

Mental fatigue, motivation and action monitoring

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Abstract

In this study we examined whether the effects of mental fatigue on behaviour are due to reduced action monitoring as indexed by the error related negativity (Ne/ERN), N2 and contingent negative variation (CNV) event-related potential (ERP) components. Therefore, we had subjects perform a task, which required a high degree of action monitoring, continuously for 2 h. In addition we tried to relate the observed behavioural and electrophysiological changes to motivational processes and individual differences.

Changes in task performance due to fatigue were accompanied by a decrease in Ne/ERN and N2 amplitude, reflecting impaired action monitoring, as well as a decrease in CNV amplitude which reflects reduced response preparation with increasing fatigue. Increasing the motivational level of our subjects resulted in changes in behaviour and brain activity that were different for individual subjects. Subjects that increased their performance accuracy displayed an increase in Ne/ERN amplitude, while subjects that increased their response speed displayed an increase in CNV amplitude. We will discuss the effects prolonged task performance on the behavioural and physiological indices of action monitoring, as well as the relationship between fatigue, motivation and individual differences.

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1. Introduction

1.1. Mental fatigue and action monitoring

Fatigue due to prolonged task performance is a common phenomenon in our everyday lives. When people become fatigued, they usually experience difficulties in maintaining task performance at an adequate level. This can have major consequences: for example, in a recent study by [Campagne et al. \(2004\)](#) in which subject were required to drive a car (in a simulator) for about 3 h, it was found that with increasing fatigue, performance deteriorated. Driving errors such as large speed variations and even running of the road became increasingly frequent. Comparable results have been obtained for truck and

train drivers ([Kecklund and Akerstedt, 1993](#); [Torswall and Akerstedt, 1987](#)). It seems that the problems that fatigued people experience in these circumstances result to a large extent from the fact that they monitor their actions insufficiently.

To be able to behave in a coherent and adaptive manner, it is imperative to monitor ones actions ([MacDonald et al., 2000](#)). In doing so, information is gained which can be used to adjust ongoing behaviour. To keep with our example: if the subjects in the car simulator would have monitored their actions adequately, they would have detected their deviations in speed and position on the road earlier, resulting in less driving errors.

In the present study we examined the effects of fatigue on action monitoring processes, using event-related potentials (ERPs). Different indices of action monitoring can be discerned in the ERP. The error related negativity (ERN) or error negativity (Ne) consists of a large negative shift in the response locked ERP occurring after subjects made an erroneous response. First reported by [Falkenstein et al. \(1990\)](#) and [Gehring et al. \(1990\)](#), the Ne/ERN was thought to be specifically related to error detection processes, in the sense of a mismatch signal when representations of the actual response and the required response are compared.

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Peaking at 50–150 ms after response execution, the Ne/ERN is most prominent at fronto-central scalp positions (e.g., Fz, FCz and Cz). Localization of the Ne/ERN with dipole localization algorithms (BESA) has led most authors to conclude that the Ne/ERN is generated in the anterior cingulate cortex (ACC, Dehaene et al., 1994; Gehring and Knight, 2000; Wijers and Boksem, 2005). These findings are corroborated with results from fMRI studies (Carter et al., 1998; Kiehl et al., 2000; Van Veen and Carter, 2002a).

A second ERP component associated with action monitoring is the N2 (Van Veen and Carter, 2002b). This stimulus locked ERP component has a similar scalp topography as the Ne/ERN and has also been localized in the ACC (Lange et al., 1998; Liotti et al., 2000). In contrast to the Ne/ERN, the N2 occurs prior to response execution on correct trials and is thought to reflect response conflict (Lange et al., 1998; Kopp et al., 1996; Liotti et al., 2000; Swick and Turken, 2002). Response conflict occurs when a stimulus activates more than one response channel (the correct and an incorrect channel).

To resolve the detected conflict, the action monitoring system recruits greater top-down control from other prefrontal structures to improve task performance and thereby reduce conflict (Botvinick et al., 2001; Carter et al., 1998; Gehring and Knight, 2000; Menon et al., 2001). The contingent negative variation (CNV) is thought to reflect anticipatory and preparatory processes, and has been shown to correlate with performance accuracy (Hohnsbein et al., 1998). The CNV is elicited by providing the subject with a warning stimulus (e.g., a cue) followed at some fixed interval by a second ‘imperative’ stimulus. The CNV is observed as a large negative deflection in the ERP between the warning and the imperative stimulus.

Action monitoring is a prerequisite for the ability to optimize ongoing behaviour. To modify behaviour, remedial actions should be implemented when errors are made. These remedial actions can consist of immediate corrections and/or post error slowing (Rabbitt, 1966). Post error slowing refers to the phenomenon that, after making an error, subjects typically respond with increased reaction times on the following trial. This probably reflects a strategic adjustment in response generation. Gehring et al. (1993) noted that the Ne/ERN was larger on trials in which errors were immediately corrected and that larger Ne/ERNs were related to a slower response on the subsequent trial (see also Scheffers et al., 1996). Moreover, Fiehler et al. (2004) reported a significantly greater haemodynamic response for corrected than for uncorrected errors in the rostral cingulate zone, an area identified to play an important role in error detection.

