proceedings of the National Academy of Sciences*, 113(46), E7277–E7286. <https://doi.org/10.1073/pnas.1608434113>
- De Smedt, B., Holloway, I. D., & Ansari, D. (2011). Effects of problem size and arithmetic operation on brain activation during calculation in children with varying levels of arithmetical fluency. *NeuroImage*, 57(3), 771–781. <https://doi.org/10.1016/j.neuroimage.2010.12.037>
- Dehaene, S. (1992). Varieties of numerical abilities. *Cognition*, 44, 1–42. [https://doi.org/10.1016/0010-0277\(92\)90049-N](https://doi.org/10.1016/0010-0277(92)90049-N)
- Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, 134(1), 9–21. <https://doi.org/10.1016/j.jneumeth.2003.10.009>
- Dosenbach, N. U. F., Fair, D. A., Miezin, F. M., Cohen, A. L., Wenger, K. K., Dosenbach, R. A. T., ... Petersen, S. E. (2007). Distinct brain networks for adaptive and stable task control in humans. *Proceedings of the National Academy of Sciences*, 104(26), 11073–11078. <https://doi.org/10.1073/pnas.0704320104>
- Egner, T., & Hirsch, J. (2005). Cognitive control mechanisms resolve conflict through cortical amplification of task-relevant information. *Nature Neuroscience*, 8(12), 1784–1790. <https://doi.org/10.1038/nn1594>
- Elbert, T. (1993). Slow cortical potentials reflect the regulation of cortical excitability. In *Slow potential changes in the human brain* (pp. 235–251). Boston, MA: Springer, US. [https://doi.org/10.1007/978-1-4899-1597-9\\_15](https://doi.org/10.1007/978-1-4899-1597-9_15)
- Fries, P. (2015). Rhythms for cognition: Communication through coherence. *Neuron*, 88(1), 220–235. <https://doi.org/10.1016/j.neuron.2015.09.034>
- Frost, B. G., Neill, R. A., & Fenelon, B. (1988). The determinants of the non-motoric CNV in a complex, variable foreperiod, information processing paradigm. *Biological Psychology*, 27(1), 1–21. [https://doi.org/10.1016/0301-0511\(88\)90002-6](https://doi.org/10.1016/0301-0511(88)90002-6)
- Gitelman, D. R., Nobre, A. C., Parrish, T. B., LaBar, K. S., Kim, Y. H., Meyer, J. R., & Mesulam, M. (1999). A large-scale distributed network for covert spatial attention: Further anatomical delineation based on stringent behavioural and cognitive controls. *Brain*, 122(6), 1093–1106. <https://doi.org/10.1093/brain/122.6.1093>
- Gómez, C. M., Flores, A., & Ledesma, A. (2007). Fronto-parietal networks activation during the contingent negative variation period. *Brain Research Bulletin*, 73(1), 40–47. <https://doi.org/10.1016/j.brainresbull.2007.01.015>
- Gratton, G., Coles, M. G. H., & Donchin, E. (1992). Optimizing the use of information: Strategic control of activation of responses. *Journal of Experimental Psychology: General*, 121(4), 480–506. <https://doi.org/10.1037/0096-3445.121.4.480>
- Grent't-Jong, T., & Woldorff, M. G. (2007). Timing and sequence of brain activity in top-down control of visual-spatial attention. *PLOS Biology*, 5(1), e12. <https://doi.org/10.1371/journal.pbio.0050012>
- Haegens, S., Händel, B. F., & Jensen, O. (2011). Top-down controlled alpha band activity in somatosensory areas determines behavioral performance in a discrimination task. *Journal of Neuroscience*, 31(14), 5197–5204. <https://doi.org/10.1523/JNEUROSCI.5199-10.2011>
- Haegens, S., Nacher, V., Luna, R., Romo, R., & Jensen, O. (2011). Alpha-oscillations in the monkey sensorimotor network influence discrimination performance by rhythmical inhibition of neuronal spiking. *Proceedings of the National Academy of Sciences*, 108(48), 19377–19382. <https://doi.org/10.1073/pnas.1117190108>
- Hernández-López, S., Bargas, J., Surmeier, D. J., Reyes, A., & Galarraga, E. (1997). D1 receptor activation enhances evoked discharge in neostriatal medium spiny neurons by modulating an L-type Ca<sup>2+</sup>-conductance. *Journal of Neuroscience*, 17(9), 3334–3342.
