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Research report

Impaired cognitive control and reduced cingulate activity during mental fatigue

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Abstract

Neurocognitive mechanisms underlying the effects of mental fatigue are poorly understood. Here, we examined whether error-related brain activity, indexing performance monitoring by the anterior cingulate cortex (ACC), and strategic behavioural adjustments were modulated by mental fatigue, as induced by 2 h of continuous demanding cognitive task performance. Findings that (1) mental fatigue is associated with compromised performance monitoring and inadequate performance adjustments after errors, (2) monitoring functions of ACC and striatum rely on dopaminergic inputs from the midbrain, and (3) patients with striatal dopamine deficiencies show symptomatic mental fatigue, suggest that mental fatigue results from a failure to maintain adequate levels of dopaminergic transmission to the striatum and the ACC, resulting in impaired cognitive control.

Theme: Neural basis of behavior
Topic: Cognition

Keywords: Mental fatigue; Cognitive control; Anterior cingulate cortex; Error-related negativity; Post-error slowing

1. Introduction

Mental fatigue refers to the effects that people experience following and during the course of prolonged periods of demanding cognitive activity, requiring sustained mental efficiency. It is, at least to some extent, a common part of many daily-life activities, such as taking part in traffic, or operating complex computer programs or machinery. Mental fatigue may lead to sub-optimal functioning or even human error. In extreme cases, these failures give rise to catastrophic events such as traffic accidents or surgical imprecision. Despite these obvious perils, little is known about the cognitive processes affected by mental fatigue or the neurocognitive mechanisms underlying these effects [7,19,20].

Here, we examined the hypothesis that the effects of mental fatigue on neurocognitive function involve mechanisms of cognitive control. Cognitive control refers to those emergent 'higher-order' mental functions that oversee and regulate more basic cognitive functions in accordance with internal intentions [17,24]. Theories of cognitive control suggest that these control mechanisms are implemented in the brain in a distributed network, involving closely interacting components that are engaged in monitoring and evaluating behaviour (overseeing) and in the implementation of executive control (regulation) when adjustments in control are needed [6,22,23]. The engagement of cognitive

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control is crucial especially under novel and complex task demands, conditions under which fatigued individuals most prominently experience performance difficulties.

Neuroimaging studies and event-related brain potential research have established that the ACC is central to performance monitoring [3,13,21,34]. ACC is thought to detect the activation of erroneous or conflicting responses and to signal the need to activate adaptive control processes, serving to instigate remedial performance adjustments that minimise the risk of subsequent error [1,6,18]. Such interventions may involve immediate corrective actions (e.g., post-error slowing) or long-term strategic adjustments (e.g., tonic changes in speed/accuracy balance) [13,28]. Neural activity in the ACC has been found to change with time-on-task [5,26], suggesting that alterations in ACC functioning are a possible mechanism of mental fatigue. The monitoring function of ACC relies on the mesencephalic dopamine system [2,16], which projects diffusely to the cortex and the striatum [16]. Disturbances in the striatal system have also been related to mental fatigue [4], supporting the dopaminergic involvement in mental fatigue. If prolonged periods of demanding cognitive activity result in reduced mesencephalic dopaminergic projections to ACC, the consequence may be impaired performance monitoring and inadequate performance adjustment.

An electrophysiological index of performance monitoring in ACC is the error-related negativity (ERN or Ne) [8,14], which occurs immediately following the response. This event-related brain potential (ERP) is observed when subjects generate an error or when task conditions elicit high levels of response conflict [1,3,16,21,35]. Based on the association between ERN/Ne amplitude and the role of ACC in error monitoring, observed consistently in the literature [3,13,16,21,34], the ERN/Ne can be used to examine the effects of psychoactive substances, such as alcohol [30], or state variables, such as fatigue [9,32] on cognitive control mechanisms. The ERN/Ne amplitude was observed to be reduced after sleep deprivation [32]. Consistent with observations that cognitive failures associated with sleep-deprivation can be counteracted by caffeine [36], ERN/Ne amplitude is increased after moderate doses of caffeine consumption [33].

