

Subtle Effects of Sleepiness on Electrocortical Indices of
Attentional Resources and Performance Monitoring

by

Timothy Ian Murphy

A thesis

presented to the University of Waterloo

in fulfillment of the

thesis requirement for the degree of

Doctor of Philosophy

in

Psychology

Waterloo, Ontario, Canada, 2007

© Timothy Ian Murphy 2007

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

I understand that this thesis may be made electronically available to the public.

Abstract

In this dissertation, the effect of mild sleep deprivation on attentional allocation and performance monitoring was investigated using a variety of event-related potential (ERP) paradigms with ecologically realistic periods of sleep deprivation. Seventeen female young adults completed several tasks under alert and sleepy conditions, after 3 and 20 hours of wakefulness, respectively. Objective behavioural measures of response times and error rates indicated virtually no decrements that could be attributed exclusively to sleepiness; however, there were consistent alterations in the ERPs indicative of subtly reduced attentional resources and performance monitoring.

The first study (Chapter 2) examined the effect of distraction on the P300, an ERP component related to attention and stimulus processing. Participants performed an auditory oddball task with and without a secondary visual working memory task. Response times (RTs) and P300 amplitudes were affected by the addition of the secondary working memory task. However, an interaction showed that the P300 latency was significantly increased by the secondary task only in the sleepy condition, indicating that processing speed is impaired by a secondary task only when the participant is sleepy. The next study (Chapter 3) used a Go/NoGo contingent negative variation (CNV) task. The CNV is reflective of sustained attention, and is known to be associated with frontal lobe functioning. This task was performed twice, with and without a financial incentive for fast responses, to assess the effect of motivation. The P300 amplitude to the first stimulus and CNV prior to the second were clearly larger to Go stimuli for both levels of alertness when the participant was motivated by

the financial incentive. However, with no incentive in the sleepy condition, there was reduced differentiation of the two types of stimuli, indicating a reduced ability to discriminate between important and less important information.

In chapters 4 and 5, performance monitoring was examined using two tasks, the Eriksen Flanker task and the Anti-Saccade task, producing an ERP related to errors with two basic components: the error-negativity (Ne/ERN) and error-positivity (Pe), thought to be related to error recognition and error evaluation, respectively. In both data sets, the amplitude of the Ne/ERN was not significantly reduced by sleep deprivation, but the amplitude of the Pe was. In addition, smaller anti-saccade errors produced reduced Ne/ERN amplitudes compared to larger anti-saccade errors. Another marker of performance monitoring is post-error slowing, which was present in the flanker task only during the alert condition. These results indicate that error detection or recognition (Ne/ERN) appears to be relatively preserved during sleep deprivation, but further error evaluation (Pe) and compensation (post-error slowing) are impaired.

Taken together, the findings demonstrate that even mild sleep deprivation has a subtle but reliable effect on electrocortical activity associated with attention and performance monitoring despite an absence of behavioural changes, indicating deleterious effects before behavioural changes are observed. Therefore, relying on behavioural tests to determine at what point an individual becomes unsafe to operate machinery or perform various tasks may be misleading.

Acknowledgements

There are always many people associated with a project of this size. First and foremost, this work could not have been completed without the guidance, support and patience of my supervisor and good friend Sid Segalowitz. I consider myself exceptionally fortunate to have had the privilege to work with and learn from him for the last 15 years. Equally supportive and important to me even though she was not officially associated with this work was Jane Dywan. They have taught me a great deal, not only in terms of research and academics, but also about the more important things in life. Their consistently optimistic and enthusiastic personalities made this work so much easier and enjoyable. They supported me, stood by me during some of the darkest times in my life, and were always encouraging and available. Sid and Jane have become my academic family and I look forward to many more years of collaboration and friendship with both of them.

I also want to thank Barb Bulman-Fleming. Over the years, I undoubtedly tested her patience but she always remained friendly and supportive and I knew I could count on her anytime I needed advice. I am grateful to my other committee members: Colin Ellard, Dan Smilek and Richard Steffy for their help. In addition, I was lucky to have an unofficial committee of good friends and collaborators from whom I could seek advice and discuss my ideas and findings, and with whom I shared many good times. Hiroaki Masaki, Tricia Pailing, Wilma Veenhof, Melonie Hopkins, Helene Chevalier, James Desjardins, Karen Mathewson, Bill Tays, Gillian Munro, Tomoka Takeuchi and Bob Ogilvie all contributed in various ways over the years to my research and my life was enriched by knowing them. Mary Richard deserves special thanks. She worked with me on this project for over two years, endured many sleepless nights to help collect data, many frustrating days scoring that data and through it all became one of my closest friends.

Lastly, I could not have attained what I have if it were not for my family. My sister Kathy Oakleaf and her husband John who graciously provided me with a place to stay during my time in Waterloo, and especially my parents Lillian and Charles Murphy. They instilled a love of learning, an expectation of achievement and were unstintingly supportive of my academic pursuits. Unfortunately, neither lived to see me complete this degree, but their support and encouragement of my education and therefore contribution to this document is undeniable.

Dedication

The dedication in my master thesis simply read “To my best friend and wife, Wendy”. I still feel the same way but those few words do not truly convey what she means to me. Wendy was the impetus and inspiration for me to return to academics. Wendy and I shared our love of education, our lives and our dreams. We supported and pushed each other in our academic endeavors. In many ways I owe everything I have accomplished and become to her. Wendy was taken from me just as we began our Ph.D. studies, but her memory and love still inspire me. I miss her more than words can express and she was on my mind a great deal during the last few months of this work. A journey we began together, I had to complete alone. I dedicate not only this document, but also my academic career to Wendy, the love of my life.

Table of Contents

CHAPTER 1	1
Introduction to Sleepiness, Performance and Event-Related Potentials	1
Past Research into Problems Caused by Sleepiness	3
Predicting Sleepiness	4
Brain Alterations in Sleepiness: Frontal Lobe Decline?	6
“Core” sleep, the frontal lobes, and behavioural performance	8
How can we look at these issues?	10
Attention, and attentional allocation	10
Frontal lobe functioning	11
Performance monitoring	12
The Current Study	14
CHAPTER 2	16
Attentional Allocation during Sleep Deprivation	16
Method	19
Participants	19
Procedure	20
Instrumentation	20
Tests Administered	21
Results	23
Self-ratings and behavioural performance	23
Electrophysiological results	24
Discussion	28
CHAPTER 3	31
Effects of Sleepiness and Incentive on the P300 and Contingent Negative Variation	31
P300, Attention, Motivation, Salience and Arousal	32
Sleepiness and Frontal Lobe Functioning	33
Contingent Negative Variation (CNV)	33
Go/NoGo CNV task	35
CNV and Arousal	36
CNV and Attention/Motivation	36
P300, the CNV and arousal-attention	38
Rationale of the study	38
Method	40
Results	43
Discussion	51

CHAPTER 4	57
Performance Monitoring and Sleepiness	57
Error Negativity/Error-Related Negativity (Ne/ERN).....	58
Ne/ERN and Lowered Arousal due to Sleepiness or Alcohol Consumption	60
Ne/ERN and Motivation	60
Error Positivity (Pe)	61
Method	62
Discussion.....	67
 CHAPTER 5	 71
Performance Monitoring and Size of Error using an Anti-Saccade Task	71
Error-Related Negativity (Ne/ERN)	72
Error Positivity (Pe)	74
Sleepiness and the Ne/ERN	75
Saccades.....	76
Conscious awareness of errors and the Ne/ERN	76
Size of the error the Ne/ERN	77
Method	79
Results.....	82
Discussion.....	85
 CHAPTER 6	 94
General Discussion	94
Attentional Allocation and Frontal Lobe Functioning.....	95
Performance (Error) Monitoring.....	97
Importance of ERP measures.....	99
Sleepiness and Motivation	99
Limitations.....	100
Practical Applications.....	100
References.....	102
 Appendix A: Health and History Questionnaire.....	120
Appendix B: Screening Questionnaire	122
Appendix C: Circadian Rhythm Questionnaire	123
Appendix D: Circadian Rhythm Questionnaire (Scoring Instructions).....	127
Appendix E: Epworth Sleepiness Scale.....	132
Appendix F: Epworth Sleepiness Scale (Scoring Instructions)	134
Appendix G: Daily Sleep Log	135
Appendix H: Task Instructions	136
Appendix I: Visual Analogue Scales.....	140
Appendix J: Sample Ne/ERN/Pe from one Individual	141

List of Figures

Figure 2.1. Mean response times for alert and sleepy conditions.....	24
Figure 2.2. P300 amplitude of single and dual task by sleepiness condition.	25
Figure 2.3. P300 latency of single and dual task by sleepiness condition.....	26
Figure 2.4 Grand average ERP's showing the four conditions.....	27
Figure 3.1 Subjective Sleepiness (Alertness by Incentive).....	44
Figure 3.2; Mean Response Time by Incentive and Alertness	45
Figure 3.3 Waveforms showing a clear differentiation between the Go and NoGo stimuli during incentive trials..	47
Figure 3.4 Waveforms showing how without the incentive the differentiation between Go and NoGo stimuli is much less clear.	48
Figure 3.5 Amplitude of the P300 to the first stimulus.	49
Figure 3.6 CNV amplitudes of GO trials after Controlling for NoGo Trials	50
Figure 3.7 Difference waves (Go – NoGo) for the CNV.....	51
Figure 4.1: Response-locked EEG averages (Ne/ERN & Pe marked) to correct responses and errors in the Flanker task in both the alert and sleepy conditions.....	66
Figure 4.2: Mean response time for correct trials following correct and error trials following error trials in both alert and sleepy conditions.....	67
Figure 5.1: EOG group averages for correct responses, small and large errors for left and right saccades.....	80
Figure 5.2: Grand-averaged response-locked ERPs for large and small errors.....	85

CHAPTER 1

Introduction to Sleepiness, Performance and Event-Related Potentials

Sleepiness is a fundamental fact of life, and is experienced daily by most people. Prior to the invention of convenient artificial methods of lighting our world, people slept longer (Kleitman, 1963). Unfortunately, mild sleep deprivation (continuous wakefulness of 18-20 hours) has become increasingly common, and individuals are often expected to perform tasks efficiently while sleepy. These tasks are often relatively innocuous and can be performed safely, but some tasks require optimal, or near optimal, attention because of their nature. The potential outcomes of performance failure while operating machinery, driving, or performing medical procedures can be disastrous.

As a person becomes tired and reaches the point at which it becomes increasingly difficult to fight sleepiness, he/she may fall victim to an unexpected sleep onset or lapse in attention (Loh, Lamond, Dorion, Roach, Dawson, 2004). People can often fight the fatigue and regain concentration and ability to function through increased effort, but this effect is typically short lived and has its own costs (Dinges et al., 1997). Is performance under these conditions comparable to that done while fully awake? How does the brain compensate for the decreased ability to perform and what are the costs of these compensations? Motivation can often reverse or mask the effects of sleepiness; but, when sleepy performance is improved by increased motivation so that it is now comparable to alert performance, does the brain show similar patterns of activation as in alert performance?

The majority of previous research has focused on periods of sleep deprivation not

commonly encountered by the majority of people. Wakefulness has been extended to 24, 36, 48, even 72 hours or more in many studies (e.g., van Dongen, Baynard, Maislin, & Dinges, 2004; Drummond, Meloy, Yanagi, Orf, & Brown, 2005; Lieberman, Tharion, Shukitt-Hale, Speckman, & Tulley 2002). The effects of these levels of sleep deprivation on both performance and cognitive function are well noted. Virtually every aspect of human functioning is affected from increased response time (Scott, McNaughton, & Polman, 2006), reductions in motor coordination (Lieberman et al., 2002), eye movements (Bocca, & Denise, 2006), and mood (Lieberman et al., 2002); increased errors (Smith, McEvoy, & Gevins, 2002), or reduced driving (Arnedt, Owens, Crouch, Stahl, & Carskadon, 2005) as well as reduced cognitive efficiency in terms of decision making (Killgore, Balkin, & Wesensten, 2006), learning tasks (Drummond et al., 2005) and increased error rates (Morris & Miller, 1996). There are also significant physiological responses to sleep deprivation such as changes in brain function as indexed by electroencephalogram (EEG), event-related potentials (ERPs) and fMRI. In short, there is nothing positive about sleep deprivation other than perhaps some mixed findings that it may temporarily relieve the symptoms of depression (Wu et al., 1999).

The minimum threshold of 24 hours implicitly used by several researchers to denote sleep deprivation is likely used because it represents one day and makes a useful unit that people can relate to. However, the pronounced effects observed after 24-60 hours of wakefulness likely have their beginnings much earlier. In fact, virtually everyone has been in the situation of attempting to work after 18-20 hours of wakefulness and had the subjective

experience of being able to function adequately, yet knowing that it was more difficult, or being accomplished in a different manner than usual. It is because working after 18 to 20 hours of wakefulness has become increasingly commonplace that this time-frame for mild sleep deprivation was chosen.

Past Research into Problems Caused by Sleepiness

Sleepiness has often been studied as it relates to vehicle operation (e.g., Pack, Cucchiara, Schwab, Rodgman, & Pack, 1994) or industrial accidents (see Akerstedt, 1991 for a review). Akerstedt, using continuous ambulatory EEG monitoring in a variety of settings, has shown that serious bouts of fatigue and even inadvertent sleep at work is not an uncommon occurrence among shift workers (see Folkard & Akerstedt, 1991).

Accidents related to (if not caused by) sleepiness are very costly in terms of lives and dollars. Leger (1994) estimates that in the United States, between 43 and 56 billion dollars were lost in 1988 as a result of sleep-related accidents of all types (vehicular, industrial, home). Leger (1994) points out that the actual number of accidents which can be directly linked to sleepiness is difficult to assess. However, 41.6% of vehicular accidents (769,184 serious injuries) and 36.1% of fatalities (17,689 deaths) occurred during the times when sleepiness would be at its highest level due to circadian and environmental factors (Leger, 1994). Leger (1994) also produced similar statistics for work-related accidents (5,565 deaths, 945,000 disabling accidents), and home-related accidents (2,346 deaths, 408,762 disabling accidents).

These figures have been criticized (Webb, 1995) because they are based on numbers

of accidents occurring during known times of increased sleepiness, not actual data in which the accidents were shown to be sleep related. Webb cites more conservative estimates of sleep-related accidents (under 2%). However, many states do not have consistent or reliable methods for investigators to indicate sleepiness or inadvertent sleep onset as the cause of an accident (Pack, Willis, & Pack, 1995) so the official estimates like those quoted by Webb (1995) are, in all likelihood, too low (McCartt, Pack, Walsleben, Hammer, & Pack, 1995). The true values undoubtedly lie somewhere between Leger's (1994) and Webb's (1995) estimates, but the problem of sleepiness in potentially dangerous situations is obvious.

The problem of sleepiness has also been associated with some of the world's most notable modern disasters. Sleepiness has been cited as a contributing factor in the disasters associated with Chernobyl, Exxon Valdez, Challenger, Three Mile Island, and Bhopal (Mittler, Carskadon, Czeisler, Dement, Dinges, & Graeber, 1988). Attempting to perform tasks while sleepy can have profound implications, not only for the individuals performing the task but the (sometimes thousands) of people affected by their actions. A better understanding of the changes our brains undergo as we become sleepy may someday help researchers identify people who are dangerously sleepy or the point at which the natural process of sleep onset overpowers any intent to remain awake. The research in the present study is to designed better understand the effect of sleepiness on attention and performance-related processes in the brain.

Predicting Sleepiness

Many researchers have attempted (with good success) to predict the probability of

sleep onset in various situations (Webb, 1994; Akerstedt & Folkard, 1994). Akerstedt and Folkard (1994) and Webb (1994) have developed three-process models based on the two-factor Borbely-Daan model (Daan, Beersma, & Borbely, 1984). The initial two-factor model (Daan et al., 1984) used the circadian tendency (process C) and sleep demand (process S) to estimate sleepiness or sleep tendency.

Akerstedt and Folkard (1994) added the influence of sleep inertia (the time required to attain full arousal after awakening) as their third factor. Using this model they can account for 88% of the variance in sleep onset latencies. Although 88% is a very large amount of variance to be able to predict, these types of studies are based on 24-hour periods, a time spread during which there is considerable variance. Despite the amount of variance which can be accounted for by these models in predicting sleep onset latency, they are still inadequate when attempting to predict sleep onset on a moment to moment basis. The likelihood of sudden sleep onset, or performance failure is dependent on other factors.

The third factor used in Webb's model (1994) deals with behavioural facilitation or inhibition. The behavioural component in this model consists of such variables as body position, current activity, noise, intention, etc. He points out, however, that these behavioural factors cannot easily be quantified and added to the equation containing the sleep demand and circadian variables. One variable that could play a critical role in alertness is motivation. However, one counterintuitive fact about human endurance and performance is that even with high motivation, concentration, and effort, humans will still begin to show deterioration in performance as the length of time awake increases, even in life-threatening

situations. A common and familiar example of this is driving late at night. The motivation to drive safely should be high (failure to do so could result in death), concentration may be high (much mental effort is being used to remain awake) and effort to maintain arousal may be high (windows rolled down, driver singing along with the radio) but yet performance may quickly deteriorate (Horne & Pettitt, 1985). The car may drift over the centre line or off the shoulder. These lapses occur despite the driver's best intentions and under some conditions after a surprisingly short length of time awake (Reyner & Horne, 1997). Therefore, any thorough evaluation of brain function and performance while sleepy must contain a motivation manipulation to assess its effect.

Brain Alterations in Sleepiness: Frontal Lobe Decline?

What are the characteristics of our brains or brain function that change as we become sleepy, and what processes and changes are required to maintain or regain concentration and the ability to perform once again despite the fatigue? With sufficient attention and arousal, adequate performance, or ability, will follow naturally. Of course, all this is predicated on an acceptable level of motivation; however, if one is fighting to retain good performance at whatever task is being attempted then some motivation must, by definition, be present or performance would deteriorate at the first signs of fatigue and sleep would soon follow. Drummond and colleagues (1999, 2000, 2001, 2005) have shown that while performing various tasks during sleep deprivation, humans demonstrate (or undergo) dynamic changes in brain function. Blood flow to various areas of the frontal lobes, as measured by fMRI, increases in some areas and decreases in others; however, the specific areas of activation and

deactivation vary by task. Drummond has interpreted these differential alterations in blood flow as indications of declines in cognitive functions and compensation. Despite varying results across several studies, we can conclude that there are losses in specific subregions in sleep deprivation rather than a global reduction in activation.

Alterations in frontal lobe functioning have also been demonstrated using EEG (Cajochen, Foy, & Dijk, 1999). Calochen and colleagues found an increase in the delta and theta activity at frontal scalp sites (measured at Fz and Cz) compared to more posterior areas (Pz and Oz) after 16-40 hours of wakefulness and have concluded that some aspects of sleep onset may be quite local. Thomas et al. (2000) found that metabolic rate decreased throughout the brain after 24 hours of wakefulness but noted specifically that there were reductions in the activity in the anterior cingulate, lateral posterior parietal cortices, prefrontal cortices and thalamus. They found no areas where metabolic rate increased. These findings stand in contrast to those of Drummond (1999, 2000, 2001, 2005), but were attributed to the potential confounds due to differences task difficulty, task duration and techniques for measuring metabolic rate among the studies. Gosselin, De Koninck and Campbell (2005) have also shown reductions in the amplitude of the P3a, measured at Fz, using a novelty P3 paradigm. The novelty P3 has been shown in the past to be related to frontal lobe functioning (Knight, 1984).

Thus, frontal lobe function has been shown to be affected by sleep loss across a variety of paradigms and measurement techniques. Several studies in the past have made claims involving the importance of the frontal lobes for a variety of tasks including those

requiring divided attention, executive function(s), inhibition, planning, working memory etc. (Fuster, 1999). Therefore, if frontal lobe decline observed in sleepiness after 24+ hours awake causes reductions in an individual's ability to perform tasks requiring these higher order cognitive functions, when does this effect begin? Decrements in brain function associated with these cognitive functions very likely begin well before the 24-hour threshold employed by most studies, but it is not easily observed in behavioural tasks.

“Core” sleep, the frontal lobes, and behavioural performance

Horne (1991) has postulated that sleep can be divided into two basic types: core and optional. The pre-frontal cortex is the most metabolically active area of the brain during wakefulness and shows the largest decrease in metabolic rate after one full night of sleep loss (Horne, 1993). The frontal lobes also show the highest amount of delta (slow wave or deep) sleep during the early portions of the night or after sleep deprivation (Cajochen, et al., 1999). Hence, Horne argues that the first 4 cycles of sleep (approximately 6 hours) represent required “core” sleep for cerebral recovery, while any additional sleep is “optional” and can be reduced or eliminated without significant impairment. Because the frontal lobes appear to be the most active during wakefulness and therefore in the greatest need of rest during sleep, sleep deprivation should affect these areas most. However, some research has shown that the behavioural effects of sleep deprivation may not become evident until long after most people would become sleepy (Jones & Harrison, 2001).