To investigate whether action monitoring processes are compromised when people are fatigued, we had subjects perform a task in which response conflict was high and required a high degree of action monitoring, for 2 h. The task we used was a modified version of the Simon task. In this kind of task, targets which are assigned to different effectuators (in this case hands) are displayed either left or right of fixation. The Simon effect (or congruency effect), first described by Simon and Small (1969) refers to the phenomenon that people respond faster (typically 20–30 ms; Lu and Proctor, 1995) when the side

of stimulus presentation corresponds to the response side. This kind of task induces response conflict as the presentation of the stimulus automatically activates the spatially corresponding response. In the incongruent condition however, one has to override this automatically activated response in order to give the required response, which relies heavily on adequate action monitoring.

1.2. *Mental fatigue and motivation*

A second important issue we addressed in the current study is the relationship between fatigue and (lack of) motivation to continue task performance. Chaudhuri and Behan (2000) noted that in their patients fatigue is, at least in part, due to a deranged motivation in self-initiated tasks. Topp et al. (2004) proposed that mental fatigue can be viewed as an effort/reward imbalance: as long as one feels that the invested effort in the end will result in sufficient rewards, one will continue working. However, when the perceived effort becomes too great and the reward no longer compares to this, the motivation to continue will dissipate and one will want to disengage from the task, feeling fatigued.

To test this, we manipulated motivation by offering our subjects a certain amount of money if they performed well in the remainder of the task, after they had performed the task for 2 h. If fatigue can indeed be viewed as an effort/reward imbalance, the increased reward should lead to a better balance between effort and reward, thus counteracting the effects of fatigue. However, there are large individual differences in the way people respond to motivation and what kinds of rewards are perceived as motivating. Here, we chose to motivate our subjects by offering them a monetary reward, as well as stressing that their performance would be compared to that of other participants (social comparison). We stressed both accuracy and performance speed, so that subjects were free to choose the way in which they could improve their performance. This allowed us to investigate individual differences in response strategies.

Interestingly, many studies have shown the Ne/ERN to be related to motivational processes: when by task instructions the motivation to perform well is reduced, a reduction in Ne/ERN amplitude can be observed (Gehring et al., 1993). Motivation appears to be essential for observing a robust Ne/ERN (Gehring et al., 1993; Gehring and Knight, 2000; Tucker et al., 1999; Dikman and Allen, 2000; Luu et al., 2000). Bush et al. (2000) argue that Ne/ERN and related ACC activity represent a general evaluative system that processes the motivational significance of events including, but not limited to errors and conflict. In addition, Falkenstein et al. (2003) have shown the CNV to be sensitive to motivational manipulations as well. In their study, CNV amplitude was larger on trials when subjects were asked for an effortful improvement of performance compared to trials when no such performance improvement was demanded.

In this study we will investigate whether the effects of fatigue on behaviour are due to reduced action monitoring as indexed by the Ne/ERN, N2 and CNV ERP components. In addition we will relate these changes to motivational processes.

2. Methods

2.1. Subjects

Nineteen healthy participants (nine males), between 18 and 26 ($M = 22$) years of age, were recruited from the university population. They were paid for their participation and had normal or corrected-to-normal vision. All participants described themselves as being right handed. None of the subjects worked night shifts or used prescription medication. Written informed consent was obtained prior to the study.

2.2. Stimuli

All stimuli were presented white on a black background. The fixation point in the centre of the screen was indicated by an asterisk. Every trial started with the presentation of an arrow cue (150 ms), 0.6° above the fixation point. The arrow indicated the hand that would have to be used for response for the upcoming stimulus. This cue was valid in 80% of the trials. One thousand milliseconds after cue onset, the imperative stimulus was presented. Stimuli consisted of an H or an S (0.5° visual angle). Participants were instructed to make a left-hand button-press response if the stimulus was an H, and a right hand button-press response if the stimulus was an S. Stimuli were presented 2.2° left or right of the fixation point. When stimulus location and response are on the same side, the stimulus is called congruent (for example an H presented on the left side of the screen). When stimulus location and response are on opposite sides, the stimulus is called incongruent (for example an H presented on the right side of the screen). Congruent and incongruent stimuli were equiprobable. Stimuli remained on the screen until a response was made or until 1200 ms had elapsed. After this, there was a 500 ms interval, in which subjects had the opportunity to correct their erroneous response by giving the correct response. Finally, there was an interval of 400–600 ms before the start of the next trial.

2.3. Procedure

Subjects were instructed to abstain from alcohol 24 h before the experiment and from caffeine containing substances 12 h before the experiment. Subjects were told the study was aimed at investigating the neural correlates of cognitive control, they were unaware the study was about mental fatigue and motivation.

After arrival at the laboratory (between 12 and 1 p.m.), the subjects surrendered their watches. They had no knowledge of the length of the session other than that it would not last beyond 18.00 h. Before the start of the experiment, subjects were given written task instructions, where after they were trained in performing the task, for 15 min.

Following the application of the electrodes, subjects were seated in a dimly lit, sound-attenuated, electrically shielded room at 0.90 m from a 17 in. PC monitor. Their index fingers rested on touch-sensitive response boxes. Subjects were instructed to lift their finger from the response button as quickly as possible when a target was presented, maintaining a high level of accuracy. The experiment started between 13:30 and 14:30 h and lasted for 2 h and 20 min. Subjects completed between 3500 and 4000 trials during the entire experiment. In the first 2 h subjects performed the task to induce fatigue. Before the start of the last 20 min, a text was displayed on screen that informed the subject that from that time on, his performance would be compared to that of other subjects and that the subjects who performed best would receive € 25 extra payment. No rest pauses were given during task performance.