- Hopfinger, J. B., Buonocore, M. H., & Mangun, G. R. (2000). The neural mechanisms of top-down attentional control. *Nature Neuroscience*, 3(3), 284–291. <https://doi.org/10.1038/72999>
- Janssens, C., De Loof, E., Boehler, C. N., Pourtois, G., & Verguts, T. (2018). Occipital alpha power reveals fast attentional inhibition of incongruent distractors. *Psychophysiology*, 55(3), e13011. <https://doi.org/10.1111/psyp.13011>

- Janssens, C., De Loof, E., Pourtois, G., & Verguts, T. (2016). The time course of cognitive control implementation. *Psychonomic Bulletin & Review*, 23, 1266–1272. <https://doi.org/10.3758/s13423-015-0992-3>
- Jensen, O., Bonnefond, M., & VanRullen, R. (2012). An oscillatory mechanism for prioritizing salient unattended stimuli. *Trends in Cognitive Sciences*, 16(4), 200–206. <https://doi.org/10.1016/j.tics.2012.03.002>
- Jensen, O., & Mazaheri, A. (2010). Shaping functional architecture by oscillatory alpha activity: Gating by inhibition. *Frontiers in Human Neuroscience*, 4(Nov), 1–8. <https://doi.org/10.3389/fnhum.2010.00186>
- Kappenman, E. S., & Luck, S. J. (2011). *The Oxford handbook of event-related potential components*. Oxford, UK: Oxford University Press. <https://doi.org/10.1093/oxfordhb/9780195374148.001.0001>
- Karayanidis, F., Provost, A., Brown, S., Paton, B., & Heathcote, A. (2011). Switch-specific and general preparation map onto different ERP components in a task-switching paradigm. *Psychophysiology*, 48, 559–568. <https://doi.org/10.1111/j.1469-8986.2010.01115.x>
- Kastner, S., & Ungerleider, L. G. (2000). Mechanisms of visual attention in the human cortex. *Annual Review of Neuroscience*, 23, 315–341. <https://doi.org/10.1146/annurev.neuro.23.1.315>
- Kelly, S. P., Lalor, E. C., Reilly, R. B., & Foxe, J. J. (2006). Increases in alpha oscillatory power reflect an active retinotopic mechanism for distracter suppression during sustained visuospatial attention. *Journal of Neurophysiology*, 95(6), 3844–3851. <https://doi.org/10.1152/jn.01234.2005>
- Kong, J., Wang, C., Kwong, K., Vangel, M., Chua, E., & Gollub, R. (2005). The neural substrate of arithmetic operations and procedure complexity. *Cognitive Brain Research*, 22(3), 397–405. <https://doi.org/10.1016/j.cogbrainres.2004.09.011>
- Kool, W., McGuire, J. T., Rosen, Z. B., & Botvinick, M. M. (2010). Decision making and the avoidance of cognitive demand. *Journal of Experimental Psychology: General*, 139(4), 665–682. <https://doi.org/10.1037/a0020198>
- Krebs, R. M., Boehler, C. N., Roberts, K. C., Song, A. W., & Woldorff, M. G. (2012). The involvement of the dopaminergic midbrain and cortico-striatal-thalamic circuits in the integration of reward prospect and attentional task demands. *Cerebral Cortex*, 22(3), 607–615. <https://doi.org/10.1093/cercor/bhr134>
- Landau, A. N., Schreyer, H. M., Van Pelt, S., & Fries, P. (2015). Distributed attention is implemented through theta-rhythmic gamma modulation. *Current Biology*, 25(17), 2332–2337. <https://doi.org/10.1016/j.cub.2015.07.048>
- Laufs, H., Kleinschmidt, A., Beyerle, A., Eger, E., Salek-Haddadi, A., Preibisch, C., & Krakow, K. (2003). EEG-correlated fMRI of human alpha activity. *NeuroImage*, 19(4), 1463–1476. [https://doi.org/10.1016/S1053-8119\(03\)00286-6](https://doi.org/10.1016/S1053-8119(03)00286-6)
- Lieder, F., Shenhav, A., Musslick, S., & Griffiths, T. L. (2018). Rational metareasoning and the plasticity of cognitive control. *PLOS Computational Biology*, 1–27. <https://doi.org/10.1371/journal.pcbi.1006043>
- Macar, F., & Vidal, F. (2003). The CNV peak: An index of decision making and temporal memory. *Psychophysiology*, 40, 950–954. <https://doi.org/10.1111/1469-8986.00113>
- Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods*, 164(1), 177–190. <https://doi.org/10.1016/j.jneumeth.2007.03.024>