Some researchers have claimed that moderate sleep deprivation (under 36 hours) does not impair “higher cortical functioning” (Binks, Waters, & Hurry, 1999) or “frontal”

measures (Jones & Harrison, 2001). Binks et al. (1999) found no differences in WAIS-R I.Q., PASAT, WCST or word fluency between a group which had been sleep-deprived for 36 hours and controls, even though there were significant differences in subjective sleepiness. Jones and Harrison (2001), incorporating the results from a series of studies, claims that behavioural tests of frontal lobe functioning (WCST, divergent thinking, word fluency, complicated business games, etc.) do not show significant decrements for the first 36 hours of wakefulness. Nilsson et al., (2005) reported that individuals subjected to 32 hours of wakefulness awake, performed more poorly than a rested control group on the Six Elements Test (a test of executive function); however, there were no group differences on other tasks involving working memory or psychomotor vigilance.

However, these researchers have used behavioural data and, in the case of Binks et al. (1999) and Horne's and colleagues series of experiments (see Jones & Harrison, 2001), undergraduate populations with mean ages of under 23. Perhaps for these samples of young undergraduates, their relative youth and cognitive flexibility enabled them to delay and/or compensate for the effect of sleep loss. In even a slightly older, more diverse population the effects may manifest themselves earlier. Also, even though behavioural performance of the sleep-deprived subjects in these studies may have been largely maintained, the effort expended may have been much greater. These studies had no electrophysiological measurements. With measures such as EEG and averaging techniques such as ERPs, which are more sensitive to process rather than outcome, any difference in mental effort may be documented.

In a paper reviewing the literature on sleep deprivation and decision making, Harrison and Horne (2000) reiterate that the majority of studies employ relatively simple functions that require a long testing session in order to induce monotony before effects are observed. They also point out that higher-level decision-making processes that involve innovation, distraction, and unexpected events do suffer after relatively moderate levels of sleep deprivation. Harrison and Horne (2000) cite studies wherein participants, when placed in more realistic settings or given more complicated or distracting tasks showed decrements in performance, even when performing at baseline on simpler tasks. However, once again, virtually all the studies cited used periods of sleep deprivation that exceeded 24 hours.

How can we look at these issues?

How can these issues of sleepiness, performance, and brain function be evaluated? A logical comparison would be between conditions of alertness and mild sleep deprivation (<24 hours) involving a wide variety of tasks that have been demonstrated to assess the constructs of interest. Attentional allocation, frontal lobe functioning, performance (error) monitoring as well as behaviour measures must be compared. In addition, because variations in motivation and effort will affect performance and brain function, these must be assessed. I will briefly describe the measures used and the rationale of a series of analyses here. Additional details will follow in each specific chapter relating to the various tasks.

Attention, and attentional allocation

One of the most often used event-related potentials related to attention is the P300.

The amplitude of the P300 has been shown to be positively related to task difficulty, effort, and negatively related to distraction (see Polich & Criado, 2006 for a review). The P300 can be broken down into a P3a and P3b. The P3a is associated with novelty processing and is typically measured at Fz whereas the P3b is maximal over Pz and is thought to be related to memory updating (see Polich & Criado, 2006). In this thesis the P300 referred to is the P3b, which is maximal over the parietal area and thought to be related to attention allocation and memory updating (Donchin, 1981). The P300 produced by standard oddball paradigm has been repeatedly shown to be reduced in amplitude during sleep onset (Cote, De Lugt, & Campbell, 2002; Ogilvie, Simons, Kuderian, MacDonald, & Rustenburg, 1991) or during sleep deprivation (Corsi-Cabrera, Arce, Del Rio-Portilla, Perez-Garci, & Guevara, 1999) and the novelty P3 is also reduced after sleep deprivation (Gosselin et al. 2005). The amplitude of the P300 is also reduced by a dual task (Nash & Fernandez, 1996); however, these conditions have not been studied together, so it is uncertain what the effect of distracting tasks are on the P300 during sleep deprivation. As Harrison and Horne (2000) pointed out, unexpected or distracting tasks appear to be particularly affected by sleep deprivation behaviourally, so an investigation of the ERP most commonly associated with attention under a dual-task situation seems warranted.

Frontal lobe functioning

The Contingent Negative Variation (CNV) (Walter, Cooper, Aldridge, McCallum, & Winter, 1964) is an ERP that has been shown to be related to frontal lobe functioning (Basile,

Brunder, Tarkka & Papanicolaou, 1997). It has been shown to correlate with behavioural measures related to frontal lobe functioning such as the Wisconsin Card Sorting Task (Segalowitz et al., 1992a; Segalowitz et al., 1992b; Dywan, et al., 1994). The CNV has also been shown to be sensitive to effort. Increasing the effort or motivation during a CNV task will also increase the amplitude of the CNV (Davies & Segalowitz, 2000). Horne and colleagues have shown that many behavioural tasks that require frontal lobe involvement due to their complexity (business games, etc.) can be performed at baseline levels even after 36 hours of sleep deprivation if the participant is motivated. Therefore, employing the CNV, an electrophysiological correlate of frontal lobe functioning, will allow assessment of frontal lobe activity. Previous research has shown that the amplitude of the CNV decreases after sleep deprivation. However, when a reward manipulation to increase motivation and effort is then added, behavioural performance improves and CNV amplitude increases. We can ask whether this manipulation will compensate for the effects of sleep deprivation.

Performance monitoring

Actual performance on a task is important, but perhaps an even more important feature is performance monitoring. Recognizing inadequate performance or errors is an important step in improving performance. One method of assessing performance monitoring that has been developed is the error negativity (Ne) (Falkenstein, Hohnsbein, Hootmann, & Blanke, 1991) or error-related negativity (ERN) (Gehring, Goss, Coles, Meyer, & Donchin,

1993)¹. The Ne/ERN is a negative deflection in the ongoing EEG that is typically observed approximately 80 msec after an error. This ERP has been shown to be related to error detection and is generated by the anterior cingulate cortex (ACC). Following sleep deprivation, the ACC has been shown to have a reduced metabolic rate (Thomas et al., 2000). It has also been proposed that the Ne/ERN is actually a reflection of response conflict (van Veen & Carter, 2002), but recent research has cast doubt on this theory (Masaki & Segalowitz, 2004).

Following the Ne/ERN is the error positivity (Pe) (Falkenstein, 2004). This component occurs approximately 200-400 msec after an error and is theorized to reflect further (possibly emotional) evaluation of the error (Falkenstein, 2004). The topology (maximal over Pz) and timing of the Pe have led some to speculate that the Pe may be a P3b related to the error detection (Davies, Segalowitz, Dywan, & Pailing, 2001). There is even some research to suggest that the Pe may be related to conscious recognition of the error (Nieuwenhuis, Ridderinkhof, Blom, Band, & Kok, 2001).

The Ne/ERN (Scheffers, Humpfrey, Stanny, Kramer, & Coles, 1999); Tsai, Young, Hsieh, & Lee, 2005) and the Pe (Tsai et al., 2005) have been shown to be reduced by 24-28 hours of sleep deprivation; however, no research has been done after 18-20 hours of sleep deprivation. As in the vast majority of previous research, sleep deprivation of over 24 hours was employed in these studies. However, no detailed, electrophysiological work has been

¹ The Error-Related Negativity (ERN) (Gehring, Goss, Coles, Meyer, & Donchin, 1993) and Error Negativity (Ne) (Falkenstein et al., 2000) refer to the same phenomenon. The two terminologies arose from essentially identical research carried out in North America (ERN) and Europe (Ne) during the early 1990's. In this paper we will use the term Ne/ERN, but Ne or ERN would have been equally appropriate.

done on more realistic levels of sleepiness (18-22 hours awake) despite the fact that only a select, relative small subset of individuals is typically required to perform after more than 24 hours of wakefulness. Therefore, an examination of the effect of mild sleep deprivation on these measures of performance (error) monitoring would be of value.

The Current Study

To address the issues discussed above, this thesis research employs several standard, well established ERP paradigms to assess these various indices of brain function in both alert and sleepy conditions. These tasks, the exact protocols, and more detailed justification will follow in the next four chapters. Chapter two describes the analysis of a standard oddball paradigm to elicit a P300. This was done with and without a distracting second task to examine the effect of distraction. In Chapter three, a Go/NoGo CNV task was used, with and without an incentive manipulation to determine the effects of motivation and stimulus discrimination. The experiments described in chapters four and five employ two tasks designed to produce Ne/ERN/Pe responses. In Chapter four, a standard Eriksen Flanker (Eriksen & Eriksen, 1974) was used, and in Chapter five an anti-saccade task was employed. The Eriksen Flanker produces the standard Ne/ERN/Pe whereas the anti-saccade task also allowed for the assessment of degree (size) of error to be evaluated. In all these tasks it is expected that behavioural performance, as measured by response time and error rate, will not significantly differ between the conditions. This is an important aspect because it allows the examination of changes in the ERP due to sleepiness without the confound of altered

behaviour.

In all studies, subjective measures of sleepiness, effort and performance were taken. The sleepiness measure was taken to both confirm that the sleep-deprivation manipulation was effective and measure the subjective degree of sleepiness. It could be argued that reductions in performance or changes in any ERP components during sleepiness are actually due to reduced effort. Therefore, effort and performance measures were taken to determine if effort was maintained during sleepiness and if subjective performance was affected.

CHAPTER 2

Attentional Allocation during Sleep Deprivation

The effects of sleepiness on both cognitive and behavioural mechanisms have been well studied and it has been found that people do not function at their maximum potential when they lack sleep. Sleep deprivation typically results in an increase in response time, a decrease in concentration level, impaired motor responses, and poorer performance on memory tasks (Cote, 2002; Drummond, et al. , 2000). This is demonstrated by an increase in errors and completion time on visual and auditory tests and an overall decline in performance of these tasks, which suggests serious repercussions for those required to work or perform complex tasks after prolonged periods of wakefulness. However, many of the past studies expose subjects to unrealistically large amounts of sleep deprivation. Therefore, more moderate levels of sleepiness should be examined to determine behavioural and electrophysiological responses that are likely to be encountered in everyday life.

Distraction or multi-tasking can also negatively affect an individual's performance. When people are required to complete two tasks simultaneously, they finish with more difficulty than those who are asked to complete a single task (Jolicoeur and Dell'Acqua, 1999 ; Shucard, Abara, McCabe, Benedict, & Shucard, 2004). Garcia-Larrea, Perchet, Perrin, and Amenedo (2001) observed subjects completing a visual task while talking on a cell phone. These participants had a significantly longer response times when their attention was divided.

In addition to behavioural measures taken during sleep and attention deprived states, there are electrophysiological measures that can be used to examine neurological changes that occur. One specific method is to examine event-related potentials (ERPs). ERPs are taken by averaging the ongoing EEG, time-locked to either a stimulus or. ERPs are sensitive to psychological aspects of the events, as well as physiological aspects of the individual being tested (Polich & Criado, 2006). One component of an ERP elicited by novel or rare stimuli is the P300. The P300 is a late, positive deflection in averaged EEG that occurs approximately 300 ms after presentation of a stimulus, and is one of most commonly studied ERP components. It is thought to represent the higher cognitive functions of information processing, working memory, or stimulus categorization (Verleger, Jaskowski, & Washer, 2005). One of the most common and effective paradigms to elicit a P300 is the auditory oddball task. In this paradigm participants must respond to rare, or less frequent tones, which occur on approximately 20 percent of the trials.

Changes in both the amplitude and the latency of P300 have been observed during periods of sleep deprivation (e.g. Corsi-Cabrera et al., 1999) and attentional impairments (Polich & Criado, 2006). ERPs recorded during both distracted and sleep-deprived states indicate that an individual's cortical responses to this task are impaired during these altered states. The examination of the P300 after long periods of sleep deprivation shows a decrease in amplitude, indicating an interference in cognitive functioning (Campbell & Colrain, 2002; Lee, et al., 2004; Muller-Gass & Campbell, 2002; Shucard et al., 2004).

Similarly, when participants must simultaneously complete an additional, distracting task, the P300 amplitude decreases. Ramirez, Bomba, Singhal and Fowler (2005) found that the addition of a secondary visual task decreased the amplitude and increased the latency of the auditory P300. P300 latency is also affected by both sleep deprivation and attentional lapses. When a person is subjected to sleep deprivation, the cognitive processing has been shown to be delayed (Lee, Kim, & Suh, 2003). Lee et al. (2003, 2004) found that the P300 latency to an auditory, single task was increased by approximately 30 ms after 24 hours of sleep deprivation. Similarly, decreased attentional resources can cause an increase in P300 latency. Shucard et al. (2004) revealed that participants had a later-occurring P300 when they performed an auditory dual task. Furthermore, an even greater increase to latency was detected when the target sound was degraded, suggesting the more difficult the task is, the larger the effect on cognitive performance.

Similar physiological research using functional magnetic resonance imaging (fMRI) has also shown impairments in cognitive processing during sleep deprivation. The fMRI indicates levels of brain activity through measurement of blood flow and hence metabolic rate in various areas of the brain. Significant changes in metabolic rate in frontal regions of the brain during the sleep-onset period have been noted in previous research (Drummond & Brown, 2001). Drummond et al. (1999) examined participants' brain blood flow as they completed a serial arithmetic task and found that there was a significant decrease in frontal and parietal lobes after sleep deprivation. This indicates that as a person gets tired, there is reduced brain activity, especially in higher-order functioning frontal areas, confirming that

cognitive processing is impaired by sleep deprivation. Behavioural reactions were also impaired, as subjects' overall level of correct responses also significantly decreased when they were sleepy.

Although both behavioural and cognitive deficits have been noted during sleep-deprived and distracted states, it may be that similar effects are the result of two relatively separate mechanisms. It is quite clear from past research that low levels of both arousal and attention cause impairments to normal cognitive and behavioural functioning; however, the combined effect has not yet been examined. Since both divided attention and sleep deprivation have an effect on cognition, the hypothesis is that there will be an interaction effect of distraction and sleep deprivation that will cause a further decrease in amplitude and increase in latency of the P300 that is greater than the cumulative effect.

Method

Participants

Seventeen females (aged 19-45, $M=26$, $SD=7$) were recruited through the use of advertising at Brock University. They were free of previous head injury, serious sleep disorders, excessive daytime sleepiness, neurological problems, and medications, which may affect alertness (all measured by questionnaire and interview, see appendices A and B). They scored in the mid-range on the morningness/eveningness scale (Horne & Ostberg, 1976, appendices C and D) as well as a modified version of the Epworth Sleepiness Scale (ESS) (John, 1991; see appendices E and F) and had typical sleep patterns, defined as a

typical bedtime of 22:00-0:00 and a rising time of 6:00-8:00. Participants completing the entire protocol were paid an honorarium for their participation.

Procedure

Participants were given a sleep log to complete for two weeks to assess their typical sleep and activity patterns, as well as food, caffeine and alcohol intake (see appendix G). Participants were instructed not to use alcohol or caffeine the night before or day of testing, to sleep 7-8 hours the night before testing, awaken at their normal time and not nap the day of testing. The procedure took place during three separate sessions. The first session was to explain the procedures that were to take place. Participants were familiarized with the equipment and given abbreviated versions of each test, but no EEG was recorded. The purpose of this session was to diminish arousing effects of the situation or tests being administered. The next two sessions involved identical procedures, but one was completed in an alert state, typically began 2-3 hours after participants would wake up (9am-10am) whereas the other was completed in a sleepy state, and typically began 2-3 hours after normal bedtime (2am-3am). Sessions were counterbalanced across participants.

Instrumentation

Participants were required to arrive at the lab one hour prior to testing. Forty-four electrodes were then applied using an electrode cap (Electro-Cap International, Inc.). Electrodes were also placed on each earlobe, as well as the outer cantus and supraorbital ridge of the right eye. All EEG electrodes, as well as the left ear, were referenced to the right

ear, and a mastoid electrode served as ground. Bipolar EOG (outer canthus-supraorbital ridge) was recorded to monitor eye movements and blinks. All electrodes' impedances were maintained below 5 kΩ. EEG and EOG data were converted from analogue to digital signals with a window of 12-bit resolution using a frequency of 256 Hz, and a band-pass frequency of .1 to .30 Hz with the exception of the Flanker Task (Chapter 4) for which the sampling rate was 512 Hz with a band-pass frequency of .1 to 100 Hz. The EEG signals were amplified at a gain of 10,000 using a Sensorium, Inc. amplifier system. INSTEP (a commercial data-acquisition program) was used to present and record data.

Tests Administered

A total of 14 tasks, requiring approximately 2 hours of testing, were administered (see appendix H); however, only the results associated with the two tests pertaining to this chapter are discussed here. These were the second and fifth tasks done within the test battery and described below. Therefore, they were performed after approximately 3 and 21 hours of wakefulness, respectively. Other results will be reported in subsequent chapters.

Auditory Oddball (P300) Task.

A standard (easy) oddball consisting of 40 targets and 160 non-targets was used. The target tones were 800 Hz tone and the non target tones 1000 Hz. All tones were 100 ms in duration with a rise/fall time of 5ms. The ISI varied between 1.3 and 1.6 seconds (mean 1.45 seconds). Participants were required to press the space bar each time they detected a target tone.

Dual Tasks.

The dual task was simply the combination of the same auditory oddball task described above with a visual working memory task performed simultaneously. In the working memory task, the participant was presented with a series of numbers presented sequentially on the computer screen and was required to respond with the left hand each time three consecutive odd (e.g. 2, 3, 5, 1 respond), increasing (e.g. 3, 2, 3, 4 respond) or decreasing (e.g., 4, 7, 6, 5, respond) numbers appeared.

ERP averaging and scoring.

The effects of eye movements and blink artifacts were corrected for using a regression procedure that displays the residual scalp ERP with the eye-channel signal removed on a trial-to-trial basis. This procedure permits manual rejection of the trial in the rare case when there is overcorrection. This method thus reduces noise introduced by overcorrection that is occasionally found in automated eye-correction procedures.

Subjective Measures.

Visual analogue scales were used to measure subjective sleepiness, effort and performance (see Appendix I). These scales consist of a 10cm line with opposing descriptors of the attribute being measured at either end. Participants were asked to rate themselves along each continuum. The following measures were taken: Visual Analog Sleepiness Scale (Very Alert/Very Sleepy); Visual Analogue Performance Scale (Very Poorly/Very Well); Visual Analogue Effort Scale (No Effort/Maximum Effort). In addition, after the Flanker Task, participants were asked to estimate the number of errors they had made.

Results

Self-ratings and behavioural performance

A series of two (alert/sleepy) by two (single/dual task) within-subjects analyses of variance (ANOVA) were conducted to examine the visual analogue scales (subjective rating of sleepiness, effort, and performance).

Analysis of the visual analogue scales revealed that participants rated themselves significantly less alert in the sleepy condition ($F(1,12)=17.7, p=.001$) for both the oddball task ($M=20.2, SD=9.6$) and the dual task ($M=29.8, SD=27.6$), as compared to the oddball ($M=52.9, SD=26.3$) and dual task ($M=56.4, SD=28.9$) in the alert condition. There was no significant arousal difference found in relation to task ($F(1,12)=1.77, p=.21$). These results confirm that the participants were indeed more tired in the sleep-deprived state. Participants' subjective effort was significantly higher for the dual task ($F(1,12)=31.2, p<.001$) in both the alert ($M=81.08, SD=14.86$) and sleepy condition ($M=83.46, SD=12.21$) than for the single task in the alert ($M=47.62, SD=31.17$) and sleep-deprived states ($M=50.31, SD=25.14$). There was no significant difference in individuals' effort level as a function of sleepiness ($F(1,12)=.26, p=.62$).

Similarly, subjects rated themselves as performing significantly worse on the dual-task in both the alert ($M=45.0, SD=31.6$) and sleepy ($M=36.62, SD=25.9$) conditions, as compared to the oddball alert ($M=70.7, SD=28.6$) ($F(1,12)=44.34, p<.001$). Again, no significant difference was found for alertness level upon subjective performance ($F(1,12)=1.92, p=.191$). The results for reaction times indicate no significant effect for

arousal ($F(1,16)=1.51, p=.24$). Participants reacted similarly to a single task whether they were sleepy ($M=356.5, SD=48.4$) or alert ($M=376.8, SD=82.3$) as well as in the dual task whether sleepy ($M=585.6, SD=126.8$) or alert ($M=599.9, SD=120.5$). No interaction effect was found ($F(1,16)=.056, p=.816$). However, there was a large effect of attention on response times ($F(1,16)=114.2, p<.001$). Mean response times for the dual task were 226.28 (SE=21.2) ms longer than in the single condition (see Figure 2.1). This suggests that distractions cause a significant delay in response time, regardless of whether a person is sleepy or alert.