The current investigation was designed to assess whether performance monitoring involving the ACC, as indexed in the ERN/Ne, and related post-error adjustments in behaviour, were modulated by mental fatigue, induced by 2 h of prolonged task performance. To this end, we examined ERPs in a study designed to track the effects of fatigue on error monitoring, as well as remedial behavioural adjustments subsequent to errors. Participants performed a variant of the Eriksen flanker task, in which they searched for a centrally presented target letter that was flanked by distracter stimuli, associated either with the same response as the target (compatible condition) or with the opposite response (incompatible condition). The subjects' task was to respond to the target letter and ignore distracting information. This task was selected because of its demonstrated success at eliciting ERNs/Nes [1,16].

2. Materials and methods

2.1. Participants

Fifteen healthy young women, ranging in age from 19 to 25 years (M = 21.1, SD = 1.8), participated in the study. All reported to be non-smokers, to have normal sleep patterns, not to work night shifts, and not to use prescription medication. They all had normal or corrected-to-normal visual acuity and were right-handed according to self-report. Subjects received a monetary bonus in return for their participation. Informed consent was obtained from all subjects prior to the study.

2.2. Stimuli and apparatus

Stimuli were presented in the centre of a computer screen positioned at a viewing distance of 80 cm. On each trial, the participants were presented with a horizontal array of three uppercase letters, the central one of which was the target letter and the remaining letters were the flankers. The participants were instructed to make a speeded left-hand response if the central letter was an H and a right-hand response if the central letter was a S. The letter array remained on the screen until a response was given, or in case no response was issued the letters disappeared after 1200 ms. If the first response was considered incorrect, the subject was allowed to correct it by a second response within 500 ms following the initial response.

The target letter was presented in red in 50% of the trials or in green, on the other half of the trials, against a black background. On half of the trials, the flankers had the same identity and colour as the target letter (e.g., HHH or SSS: compatible). In the other half of the trials, flankers had a different identity and colour than the target letter (e.g., SHS or HSH: incompatible). The different stimulus categories were presented in random order but with equal probability. A pre-cue, appearing 1000 ms before the three letters, was presented for 150 ms, designating either the colour of the target letter (the Dutch word for 'red' or 'green') or the response hand (the Dutch word for 'left' or 'right')[1]. Hand and colour cues were presented in random order with equal probability. The cues were valid on 80% of the trials. During the trial, a fixation mark remained visible on the screen (an asterisk of 0.5 × 0.5 cm). Stimuli were presented 0.5 cm above this fixation mark and the visual angle per stimulus letter was 0.18° × 0.18°. The interval

[1] In addition to the relation between mental fatigue and performance monitoring, we were interested in the effect of type of information provided before a stimulus was presented. Results concerning this research question will be discussed elsewhere.

between the (initial) response to one trial and the onset of pre-cue presentation on the next trial varied randomly between 900 and 1100 ms.

2.3. Procedure

The experimental sessions started around 1.00 p.m. and lasted 3 h. After the subject arrived at the laboratory, the EEG montage (see below) was applied and the experimental procedure was explained, without giving specific information about the duration of the experimental task. Subsequently, the subject was seated in a dimly illuminated, sound attenuated electrically shielded room. The subject was instructed to respond as quickly as possible, maintaining a high level of accuracy, and to minimise eye movements and blinking during task performance. A 2-h experimental block without breaks followed a practice block of 80 trials. Written informed consent was obtained from all subjects prior to the experiment after the nature and possible consequences (but not the duration) of the study were explained to them. The experiment was performed in compliance with relevant laws and institutional guidelines and was approved by the ethical committee of the Department of Psychology of the University of Groningen.

2.4. EEG recordings

EEG was recorded from 22 scalp sites, using *Sn* electrodes attached to an electrode cap (ElectroCap International). Standard 10–20 sites were F7, F3, Fz, F4, F8, T7, C3, Cz, C4, T8, P7, P3, Pz, P4, P8, O1, Oz, and O2. Additional intermediate sites were FC5, FC1, FC2, and FC6. The electrodes were referenced to electronically linked earlobes. Electro-oculograms were recorded bipolarly with *Sn* electrodes from the outer canthi of both eyes and from above and below the left eye. An *Ag*/*AgCl* ground electrode was placed on the sternum. Electrode impedance was reduced to less than 5 kΩ. The signals were amplified with a bandpass set at 30 Hz and a time constant of 10 s and digitised at a rate of 100 Hz.