2.4. Recording

The electroencephalogram (EEG) was recorded using 22 Sn Electrodes attached to an electro cap (Electro-Cap International), from positions F7, F3, Fz, F4, F8, Fc5, Fc1, Fc2, Fc6, T7, C3, Cz, C4, T8, P7, P3, Pz, P4, P8, O1, Oz and O2. All electrodes were referenced to linked earlobes. The electro-oculogram (EOG) was recorded bipolarly from the outer canthi of both eyes and above and below the left eye, using Sn electrodes. Electrode impedance was kept below 5 k Ω . EEG and EOG were amplified with a 10 s time constant and a 200 Hz low pass filter, sampled at 1000 Hz, digitally low pass filtered with a cut-off frequency of 30 Hz, and online reduced to a sample frequency of 100 Hz.

2.5. Data analysis

To investigate the effects of time on task, the data were divided into six time intervals of 20 min each. Data were subjected to SPSS ANOVA for repeated measurements, using the ϵ -adjustment procedure recommended by Quintana and Maxwell (1994). When the main analysis indicated a significant interaction ($p < .05$) between factors, follow-up analyses were performed, adjusting error rates according to Bonferroni.

2.5.1. Performance

For the different stimulus conditions mean reaction times (RTs) were calculated. Reactions occurring within a 150–1000 ms interval after stimulus presentation were considered as hits. The percentage of misses and false alarms were also determined. We tested the factors time on task (TOT, six levels), cue validity (VAL, two levels) and congruency (CON, two levels).

2.5.2. ERPs

In addition to the Ne/ERN, N2 and CNV, we also measured P3 amplitude and latency. All ERP analyses were performed using the Brain Vision Analyser software (Brain Products). ERPs were averaged off-line. Out of range artefacts were rejected and eye movement artefacts were corrected, using the Gratton and Coles method (Gratton et al., 1983). A baseline voltage over the 100 ms interval preceding the cue (CNV), stimulus (N2 and P3) or response (Ne/ERN), was subtracted from the averages. The ERPs were averaged over replications and calculated separately for each subject, time on task interval and stimulus category.

Using the grand averages, we determined the electrodes showing the largest amplitudes for each of the ERP deflections of interest (Ne/ERN, N2 and P3). For these electrodes we automatically detected peak amplitudes and latency. Peak detection for the Ne/ERN was performed in the 50–200 ms latency range, N2 peak detection was performed in the 250–350 ms latency range and peak detection for the P3 was performed in the 300–600 ms latency range. For the Ne/ERN, N2 and P3, we selected the average amplitude of the respective ERP components in a time window from 20 ms before the peak until 20 ms after the peak for statistical analysis. For the CNV we tested the amplitude in the 600 ms–1000 ms time window after cue onset.

The Ne/ERN was maximal on Cz (Fig. 1). Because of the limited number of errors made by the subjects, these ERPs were averaged over stimulus categories, leaving only the factor TOT for statistical analyses. As the N2 amplitude was maximal on Cz, we used this electrode to test the factors TOT, VAL and CON. For the P3 we tested the same factors on Pz, where this component had its maximum. For the CNV, we tested the factors TOT and CUE (left or right) in the specified time window at electrode Cz, where visual inspection indicated that the CNV was maximal.

2.5.3. Motivation

To investigate the effects of motivation on the behaviour and brain activity of fatigued subjects, we tested the difference on all the measures described above between the last interval before the motivation manipulation (interval six) and the interval after the motivation manipulation (interval seven). RTs and the

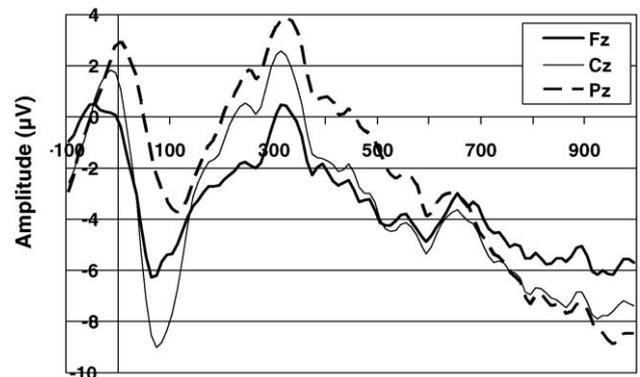


Fig. 1. Ne/ERN amplitude at Fz, Cz and Pz for interval 1. The Ne/ERN had a maximal amplitude at Cz.

proportion of correct responses in interval seven were converted to standard scores for each participant. An index of speed-accuracy trade-off was then calculated according to the method of Nietfeld and Bosma (2003). Based on this index, we divided our subjects (median split) in a group that responded to the motivational instructions with increased accuracy and one that responded with increased speed (the 'accuracy' and the 'speed' group).