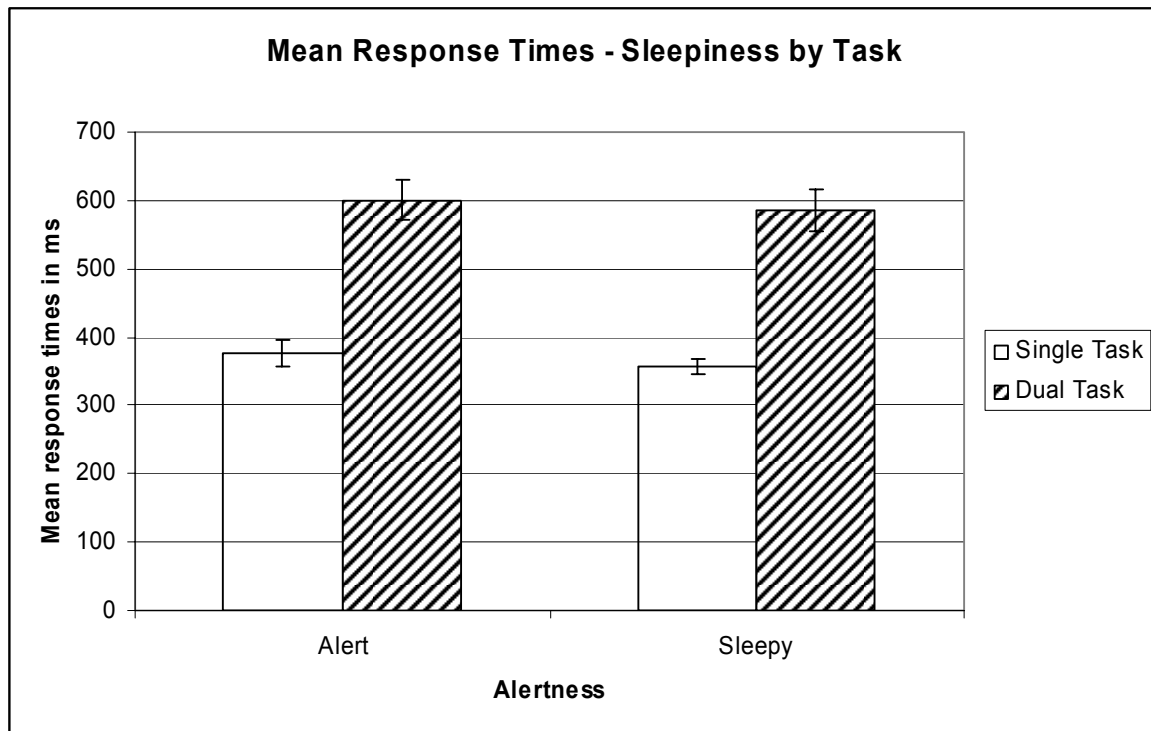


Figure 2.1. Mean response times for alert and sleepy conditions.

Electrophysiological results

In regards to the P300 component, amplitude was significantly decreased for the dual task ($F(1,16)=47.3, p<.001$), whether participants were alert ($M=7.7, SD=3.4$) or sleepy ($M=7.3, SD=5.6$), as compared to the single task performed in the alert ($M=12.4, SD=4.4$) and sleep-deprived condition ($M=12.5, SD=5.4$). There was no significant difference in P300 amplitude as a result of sleep deprivation ($F(1,16)=.04, p=.85$) and no interaction effect for alertness and attention was found ($F(1,16)=.09, p=.76$). (see Figure 2.2)

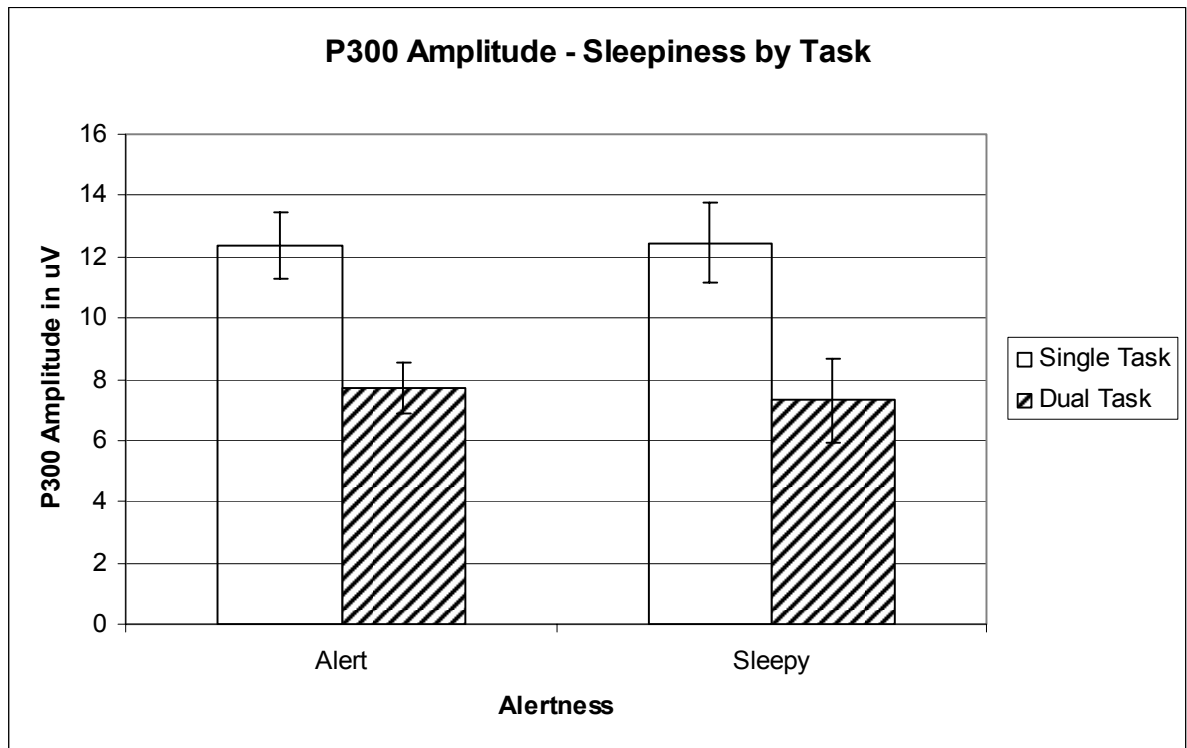


Figure 2.2. P300 amplitude of single and dual task by sleepiness condition.

Although alertness effects on P300 latency also fell short of significance for the alertness condition ($F(1,16)=3.28, p=.09$), they were in the expected direction. However, latency was found to be significantly prolonged in the distraction condition ($F(1,16)=7.66,$

$p=.01$). Furthermore, an interaction effect was found for P300 latency ($F(1,16)=9.77, p=.007$), indicating that cognitive processing was delayed the most when participants were both sleepy and had their attention divided (see Figures 2.3 and 2.4). These results indicate that when the participant was sleepy the P300 latency was affected by levels of attention. The P300 latency associated with the single and dual-task when alert and the single task when sleepy did not significantly differ. However, the combined effect of sleep deprivation and attentional distraction did increase the P300 latency (see Figure 2.3).

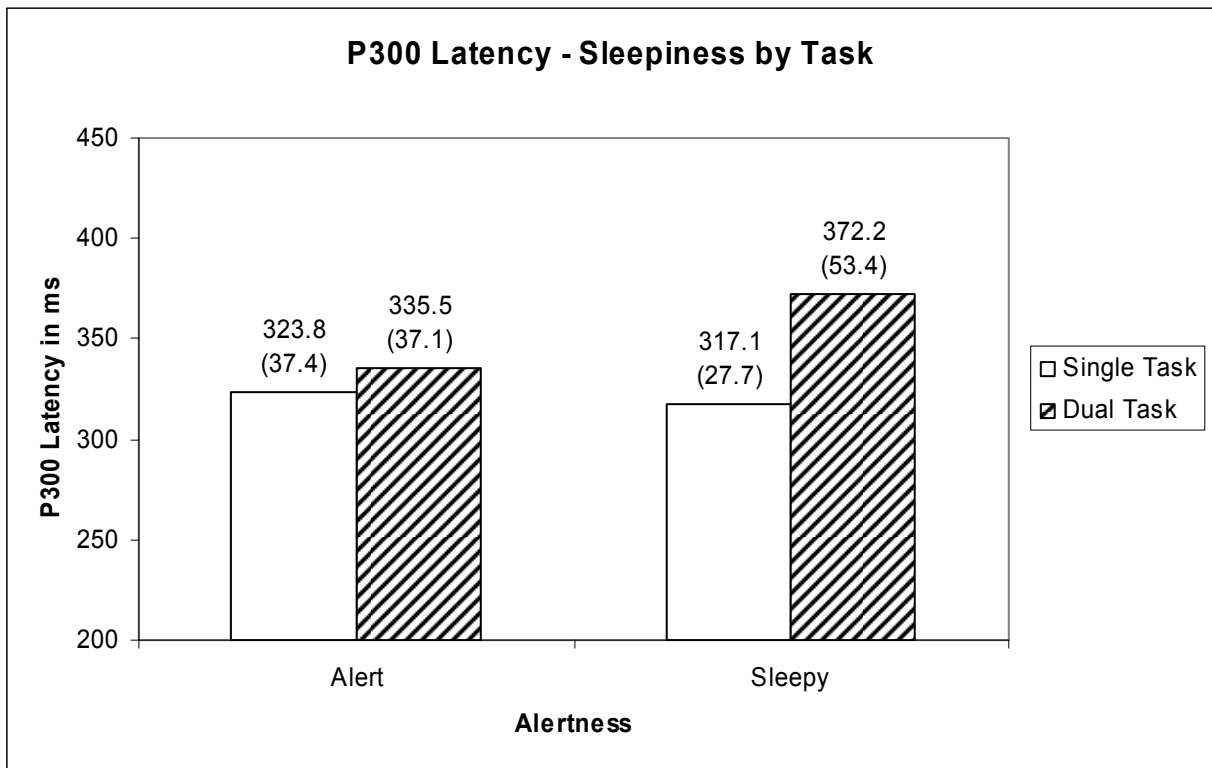


Figure 2.3. P300 latency of single and dual task by sleepiness condition. Note the increased latency the sleepy/dual condition.

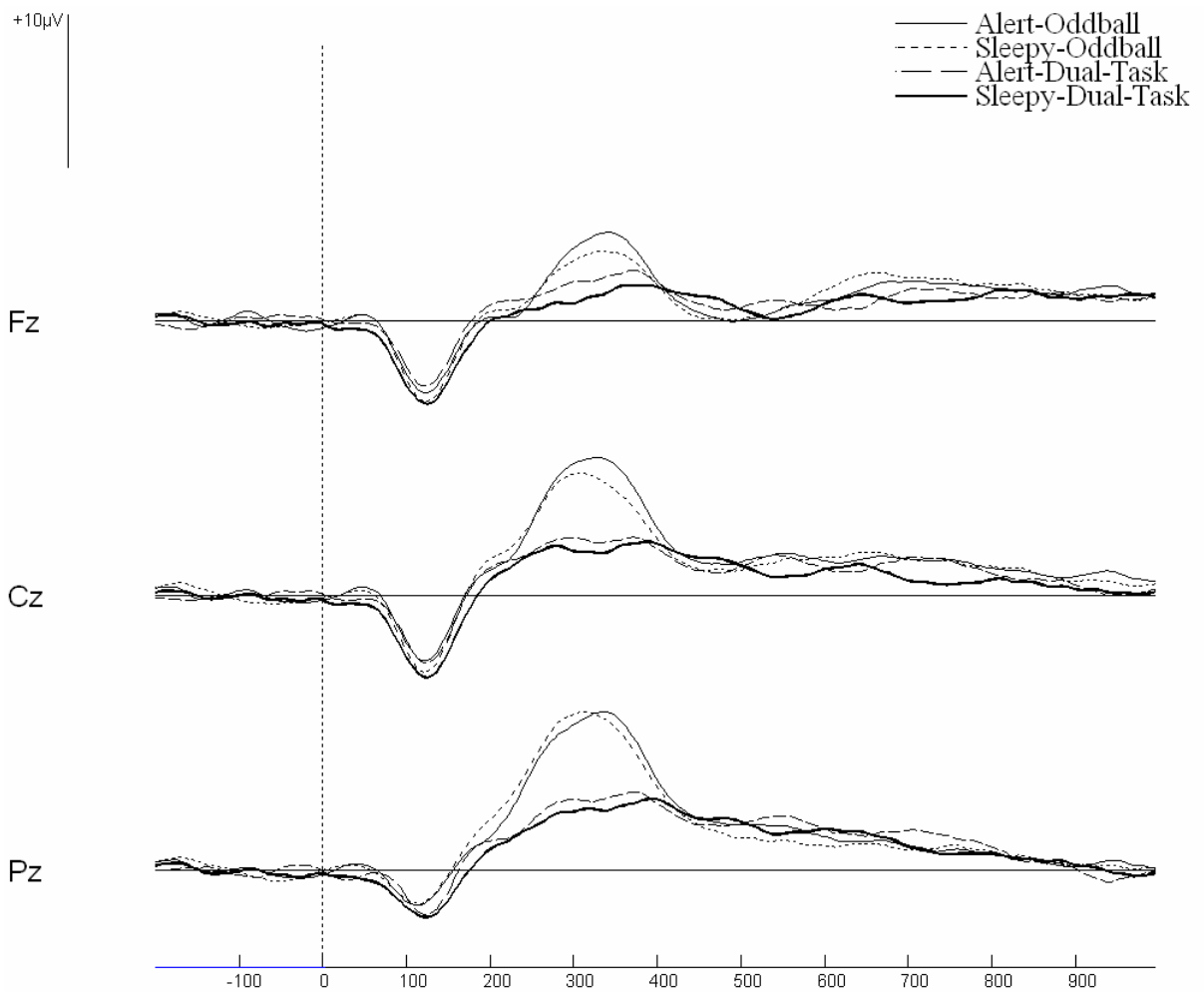


Figure 2.4 Grand average ERP's showing the four conditions.

Discussion

These results add to the growing body of research demonstrating the impact of relatively mild to moderate levels of sleepiness (20-21 hours of wakefulness) on information processing. The sleep deprivation manipulation was successful. Participants reported feeling significantly more tired during the sleep-deprivation condition. However, in the present study there were no behavioural effects of sleepiness. The response times were only affected by the distracting task. The addition of a secondary working memory task increased response times by 233 ms in the alert condition and 229 ms in the sleepy condition. There were also no subjective effects of sleepiness. Subjective reports of performance and effort were also only affected by the addition of the secondary task but not time awake. Interestingly, although perhaps not surprisingly, subjective ratings of effort significantly increased for the dual task while ratings of performance decreased. Therefore, even though they were increasing their effort in an attempt to compensate for the additional working memory task, participants still felt that their performance deteriorated.

The amplitude of the P300 was also affected only by addition of the secondary task, but not sleepiness. Similar to previous research (Nash & Fernandez, 1996) addition of a secondary, distracting task reduced the amplitude of the P300 in both conditions. This is attributable to the reduction in attention to the task (Polich, 1986). Previous research has shown that the amplitude of the P300 is decreased by sleep deprivation (Gosselin et al., 2005). In fact, analysis of the P300 amplitude to the first stimulus of a Go/NoGo two-stimulus task on these same participants later in the test session showed a decrease in

amplitude in the sleepy condition (Chapter 3). However, this typical reduction in P300 amplitude after sleep deprivation was not observed in the current data set. It may be that participants were not adequately fatigued to affect P300 amplitude because the auditory oddball and dual task were among the first in the test battery (approximately 15 and 45 minutes respectively). Comparison across the tasks (Chapters 2 and 3) indicates that subjective ratings of sleepiness after the Go/NoGo tasks, performed approximately 100-110 minutes into the test battery, were higher than after the dual task ($p=.04$). Therefore, perhaps participants were simply not sleepy enough. Of course, we cannot separate the timing factor from the nature of the task (auditory oddball versus visual Go/NoGo).

The lack of any significant differences in P300 amplitude due to sleepiness stands in stark contrast to the increase in P300 latency during the sleepy-dual task condition. During the alert condition, the participants P300 latency during the dual task increased only 12ms compared to the auditory oddball; however, in the sleepy condition this difference was 45 ms. This effect also occurred despite no similar effect in terms of response times. This is further clear evidence supporting the contention that response times and P300 latency represent two distinct mechanisms.

This research indicates the importance for skilled professionals, such as doctors, aircraft pilots, truck drivers, etc., to have adequate amounts of rest while on the job, especially when they are expected to perform multiple tasks. Furthermore, the significant decrease in the efficiency of information processing (as indexed by decreased P300 amplitude) when an individual is distracted adds support to the ongoing debate regarding

legislation to ban distractions (e.g. cell-phone use) while driving. The detected interaction effect of the P300 latency implies even greater impairments to brain processing during sleep deprivation. Therefore, a driver who is both sleepy and using a cell phone runs the serious risk of a serious slowing in information processing and decision making as evidenced by the P300 latency.

CHAPTER 3

Effects of Sleepiness and Incentive on the P300 and Contingent Negative Variation

The study presented in Chapter two demonstrated how sleepiness and distraction can interact to affect the latency of the P300 in a relatively simple auditory oddball task. However, it not always the case that distraction is the only element that can complicate performance of a task when one is sleepy. We are presented with a multitude of stimuli each moment we are awake, for that matter when asleep as well, and we must differentiate between those stimuli that are important to attend to and those that are of less, or no, importance.

Another key feature in assessing or examining performance while sleepy is motivation. Performance will typically be enhanced by increased motivation and this may be especially true for sleep-deprived individuals (see Harrison & Horne, 2000 for a review). Individuals can return to baseline levels of performance for short periods of time, even after relatively long periods without sleep. Therefore, an assessment of the effects of stimulus discrimination and motivation is warranted.

Sleep restriction and sleep deprivation have been shown to be associated with a large variety of behavioural, medical and mental problems (van Dongen, Maislin, Mullington, & Dinges, 2003) but the mechanisms underlying these problems are still not clearly understood. Among the prominent, negative outcomes of being forced to perform various tasks while sleepy is an apparent reduction in the ability to attend to tasks. This can sometimes be seen behaviourally in lapses, when an individual fails to respond appropriately to a task (Lubin,

1967). These lapses, sometimes referred to as micro sleeps, can occur even in well rested individuals if the task is very long or very monotonous but become much more common during extended wakefulness (van Dongen, Baynard, Maislin, & Dinges, 2004). These failures to attend can even occur in the absence of EEG measures that would typically indicate a sleep (or micro-sleep) episode has taken place (Santamaria & Chiappa, 1987). Also dangerous, but more insidious, is the slow degradation of the ability to perform tasks with or without lapses in performance. This slow process may be observed earlier through the use of event-related potential (ERP) components that reflect cortical processes critical for good performance, such as the P300, an index related to attention and working memory (Kok, 2001) or the contingent negative variation, a measure reflecting sustained attentional processes (Walter et al., 1964).

P300, Attention, Motivation, Salience and Arousal

The P300 is likely the most extensively studied ERP component, being associated with a wide variety of cognitive constructs and experimental manipulations relating to target salience, attention, and arousal. Several studies have shown that the P300 to attended targets is larger than that to unattended targets (see Kok, 2001 for a review). The P300 is also larger to more relevant stimuli, suggesting more attentional resources (or mental effort) are devoted to the evaluation of these more important stimuli. The P300 is also known to be reduced in distraction or multi-task paradigms in which reduced attentional resources are available to be devoted to the task eliciting the P300 (Nash & Fernandez, 1996).

The P300 is also sensitive to motivation. There have been several reports of a

positive relation between P300 amplitude and task priority (Kok, 2001). Carrillo-de-la-Pena and Cardaveira (2000) found that if participants were instructed that their performance was being monitored and would be compared to that of others the response times were reduced and the P300 amplitude increased.

The amplitude of the P300 reduces as arousal levels decline. Gosselin et al. (2005) report that as time awake increases, the amplitude of the novelty P300 is reduced. As one enters sleep, the P300 amplitude continues to be reduced in size (Ogilvie et al., 1991). This has been hypothesized to relate to the reduction in attention that can be directed towards a task as arousal levels decrease (Segalowitz, Velikonja, & Baker, 1994).

Sleepiness and Frontal Lobe Functioning

Another consequence of extended wakefulness is the eventual reduction in the effectiveness of frontal lobe functioning (Jones & Harrison, 2001). The frontal lobes are associated with executive functions and higher order mental processes (Fuster, 1999). They are the most active, in terms of metabolic rate, during the day and least active during sleep (see Harrison & Horne, 2000 for a discussion), so it is likely that they would be among the first to show signs of sleep deprivation. Symptoms of frontal lobe deficits (decreased working memory capacity, inability to concentrate, irritability, etc.) are all also associated with sleepiness.

Contingent Negative Variation (CNV)

One electrophysiological measure associated with frontal lobe functioning is the contingent negative variation (CNV) (Walter et al., 1964). The CNV is an ERP component

consisting of a negative deflection that occurs between two stimuli presented as a pair. The first stimulus (S1) serves as a warning that a response is required after the presentation of the second (or imperative) stimulus (S2). The warning stimulus produces anticipation that the participant must respond when the imperative response stimulus is presented. The CNV is typically thought of as being composed of at least two components (Tecce & Cattanach, 1993). The first earlier component, called the O-wave (orienting), is a negative deflection in response to the warning stimulus (S1), and reflects an orienting response to this initial stimulus. This O-wave follows the P300 that occurs in response to the S1. The second component, called the E-wave (expectancy), grows as the expectancy of the second stimulus (S2) increases following some short interval after S1. Normally, the E-wave appears simply as a continuation of the O-wave negativity. In order to see a separation of the O- and E-waves, the interval between S1 and S2 should be at least 2 seconds (Elbert, Ulrich, Rockstroh, & Lutzenberger, 1991). The CNV and P300 can be collected using a variety of stimuli (auditory, visual, etc.) and are both relatively stable over time.