2.5. EEG data reduction

Averaged stimulus-locked and response-locked ERPs were computed separately for each combination of conditions, the conditions being time-on-task interval (first/second/third/fourth half hour), cue type (colour/hand), and performance accuracy (correct/incorrect hand). For stimulus-locked ERPs, the averaging epoch started 100 ms prior to stimulus onset and lasted until 1000 ms post-stimulus. For response-locked ERPs, the averaging epoch started 200 ms prior to the response and lasted until 500 ms thereafter. Standard psychophysiological procedures were applied to correct for eye movement artefact [15], excluding trials containing other types of movement artefacts or amplifier saturation. All stimulus-locked averages were aligned to a 100 ms pre-stimulus baseline; response-locked averages were synchronised to a 100 ms pre-response baseline.

3. Results

Dependent variables were entered into univariate repeated-measures analysis of variance in SPSS, using the ε˜*-adjustment procedure recommended by Quintana and Maxwell [27]. For clarity, uncorrected *df* values are presented.

3.1. Overall performance[2]

The number of trials performed during the experimental session decreased as a function of time-on-task ($F(3,42) = 6.27$, $P = 0.010$), from 732 (SD = 24) during the first 30-min interval to 716 (SD = 30) in the fourth 30-min interval. In 2% of the trials, subjects failed to give a response. This number was not affected by time-on-task. Error rate was quantified as the proportion of hand errors within each condition. Response times (RT) were determined for trials in which the first response was correct. Trials containing motor responses considered being too fast (<50 ms) were excluded from RT analysis.

In line with previous studies, we found incompatible trials to be associated with longer RTs and higher error rates than compatible trials ($F(1,11) = 36.16$, $P < 0.001$ and $F(1,14) = 79.59$, $P < 0.001$, for reaction times and proportion of errors, respectively; see Table 1). Importantly, RT was modulated by time-on-task. While subjects performed relatively stable during the first 90 min of prolonged task performance, after 90 min RTs increased with on average 22 ms (contrast between third and fourth interval: $F(1,12) = 6.99$, $P = 0.021$). This decrease in speed of performance was independent of the identity of the distracters. Notably, performance accuracy was not affected by prolonged task performance, indicating that the observed time-on-task effects on RT were not likely confounded with a change in speed/accuracy trade-off and related strategy shifts.

3.2. ERP analyses

In the response-locked ERP waveforms, the negative-going component, peaking approximately 60 ms after the incorrect response, was identified as the ERN/Ne. Inspection of the scalp topographies showed that the ERN/Ne was maximal at Cz; therefore, values obtained from Cz were used for statistical analysis (dependent

[2] RT data of three subjects contained either one or two missing data points and were rejected from part of the statistical analyses.

Table 1
Mean reaction time (RT) and proportion of errors and misses during different time-on-task intervals for compatible and incompatible stimuli

		0–30 min	31–60 min	61–90 min	91–120 min
Mean RT (ms)	Compatible	447	446	446	469
	Incompatible	476	483	478	500
Proportion of errors	Compatible	0.10	0.10	0.10	0.10
	Incompatible	0.17	0.16	0.18	0.17
Proportion of misses	Compatible	0.01	0.02	0.02	0.04
	Incompatible	0.01	0.01	0.02	0.04

variables were time-on-task interval (first/second/third/fourth half hour), cue type (colour/hand), and performance accuracy (correct/incorrect hand). The amplitude of the ERN/Ne was defined for each subject as the amplitude of the largest negative peak in the 40–80 ms post-response interval. The proportion of compatible errors relative to the proportion of incompatible errors remained stable during the experiment, allowing us to pool incompatible and compatible trials [14]. ERNs/Nes were observed much more prominently after incorrect compared to correct responses ($F(1,14) = 12.28$, $P = 0.004$; Fig. 1). The ERN/Ne peak amplitude decreased significantly with time-on-task ($F(3,42) = 4.27$, $P = 0.015$), indicating that performance monitoring is affected by prolonged task performance. As can be seen in Fig. 2, this time-on-task effect is due mainly to a decrease in ERN/Ne amplitude from the second to third 30-min interval ($F(1,14) = 8.99$, $P = 0.010$).