3. Results

3.1. Performance

3.1.1. RTs and accuracy

Processing speed was reduced by time on task, from 457 ms in the first interval to 485 ms in the sixth interval (Table 1, $F(5,90) = 3.03$, $p < 0.05$). In addition, we found that RT variability increased with time on task, $F(6,108) = 6.18$, $p < 0.005$ (Table 1). Mean correct RTs for incongruent trials were slower, compared to the RTs for congruent stimuli (483 ms versus 451 ms, $F(1,18) = 48.13$, $p < 0.001$). However, the magnitude of this typical congruency effect was not modulated by time on task (TOT \times CON, $F(5,90) = 0.69$, ns). The difference in RT for valid (446 ms) and invalidly cued stimuli (488 ms) also proved to be significant ($F(1,18) = 21.99$, $p < 0.001$). Furthermore, we found an interaction between congruence and validity ($F(1,18) = 8.58$, $p < 0.01$). The difference in RT between congruent and incongruent stimuli was larger when validly cued (valid: $F(1,18) = 60.70$, $p < 0.001$), Invalid: ($F(1,18) = 19.32$, $p < 0.001$), although there was a congruency effect in both validity conditions.

Accuracy was determined as percentage incorrect per stimulus category (i.e. false alarms). The performance in terms of accuracy decreased from 9.2% errors in the first interval, to 12.9% errors in the sixth interval (Table 1, $F(5,90) = 3.61$, $p < 0.05$). Subjects made more errors on incongruent trials (15.3%) than on congruent trials (7.5%, $F(1,18) = 34.49$, $p < 0.001$). As with the RTs, the magnitude of this congruency effect was not modulated by time on task (TOT \times CON, $F(5,90) = 1.77$, ns). Validly cued trials resulted in less errors (7.1%) than invalidly cued trials (15.7%, $F(1,18) = 17.50$, $p < 0.001$). Contrary to what we found for RTs, the difference in percentage of errors between congruent and incongruent trials was larger when invalidly cued, $F(1,18) = 17.34$, $p < 0.001$, (valid: $F(1,18) = 23.87$, $p < 0.001$, invalid: $F(1,18) = 30.57$, $p < 0.001$). Again, we obtained a congruency effect in both validity conditions.

Table 1
Changes in RT, S.D. of RTS and Errors with time on task (interval 1–6) and with motivation (interval 7), collapsed over stimulus categories

Interval	RT (ms)	S.D. (ms)	Errors (%)
1	457 (13.3)	121 (08.2)	9.2 (1.4)
2	463 (14.8)	129 (09.1)	10.4 (1.3)
3	460 (16.0)	136 (08.9)	11.4 (1.7)
4	464 (14.0)	145 (09.4)	12.2 (1.8)
5	473 (14.5)	156 (12.3)	12.5 (2.0)
6	485 (15.1)	145 (10.2)	12.9 (1.8)
7	463 (14.2)	150 (12.3)	12.7 (1.9)

Standard errors in parenthesis.

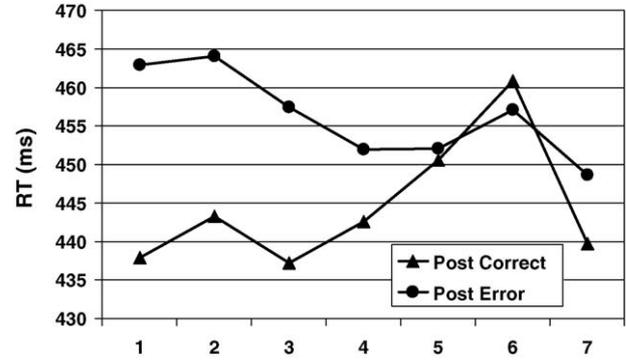


Fig. 2. Changes in post error slowing with time on task (interval 1–6) and with motivation (interval 7), collapsed over stimulus categories.

3.1.2. Post error slowing and immediate corrections

On average, subjects were slower on trials following an erroneous response compared to a correct response (458 versus 445 ms, $F(1,18) = 5.44$, $p < 0.05$). However, this difference disappeared with time on task (Fig. 2, $F(5,90) = 3.06$, $p < 0.05$).

The percentage of immediately corrected responses decreased from 73% in the first interval, to 39% in the sixth interval ($F(5,90) = 5.43$, $p < 0.01$).

3.2. ERPs

3.2.1. Ne/ERN

Ne/ERN amplitude decreased with time on task, (Fig. 3; $F(5,90) = 9.70$, $p < 0.001$) from $-9.5 \mu\text{V}$ in interval 1 to $-3.5 \mu\text{V}$ in interval 6. Ne/ERN latency remained unchanged.

3.2.2. N2

N2 latency and amplitude were significantly greater for invalidly cued stimuli compared to validly cued stimuli (296 ms versus 288 ms, $F(1,18) = 9.18$, $p < 0.01$; $2.6 \mu\text{V}$ versus $1.9 \mu\text{V}$, $F(1,18) = 9.10$, $p < 0.01$). N2 amplitude was greater for incongruent stimuli compared to congruent stimuli ($2.5 \mu\text{V}$ versus $2.0 \mu\text{V}$, $F(1,18) = 7.35$, $p < 0.05$). Importantly, the difference in amplitude between congruent and incongruent trials disappeared with time on task (Fig. 4), $F(5,90) = 6.41$, $p < 0.001$. Specifically, the N2 amplitude in the incongruent