- Mazaheri, A., Nieuwenhuis, I. L. C., Van Dijk, H., & Jensen, O. (2009). Prestimulus alpha and mu activity predicts failure to inhibit motor responses. *Human Brain Mapping*, 30(6), 1791–1800. <https://doi.org/10.1002/hbm.20763>
- McAdam, D. W. (1969). Increases in CNS excitability during negative cortical slow potentials in man. *Electroencephalography and Clinical Neurophysiology*, 26(2), 216–219. [https://doi.org/10.1016/0013-4694\(69\)90213-2](https://doi.org/10.1016/0013-4694(69)90213-2)
- Nicola, S. M., Surmeier, D. J., & Malenka, R. C. (2000). Dopaminergic modulation of neuronal excitability in the striatum and nucleus accumbens. *Annual Review of Neuroscience*, 23(1), 185–215. <https://doi.org/10.1146/annurev.neuro.23.1.185>
- Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J. M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience*, 2011, 1–9. <https://doi.org/10.1155/2011/156869>
- Padmala, S., & Pessoa, L. (2010). Interactions between cognition and motivation during response inhibition. *Neuropsychologia*, 48(2), 558–565. <https://doi.org/10.1016/j.neuropsychologia.2009.10.017>
- Padmala, S., & Pessoa, L. (2011). Reward reduces conflict by enhancing attentional control and biasing visual cortical processing. *Journal of Cognitive Neuroscience*, 23(11), 3419–3432. [https://doi.org/10.1162/jocn\\_a\\_00011](https://doi.org/10.1162/jocn_a_00011)
- Ritter, P., Moosmann, M., & Villringer, A. (2009). Rolandic alpha and beta EEG rhythms' strengths are inversely related to fMRI-BOLD signal in primary somatosensory and motor cortex. *Human Brain Mapping*, 30(4), 1168–1187. <https://doi.org/10.1002/hbm.20585>
- Rockstroh, B., Mi, M., Wagner, M., Cohen, R., & Elbert, T. (1993). “Probing” the nature of the CNV. *Electroencephalography and Clinical Neurophysiology*, 87, 235–241. [https://doi.org/10.1016/0013-4694\(93\)90023-O](https://doi.org/10.1016/0013-4694(93)90023-O)
- Rohrbaugh, J., Syndulko, K., & Lindsley, D. (1976). Brain wave components of the contingent negative variation in humans. *Science*, 191(4231), 1055–1057. <https://doi.org/10.1126/science.1251217>
- Roux, F., & Uhlhaas, P. J. (2014). Working memory and neural oscillations: Alpha-gamma versus theta-gamma codes for distinct WM information? *Trends in Cognitive Sciences*, 18(1), 16–25. <https://doi.org/10.1016/j.tics.2013.10.010>
- Ruchkin, D. S., Sutton, S., Mahaffey, D., & Glaser, J. (1986). Terminal CNV in the absence of motor response. *Electroencephalography and Clinical Neurophysiology*, 63(2), 445–463. [https://doi.org/10.1016/0013-4694\(86\)90127-6](https://doi.org/10.1016/0013-4694(86)90127-6)
- Schevernels, H., Krebs, R. M., Santens, P., Woldorff, M. G., & Boehler, C. N. (2013). Task preparation processes related to reward prediction precede those related to task-difficulty expectation. *NeuroImage*, 84C, 639–647. <https://doi.org/10.1016/j.neuroimage.2013.09.039>
- Seitz, A. R., Kim, D., & Watanabe, T. (2009). Rewards evoke learning of unconsciously processed visual stimuli in adult humans. *Neuron*, 61(5), 700–707. <https://doi.org/10.1016/j.neuron.2009.01.016>
- Shenhav, A., Botvinick, M. M., & Cohen, J. D. (2013). The expected value of control: An integrative theory of anterior cingulate cortex function. *Neuron*, 79(2), 217–240. <https://doi.org/10.1016/j.neuron.2013.07.007>
- Silvetti, M., Nuñez Castellar, E., Roger, C., & Verguts, T. (2014). Reward expectation and prediction error in human medial frontal cortex: An EEG study. *NeuroImage*, 84, 376–382. <https://doi.org/10.1016/j.neuroimage.2013.08.058>
- Silvetti, M., Vassena, E., Abrahamse, E. L., & Verguts, T. (2018). Dorsal anterior cingulate-brainstem ensemble as a reinforcement meta-learner. *PLOS Computational Biology*, 14(8), e1006370. <https://doi.org/10.1371/journal.pcbi.1006370>

- Tecce, J. J. (1972). Contingent negative variation (CNV) and psychological processes in man. *Psychological Bulletin*, 77(2), 73–108. <https://doi.org/10.1037/h0032177>