In the stimulus-locked ERP waveforms, no effects of time-on-task were apparent. For instance, as can be seen in Fig. 3, the amplitude of the P3 component (largest at Pz, as typical) remained unaffected by time-on-task (analyses were performed on mean amplitudes in 50 ms windows; between 350–500 ms: $F(3,42) < 1.13$, n.s). This observation attests to the specificity of time-on-task effects on ERN/Ne amplitude.

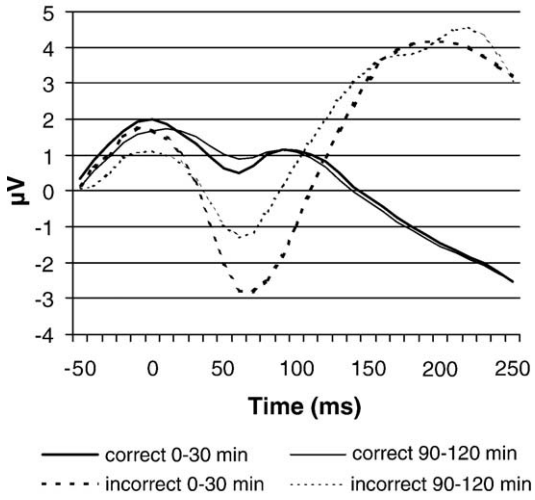

Fig. 1. Response-locked event-related potentials from the vertex (Cz) electrode for correct (straight lines) and incorrect trials (dashed lines) in the 0–30 min interval and in the 90–120 min interval.

3.3. Corrective actions

If a reduction of the ERN/Ne component implies a failure of response monitoring, performance adjustments are expected to be less efficient with increasing time-on-task. As a behavioural index of error correction, we first examined the proportion of error trials on which the erroneous response was followed immediately (within 500 ms) by a correct response [11,13,28]. Of all incorrect responses, 78% was corrected by a subsequent, correct response (SD = 17%). Note that these second responses were true error corrections, as very few *correct* responses were 'corrected' by errors (0.8%, SD = 1.4%). The percentage of corrected errors was smaller for compatible compared to incompatible trials ($F(1,11) = 8.85$, $P = 0.013$). Remarkably, however, these immediate performance adjustments were unaffected by the time spent on task performance. Thus, the decrease in ERN/Ne amplitude with time-on-task was not accompanied by a corresponding decrease in immediate error corrections with prolonged task performance.

As a second behavioural index of behavioural adjustment after errors, we examined speed/accuracy adjustments in trials subsequent to incorrect trials. In particular, we analysed time-on-task effects on post-error slowing. In correct trials following error trials, subjects slowed down compared with RTs in trials following correct trials ($F(1,14) = 4.70$, $P = 0.048$). Most important, however, this post-error slowing disappeared with time-on-task (time-on-task × trial type:

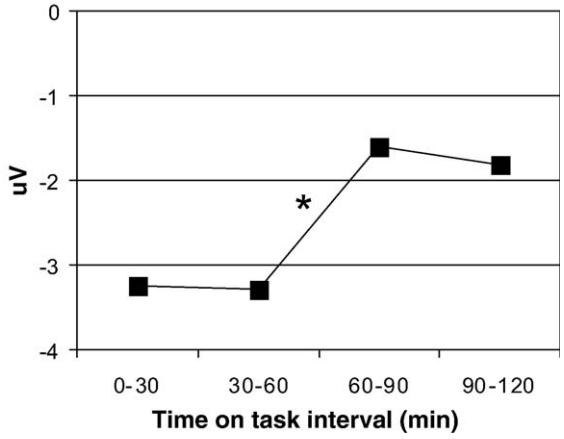

Fig. 2. Mean ERN/Ne amplitude for incorrect trials in different time-on-task intervals (asterisk indicates significant difference ($P < 0.01$) between ERN/Ne amplitudes in successive time-on-task intervals).