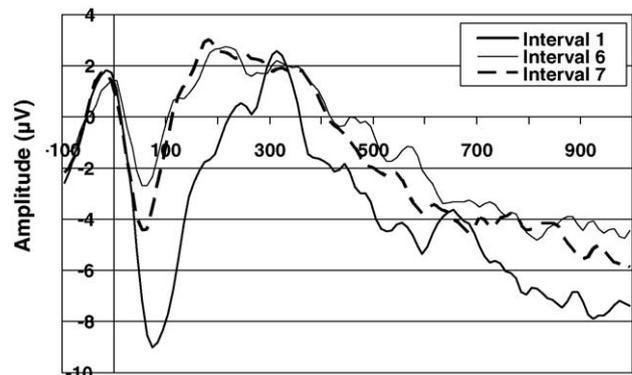


Fig. 3. Ne/ERN amplitude for interval 1 (non-fatigued), interval 6 (fatigued) and interval 7 (fatigued and motivated).

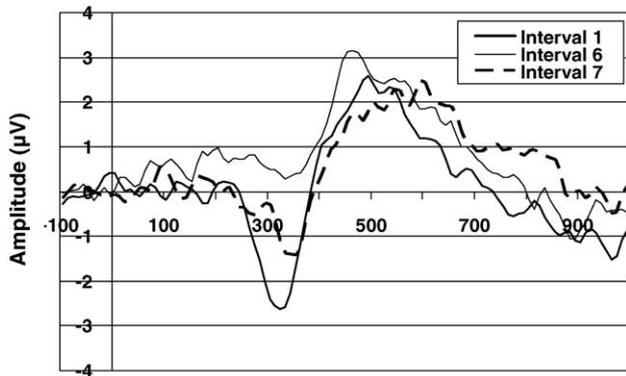


Fig. 4. N2 amplitude (difference waves; incongruent–congruent) for interval 1 (non-fatigued), interval 6 (fatigued) and interval 7 (fatigued and motivated).

conditions was significantly reduced with time on task ($F(5,90) = 7.67$, $p < 0.001$), while the amplitude in the congruent conditions remained the same across time on task intervals ($F(5,90) = 0.095$, ns).

3.2.3. CNV

CNV amplitude was maximal on Cz and decreased with time on task, (Fig. 5; $F(5, 90) = 3.07$, $p < 0.05$), from $-2.6 \mu\text{V}$ in interval 1 to $-1.2 \mu\text{V}$ interval 6.

3.2.4. P3

Amplitude of the P3 component was larger for validly cued trials compared to invalidly cued trials ($13.6 \mu\text{V}$ versus $12.0 \mu\text{V}$), $F(1,18) = 23.03$, $p < 0.001$. Although P3 amplitude did not change with time on task, P3 latency did change. Latency increased from 381 to 399 ms, $F(1,18) = 5.68$, $p < 0.001$. Also, P3 latency was greater for invalidly cued trials compared to validly cued trials (402 ms versus 385 ms), $F(1,18) = 13.31$, $p < 0.005$, and for incongruent stimuli compared to congruent stimuli (400 ms versus 386 ms), $F(1,18) = 29.09$, $p < 0.001$.

3.3. Motivation and individual differences

When comparing the last interval before subjects were motivated (interval 6), and the interval after which subjects were motivated (interval 7), a number of changes can be

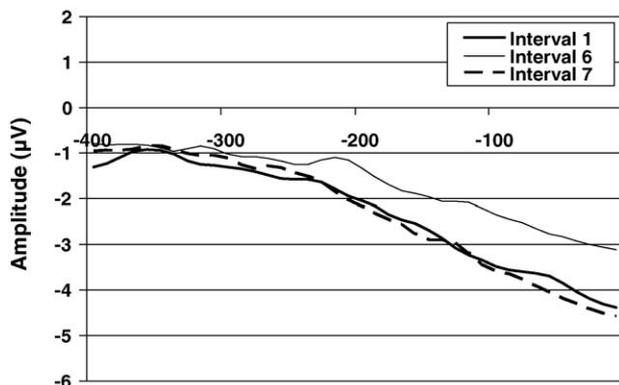


Fig. 5. CNV amplitude for interval 1 (non-fatigued), interval 6 (fatigued) and interval 7 (fatigued and motivated).

observed. Behaviourally, reaction times decrease (Table 1; $F(1,18) = 10.60$, $p < 0.005$), while accuracy remains unaffected (Table 1; $F(1,18) = 0.03$, ns). Interestingly, the post error slowing that had disappeared with time on task in the previous intervals once again emerged (Fig. 2; $F(1,18) = 4.63$, $p < 0.05$). Visual inspection of the ERP averages suggests that this increase in post error slowing was accompanied by an increase in Ne/ERN amplitude (Fig. 3). However this increase was not significant ($F(1,18) = 1.39$, ns). N2 amplitude also did not increase significantly, (Fig. 4; $F(1,18) = 0.18$, ns.). In contrast, CNV amplitude increased to the level of the first interval after motivation, (Fig. 5; $F(1,18) = 8.98$, $p < 0.01$). P3 amplitude also increased after motivation, $F(1,18) = 7.06$, $p < 0.05$, while latency remained unchanged.