Klein and Berg (2001) showed that CNVs remained largely unchanged after a four-week period, and Segalowitz and Barnes (1993) demonstrated that P300 amplitudes are consistent over a two-year period. Also, Geisler and Polich (1990) showed that P300 amplitudes are not directly affected by circadian rhythms although other influences such as food intake can increase P300 amplitude. However, more recent work (Hoffman & Polich, 1998) showed no significant change in P300 amplitude after smaller amounts of food intake and Hoffman and Polich hypothesized that the effects of food intake may be related more to

general arousal. Therefore, P300s and CNVs collected within a relatively short time frame (less than 2 weeks) should be consistent unless otherwise affected by experimental manipulations.

Go/NoGo CNV task

A common variation of the basic CNV task is the Go/NoGo paradigm. In this version, the initial or warning stimulus (S1) contains information regarding whether or not the second or imperative stimulus (S2) is to be responded to. In a Go/NoGo paradigm, a P300 is typically produced to both stimuli; however, the amplitude of the E-wave of the NoGo CNV is sharply reduced in comparison to the Go CNV indicating recognition of the lack of the expectation to respond to the second stimulus.

The neural generators of the CNV vary depending on the task, but are thought to be among the basal ganglia, dorsolateral pre-frontal cortex (DLPFC), and ventral and medial pre-frontal cortex (Bares & Rektor, 2001; Basile, Rogers, Bourbon, & Papanicolaou, 1994; Roshal & Knight, 1995). Evidence of the association between the CNV and frontal lobe functioning also comes from research showing the relation between the CNV and psychometric measures of executive function in various populations including the elderly (Dywan, et al., 1994), adolescents (Segalowitz et al., 1992a) and those with acquired brain injury (Segalowitz et al., 1992b). In terms of the last group, individuals with acquired brain injury are very likely to have damage to the frontal cortex whereas the first two groups have developmental limitations to some frontal structures. In a Go/NoGo paradigm, some individuals with a brain injury do not produce a negativity (CNV), but others will show a

comparable negativity to both the Go and NoGo stimuli. This second outcome has been hypothesized as reflecting damage to the orbital frontal cortex (Campbell, Suffield, & Deacon, 1990).

CNV and Arousal

Several studies have explored the relation between physiological arousal and the CNV through the use of sleep deprivation ranging from 24 hours (Yamamoto, Saito, & Endo, 1984) to 48 consecutive hours (Gauthier & Gottsmann, 1984; Naitoh, Johnsonm & Lubin, 1971). A consistent relationship has been found between physiological arousal and CNV amplitude. Sleep deprivation reduces the amplitude of the CNV (Gauthier & Gottesmann, 1984; Naitoh et al., 1971; Yamamoto et al., 1984). Subsequent nights of sleep deprivation have even resulted in the abolition of the CNV in some participants (Naitoh et al., 1971). These studies demonstrate that as a physiological measure, the CNV is sensitive to sleepiness in human populations. However, considering the classic relation between arousal and attention, the mechanism may be through attentional processes.

CNV and Attention/Motivation

Similar to results reported from P300 research, CNV amplitude has also been linked to attentional processes (Tecce, 1972; Tecce & Cattanach, 1993). Typically, as the amount of attention to a task increases or decreases so does the amplitude of the CNV. With respect to specific CNV components, it is argued that the late component (the E-wave) is influenced by allocation of more attention resources, resulting in increased CNV amplitudes (Tecce & Cattanach, 1993). Travis and Tecce (1998) showed that late CNV amplitudes were

significantly attenuated when a distracting memory task was presented during the stimulus interval. CNV amplitudes were also enhanced when the distracting task was unexpectedly withheld. These results show that CNV amplitudes are sensitive to manipulations of attention, with larger amplitudes being generated when individuals could direct their undivided attention to the task.

Researchers have also investigated the motivational effects of a performance incentive on the CNV. Davies and Segalowitz (2000) used a visual Go/NoGo paradigm to elicit CNVs. Participants were offered an incentive of \$0.25 for each correct response that was faster than 200ms. Results showed that payment increased the difference in CNV amplitudes between Go and NoGo trials compared to the no-payment condition. When payment was offered, the negative deflection was larger in the late CNV component (E-wave), but increased the positive deflection in the early CNV (O-wave) because of a greater amplitude of the P300 to the warning stimulus. In other words, increased incentive produced a larger P300 to S1 and along with it a more positive O-wave, but also a more negative E-wave. All of these are indicative of increased attention allocation to the task (Davies & Segalowitz, 2000).

In a study examining mental fatigue and the CNV, Boksem, Meijman and Lorist (2006) had participants complete seven, 20-minute blocks of a CNV task without rest (~4000 trials) to induce mental fatigue. Before the 7th block participants were informed that the subjects who performed best relative to the other participants would be paid a bonus. Approximately half the participants appeared to choose to focus on accuracy (by making

fewer errors) while the other half focused on speed (reducing response times). The amplitude of the CNV increased for those who focused on speed. These studies showed that the CNV amplitude is sensitive to changes in motivation when manipulated by performance incentives.

P300, the CNV and arousal-attention

Because the O-wave immediately follows the P300 to the warning stimulus, the dynamics of the P300 to the warning stimulus are critical, i.e., a larger P300 amplitude to S1 may reduce or delay the O-wave. The P300 is the primary ERP component to reflect attentional allocation to a salient stimulus, and can be easily manipulated by motivating task instructions (Carrillo-de-la-Pena & Cadaveira, 2000). Within sleep paradigms, the P300 is consistently seen to be attenuated (Cote et al., 2002; Ogilvie et al., 1991). However, the amplitude of the P300 to the initial stimulus does not necessarily affect the later E-wave component of the CNV. Davies and Segalowitz (2000) showed that a larger P300 to the initial stimulus can still be associated with a larger E-wave.

Rationale of the study

Sleepiness is known to have an impact on frontal lobe functioning (Jones & Harrison, 2001). Sleep deprivation also reduces the amplitude of the P300 (Corsi-Cabrera et al., 1999) and CNV (Gauthier & Gottesmann, 1984; Naitoh et al., 1971; Yamamoto et al., 1984). However, increased attention and perhaps arousal through the use of monetary motivation will also increase the amplitude of the P300 and CNV. No research has examined whether motivational effects on the P300 and CNV, which presumably reflect activity of the frontal

attentional systems, are especially affected by sleep deprivation. Previous research has shown that even after 24 hours of sleep deprivation, if participants are properly motivated many simple measures will remain at, or return to, baseline levels (Nilsson et al., 2005), but the question of brain mechanisms has not been addressed. This study examines the combined effects of sleepiness and motivation using a Go/NoGo CNV paradigm.

If the behavioural performance and the amplitude of the P300 and CNV are reduced by sleepiness, can financial incentives return one or more of these measures to baseline? It is hypothesized that similar to previous research, behavioural measures (response times) will be improved when incentives are offered, and may even return to baseline standards, but that the P300 and CNV amplitudes will not recover fully. It is also hypothesized that contrary to previous studies reporting that at least 24 hours of sleep deprivation are needed for behavioural effects, we expect that the P300 and CNV amplitudes will be reduced and that the P300 and CNV to the Go and NoGo stimuli will be more similar after more moderate sleep deprivation. This would indicate not only a reduction in attention but also a reduced ability to respond to stimulus salience and external motivations.

If the hypothesized results are found it will have profound implications for people who must interpret, assess, or decide when individuals are sufficiently competent to perform various tasks under sleep-deprived conditions. A multitude of jobs upon which peoples lives are literally dependent (e.g., air traffic controller, professional driver) require individuals to make the proper interpretation and reaction to various and often multiple stimuli. If people performing these jobs have impaired ability to control their allocation of attention due to

extended wakefulness as measured by these electrophysiological measures (P300 and CNV) even before significant behavioural evidence is observed of any deficits, then they will be more prone to error if a situation arises that increases their cognitive load. Also, if incentives are not completely effective in compensating for these decrements in cognitive function then the common assumption that simply concentrating harder will alleviate the symptoms of sleepiness will be shown to be false.

Method

The participants and procedure were described in Chapter 2.

Procedure

Go/NoGo Task.

Stimuli consisted of red, green and blue squares (3.5cm²) presented one at a time at the centre of a computer monitor. To elicit a CNV, stimuli were presented as pairs with inter-stimulus interval of 2000 ms and inter-trial intervals of between 5500 and 7500 ms, and duration of 250ms. Participants were instructed that the stimuli would appear in pairs separated by 2 seconds and that the second stimulus would always be blue. If the first stimulus was a green square, this was a “Go” trial and when the blue square appeared participants were to press the space bar as quickly as possible. However, if the first square was red this was a “NoGo” trial and they were to wait for the blue square but not press the space bar. Participants were instructed to use the first stimulus as a warning and to anticipate the second stimulus, but also wait until they saw it to respond and not attempt to simply time

their response to coincide with the appearance of the second stimulus. Individuals were also instructed to fix their eyes on the centre of the monitor, keeping eye blinks to a minimum.

The non-incentive and incentive CNV tasks were situated as the 10th and 11th tasks in a 14-task, 2-hour test battery. Therefore, for most participants these tasks were done at approximately 10:30-11:00 a.m. and 3:30-4:00 a.m., respectively, for the alert and sleepy sessions, i.e., after approximately 3 and 21 hours of wakefulness, respectively.

Incentive Manipulation.

Following the completion of the first Go/NoGo paradigm, participants were told that they had an opportunity to earn additional money during the next task. They were instructed that the task they just completed would be repeated; however, this time they would earn an extra \$0.10 for each correct response that was faster than 250ms, but lose \$0.10 for each error (failing to respond on a Go trial or responding to a NoGo trial). They were also cautioned not to attempt to anticipate the second stimulus because response times of less than 100 ms would be considered errors. This manipulation was intended to reward participants for quick and accurate responses, and therefore their allocation of attention to the experimental task. Participants were occasionally verbally encouraged to maintain their effort in the incentive condition, but seldom achieved the criterion of less than 250 ms. Feedback was not given on individual trials. However, participants were informed that they had earned a minimum additional \$.80 at the end of the first testing session in order to promote sustained effort in the incentive CNV during the second testing session. The order

of the non-incentive and incentive sessions was not counterbalanced. Counterbalancing of these conditions was deemed to be not feasible because of potential carry-over effects. If the incentive condition was performed first then the non-incentive condition would have been affected. There was no indication before the incentive condition was performed the first time, or during the second testing session, that the participant would have an opportunity to do the same task again. If participants inquired whether or not they would be doing the task twice during the second session they were told to simply do the task at hand and that information would be revealed later.

ERP averaging and scoring.

The effects of eye movements and blink artefacts were corrected for using the procedure described in Chapter 2. Once all possible trials had been selected (including those with eye-movement correction), all correct responses were averaged based on the 2 (alert/sleepy) by 2 (no-incentive/incentive) by 2 (Go/NoGo) design to yield 8 CNV waveforms for each participant. The P300 amplitudes to both first and second stimuli were measured using a -200 to 0 pre-stimulus baseline (respectively) and measured at Pz, the site of maximal P300 deflection. The CNV (E-wave) was calculated as the mean amplitude between 1600 and 2000 ms post initial stimulus (i.e., the last 400 ms before S2) using a pre-stimulus baseline of -200 to 0 ms and measured at Cz, the site of maximal deflection. To control for differences in CNV amplitude among participants, the amplitude of the NoGo CNVs will be regressed out of the Go CNV and standardized residuals saved. These will

then be used in a 2 (alert/sleepy) by 2 (Incentive/non-Incentive) repeated measures ANOVA.

Results

Subjective and objective data were analyzed using 2 (alert/sleepy) by 2 (non-incentive/incentive) repeated-measures ANOVAs with summary data reported as condition means (M) with standard error (SE) except where indicated.

Subjective Sleepiness, Effort and Performance

Participants reported feeling less alert during the sleepy $M=11.4$ (2.8), than alert, $M=51.4$ (6.4) session, $F(1,13)=51.1$, $p<.001$; they also reported being more alert after the incentive condition, $M=33.1$ (4.0) versus non-incentive, $M=29.7$ (4.3), $F(1,13)=5.29$, $p=.04$. However, the main effect of incentive was relatively small and was superceded by an interaction in which alertness was higher in the incentive condition during the alert session, but more comparable across conditions during the sleepy session $F(1,13) = 11.01$, $p = .005$ (see Figure 3.1).

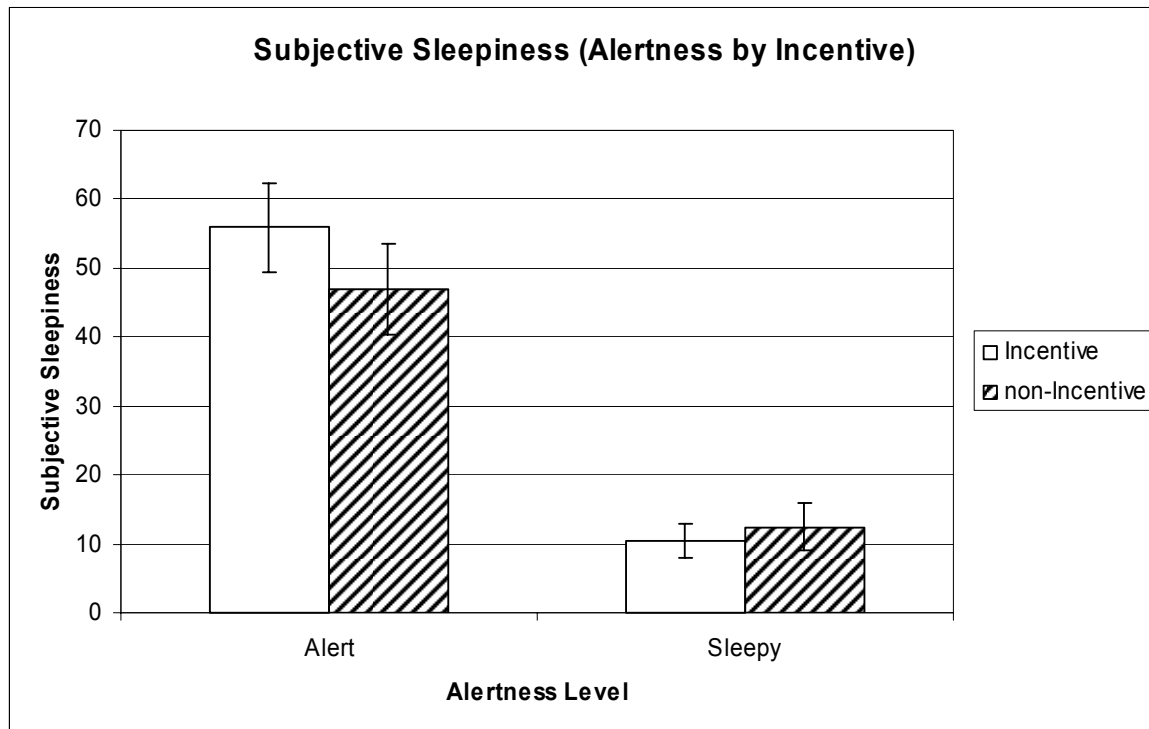


Figure 3.1 Subjective Sleepiness (Alertness by Incentive)

In terms of subjective effort and performance, there were only main effects of alertness. Participants reported higher perceived performance in the alert session, $M=67.5$ (4.5) than the sleepy session, $M=46.4$ (7.1), $F(1,13)=10.9$, $p=.01$. However, they also reported exerting more effort in the sleepy, $M=69.2$ (4.3) than the alert session, $M=56.2$ (6.6), $F(1,13)=7.13$, $p=.02$. In terms of effort, there was also a difference in the expected direction comparing the non-incentive, $M=58.6$ (6.6) versus incentive, $M=66.9$ (4.2) condition, but this failed to reach significance, $F(1,13)=3.09$, $p=.10$. Participants also perceived their performance as better in the alert session, $M=67.5$ (4.5) than the sleepy session, $M=46.4$ (7.1), $F(1,13)=10.92$, $p=.01$. Therefore, based on these subjective results we feel confident

that the manipulations were effective.

Objective Performance

In terms of response times, participants were faster for incentive trials, $M=320.6$ (11.9) than non-incentive trials, $M=379.1$ (12.6), $F(1,16)=18.4$, $p=.001$. This was true for both the alert condition, when participants improved their response times by 71.9 (19.9) ms, $t(16)=3.61$, $p=.002$, and the sleepy session, when response times improved by 45.1 (73.3) ms, $t(16)=2.54$, $p=.02$. There were no significant differences in response times based on alertness for either the non-incentive or incentive conditions. However, interestingly there was a significant difference between the mean response times for the alert non-incentive, $M=389.5$ (17.3) versus sleepy incentive, $M=323.5$ (11.7) conditions $t(16)=3.23$, $p=.005$ (see Figure 3.2)

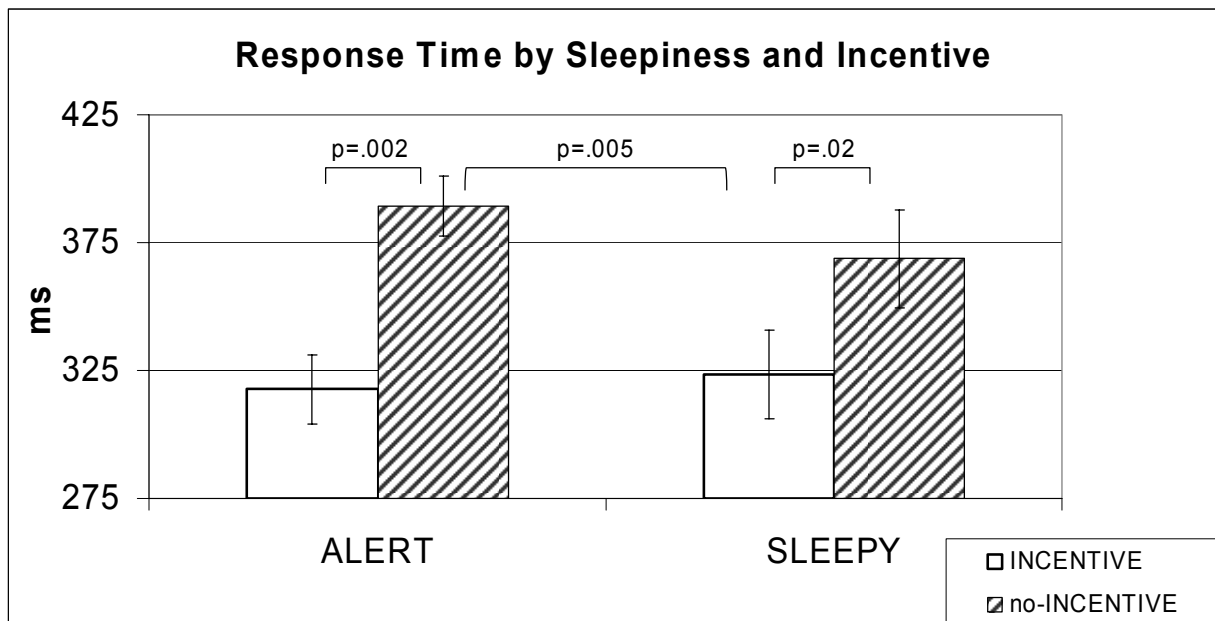


Figure 3.2; Mean Response Time by Incentive and Alertness

Event-Related Potentials (P300 and CNV)

All ERPs were analyzed using 2 (alert/sleepy) by 2 (non-incentive/incentive) by 2 (Go/NoGo) repeated-measures ANOVAs except where indicated.

P300 amplitudes.

The P300 amplitude after the first stimulus produced a 3-way interaction, $F(1,16)=5.62$, $p=.03$. As seen in Figures 3.3 and 3.4, there was a clearer distinction between the Go and NoGo P3s elicited during the incentive condition. When the incentive-only trials are considered, there is only a main effect of Go/NoGo (see Figure 3.3). The P300 amplitudes in the Go trials, $M=26.8$ (2.4) were larger than in the NoGo trials, $M=18.9$ (1.6), $F(1,16)=15.1$, $p=.001$. However, when only the non-incentive trials are examined (Figure 3.4) there is not only a main effect of trial type, whereby the P300 amplitude for the Go trials $M=23.6$ (2.5) is larger than those for the NoGo trials, $M=18.8$ (1.9), $F(1,16)=7.38$, $p=.015$, but also a near interaction such that the difference between the P300 amplitudes in the alert condition [Go $M=25.5$ (2.9), NoGo $M=18.8$ (1.9)] is larger than in the sleepy condition [Go $M=21.8$ (2.6), NoGo $M=19.3$ (1.8), $F(1,16)=3.96$, $p=.06$; see Figures 3.4 and 3.5)]. Therefore there appears to be a differentiation to the first (Go/NoGo) stimulus in the alert condition that does not occur in the sleepy condition.

The second (blue) stimulus produced only a main effect of trial type (Go/NoGo) in the P300 amplitude, with amplitudes on Go trials, $M=25.8$ (1.6) larger than on NoGo trials, $M=13.1$ (1.2), $F(1,16)=72.6$, $p<.001$.