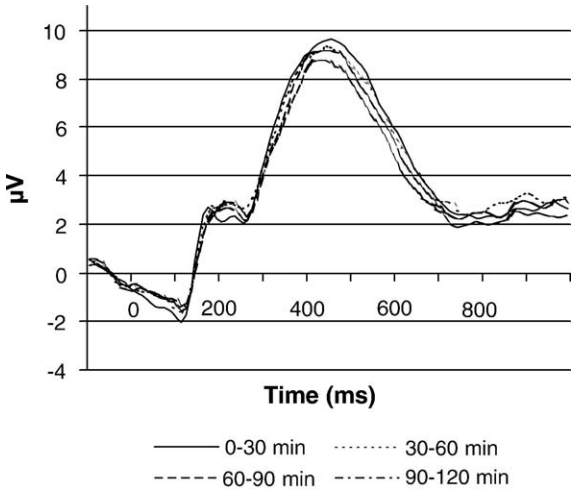

Fig. 3. Stimulus-locked event-related potentials from the parietal (Pz) electrode elicited in different time-on-task intervals.

$F(3,42) = 5.25$, $P = 0.004$). As can been seen in Fig. 4, the post-error slowing observed in the first half hour ($F(1,14) = 12.77$, $P = 0.003$) had disappeared in all subsequent 30-min intervals (all $F(1,14) < 2.22$, all $P > 0.05$).

In summary, although the incidence of errors remained stable across prolonged task performance, the amplitude of the ERN/Ne decreased with time-on-task and performance adjustments subsequent to errors declined with time-on-task, as well. During the first 30-min of task performance, errors were followed by post-error slowing, an adjustment that can be interpreted as a transient shift in speed/accuracy balance in an attempt to prevent subsequent errors. This tendency to adopt a more conservative strategy following the occurrence of errors disappeared during the course of prolonged task performance.

4. Discussion

Although performance detriments as a function of mental fatigue have been documented across a broad spectrum of cognitive tasks [7,19,20], the neurocognitive mechanisms underlying these effects have remained elusive. Building on the hypothesis that these effects involve mechanisms of cognitive control, we examined the effects of prolonged task performance on error processing. The present study documents that mental fatigue results in compromised error monitoring as reflected in a significant attenuation of the ERN/Ne, as well as in adjustment failures in post-error performance. However, subjects seemed to compensate for the reduction in performance efficiency due to prolonged task performance by increasing RTs, preventing the occurrence of errors and related demands placed on ACC functioning.

Thus, a change in the internal state of humans due to 2 h of prolonged task performance has major effects on one of the key features of cognitive control: the extraction of goal-relevant features of past experiences to orchestrate future behaviour in accord with intentions. To verify whether this impairment is specific to error monitoring, it was important to establish that time-on-task uniquely affected ERN/Ne amplitude and did not generalise to other ERP components that are not related to error processing. In addition, it was important to establish that any effects of mental fatigue on error detection were not contaminated by concomitant reductions in interference control or in accuracy, since the latter affects could potentially mediate the effects on ERN/Ne amplitude [2,30]. As both conditions were satisfied, the present data reveal that mental fatigue affects the error-monitoring processes expressed in the ERN/Ne.

The capacity to monitor error performance, as reflected in ERN/Ne amplitude, is thought to rely predominantly on intact ACC functioning [1,3,13,16,21,34]. In addition to the monitor function, the ACC serves to signal the need for enhanced cognitive control after a performance error has occurred. Subjects typically slow down on the trial after an incorrect response [1,28]. We observed that these remedial adjustments were limited to the first 30-min period of task performance. Although the precise relationship between the ERN/Ne and subsequent post-error slowing is still unclear [12,25], the present findings suggest that the ability to use information from previous trials to strategically adapt behaviour is severely deteriorated already after half an hour of task performance. By contrast, remedial actions in the form of immediate corrections were not affected by time-on-task. To understand this differential sensitivity to mental fatigue, note that post-error performance adjustments are subject to strategic modulation [11,30] while immediate error correction is a relatively automatic process that cannot be consciously suppressed [11,29]. After a premature execution of the first incorrect response tendency, stimulus processing continues and can result in a corrective response. Note that these immediate corrections are based on the stimulus-driven second response tendency, which does not

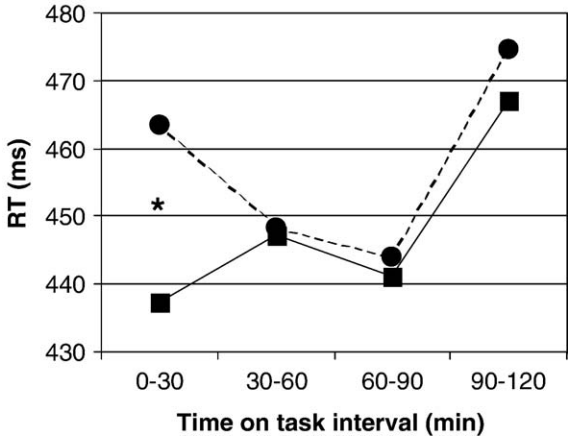

Fig. 4. Mean reaction time for correct trials following a correct response (straight line) and correct trials following an incorrect response (dashed line; asterisk indicates significant difference ($P < 0.01$) between reaction times in specific time interval).