Inspection of the data of the individual subjects revealed that subjects did not all react in the same way to the motivational instructions. The instructions stressed accuracy as well as speed. It appeared that subjects never improved their performance on both speed and accuracy. Instead they chose a strategy for themselves in which they focussed on either speed or accuracy. To investigate whether these different strategies were accompanied by different patterns of brain activity, we divided our subjects in to two groups. One group tended to improve most on speed ($n = 10$), the other most on accuracy ($n = 9$). Subjects in the accuracy group increased their response speed to a much lesser extent than subjects in the speed group ($F(1,17) = 3.29$, $p < 0.05$, one-tailed). Moreover, subjects in the accuracy group responded to the motivation with increasing their accuracy, while subjects in the speed group even made more errors than before the motivation (Fig. 6; $F(1,17) = 10.92$, $p < 0.005$, one-tailed).

At the physiological level, the Ne/ERN amplitude is differentially affected by the motivation manipulation, as indicated by the $\text{TOT} \times \text{GROUP}$ interaction, $F(1,17) = 10.32$, $p < 0.005$. As show in Fig. 7, Ne/ERN amplitude increases only for subjects in the accuracy group. The post error slowing seems to follow the same pattern, but the difference between the groups failed to reach significance, $F(1,17) = 0.72$, ns. Likewise, the N2 amplitude showed no difference between groups, $F(1,17) = 1.38$, ns. In contrast, CNV amplitude increased only for subjects in the speed group, $F(1,17) = 9.10$, $p < 0.01$. The effect of motivation on P3 amplitude and latency was not different for the two groups.

4. Discussion

4.1. Mental fatigue and action monitoring

In the following, we will discuss the effects of 2 h of continued task performance on the behavioural and physiological indices of action monitoring. In addition, the relationship between fatigue, motivation and individual differences will be discussed.

Apparent in ERPs associated with erroneous responses, there was a clear Ne/ERN that had its maximum at fronto central scalp positions. This negative deflection was absent in ERPs associated with correct responses. Ne/ERN amplitude

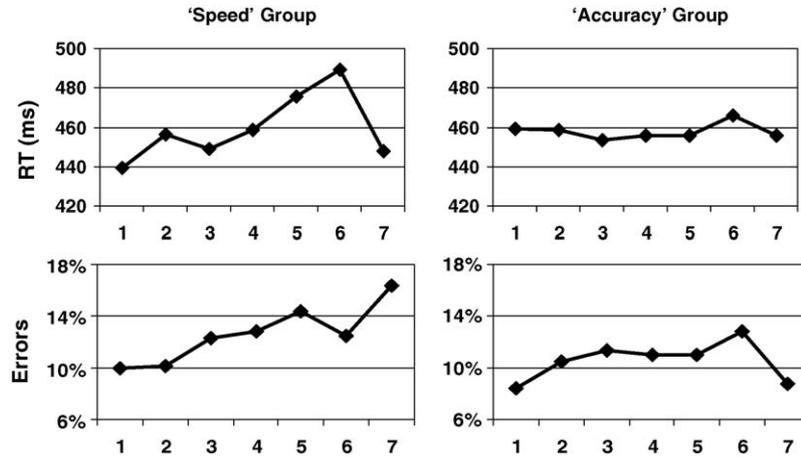


Fig. 6. RT (top panels) and errors (lower panels) for subjects in the 'speed' group (left panels) and the 'accuracy' group (right panels). Subjects in the speed group responded to the motivation with decreased RTs, while subjects in the accuracy group responded with increased accuracy.

was substantially reduced during the 2 h of task performance, indicating that action monitoring is impaired in fatigued subjects (see also Lorist et al., 2005; Scheffers et al., 1999). In addition to reflecting action monitoring, the Ne/ERN also serves to signal the need to initiate performance adjustments after errors (Gehring and Knight, 2000). As a reduction in Ne/ERN amplitude indicates that the cognitive system fails to detect erroneous behaviour, this should have direct consequences for the initiation of remedial actions. Indeed, subjects corrected their incorrect responses less often when they were fatigued. In addition, fatigued subjects no longer slowed down after committing an error. These results suggest that the ability to strategically adjust behaviour after incorrect actions is reduced in fatigued subjects.

This inability to strategically adjust behaviour with mental fatigue is also reflected in the observed decrease in CNV amplitude. Subjects could use the advance information provided by the cue to prepare themselves for the upcoming

stimulus. However, fatigued subjects did not seem to prepare themselves as well for the upcoming trial, resulting in a decrease in response speed and reduced accuracy. This replicates previous findings of Lorist et al. (2000). The validity of the cue influenced the magnitude of the congruency effect. This replicates previous findings: cueing the side of the required response results in an increased congruency effect on validly cued trials (Wascher and Wolber, 2004). This effect of validity however, did not change with time on task.