- Thut, G., Nietzel, A., Brandt, S. A., & Pascual-Leone, A. (2006). Alpha-band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. *Journal of Neuroscience*, 26(37), 9494–9502. <https://doi.org/10.1523/JNEUROSCI.0875-06.2006>
- van den Berg, B., Krebs, R. M., Lorist, M. M., & Woldorff, M. G. (2014). Utilization of reward-prospect enhances preparatory attention and reduces stimulus conflict. *Cognitive, Affective & Behavioral Neuroscience*, 14, 561–577. <https://doi.org/10.3758/s13415-014-0281-z>
- van Noordt, S. J. R., Desjardins, J. A., Gogo, C. E. T., Tekok-kilic, A., & Segalowitz, S. J. (2017). Cognitive control in the eye of the beholder: Electrocorical theta and alpha modulation during response preparation in a cued saccade task. *NeuroImage*, 145(Apr), 82–95. <https://doi.org/10.1016/j.neuroimage.2016.09.054>
- Vanlessen, N., De Raedt, R., Mueller, S. C., Rossi, V., & Pourtois, G. (2015). Happy and less inhibited? Effects of positive mood on inhibitory control during an antisaccade task revealed using topographic evoked potential mapping. *Biological Psychology*, 110, 190–200. <https://doi.org/10.1016/j.biopsycho.2015.07.004>
- Vassena, E., Silvetti, M., Boehler, C. N., Achten, E., Fias, W., & Verguts, T. (2014). Overlapping neural systems represent cognitive effort and reward anticipation. *PLoS ONE*, 9, 1–9. <https://doi.org/10.1371/journal.pone.0091008>
- Verguts, T. (2017). Binding by random bursts: A computational model of cognitive control. *Journal of Cognitive Neuroscience*, 6, 1103–1118. <https://doi.org/10.3837/tiis.0000.00.000>
- Verguts, T., Vassena, E., & Silvetti, M. (2015). Adaptive effort investment in cognitive and physical tasks: A neurocomputational model. *Frontiers in Behavioral Neuroscience*, 9, 1–17. <https://doi.org/10.3389/fnbeh.2015.00057>
- Voloh, B., Valiante, T. A., Everling, S., & Womelsdorf, T. (2015). Theta-gamma coordination between anterior cingulate and prefrontal cortex indexes correct attention shifts. *Proceedings of the National Academy of Sciences*, 112(27), 8457–8462. <https://doi.org/10.1073/pnas.1500438112>
- Walter, W. G., Cooper, R., Aldridge, V. J., McCallum, W. C., & Winter, A. A. L. (1964). Contingent negative variation: An electrical sign of sensorimotor association and expectancy in the human brain. *Nature*, 203, 380–384.
- Weissman, D. H., Warner, L. M., & Woldorff, M. G. (2004). The neural mechanisms for minimizing cross-modal distraction. *Journal of Neuroscience*, 24(48), 10941–10949. <https://doi.org/10.1523/JNEUROSCI.3669-04.2004>
- Westbrook, A., & Braver, T. S. (2015). Cognitive effort: A neuroeconomic approach. *Cognitive, Affective, & Behavioral Neuroscience*, 15(2), 395–415. <https://doi.org/10.3758/s13415-015-0334-y>
- Womelsdorf, T., Ardid, S., Everling, S., & Valiante, T. A. (2014). Burst firing synchronizes prefrontal and anterior cingulate cortex during attentional control. *Current Biology*, 24(22), 2613–2621. <https://doi.org/10.1016/j.cub.2014.09.046>
- Womelsdorf, T., Johnston, K., Vinck, M., & Everling, S. (2010). Theta-activity in anterior cingulate cortex predicts task rules and their adjustments following errors. *Proceedings of the National Academy of Sciences of the United States of America*, 107(11), 5248–5253. <https://doi.org/10.1073/pnas.0906194107>
- Worden, M. S., Foxe, J. J., Wang, N., & Simpson, G. V. (2000). Anticipatory biasing of visuospatial attention indexed by retinotopically specific alpha-band electroencephalography increases over occipital cortex. *Journal of Neuroscience*, 20(6), 63.

**How to cite this article:** De Loof E, Vassena E, Janssens C, et al. Preparing for hard times: Scalp and intracranial physiological signatures of proactive cognitive control. *Psychophysiology*. 2019;e13417. <https://doi.org/10.1111/psyp.13417>