require error detection [11]. The present data provide support for the notion that post-error slowing and overt response correction are different phenomena and suggest that mental fatigue mainly affects higher-level cognitive control mechanisms, while reflexive reactions seem relatively insensitive to prolonged task performance.

Different brain structures are involved in monitoring performance, deciding how and when to allocate attention and for the implementation of control or behavioural adjustments [18,31]. The results of the present study suggest that these different brain areas are differentially sensitive to the effects of mental fatigue. The ERN data indicate that monitoring processes, mediated by the ACC, were compromised after 60 min of continuous task performance. However, the implementation of control, which may be mediated by response preparation areas, seemed more vulnerable to the effects of mental fatigue; post-error slowing already was absent after half an hour of task performance.

Taking into consideration the attenuation of the ERN observed after 60 min of task performance, indicating that monitoring processes are compromised with time-on-task, and the disappearance of strategic behavioural adjustments after half an hour of task performance, it was surprising that even after 2 h no decline in performance accuracy was observed. However, subjects did show a general reduction in speed of performance with time-on-task, irrespective of accuracy on previous trials.

In previous studies [20], we have observed that subjects seemed to be able to perform at a rather stable speed level during the first hour of task performance; thereafter, a sudden increase in RTs was observed. The occurrence of errors, however, increased gradually during the experiment. These results indicate that, with time-on-task, subjects tried to maintain their speed of performance, as was stressed in the task instructions, and in order to do so they sacrificed accuracy. After 60 min of task performance, however, subjects seemed to readjust their strategy; in addition to sacrificing accuracy, they also modified their speed levels [20].

In the present study, subjects were able to respond relatively stable for 60 min of task performance, whereafter the ERN amplitude attenuated, indicating that monitoring processes were compromised. The instructions stressed both speed and accuracy; however, subjects were told that they were able to correct incorrect reactions. This additional instruction stressed accuracy. It might be argued that the increase in RTs after 90 min of task performance indicates that subjects sacrificed speed in order to maintain accuracy levels.

Slowing down may allow a more complete accumulation of evidence concerning the correct response, thus preventing premature incorrect reactions. The general slowing observed with time-on-task thus might be a dynamic adaptation allowing subjects to compensate for the reduction in performance efficiency due to prolonged task performance and can be considered a functional strategy to cope with sub-optimal internal states (i.e., mental fatigue).

Beyond these demonstrations, the present data provide initial support for the notion that mental fatigue involves dopamine-mediated mechanisms of cognitive control, thereby providing the initial contours of a neurocognitive theory of mental fatigue. Although the neuroanatomical pathways and the neurochemical substrates for mental fatigue remain far from clear, the genesis of symptoms related to fatigue has been argued to involve the striatum [4]. Patients suffering from ischaemic vascular diseases involving the basal ganglia or from progressive neurodegeneration affecting the striatum (like in Parkinson's disease) frequently report symptoms of mental fatigue. Moreover, Falkenstein et al. [10] have shown that patients with Parkinson's disease have a reduced ERN/Ne (but see [16]). These clinical observations suggest the possible involvement of mesencephalic dopaminergic projection systems comprising the striatum and frontal cortical structures, in particular ACC. A role of ACC in mental fatigue is suggested also by reports of modulations in neural activity as a function of time-on-task [5,26]. The present finding that two key functions of ACC in action monitoring, error detection and signalling the need for remedial action, decline during prolonged periods of demanding cognitive activity, combined with the notion that these monitoring functions of ACC rely on dopaminergic inputs [2,16], suggests that mental fatigue results from a failure to maintain adequate levels of dopaminergic transmission in the striatum and ACC. The result is impaired cognitive control, expressed in the present case as compromised performance monitoring and inadequate performance adjustment.

Acknowledgments

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