According to Van Veen and Carter (2002a,b), the N2 reflects the conflict that occurs when an incorrect response is overridden by the correct response. When our subjects were not fatigued, they clearly monitored their actions in terms of detecting the conflict that occurred on incongruent trials. This is reflected by the larger N2 on incongruent compared to congruent trials. On the behavioural level, subjects made more errors on incongruent trials and also RTs were longer on incongruent trials. However, when subjects were fatigued, there

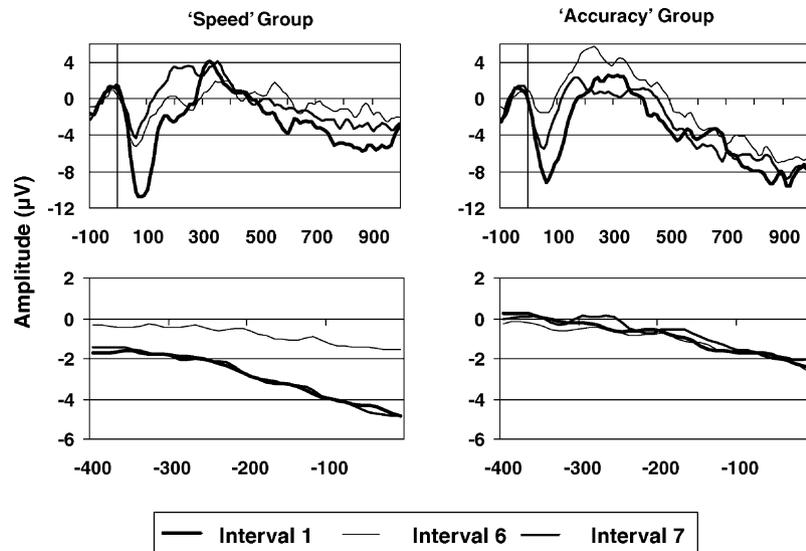


Fig. 7. Ne/ERN (top panels) and CNV (lower panels) for subjects in the 'speed' group (left panels) and the 'accuracy' group (right panels). Subjects in the speed group responded to the motivation with increased CNV amplitude, while subjects in the accuracy group responded with an increase in Ne/ERN amplitude.

no longer was a difference in N2 amplitude between congruent and incongruent trials. More specifically: the N2 amplitude on incongruent trials is reduced to the level of the amplitude observed on congruent trials. So, it seems that the conflict that arises by the activation of the incompatible responses is no longer detected. Various studies using source localization have found that the N2, like the Ne/ERN is generated in the ACC. The decrease in N2 amplitude together with the decrease in Ne/ERN amplitude can thus be viewed as converging evidence that the action monitoring functions of the ACC are negatively affected by mental fatigue.

Remarkable is that, despite the differential effect of mental fatigue on N2 amplitude in congruent and incongruent trials, the congruency effect at the behavioural level remains unaffected. The decrease in N2 amplitude on incongruent trials suggests that subjects no longer detect the conflict that occurs on these trials. This would result in an increased number of errors and/or greater response latencies on incongruent trials specifically, increasing the congruency effect. This is not what we observe in our data. Instead, subjects increased their response latency on all trials (from 457 to 485 ms) when they became fatigued. Studies on the Simon effect have shown that when subjects postpone their response, the difference in response latency between congruent and incongruent stimuli becomes smaller. In the present study, subjects appear to have used these larger response latencies to counteract the effects of reduced conflict detection to keep performance at an acceptable level. Subjects seemed to have switched from a controlled, effortful strategy, requiring the detection of conflict, to a more passive strategy in which they increased their overall response latency. This increase is probably due to the fact that subjects took more time to evaluate the stimuli, before responding. The finding that P3 latency increases when subjects become fatigued corroborates this interpretation. The latency of the P3 component covaries with target detection processes involved in stimulus evaluation and categorization, with the peak of this component indicating the termination of these evaluation processes (Duncan-Johnson, 1981; Duncan-Johnson and Donchin, 1982).

This kind of strategy change when people become fatigued has been observed in other task situations as well. For example Sperandio (1978) showed that air traffic controllers shifted to cognitively less demanding strategies when they had worked under high workload for a considerable period of time. In the present task however, the effectiveness of the strategy change was limited, as the number of errors still increased as subjects became more fatigued.

4.2. *Mental fatigue and motivation*

As already mentioned in the introduction, there is a strong link between fatigue and motivation: fatigue may be considered a lack of motivation or drive to perform. Tops et al. (2004), have argued that fatigue may result from an 'effort/reward imbalance': as long as one feels that the invested effort in the end will result in sufficient rewards, one will continue working. However, when the perceived effort becomes to great

and the reward no longer compares to this, the motivation to continue will dissipate and one will want to disengage from the task, feeling fatigued. When our subjects are motivated after 2 h of task performance by the promise of a financial reward if they perform as well as they possibly can, we observed a number of changes in behaviour and brain activity.

As expected, inspection of the individual data of our subjects revealed that subjects did not all respond to the motivational instructions in the same manner. The instructions stressed both speed and accuracy. Subjects however, almost never improved both their speed and their accuracy. Instead they chose a strategy for themselves to improve their performance, focussing on either speed or accuracy. Subjects that opted for improving their accuracy showed a remarkable increase in Ne/ERN amplitude, while subjects focussing on speed did not show this increase at all. Conversely, subjects who chose to improve their performance speed instead of their accuracy, exhibited an increase in CNV amplitude, while subjects that focussed on accuracy did not. This dissociation in ERP changes between the two groups of subjects reflects the strategy they chose to improve their performance. The subjects who focussed on accuracy responded to the motivation by the improving the monitoring of their actions (indicated by the increased Ne/ERN amplitude), so that they would produce less errors. The subjects who increased their response speed, however, once again prepared themselves better for the upcoming stimulus (reflected by the increase in CNV).