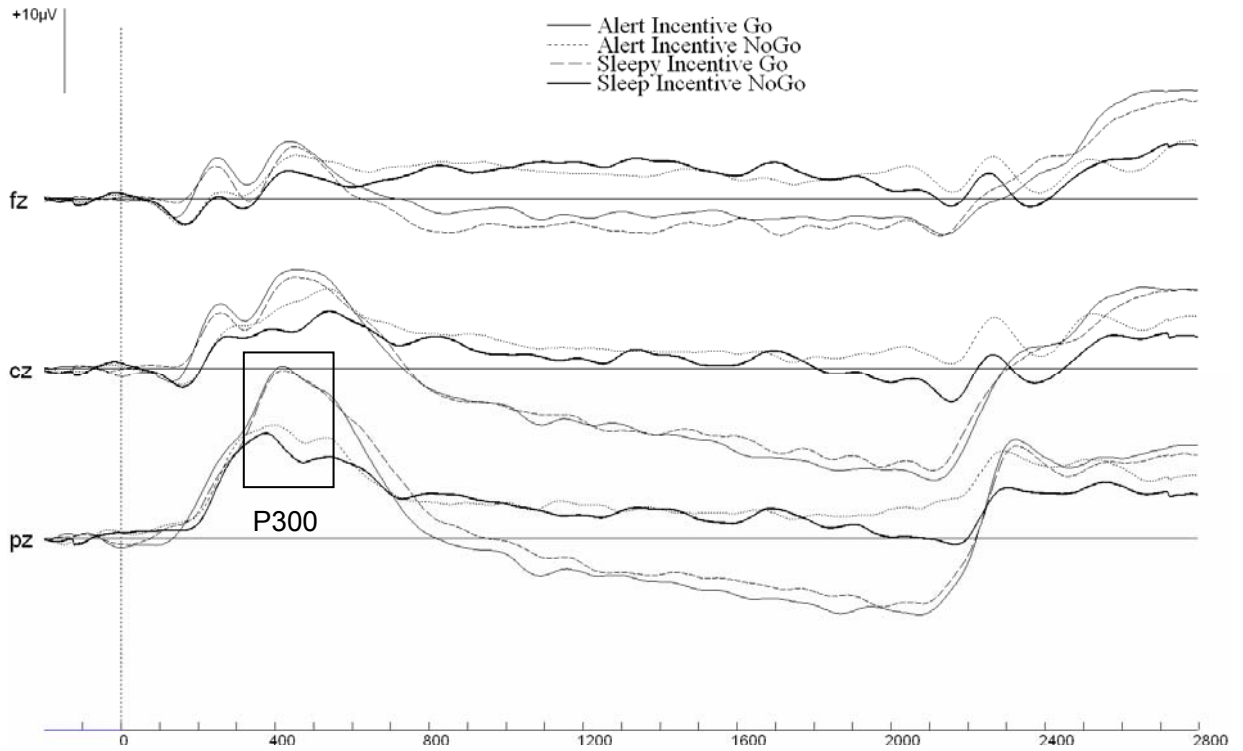


Figure 3.3 Waveforms showing a clear differentiation between the Go and NoGo stimuli during incentive trials. Note the P300 to first stimulus.

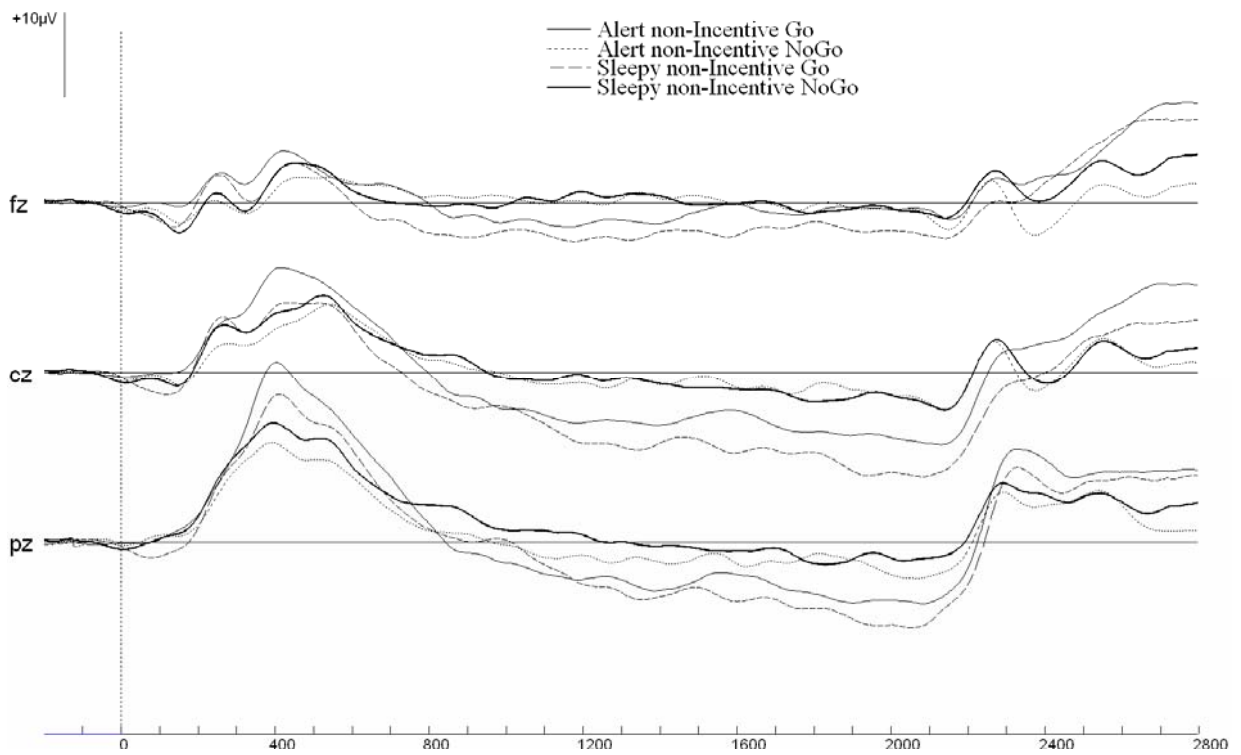


Figure 3.4 Waveforms showing how without the incentive the differentiation between Go and NoGo stimuli is much less clear. Again, note the P300 to the first stimulus.

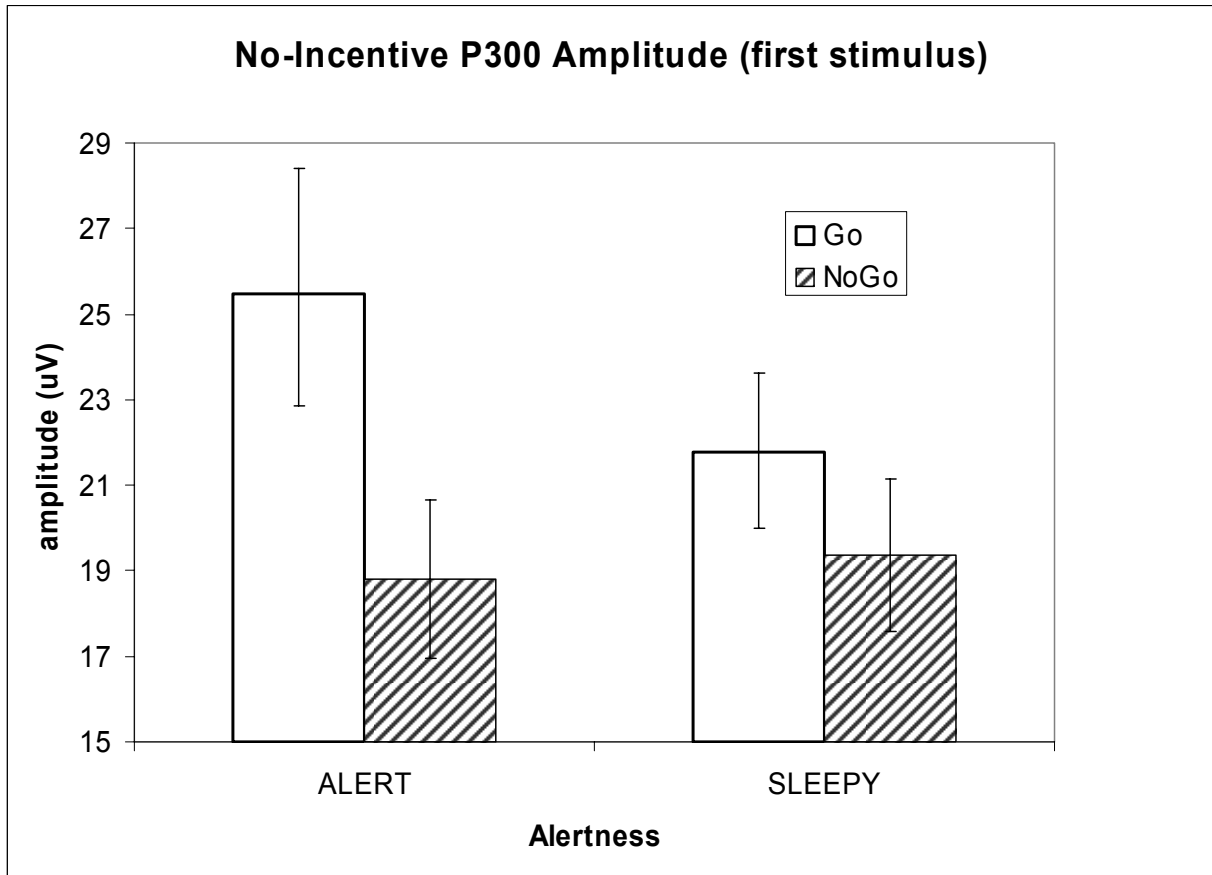


Figure 3.5 Amplitude of the P300 to the first stimulus.

CNV amplitudes.

The mean amplitude for the E-wave (1600-2000 ms post initial stimulus) was calculated for all 8 combinations (alert/sleepy by non-incentive/incentive by Go/NoGo) at Cz. The mean amplitude for the NoGo trials was then partialled out of the Go trials by regression and nonstandardized residuals were saved. These residuals were then analyzed using a 2 (alert/sleepy) by 2 (non-incentive/incentive) repeated-measures ANOVA. Analysis

revealed an essentially identical interaction for the CNV E-wave as for the P300 amplitude to the first stimulus. After the size of the NoGo CNV was controlled, there was a marginal interaction such that the amplitude difference between the non-incentive, $M=3.02$ (2.37) and incentive $M=-2.05$ (1.78) was larger in the alert condition than between the non-incentive $M=-.32$ (1.37) and incentive $M=-.66$ (1.85) trials in the sleepy condition, $F(1,16)=4.28$, $p=.055$, (see Figure 3.6). In other words, when participants were alert, the E-wave of the CNV tended to be larger when incentives were involved (mean difference of 5.07), but when participants were sleepy this difference disappeared (mean difference of .34) once again indicating a lack of differentiation between the Go and NoGo stimuli in the sleepy condition. The difference waves have been plotted in Figure 3.7 to show this effect.

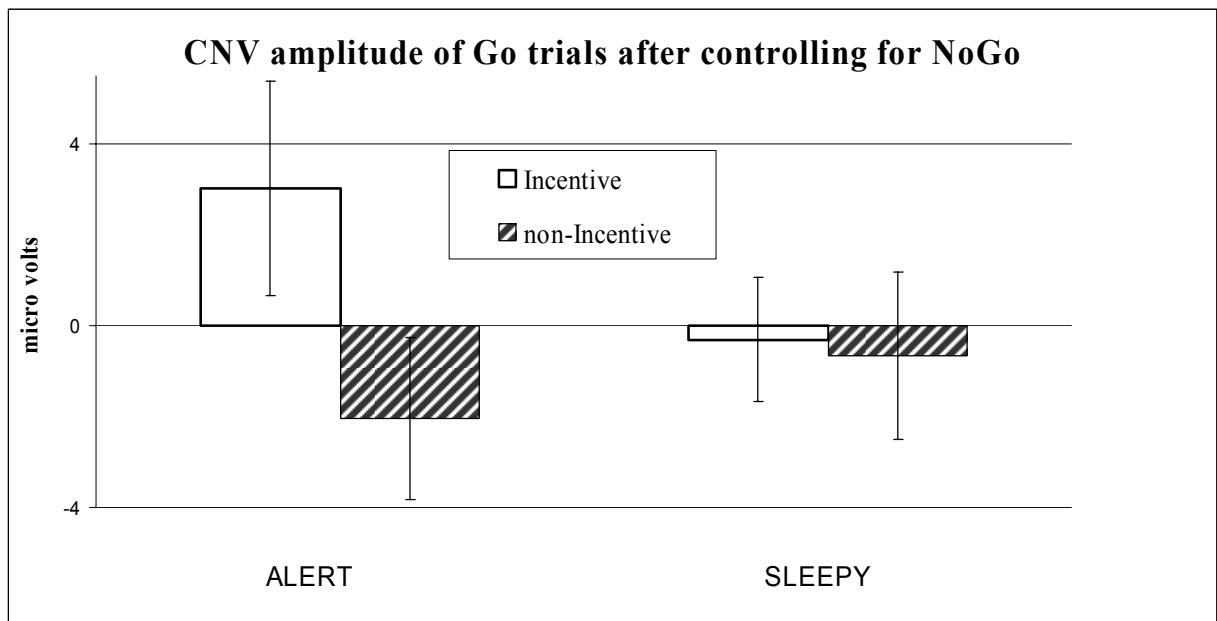


Figure 3.6 CNV amplitudes of Go trials after Controlling for NoGo Trials

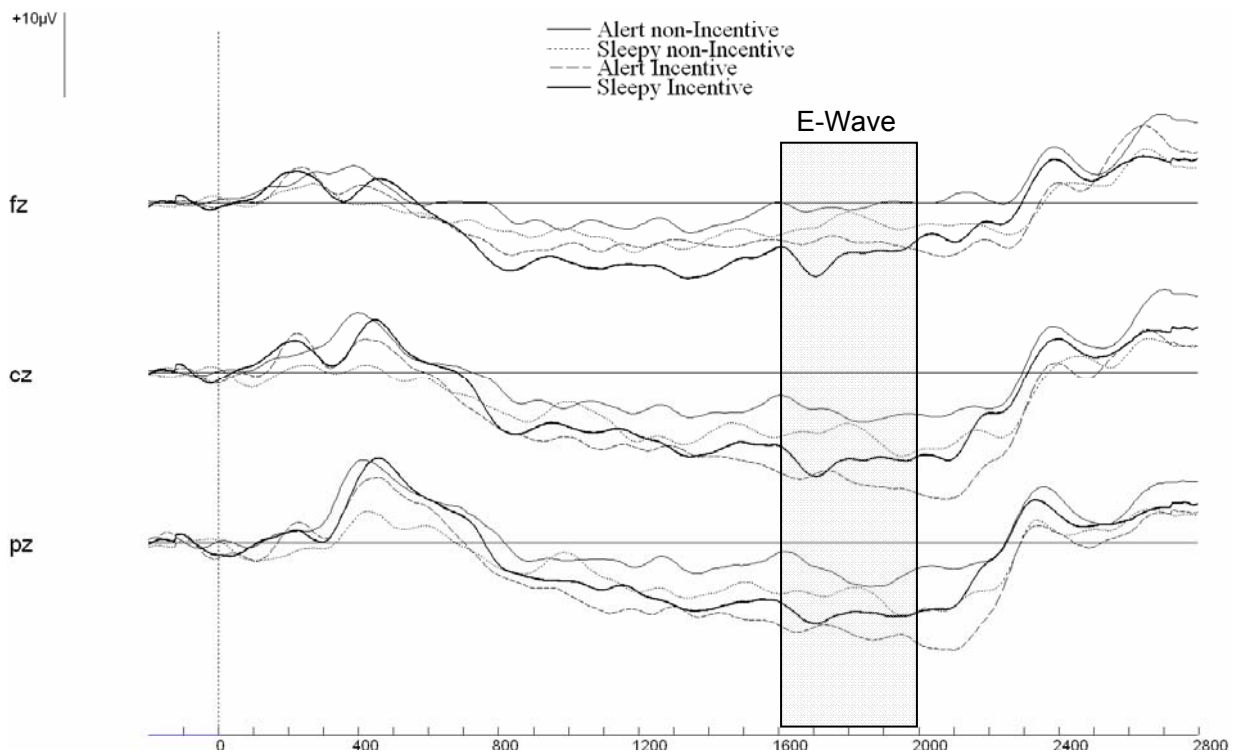


Figure 3.7 Difference waves (Go – NoGo) for the CNV. Note E-Wave (1600-2000 ms) at Cz and Pz

Discussion

This experiment was designed to test the effects of sleepiness and incentive on attention allocation and frontal lobe functioning as reflected in the P300 and CNV, especially in the context of a relatively monotonous environment. The attention allocation to the warning as reflected in the P300 amplitude and the sustained attention aspect of the CNV are of particular interest.

Both the P300 and CNV have previously been associated with both arousal (Corsi-Cabrera et al., 1999; Yamamoto et al., 1984) and attention (Jolicoeur and Dell'Acqua, 1999; Shucard et al., 2004; Teece, 1972) but often these are hard to examine in isolation because arousal and attention covary a great deal. As arousal level drops, so will attention, and any effort to maintain attention will also increase arousal. However, by manipulating both in a repeated-measures Go-NoGo design we were better able to determine how they interact.

The sleep deprivation and incentive manipulations appear to have been effective. During the sleepy condition, participants reported increased subjective sleepiness. They also reported a moderate increase in effort in the incentive condition. It was even the case that the objective measure of response time indicated that participants responded significantly more quickly under the incentive condition when sleepy (324 ms) than in the non-incentive condition when alert (390 ms). This 66 ms improvement in response time indicates that participants were able to dramatically improve their performance with increased effort/motivation.

The effects of sleepiness and incentive on the P300 and CNV were not as straightforward although both supported the basic hypotheses. The P300 has been related to several other psychological and physiological indices. For example, the P300 amplitude is known to decrease if participants are sleepy (Gosselin et al., 2005), but will increase with increasing target salience or importance (see Polich & Criado, 2006). The P300 to Go trials has been shown to be larger than that to NoGo trials (Eimer, 1993). Similarly, CNV amplitude has been positively associated with increased effort/motivation (Davies et al.,

2001) or attention (Teece & Cattanach, 1993), and negatively related to increases in sleepiness (Gauthier & Gottesman, 1984; Naitoh et al., 1971; Yamamoto et al., 1984).

In both the P300 (Figures 3.3, 3.4 & 3.5) and CNV (Figures 3.6 & 3.7) the combination of low-incentive and sleepiness resulted in a lowered ability to differentiate between more important (to be responded to Go trials), and less important (to be not responded to NoGo trials) events. The P300 amplitudes in the incentive condition when participants were paid for fast responses (Figure 3.3) showed a clear distinction between the Go and NoGo trials regardless of level of sleepiness. However in the non-incentive (unpaid) condition this distinction remained for the Go trials when the participant was alert, but not when he/she was sleepy (Figures 3.4 & 3.5). This effect was not seen for the P300 amplitudes to the second stimulus. This second stimulus required a motoric response for Go trials and by this point the decision had been made regarding whether or not to respond. Therefore, the effect on the P300 was only present during the time period when evaluation of the initial stimulus was taking place.

A similar effect was observed for the CNV. When participants were alert, incentive significantly increased the amplitude of the E-wave in the CNV. This is similar to the result of Boksem et al. (2006) who found that when response times were improved after instruction, CNV amplitudes were enhanced. Our incentive instructions were based on fast response times. However, this difference was not seen during the sleepy session for NoGo trials. The differences between the Go and NoGo trials in terms of attention allocation and frontal lobe function as reflected by both P300 and CNV were attenuated in the sleepy

condition (see Figures 3.3, 3.4, & 3.5). Therefore, the apparently reduced level of differentiation between the Go and NoGo trials in the non-incentive/sleepy condition would appear to be indicative of a general lowered ability to recognize and/or categorize stimuli in this condition.

These results suggest that when sleepy, participants do not automatically distinguish between important, to-be-attended-to, events and less important, to-be-ignored, events as efficiently, unless special incentives are applied. However, in our paradigm, the conditions were blocked, making it possible that the incentives raised arousal levels in the sleepy session. In the normal course of the day, such as in the case of a sleepy driver, a near collision raises attention and arousal levels. However, our results suggest that within a boring repetitive task, electrophysiological measures of attention allocation show a potentially dangerous drop in attention resources before simple responses do, i.e., before there is a direct warning of the person's poor performance.

Sleepiness and frontal lobe function

Evidence of altered brain function after sleep deprivation has been shown in the past. Drummond and colleagues (1999, 2000) using fMRI have shown that after sleep deprivation there appears to be recruitment of some prefrontal areas; however, this recruitment appears to be related to the difficulty of the task (Drummond et al., 2005). On relatively easy tasks, cerebral activation as indexed by fMRI remained fairly constant after sleep deprivation, but for more difficult tasks there were increases in activation seen in the dorsolateral prefrontal gyrus and the cingulate cortex (among other regions). These are also among the areas

involved in generation of the CNV (Roshal & Knight, 1995). Drummond and colleagues have not employed any two-stimulus CNV-type tasks so we cannot be certain of the brain's response to sleep deprivation in terms of this task, but further research using fMRI would be valuable in determining what areas of the brain may decrease or increase in activity in a Go/NoGo task after sleep deprivation.

This lower ability to distinguish events may have profound implications. The CNV is considered by most researchers to be indicative of frontal lobe functioning (Dywan et al., 1994), so therefore this experiment demonstrates potential frontal lobe deficits when people are sleepy that can occur simultaneously with preserved (simple) behavioural output. In the current experiment, we observed reduced response time based only on incentive with similar response times in the alert and sleepy conditions. Previous research (e.g. Jones & Harrison, 2001; Harrison & Horne, 2000) has claimed that frontal lobe deficits do not appear until at least 24-30 hours of sleep deprivation. However, these results were based on behavioural tasks such as complex business demands associated with frontal lobe functioning and not based on physiological measures (Harrison & Horne, 2000). This has implications for the type of testing that must be done to determine if there are frontal lobe deficits based on sleepiness.

Harrison and Horne (2000, page 236) reviewed the impact of sleep deprivation on decision making and suggested that “complex, rule-based, convergent and logical tasks” are unaffected by short-term sleep deprivation, perhaps because of their arousing effect, but that decisions involving unexpected outcomes, innovation, and revision are impaired. This line

of logic is supported by the current results. The P300 is a measure of attention allocation and the CNV is an index of sustained attention, but the only consistent effects are seen when the discrimination between the Go and NoGo interact with sleepiness and incentive. This is consistent with the idea that, if faced with a decision for which rapid and accurate discrimination of input is needed, then individuals who have been sleep deprived may not perform as well at these types of tasks.

CHAPTER 4

Performance Monitoring and Sleepiness

The first two studies (Chapters 2 and 3) examined measures of attention, attentional allocation and frontal lobe functioning. However, the P300 and CNV are ERP components which are only averaged across correct responses. Incorrect responses are not included in the average, but, as people become more sleepy, errors become more common so Chapters four and five will examine the brain responses to errors.

Sleepiness influences how well an individual functions. Individuals may be able to fight extreme tiredness, but lapses of attention and errors are inevitable. The behavioural, cognitive, and psychophysiological effects of sleep restriction or extended wakefulness (>24 hrs) are well known (e.g. Patrick & Gilbert, 1896; Dinges et al., 1997; Van Dongen et al., 2003); however, more realistic lengths of wakefulness (<24 hrs) have not been as thoroughly studied. As time awake increases, errors become more common and are often attributed to lapses in attention. Several researchers (e.g., Mitchell and Williamson, 2000) have reported that the number of errors made on the job begins to rise after approximately 10 or 11 hours of work, although this finding has not always been consistent (see Bendak, 2003, for a review) and much research continues to focus on reasonable hours of work and optimal scheduling. However, even once work has finished, people must continue to perform many important and often hazardous tasks such as driving a vehicle. After 20 hours of wakefulness, a situation encountered frequently by many people, errors can be just as devastating as those committed by professionals such as doctors enduring longer periods of sleep deprivation. The existence

of increasing likelihood of performance failure during sleepiness is well documented; however, useful identification of, or counter-measures for, dangerous levels of sleepiness requires a deeper understanding of the mechanisms underlying such errors and adaptiveness taken in response to performance failure.

It has typically been assumed that the increase in errors made while people are sleepy is primarily due to lapses of attention (Lubin, 1967) or even consciousness, i.e., micro-sleeps (Koslowsky and Babkoff, 1992). In other words, the person fails to notice the stimulus requiring a response. However, other research has shown that performance failure may occur even during objectively identifiable wakefulness as determined by polysomnography (McCarthy and Waters, 1997). At what level do these performance failures occur?

Research examining sleep onset has shown that ERPs such as the P300, indicative of stimulus processing (Polich, 1986) or categorization (Verleger et al., 2005), continue to occur even after objective responding (button press) has stopped (see Cote, 2002, for a review). Therefore, some processing of a stimulus must occur even after behavioural evidence of this processing has ceased. However, lapses, or failure to respond, can occur with increased frequency well before sleep onset. Also, in addition to these errors of omission, there are also errors of commission, when the individual responds inappropriately, and often quickly without adequate consideration, analysis, or adherence to the task demands. This study addresses the electrophysiological correlates of these errors.

Error Negativity/Error-Related Negativity (Ne/ERN)

Approximately 60-100 ms after an erroneous response or a response in which there is

some uncertainty regarding its correctness, there is a negative EEG deflection which has been labeled error negativity (Ne, Falkenstein et al., 1991) or the error-related negativity (ERN, Gehring, et al., 1993). It is most easily seen using response-locked averages from tasks that are simple but speeded so as to produce numerous errors (about 10-20%). The Ne/ERN is thought to be generated in the anterior cingulate cortex (Braver, Barch, Gray, Molfese, & Snyder, 2001; Stemmer, Segalowitz, Witzke & Schoenle, 2003; van Veen & Carter, 2002) . The Ne/ERN has been hypothesized to reflect either error detection (Holroyd, Coles, & Nieuwenhuis, 2002) or response conflict (Yeung, Botvinick, & Cohen, 2004).

Regardless of which account is most accurate, the Ne/ERN appears to play some role in behavioural modification. It has been shown that the amplitude of the Ne/ERN correlates with the subjective confidence of the response; the Ne/ERN is larger after trials in which the participant is most certain an error had been committed (Scheffers & Coles, 2000). Gehring et al., 1993) also found that the amplitude of the Ne/ERN correlates positively with the increase in response time on the following trial. In other words, the larger the Ne/ERN, the greater the behavioural compensation after errors.

The Ne/ERN has also been shown to be sensitive to several other manipulations and individual differences. For example, for some individuals, the Ne/ERN varies as the importance of the error (Pailing & Segalowitz, 2004a). Individuals who produce smaller Ne/ERNs tend to make impulsive errors (Pailing, Segalowitz, Dywan, & Davies, 2002) and, when given instructions to focus on speed over accuracy, people in general produce a smaller Ne/ERN to an incorrect response (Gehring et al., 1993; Ullsperger & Szymanowski, 2004).

It has been reported that conscious recognition of the error may not be required for the Ne/ERN to be observed (Nieuwenhuis et al., 2001); however, the research that links Ne/ERN amplitude with conscious evaluation of error probability (Scheffers & Coles, 2000) or degree of behavioural change (Gehring et al., 1993) suggests that Ne/ERN is associated with conscious error recognition.

Ne/ERN and Lowered Arousal due to Sleepiness or Alcohol Consumption

Scheffers et al. (1999) reported a reduction in the Ne/ERN after 24 hours of wakefulness and this effect was attributed to a failure to detect errors. However, the participants were tested a total of 9 times, in addition to practice sessions, so there may have been an effect due to the multiple testing sessions. Perhaps familiarity with the task may have interacted with sleepiness such that what is being reflected is an increased boredom or habituation factor rather than a drop in error detection. Alcohol intake can also affect the Ne/ERN. Ridderinkoff et al. (2002) found that even a moderate dose of alcohol (BAC ~ .04%) reduced the amplitude of the Ne/ERN by approximately one third, but no further reductions were seen at higher doses (BAC ~ .10%). Post-error slowing, a classic behavioural outcome associated with compensatory actions, did not occur at either level of intoxication.

Ne/ERN and Motivation

The Ne/ERN and Pe have been shown to be sensitive to both internal (e.g., personality) and external (e.g., reward or instruction) variables. The Ne/ERN is larger in individuals with obsessive-compulsive disorder (Gehring, Himle, & Nisenson, 2000) and

smaller in some contexts in individuals with a low level of socialization (Dikman & Allen, 2000; Santesso, Segalowitz & Schmidt, 2006). Hence, those people who are more concerned with performance or with what others observe about them appear to produce larger Ne/ERNs. The Ne/ERN has also been shown to be sensitive to instruction. In a task involving two stimulus factors, the size of the Ne/ERN was influenced by the amount of reward associated with the stimulus factor incorrectly responded to, although this varied with personality factors related to conscientiousness (Pailing & Segalowitz, 2004b). Therefore, the Ne/ERN appears to depend on the motivational state.

Error Positivity (Pe)

Following the Ne/ERN, a positive deflection (error positivity, Pe) (Falkenstein, 2004) has been observed, but has been less studied. The Pe is typically maximal at parietal sites, and reaches maximum amplitude between 200 and 400 ms after an erroneous response. Because of similar polarity, topography and latency, the Pe may be a P3b related to the detection of the error about to be made (as opposed to the stimulus) and research has shown that it is likely related to error recognition, response strategy or subjective error processing (see Falkenstein, 2004, for review). Scheffers et al. (1999) did not examine the Pe so the effect of sleepiness on the Pe remains unknown.

The current study examines the effect of sleepiness on the Ne/ERN and the Pe. We employed a task known to produce the Ne/ERN and Pe: the Eriksen Flanker task (Eriksen & Eriksen, 1974). In addition, we asked participants to evaluate their subjective sleepiness, effort, and performance immediately after the task was completed.

Method

The participants and procedure were described in Chapter 2.

Procedure

EEG and EOG data were converted from analogue to digital signals with a window of $\pm 250 \mu\text{V}$ (12-bit resolution) using a sampling frequency of 512 Hz and band-pass frequency of .16 to 100 Hz. The EEG signal was amplified at a gain of 10,000 using a Sensorium Inc amplifier system. InstEP (a commercial data acquisition program) was used to present stimuli and acquire data. To eliminate electrical interference, the EEG signal was further filtered offline using a 60Hz-notch filter.

Flanker Task.

The Flanker task took place approximately one hour into each two-hour testing session. Actual mean time awake before testing was 4.0 hours (SD=.8) in the alert session and 19.9 hours (SD=1.2) in the sleepy session. The Flanker task requires participants to respond quickly (ITI=1250 ms) via a forced-choice key press (counterbalanced across participants and conditions) to central target letters (H or S) from both congruent (HHHHH, SSSSS, n=160) and incongruent (HSHHH, SSHSS, n=320) arrays. They were instructed that the letters would appear rapidly so they must react quickly to perform the task; however, it was emphasized that speed and accuracy were equally important.

Subjective Measures.

Visual Analog Scales (VAS) were used to measure subjective estimates of

sleepiness, effort and performance. Each VAS was a 10-cm line with two anchor points indicating polar opposites on each dimension. The anchors used for each scale were as follows: sleepiness (very sleepy-very alert), effort (no effort-maximum effort), and performance (very poorly-very well). These measurements were taken immediately after each task was completed. In addition, each participant was asked to estimate the number of errors made on the Flanker task.

Ne/ERN and Pe Measurement.

Artifacts from eye movements were corrected, trials were separated into correct and error responses and ERPs were created based on response-locked averages and smoothed with a 5-point moving-window average. Response-locked averages still preserve the P300 to the stimulus (Verleger et al., 2005), normally within the 200 ms preceding the response, as can be seen in Figure 1. The amplitude of the P300 is typically reduced by sleepiness (Lee et al., 2004) and therefore to use the pre-response period as a baseline would confound the P300 amplitude effects with the Ne/ERN effects. Thus, to minimize any effect that the stimulus P300 had on these averages, a baseline of -600 to -400 ms relative to response was used. The amplitude of the Ne/ERN was measured as the maximum deflection between 50 and 120 ms post response. Because the Pe often had slow rising waveforms or poorly defined peaks, Pe amplitude was measured as the mean amplitude between 200-400 ms (Nieuwenhuis et al., 2001). The sites scored for analyses were FCz for the Ne/ERN, and Pz for the Pe. These are the sites of maximal deflection for these two components.

Results

Two participants were excluded from all EEG analyses because of technical problems. The recording parameters were set incorrectly for one and for the other, the original data file was corrupted. Only the 12 participants who showed a clearly formed negative deflection in the appropriate time frame were included in analysis of the Ne/ERN. In all other analyses the maximum number of available data points was used.

Subjective and Objective Behavioural Measures

Paired t-tests were conducted to assess the subjective and objective measures across conditions. During the sleepy condition, participants reported being more sleepy ($M=9.07$, $SD=8.00$ vs. $M=49.00$, $SD=25.99$) [$t(13)=6.07$, $p<.001$], and performing worse ($M=26.63$, $SD=15.70$ vs. $M=44.50$, $SD=19.62$) [$t(13)=3.04$, $p<.01$], even though neither the subjective estimate of the number of errors ($M=24.00$, $SD=11.98$ vs. $M=24.08$, $SD=10.80$) [$t(12)=.02$, $p=.99$], nor the objective number of errors made ($M=28$, $SD=17.62$ vs. $M=26.12$ $SD=12.04$) [$t(16)=.47$, $p=.64$] was significantly different across conditions. There was no significant difference in subjective effort across conditions ($M=73.71$, $SD=18.74$ vs. $M=71.29$, $SD=14.53$) [$t(13)=.54$, $p=.60$].

Error-Related Negativity

Paired t-tests showed no significant difference in Ne/ERN amplitude measured at FCz across conditions ($M=-8.22$, $SD=4.68$ vs. $M=-7.04$, $SD=5.10$) [$t(11)=.69$, $p=.50$] (see Figure

4.1). There appears to be a peak-to-peak (P300-Ne/ERN) difference in the amplitudes; however, this difference is only a trend ($M=11.08$, $SD=4.69$; $M=13.98$, $SD=4.47$), $[t(11)=1.94, p=.08]$ and is a result of a significant difference in the positive peak (P300) just prior to the Ne/ERN $[t(11)=2.65, p<.05]$. There were no significant correlations between the amplitude of the Ne/ERN and subjective number of errors, objective number of errors, subjective effort, or performance in either condition.

Error Positivity

The Pe was significantly reduced in the sleepy condition ($M=4.24$, $SD=3.15$; $M=7.50$, $SD=5.19$), $[t(14)=3.44, p=.004]$ (see Figure 4.1). It has been reported that the number of errors may influence the amplitude of the Pe (Dywan, Mathewson, & Segalowitz, 2004); however, the Pe did not correlate with the subjective number of errors, objective number of errors, subjective effort, or performance in either condition. It is therefore unlikely that the number of errors (real or perceived) influenced the amplitude of the Pe.

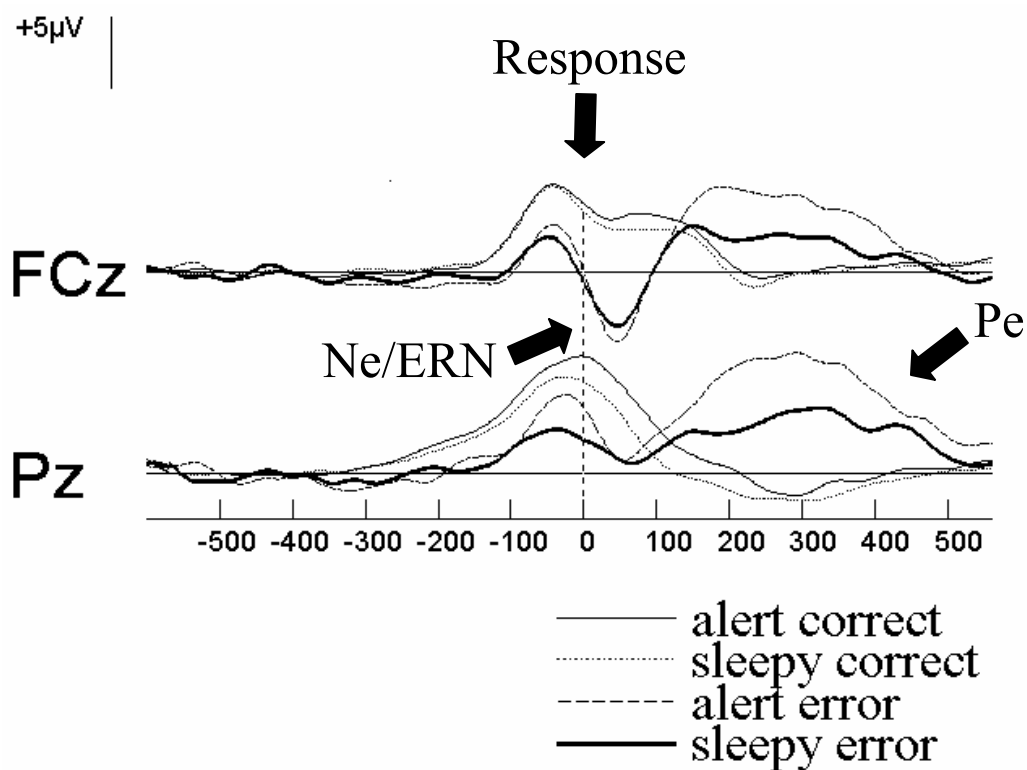


Figure 4.1: Response-locked EEG averages (Ne/ERN & Pe marked) to correct responses and errors in the Flanker task in both the alert and sleepy conditions. The similar-sized Ne/ERN ($p=.50$) but reduced Pe can be seen ($p<.001$).

Behavioural Corrections after Errors

After erroneous responses, participants typically slow down their responses to the following trial to reduce the probability of making another error (Gehring et al., 1993; Hajcak, McDonald, & Simons, 2003). To assess the behavioural effects of errors in this experiment, a 2 (alert/sleepy) by 2 (correct/error) within-subjects ANOVA was conducted using response time on correct trials following errors and following correct responses as the dependent variable. Behavioural slowing after errors was more pronounced in the alert

condition (see Figure 4.2). Response times on correct trials following errors slowed by 28.5 ms when participants were alert, but only 9.1 ms when they were sleepy [$F(1,14)=7.71$, $p=.015$].

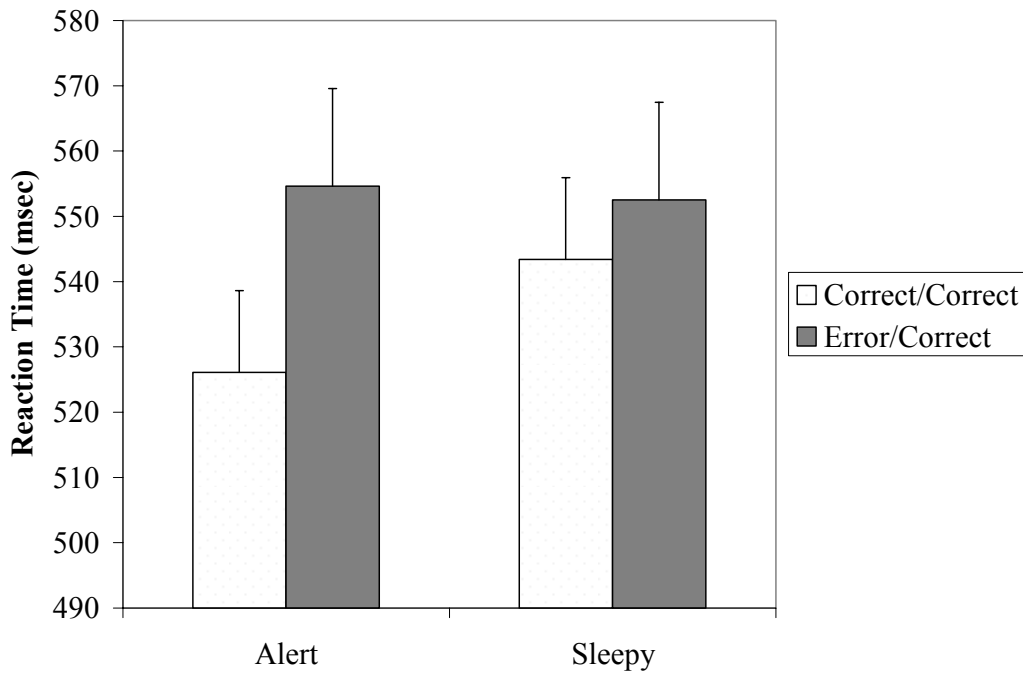


Figure 4.2: Mean response time for correct trials following correct (light bars) and correct trials following error trials (dark bars) in both alert and sleepy conditions. The interaction can be seen showing that there is less compensatory slowing after errors when one is sleepy ($p<.05$).

Discussion

This experiment was designed to assess the effect of moderate sleep deprivation on error processing. After 20 hours of wakefulness, individuals continue to react electrophysiologically to errors. This can be seen in the similarity in the Ne/ERN across the

two levels of alertness. However, post-error evaluation (reduced Pe), and remediation of these errors (reduced post-error slowing) were impaired despite participants reporting sustained effort.

Scheffers et al. (1999) have reported a reduction in the Ne/ERN after 24 hours of wakefulness. However, they used memory and visual-search tasks with multiple levels (3 and 6 items), which are not typical Ne/ERN paradigms. Although they argued that the reductions in Ne/ERN amplitude (approx 3 μ V) are primarily due to time awake, response times and error rates varied based on type of task, task load, time on task, as well as time awake. For example, the amplitude of the Ne/ERN was significantly larger in the memory search and significantly smaller with a larger memory load (6 items). Also, the response times and error rates were significantly greater in the visual-search task. Participants in the experiment conducted by Scheffers et al. (1999) were also tested multiple times. Therefore, the conclusion that reduction in the Ne/ERN is due to time awake and more specifically a “decrease in the quality of perceptual processing” may not be warranted.