These findings have some important implications for the concept of mental fatigue. It appears that fatigued subjects, when motivated, could once again monitor their actions adequately. However in doing so, they had to sacrifice their response speed. On the other hand, fatigued subjects that were, when motivated, once again able to aptly prepare for the upcoming stimulus and thus increase their response speed appeared unable to monitor their actions in an adequate manner, resulting in increasing numbers of errors. These results suggest that there is a strong motivational component involved in the processes related to mental fatigue. However this is not the whole story: fatigued, but motivated subjects were unable to improve their performance in terms of both speed and accuracy, opting instead to improving on one measure by sacrificing the other. This implies that fatigue is more than an effort/reward imbalance and involves adaptive strategies to keep performance at an acceptable level under adverse internal circumstances.

In one of our recent studies (unpublished data), we obtained additional support for this notion. The design employed in this study was comparable to the present study, only this time subjects were motivated by rewarding accuracy more than speed. The results showed that under these circumstances, all fatigued subjects chose to improve their performance in terms of accuracy and not in terms of speed. This clearly indicates that fatigue indeed involves adaptive strategies that are, at least to some extent, under voluntary control of subjects.

Returning to the present study: post error slowing increased when subjects were motivated. Although there was no significant difference between the two groups, it appears that only subjects who focussed on accuracy slowed down after

making an error. Immediate corrections also follow this pattern: subjects that focussed on accuracy corrected their actions more often when motivated, while subjects who focussed on speed did not. This fits well with the observed increase in Ne/ERN amplitude for these subjects. Because accuracy was most important for these subjects, they monitored their actions better, resulting in more immediate corrections and better strategic adaptation when performance fails in the form of slowing down after having made an error.

Of course, dividing our subjects into two groups results in rather small groups. This results in low statistical power and this is probably the reason that the differences between the groups on corrective behaviour failed to reach significance. Thus, these data should not be taken as hard evidence, but more as suggestive for underlying processes.

The same caution should be taken concerning the N2 results. Although there is no significant difference in N2 amplitude before and after motivation, visual inspection seemed to indicate that N2 amplitude does increase after motivation. No difference between the two groups of subjects were found. This may suggest that Ne/ERN and N2 are differentially affected by motivation, and may not be viewed as being different measures for the same underlying process (Falkenstein et al., 1999). This is corroborated by fMRI studies (Kiehl et al., 2000; Braver et al., 2001; Ullsperger and von Cramon, 2001) that have shown distinct areas of the ACC to be activated by conflict (N2) and errors (Ne/ERN), suggesting potentially dissociable processes.

4.3. A possible mechanism

The finding that there is a relationship between fatigue, motivation/reward and action monitoring (Ne/ERN) may suggest a common neurophysiological mechanism. We suggest that the mechanism underlying mental fatigue may involve a reduction in activity of dopaminergic (DA) projection systems, comprising the basal ganglia (BG) and medial frontal structures such as the ACC (Lorist and Tops, 2003; Lorist et al., 2005; Tops et al., 2004). The BG have long been recognized as a structure of central importance for the motivational aspect of behaviour and reward (Nauta, 1986; Schultz, 2000) and neuro-imaging and ERP studies have suggested that the response monitoring functions of the ACC rely on DA input from the BG (Holroyd and Coles, 2002). According to the theory put forward by Holroyd and Coles (2002), a response monitoring system located in the BG produces error signals that activate the mesencephalic DA system, and the Ne/ERN is elicited by the impact of this phasic DA activity on the ACC (Holroyd and Yeung, 2003). The observation that the reduction of Ne/ERN amplitude when people become fatigued can, at least in part, be undone by increasing the rewards, suggests a role of the DA system in mental fatigue.

Indeed, Chaudhuri and Behan (2000) proposed that the symptoms of mental fatigue reported by their neurological patients may be due to a failure of the DA mediated functions of the BG. Moreover, based on animal studies, Nucleus Accumbens (Nac) DA has been proposed to be central in mental fatigue, by regulating the tendency to expend energy

(Neill and Justice, 1981; Salamone et al., 1999; Szechtman et al., 1994). Salamone et al. (1999) suggested that the Nac may be involved in some kind of effort/reward analyses, setting constraints on energy expenditure such that DA depletion in the NA biases behaviour towards low effort alternatives (Lorist and Tops, 2003). Moreover, Walton et al. (2003) found that rats with lesions to the ACC, preferably selected low cost–low reward response alternatives, while control animals continued to prefer the high cost–high reward alternatives. In the present study, subjects indeed shifted to a lower demanding strategy (increasing response latency, decreasing action monitoring) when they became fatigued. Although DA turnover was obviously not measured in the present experiment, the results do provide a valuable insight in the underlying mechanisms of mental fatigue that have so far remained elusive.

5. Summary

Subjects clearly exhibited impaired action monitoring and response preparation when they became fatigued. The observation that this impairment can be alleviated by increasing rewards, suggest that mental fatigue involves an effort/reward imbalance. Continuous task performance over such a prolonged period of time requires an increase in effort of subjects to keep performance at adequate levels. When the observed rewards become insufficient, subjects disengage from the task, feeling fatigued. When rewards are increased at the end of the task, effort and reward are once again balanced, resulting in better performance. The observation that subjects differed in the way they improved their performance after the motivation, suggests that performance under conditions of mental fatigue involves adaptive strategy changes to keep performance at acceptable levels.

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