Similar to our findings, Scheffers et al. (1999) did not find evidence of behavioural slowing after errors in either task ($p=.23$ and $p=.28$). Thus, other factors may have attenuated the Ne/ERN in the participants in the sleepy condition, such as being less certain of their performance (Coles et al., 2001; Pailing & Segalowitz, 2004a) or being less motivated to perform well (Pailing & Segalowitz, 2004b). Scheffers et al. (1999) also had only male participants and the present study used only females, so gender differences cannot be ruled out.

Ridderinkhof et al. (2002) found that after alcohol consumption, the participants' Ne/ERN amplitudes were significantly reduced by approximately 2.1 μV . This reduction in Ne/ERN amplitude after participants' alcohol ingestion was also related to a failure to adjust behavioural responses after errors, even after the error rate was controlled for, and these results were interpreted as a breakdown in the recognition of errors. In contrast, the present experiment found a non-significant reduction in the Ne/ERN of approximately 1.2 μV , with a significant reduction in the Pe and a reduction in post-error slowing.

Ridderinkhof et al. (2002) claimed that alcohol impairs performance monitoring, both at an electrophysiological level of activity in the ACC and behaviourally with respect to post-error slowing. Our results suggest a somewhat different pattern: Participants when sleepy can monitor errors at the level of the ACC but they do not adjust behaviour to compensate for these errors, nor do they respond as much with the attentional-emotional response reflected in the Pe. Thus, although alcohol deteriorates performance monitoring, sleepiness reduces the motivation to adapt behaviour even when errors are detected. Further investigation into the combined effects of alcohol and sleepiness appears to be warranted. If alcohol reduces awareness of errors and sleepiness reduces evaluation, then a combination may prove more dangerous than would simply the additive effects of both conditions.

Previous research has shown that reductions in the Pe may be related to the number of errors made (Falkenstein et al., 2004; Dywan et al., 2004); however, we found that the correlation between number of errors and size of the Ne/ERN or Pe was not significant nor in fact did performance deteriorate with sleepiness. Therefore, the reduction in the Pe cannot

be attributed to an increase in errors. However, despite no significant increase in the subjective estimate of the number of errors or the objective assessment of number of errors, participants did report a subjective decline in performance. This supports Falkenstein's (2004) hypothesis that the Pe may reflect further subjective/emotional assessment of errors.

We found diminished behavioural reactivity to errors. This indicated that these participants were failing to alter their behaviour (by increasing response time after errors) in order to compensate for their impairment due to sleepiness and improve their performance. If they perceived their performance as worse and were trying to compensate, the increase in response time following errors in the sleepy condition should have been even greater than the increase when they were alert, but this was not the case.

In light of the fact that we failed to find any significant difference in effort or Ne/ERN amplitude across conditions, we conclude that although awareness (they notice) and motivation (they care) remain relatively intact, error evaluation (Pe) is impaired after extended wakefulness. This has very serious implications for anyone who finds himself in the situation of having to perform a dangerous task while sleepy. We chose the time frame of approximately 20 hours awake because this represents an amount of wakefulness (or sleep deprivation) commonly encountered by a large proportion of the population at some point in their lives. Whether it is a doctor on 24-hour call, a member of the armed forces on extended manoeuvres, a long-distance professional driver, a shift worker on a double shift, or simply someone driving home after a social evening, the failure to adequately compensate for diminished alertness can have dire outcomes.

CHAPTER 5

Performance Monitoring and Size of Error using an Anti-Saccade Task

This chapter replicates and extends the results from Chapter 4 utilizing a different task to elicit the Ne/ERN and Pe. The first several pages are somewhat redundant; however, they are included for the sake of completeness.

Sleep deprivation and sleep restriction have become ubiquitous in today's world. Individuals may be able to fight extreme tiredness for short periods of time, but lapses of attention and errors are inevitable. Extreme sleepiness can cause sudden sleep onset, or a momentary failure in attention (Sugarman & Walsh, 1989) and the results can be catastrophic. The incidents at Three-mile Island, Exxon Valdez, Chernobyl, and the Challenger disaster were all linked to critical errors involving ignored or misinterpreted warning signals that were made by sleep-deprived individuals (see Mitler et al., 1988 for a review).

Several studies have shown that performance on a variety of tasks is impaired after sleep deprivation, sleep restriction (van Dongen et al., 2003) and sleep fragmentation (Bonnet & Arand, 2003). However, aside from the rather obvious consequences of sleepiness, the precise mechanisms underlying these lapses and performance failures remain incompletely understood. Also, even though errors are more frequent after sleep deprivation, it is not simply the error itself but the recognition, evaluation, and compensation for these errors that can often determine how severe the outcome of the error is.

The majority of sleep deprivation studies have employed paradigms with enforced

wakefulness of a minimum of 24, and often 36 to 60 hours; however, this amount of wakefulness is seldom encountered in normal life by most individuals. Studies involving more realistic lengths of sleep deprivation (less than 24 hours) would be useful in assisting to determine how deleterious typically encountered amounts of sleep deprivation are.

Error-Related Negativity (Ne/ERN)

Several electrophysiological changes have been reported after sleep deprivation. There is an alteration in the respective proportions of various EEG frequencies. Lower frequencies (delta, theta and alpha) increase in power while higher frequencies (beta, gamma) diminish (Makeig & Jung, 1996). Also, there are changes in various event-related potential (ERP) components. For example, the P300 typically reduces in amplitude and increases in latency with increased time awake (Gosselin et al., 2005). Another specific ERP component affected by sleepiness that has not been thoroughly studied with respect to sleep deprivation is the error-related negativity (ERN) (Coles et al., 2001) or the error negativity (Ne) (Falkenstein et al., 2000).

The Ne/ERN is a negative deflection in the ongoing EEG that starts at approximately the same time as a response containing an error (Holroyd, Dien & Coles, 1998). Ne/ERNs are much clearer and easier to score when time locked to the participant's response rather than stimulus onset, typically have a maximum deflection between 50 and 100 ms post response, and are maximal at FCz (Falkenstein et al. 1991).

Evidence from functional imaging, source localization and lesion studies suggests that this neural response is generated from the anterior cingulate cortex (ACC) (Braver et al.,

2001; Stemmer et al., 2003; van Veen & Carter, 2002). Current models indicate that the Ne/ERN may be initiated by a drop in dopamine levels when expected and actual outcomes differ (Holroyd & Coles, 2002).

The Ne/ERN is thought by some researchers to reflect a monitoring mechanism in the brain that checks for errors in individuals' reactions to decision making. According to Coles et al. (2001), errors are detected when incompatibility between correct and actual responses is observed. Alternately, others feel that the Ne/ERN represents conflict between response representations (vanVeen and Carter 2002). This experiment will not directly address this discussion and, in fact, whether the Ne/ERN is part of an error detection system or associated with response conflict is not important in the context of performance monitoring during extended wakefulness. However, the Ne/ERN must play an initial role in correction of future erroneous responses, because the size of the Ne/ERN is positively correlated with the response time on the trial following an error (Gehring et al., 1993). This may indicate a direct link between the extent to which an error was detected, and hence the amount of remedial action taken.

Studies have typically examined the Ne/ERN through forced-choice response tasks. The Ne/ERN has been shown to be sensitive to a variety of experimental manipulations, and naturally occurring differences. These include the following: (1) salience of the target; it becomes larger if correct responses are emphasized (Pailing and Segalowitz, 2004a; Ullsperger & Szymanowski, 2004); (2) personality measures; it is larger in people who score high on a scale of socialization (Dikman & Allen, 2000; Santesso, Segalowitz & Schmidt,

2005) and impulsivity (Pailing et al., 2002), and smaller in those with sociopathic (Dikman and Allen, 2000) or antisocial (Santesso et al., 2005) tendencies. Thus, detection of an error coupled with the evaluation of it appears to correlate with the size of the Ne/ERN. The Ne/ERN is larger whether the performance sensitivity is due to intrinsic factors or task demands.

Error Positivity (Pe)

After this initial negativity, a positive component, the error-positivity (Pe) can be observed (Falkenstein et al., 1991). The Pe has received less attention than the Ne/ERN. It shares some characteristics with the P300; both are positive deflections that occur approximately 300-400 ms after the stimulus (or error in the case of Pe) and have maximal amplitude in the central/parietal area (Luu, Collins & Tucker, 2000). The Pe may be indicative of conscious recognition of the error, or may even be a P3b associated with motivational significance of the error (Overbeek, Nieuwenhuis, & Ridderinkhof, 2005; Davies et al., 2001). Furthermore, the Pe may only occur after conscious recognition of an error (Nieuwenhuis et al., 2001) and the amplitude of the Pe has also been shown to be inversely related to the error rate (Dywan, Mathewson, & Segalowitz, 2004). van Veen and Carter (2002) also demonstrated that the Pe may be at least partially generated in the rostral anterior cingulate (associated with emotional processing). Perhaps a person making a large number of errors does not consider them as important as an individual who makes relatively few errors. Therefore, although its functional significance is still unclear, the Pe is thought to be involved in the conscious recognition or emotional evaluation of errors and also possibly

the remedial response to the error or related to motivational significance (see Falkenstein, et al., 2004 or Overbeek et al., 2005 for reviews).

Sleepiness and the Ne/ERN

A reduction in the amplitude of the Ne/ERN after 24 (Scheffers et al., 1999) and 26 (Tsai et al., 2005) hours of sleep deprivation has been reported, but this effect was not observed after only 20 hours of wakefulness (Murphy, Richard, Masaki, & Segalowitz, 2006). Scheffers et al. (1999) attributed this reduction in Ne/ERN to a failure to recognize errors. However, their participants were given practice sessions and testing multiple times throughout the 24-hour paradigm so habituation may have interacted with or added to any effect that sleepiness itself had on the Ne/ERN amplitudes. Tsai et al. (2005) claimed a reduction in attentional resources as the cause for the reduction in the Ne/ERN. Tsai et al. (2005) also noted a reduction in the amplitude of the Pe, which they related to poorer performance monitoring and remedial action. Scheffers et al. (1999) did not examine the Pe.

Murphy et al. (2006, Chapter 4) studied the Ne/ERN and Pe during alert and sleepy conditions (after 3 and 20 hours of wakefulness respectively) using a standard flanker task (Eriksen & Eriksen, 1974). In contrast to Scheffers et al. (1999) and Tsai et al. (2005), they found no significant reduction in the amplitude of the Ne/ERN but a large reduction in the amplitude of the Pe. Murphy et al. (2006) also reported that the post-error slowing they observed during the alert condition did not occur during the sleepy condition. They interpreted this as an indication that even after extended wakefulness, participants were aware of their errors (preserved Ne/ERN) but were not fully evaluating them as deeply or as

seriously (reduced Pe amplitude).

Saccades

Saccades are eye movements that can be divided into two basic types, pro-saccade and anti-saccade. Pro-saccades occur when one looks towards some target or stimulus and anti-saccades when an individual looks away from a stimulus (Everling & Fisher, 1998). Our eyes are naturally drawn in the direction of a stimulus. To avoid anti-saccade errors, additional attentional and inhibitory resources are required to suppress a reflexive saccade toward a visual cue (Malone & Iacono, 2002). When an individual is asked to look in the opposite direction of a target, it is difficult, and errors may occur as a result of this type of request. Previous research has shown that it is possible to get a clear Ne/ERN and Pe to anti-saccade errors (Nieuwenhuis et al., 2001) and that at least one source of the Ne/ERN after errors in an anti-saccade task is the ACC (Polli, Barton, Vangel, Goff, Iguchi, & Manoach, 2005).

Conscious awareness of errors and the Ne/ERN

Scheffers and Coles (2000) argue that error processing must be at a conscious level in order for an Ne/ERN to be produced. However, there are other researchers who argue that the Ne/ERN occurs even in the absence of awareness. In other words, there is preconscious processing of mistakes (Nieuwenhuis, et al., 2001). This assumes that individuals have access to information based on how well they perform all the time, even at pre-conscious levels.

As evidence of their claim, Nieuwenhuis et al. (2001) used an anti-saccade task in

which participants were instructed to indicate if an error had been made after each trial. They found that during an anti-saccade task, not only was a clear Ne/ERN observed after reported errors, but that an Ne/ERN occurred even on trials when small, but unreported errors had occurred. Nieuwenhuis et al. (2001) observed Ne/ERNs to these small errors, even when participants indicated a correct response had been made, although no difference between the Pe to correct responses and unobserved errors was observed. Therefore, they concluded that the Ne/ERN may occur even without conscious awareness of an error. Thus, perhaps an Ne/ERN may be produced even during periods of sleepiness (a time during which people may be less aware of their surroundings, actions, and errors).

Size of the error the Ne/ERN

There have been few studies that have examined the size of error as it relates to the amplitude of the Ne/ERN. This is seldom studied because most errors are measured as inappropriate responses so the operational definition of an error is a binary decision (button press or other overt response). Therefore, we are also uncertain of the effect of large versus small errors on the Ne/ERN. Masaki and Segalowitz (2004) did address this issue by observing Ne/ERNs that were time-locked to EMG initiation and comparing partial (incorrect muscle initiation inhibited in time to correctly respond) and complete errors. They found that the Ne/ERNs to partial errors occurred earlier and had smaller amplitudes. These are still errors in that participants were initiating a response with an incorrect hand, even though they successfully inhibited this response and behaviourally responded with the correct hand. Analysis of errors made in an anti-saccade paradigm will allow us to assess the effect

of partial errors more clearly in that erroneous pro-saccade movements are always spontaneously corrected. The question is whether the size of the error, as measured by EOG deflection, would be reflected in the Ne/ERN.

No study thus far has examined the combined aspects of moderate sleepiness and degree of error and their combined effect on the Ne/ERN/Pe while simultaneously collecting subjective measures of effort and performance. Previous research has focused primarily only the Ne/ERN (Sheffers et al., 1999) or used longer lengths of sleep deprivation (Sheffers et al., 1999; Tsai et al., 2005). In addition, very few studies have used a paradigm that would allow for analysis based on size of error and the few that have did not involve sleepiness. The effect of moderate levels of sleepiness on error processing, especially small errors, may yield important information pertaining to how the brain recognizes and reacts to mistakes under adverse circumstances.

Therefore, we determined that using a more realistic length of sleep deprivation (likely to be encountered by a larger proportion of the population) and an anti-saccade paradigm would allow us to examine the effects of moderate sleep deprivation and size of errors. This would help address the issue of how well individuals monitor their behaviour and react to errors. Because the Ne/ERN and Pe appear to be related to error processing and evaluation, investigating how sleepiness affects these ERPs will be useful in further exploring brain functioning and performance while sleepy. If we knew more about how the brain identifies and assesses errors, especially small errors, then perhaps more effective counter measures or warning systems can be created in the future.

Method

The participants and procedure were described in Chapter 2.

Procedure

Anti-Saccade Task.

The saccade/anti-saccade task was administered in 2 sections. In order to minimize head movements, a chin rest was placed 35 cm from the computer monitor. In the first section, the participants were required to attend to the focus point in the centre of the computer monitor. A lower case “o” was presented on either the left or the right side of the monitor at a visual angle of 16° for 250 ms. The participant was instructed to look in the direction of the letter, and then return her gaze to the central focus point as quickly as possible (i.e., pro-saccade).

In the second (anti-saccade) phase the participant was instructed to look in the opposite direction of the letter, the edge of the screen, and then return to the focus point as quickly as possible. If a pro-saccade occurred it was scored as an error. All erroneous pro-saccades were spontaneously corrected by the participants. Each task consisted of 100 trials. They were randomly presented but consisted of a total of 50 right and 50 left, with an interstimulus interval (ISI) of 1.5 seconds.

The ERPs to the saccades (correct and error trials) were averaged offline. ERPs to the saccades were averaged 600 ms preceding to 400 ms following the point at which the saccade began. Saccade onsets were operationally defined as the initiation point of a

deflection in the EOG, which reached minimum amplitude of at least 4 SD above background, or baseline EOG. An in-house computer program was used to semi-automate this task, but each trial was also inspected manually to ensure accurate detection of saccade onset and corrections were made as required. Saccades were grouped and averaged based on the division of correct, large incorrect and small incorrect trials within the anti-saccade task (see Figure 5.1). The distinction between large and small errors was based on median splits of the EOG amplitude after errors per testing session. Amplitudes and latencies were measured using a custom in-house program (Segalowitz, 1999).

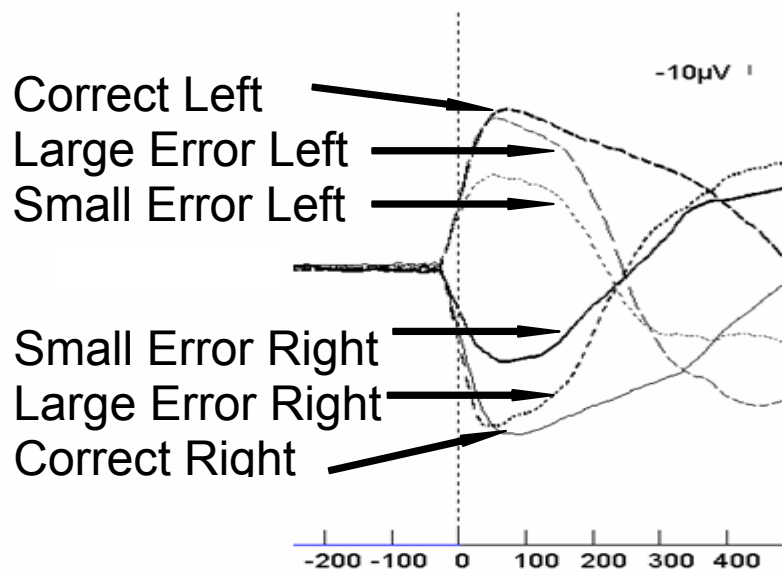


Figure 5.1: EOG group averages for correct responses, small and large errors for left (upward deflection) and right (downward deflection) saccades.

ERN and Pe Measurement.

The effects of horizontal eye movements on central scalp EEG are minimal; however, blink artefacts were corrected for using a regression procedure that displays the residual scalp ERP with the eye-channel signal removed on a trial-to-trial basis. This procedure permits manual rejection of the trial in the rare case when there is overcorrection. This method thus reduces noise introduced by overcorrection that is occasionally found in automated eye-correction procedures.

After this procedure, correct and error ERPs were created based on response-locked averages and smoothed with a 5-point moving window average. Response-locked averages still preserve the positivity related to the stimulus-generated P300, normally within the 200 ms preceding the response, as can be seen in Figure 5.2. The P300 is normally affected by sleepiness (Gosselin et al., 2005) and therefore to use the pre-response period with its positivity related to the P300 as a baseline would confound the P300 amplitude effects with the Ne/ERN effects. Thus, to minimize any effect that the stimulus-related P300 had on these averages, a baseline of -600 to -400 ms relative to response was used.

The amplitude of the Ne/ERN was measured as the maximum deflection between 50 and 120 ms post response. Because the Pe often had slow rising waveforms or poorly defined peaks, Pe amplitude was measured as the mean amplitude between 200-400 ms (Nieuwenhuis et al., 2001). The sites scored for analyses were FCz for the Ne/ERN, and Pz for the Pe as these were the sites of maximal deflection for these two components. Only 15 of the original 17 subjects were analyzed. One was excluded because of an almost complete

lack of errors and another because the original data file became corrupted and unreadable by the scoring software.

Results

Subjective ratings.

A series of paired t-tests were conducted to examine the individual subjective ratings of sleepiness, effort, and performance from the visual analogue scales. The results indicated that individuals were subjectively more sleepy in the sleepy condition ($M=46.9$, $SD=27.3$) than in the alert condition ($M=10.4$, $SD=11.1$), $t(14)=4.48$, $p<.001$. Individuals' ratings of subjective effort did not differ significantly, indicating that participants exerted a comparable amount of effort in the two conditions (alert, $M=70.1$, $SD=17.8$ vs. sleepy effort $M=75.0$, $SD=15.8$), $t(14)=1.22$, $p=.24$). Lastly, there was no significant difference in the subjective rating of performance across the conditions, $t(14)=1.88$, $p=.08$; however, the difference was in the expected direction wherein participants felt that in the sleepy condition their performance was poorer ($M=40.36$, $SD=18.6$) than when alert ($M=28.79$, $SD=22.2$). Thus, during the sleepy-condition participants reported feeling more tired, exerted a comparable amount of effort, yet may not have felt that they were performing as well as when in the alert condition.

Behavioural results.

Further investigations of response times and size of errors committed were analysed using a two (alert/sleepy) by two (small/large error) within-subjects ANOVA. There were no

differences in latency to initiate an anti-saccade based on level of alertness ($M=285.5$, $SD=36.8$ vs. $M=284.0$, $SD=38.7$, $p=.84$) or size of errors ($M=287.3$, $SD=37.9$ vs. $M=282.2$, $SD=37.7$, $p=.38$), nor was there any interaction ($p=.99$). There were also no differences in the number of errors based on alertness ($M=7.57$, $SE=.69$ vs. $M=7.57$, $SE=.94$, $p=.99$) or size of errors ($M=7.97$, $SE=.82$ vs. $M=7.17$, $SE=.78$, $p=.10$), nor was there any interaction ($p=.31$). As expected, response times to errors ($M=285.9$, $SE=7.0$) were faster than for corrects ($M=369.2$, $SE=9.96$), $F(1,13)=103.8$, $p<.001$. However, response times when participants were sleepy ($M=329.5$, $SE=9.69$) were not slower than those when they were alert ($M=325.6$, $SE=6.89$) $F(1,13)=.29$, $p=.60$) and there was no interaction, $F(1,13)=.49$, $p=.50$.

The mean response times for correct responses following errors ($M=384.1$, $SE=13.52$) were in the expected direction compared to correct responses following correct responses ($M=364.5$, $SE=9.12$) but failed to reach significance, $F(1,13)=3.38$, $p=.09$). There was no effect of alertness, $F(1,13)=.001$, $p=.98$, and no interaction, $F(1,13)=.13$, $p=.72$. However, because of the small number of errors these results may not be very illuminating or stable.

Electrophysiological results.

A similar two (alert/sleepy) by two (small/large error) repeated-measures ANOVA was conducted to examine the amplitudes and latencies of components of the Ne/ERN. To obtain a stable Ne/ERN, a minimum of 7 trials is required for averaging; however, only 7 subjects had at least 7 errors in each of the four conditions. The results reported here are based on these 7 participants; however, identical analyses of the 10 subjects with a minimum

of 5 errors per condition and all 15 participants regardless of number of errors yielded similar results. Thus, there does not appear to be any systematic bias in selecting these 7 participants (see Appendix G for examples of individual Ne/ERN/Pe waves forms).

The amplitude of the Ne/ERN measured at FCz was greater for large errors ($M = -9.24$, $SE = 1.6$) than small errors ($M = -6.02$, $SE = 1.09$), $F(1, 6) = 11.1$, $p = .016$, but was unrelated to alertness, $F(1, 6) = .13$, $p = .73$ (see Figure 5.2). The latencies of the Ne/ERN were shorter for the small errors ($M = 38.22$, $SE = 9.10$) than the large errors ($M = 59.44$, $SE = 5.20$), $F(1, 6) = 11.5$, $p = .015$. The amplitude of the Pe measured at Pz was larger during the alert condition ($M = 11.22$, $SE = 1.54$) than the sleepy condition ($M = 5.54$, $SE = 1.72$), $F(1, 6) = 9.76$, $p = .02$. However, it was unrelated to the size of the error $F(1, 6) = .25$, $p = .64$ (see Figure 5.2).

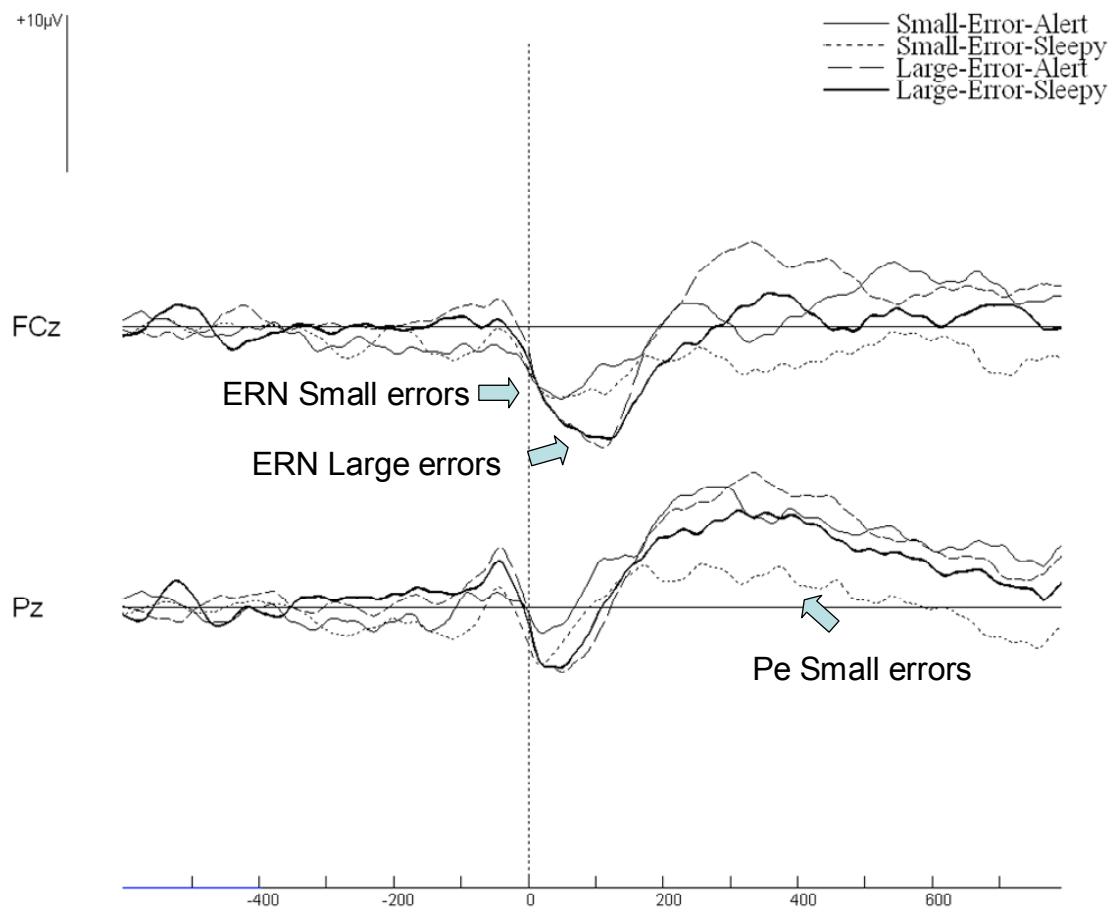


Figure 5.2: Grand-averaged response-locked ERPs for large and small errors. There was no effect of sleepiness on the Ne/ERN ($p=.73$); however, the Pe was reduced in the sleepy condition ($p=.02$). Also the Ne/ERN associated with small errors had both lower amplitude ($p=.02$) and shorter latency ($p=.02$).

Discussion

The electrophysiological response to errors can be broken down into two basic components, the Ne/ERN and Pe. These two components are increasingly thought to be largely dissociable (see Overbeek et al., 2005 for a review). In the present study, the

Ne/ERN, interpreted by some as a reaction to the detection or recognition of an error (see Falkenstein et al., 2004 for a review), was not significantly reduced by sleepiness. However, the Pe, thought to represent further, perhaps emotional evaluation of the error (see Falkenstein et al., 2004), was significantly reduced. Also, the amplitude of the Ne/ERN was related to the size of the error in both the sleepy and alert conditions.

Subjective and Behavioural Effects

Previous research has shown that Ne/ERN and Pe amplitudes can be affected by motivation (Pailing & Segalowitz, 2004b) and response times (Hajcak, Vidal & Simons, 2004), and the Pe can be affected by error rates (Dywan et al., 2004). However, in the current study, any differences in the Ne/ERN and/or Pe do not appear to be attributable to these factors. Self-reported effort, performance and objective latency to initiate the response and the number of errors were comparable across conditions and size of errors. In other words, the participants were trying just as hard and performing similarly across conditions and response sizes. As expected, the response times for errors were faster than for correct responses and post-error slowing (the response times on correct trials following errors minus those following correct responses) was in the expected direction although it did not reach significance ($p=.09$). Therefore, any observed differences in the Ne/ERN or Pe do not appear to be attributable to any behavioural factors; however, there were differences in the reported level of sleepiness. Therefore, the only significant difference between the conditions, aside from the expected differences in response times comparing errors and correct trials, was the level of sleepiness.

The effects of sleepiness on the Ne/ERN and Pe

The present result showing no significant reduction in the amplitude of the Ne/ERN after sleep deprivation is somewhat different from those of Scheffers et al. (1999) and Tsai et al. (2005), who did find a significant reduction. There are several possibilities for this discrepancy. One is the amount of time awake. The amount of sleep deprivation in the current experiment was approximately 4 hours less than that employed by Scheffers et al. (1999) and 6-7 hours less than that of Tsai et al. (2005). There may be some critical threshold between 20 and 26 hours of wakefulness when error detection becomes less effective or operates differently.

Another is the difference in baselines used. We employed a baseline of 400-600 ms prior to response. Our use of this baseline was designed to prevent contamination from the P300 and its variance to the initial stimulus into the measurement of the Ne/ERN. Scheffers and colleagues used a pre-stimulus baseline, presumably to also avoid contamination of the Ne/ERN from the preceding P3. However, Tsai et al. (2005) employed a baseline of -150 to -50 ms prior to the response in their response-locked averages. The issue here is that they also reported a significant reduction in the amplitude of the P300 (approx 1.5 μV) and mean P300 latencies of ~ 340 ms and response times of ~ 391 ms when alert and ~ 349 and ~ 391 ms, respectively, when sleepy. Therefore, the baseline they chose occurred at a time when the EEG amplitudes differed by 1 to 2 μV across conditions. They also reported a reduction in Ne/ERN amplitude of about 2.5 μV . Therefore, this reduction is likely a result, at least in part, of the baseline used in addition, of course, to the larger length of sleep deprivation in

their study.

Another potential reason for the discrepancies in these studies may be the tasks and paradigms used. Tsai et al. (2005) used an arrow Flanker, similar to the letter Flanker employed in the current study. However, Scheffers et al. (1999) used more complicated visual and memory search tasks that were repeated 9 times (including practice), so the more difficult tasks and habituation may have added to the effect attributed to sleepiness. In their experiment, Scheffers et al. (1999) reported Ne/ERN amplitude differences in not only the amount of time awake, but also in the type of task (visual versus memory) and memory load (high versus low). They also found differences in response times and error rates between the tasks, so the reported differences Sheffers et al. (1999) attribute to sleepiness may have been affected by habituation, difficulty, or some interaction among factors.

Another concern is that Tsai et al. (2005) employed instructions that were based on speed of responding. Participants were instructed to “speed up”, “maintain current speed”, or “slow down” based on response time in order to obtain approximately 15% errors. By emphasizing speed they may have altered the focus of the participants. Gehring et al. (1993) found that when participants were instructed to respond as quickly as possible (in contrast to as accurately as possible), the Ne/ERN was attenuated. The effect on the Ne/ERN and Pe by attempting to maintain a 15% error rate through alteration of response time is unknown. However, considering that mean response times and error rates still differed significantly between the alert and sleep deprived conditions, this meant that participants likely were receiving different instructions in each condition.

We found very similar results to the current study using a standard letter flanker task with the same participants (Chapter 4), reporting no significant differences in the Ne/ERN amplitude between the alert and sleep-deprived sessions; however, there was a reduction in terms of the Pe. In Tsai et al. (2005) and the current study, significant reductions were observed in the Pe after sleep deprivation which may reflect reductions in the emotional evaluation of the error, as suggest by Falkenstein (2004).

Overbeek et al. (2005) assert that the Pe may actually be more reflective of salience (emotional or cognitive), motivational significance or conscious recognition of the error. They reviewed all the literature up to August of 2005 and found only limited support for the affective-processing (emotional evaluation), and the behaviour-adaptation hypothesis (relation of Pe to post-error slowing). Therefore, the reduction we observed in the Pe may be due to a lack of further evaluation or importance of the error. Of course, in normal experience, it is difficult to dissociate these aspects of the experience.

Overbeek et al. (2005) tentatively suggested that the Pe may actually be similar to a P3b to the error but concede that the existing data are insufficient to address this issue and further research is needed to properly examine this hypothesis. We showed support for this notion earlier by making use of individual differences in the generation of the P300; individuals who produce a larger stimulus-locked P300 also tend to produce larger Pe (Davies et al., 2001). Other studies have noted that the Pe amplitude can be related to the number of errors (Dywan et al., 2004) although this was not the case in the current study.

Are the errors during the sleepy session noticed?

Nieuwenhuis et al. (2001) used an anti-saccade task to elicit Ne/ERNs and reported that there was no difference in Ne/ERN amplitude between perceived and unperceived errors; however, they did find a significant reduction in the Pe amplitude between the perceived and unperceived errors. They interpreted this as an indication that the Ne/ERN may not require conscious recognition of the error and this forms part of the logic behind the Overbeek et al. (2005) proposition that the Pe may actually be related to the conscious recognition of the error. In the Nieuwenhuis et al. (2001) study the participants were asked after each trial whether they had made an error or not. Therefore, the participant may have recognized an imminent error (hence produced an Ne/ERN) but aborted the erroneous response in time to honestly report that a correct response had been made (hence no Pe). Endrass, Franke, and Kathmann (2005) used a similar saccade countermanding task and found similar results, namely an Ne/ERN to unperceived errors and a larger Pe to perceived errors.

The Nieuwenhuis et al. (2001) and Endrass et al. (2005) experiments, while thought provoking, do not demonstrate or invalidate several previous findings that appear to indicate that the Ne/ERN may require conscious recognition of the error. Sheffers and Coles (2000) reported that the size of the Ne/ERN correlates with subjective confidence in having made an error, and findings that relate Ne/ERN amplitude to instruction (Ullsperger & Szymanowski, 2004) appear to contradict the idea that conscious awareness is not required for the Ne/ERN. Another issue in the Nieuwenhuis et al. (2001) and Endrass (2005) papers is that in both

experiments, participants were asked to make a dichotomous decision between a correct and erroneous response. There was no third option for errors that were “almost” made, such as hesitations or partial errors.

We did not require our participants to indicate whether they felt their response on each trial was correct or incorrect, but it would be interesting to speculate what the subjective experience is during a trial on which only a small error is made. Unfortunately, paradigms requiring participants to evaluate each individual trial may affect the way participants approach the task and in turn affect the Ne/ERN and Pe. To the best of our knowledge the effect of interrupting a task has not been systematically studied.

Experiments involving partial errors have shown that an Ne/ERN is observed on behaviourally correct trials when errors were originally initiated, but successfully inhibited. Masaki and Segalowitz (2004) reported that when trials were time-locked to EMG initiation and binned according to fully correct, partial error (initiation of an incorrect response measured by EMG that was successfully inhibited and followed by correct response) and full error (no correction), a clear Ne/ERN to partial errors was observed. The amplitudes were smaller and the latencies were shorter for the Ne/ERNs associated with partial errors.

We also found that for our small errors (all of which were corrected), the amplitudes and latencies were smaller. This may be because if the Ne/ERN indeed reflects awareness of an error being initiated and it is initiated soon enough, the participant has more time to detect the erroneous response and begin successful corrective action. We observed a virtually non-existent Pe after the small sleepy errors (see Figure 5.2). A visual comparison of the

Ne/ERN and Pe after small sleepy errors in the current experiment shows some striking similarities to the unrecognized errors in the Nieuwenhuis et al. (2001) paper (see their Figure 4). The preservation of the Ne/ERN but greatly reduced Pe in both situations appears to be a potentially fruitful area of future research. If the Pe does reflect either emotional assessment of the error (Falkenstein, 2004) or conscious recognition of the error (Nieuwenhuis et al., 2001; Endrass et al., 2005; Overbeek et al., 2005) then the lack of a Pe to small errors when participants are sleepy is clear evidence of the potential dangers of attempting to perform hazardous tasks while sleepy. If errors are not being recognized and/or assessed appropriately then corrective action may not be taken.

Conclusions

The present results, taken along with the results presented in Chapter 4 and previous research (Sheffers et al., 1999; Tsai et al., 2005), provide further electrophysiological evidence for the dangers associated with sleep deprivation. Sleep deprivation has long been associated with an increase in errors (e.g. Nakano, Araki, Michimori, Inbe, Hagiwara, & Koyama, 2000) but now we have evidence of impaired recognition, evaluation and remediation of errors, sometimes in the absence of increased response times and overall error rates. This has serious implications for the point at which individuals should be considered impaired because of sleepiness.

The impact of failure to detect or assess errors made while sleepy can have severe implications for individuals such as injury or death after a failure to respond appropriately while driving. More importantly, if the error is made by an individual responsible for

monitoring critical instrumentation, the results can affect (potentially kill) thousands of people and cost millions of dollars to correct (e.g., Chernobyl, Three Mile Island, and Bhopal; for a review see Mitler et al. 1988). Further research should be undertaken to try to determine the point at which the amplitudes of the Ne/ERN and Pe are reduced and if this corresponds to the onset or likelihood of performance failure.

CHAPTER 6

General Discussion

The thrust of this research was to examine the effects of relatively mild levels of sleep deprivation on performance, performance monitoring, cognitive function, attentional allocation, and frontal lobe functioning. Initial discussions for this dissertation research stemmed from my prior interest in not only performance while sleepy but also an observation that the symptoms of mild head injury, especially those associated with dysfunction of the prefrontal cortex, appeared to parallel the behavioural and subjective changes associated with sleepiness. This research was designed to test, using electrophysiological measures, the notion that the frontal lobe is especially sensitive to mild sleep deprivation, even though the previous research had failed to demonstrate any such deficits. Although the results support the basic hypotheses involving deficits in executive function in general, the electrophysiological effects do not appear to be strictly or exclusively related to the prefrontal cortex. Nonetheless, there are consistent and significant effects noted in several electrophysiological indices of attention allocation and performance monitoring, despite the absence of significant behavioural deficits.

Previous research has shown that the effects of sleep deprivation are often not observed behaviourally during mild sleep deprivation, especially if the individual is motivated to perform. Alterations in brain function after 24, 36 or more hours of wakefulness have been reported previously using fMRI (e.g. Drummond et al., 1999, 2000). In this research, changes in brain function were found after only 20-22 hours of wakefulness,

through the examination of various ERP paradigms. These results indicate that brain activation is altered and that these alterations, despite preserved behaviour on relatively simple tasks, also indicate that there are significant decrements in cognitive functioning that could lead to errors if the tasks being performed were to suddenly become more demanding.

Attentional Allocation and Frontal Lobe Functioning

The first two studies (Chapters 2 and 3) involved the anterior and posterior attentional systems. During the sleepy condition only, the latency of the P300 in the dual task increased significantly indicating slower stimulus processing. In addition, changes in the amplitude of the P300 to the first stimulus in the CNV paradigm appeared to indicate a lowered ability to discriminate between important and unimportant stimuli. Taken together these results show a pattern of subtle alterations in stimulus processing, to which we will now turn.

The P300 has a long history and has been associated with a variety of cognitive functions. The amplitude of the P300 has been shown repeatedly to be decreased by sleep deprivation (e.g. Corsi-Cabrera et al., 1999). In the context of this research, its relationship to not only sleep deprivation, but also attention and indirectly distraction was examined. The traditional interpretation of the P300 is that it is associated with stimulus updating (Donchin, 1981). In a standard oddball paradigm, each stimulus is compared to the previous (or standard) stimulus and if a change is detected then working memory is updated and the P300 is reflective of this process (Donchin, Haras, Bashore, Coles, & Gratton, 1986).

The amplitude of the P300 has also been associated with the amount of attention allotted to the task. If attention is directed (focused) on the task, the P300 amplitude is

higher. If attention is directed away from the task because of secondary, distracting task, or not directed at all because of instruction, the amplitude decreases (Polich, 1986). Thus, the decrease in P300 amplitude typically seen after sleep deprivation may mean that changes in arousal may affect attention and/or memory processes, because presumably as arousal declines, so does attention. In study 1, no significant changes in P300 amplitude were detected that could be attributed to arousal. This may have been due to the P300 tasks being early in the test battery and the level of sleep deprivation being mild. In either case, these results show that adequate memory updating or attentional allocation was taking place, and attentional levels may have been adequate.

The latency of the P300 is considered an index of processing or categorization speed (see Polich & Criado, 2006 for a review). Interestingly, P300 latency has been shown to be somewhat independent of response time. In study 1, increased P300 latency was observed in the sleepy condition with a distracting task, despite response time not being affected by sleepiness. Response times were slower for the dual task, but were stable across the two levels of alertness. This increased P300 latency under the dual conditions of distraction and sleepiness may indicate a reduced cognitive efficiency, or cognitive slowing. Increases in P300 latency have been associated with aging, cognitive decrements associated with dementia, and poorer performance on neuropsychological tests (see Polich & Criado, 2006, for a review). Therefore, the increases in P300 latency observed in the dual task of study 1 during the sleep-deprived condition, may be indicative of a system on the brink of failure.

The effect on the P300 related to the first stimulus in the Go/NoGo task reinforces

this idea of subtle reduced cognitive functioning. There was no secondary task, so there were no effects on P300 latency. The primary effect in this paradigm was associated with P300 amplitude. In the incentive (pay) condition, the only effects on the P300 amplitude were associated with the type of stimulus. The P300 amplitude was clearly diminished for the NoGo trials, but was unrelated to sleepiness (see Figure 3.3). However, in the non-incentive (un-paid) condition, there was less of a differentiation between the Go and NoGo trials (see Figure 3.4). The amplitude of the P300 has been shown to be sensitive to salience or relevance of the target (see Polich & Criado, 2006). Therefore, this interaction of P300 amplitude among sleepiness, incentive and target type indicates a reduced ability to distinguish between the important and unimportant events without special incentives. It is as if the automatic regulation of attentional allocation is less active when one is sleepy. It takes conscious motivation to bring this back to normal.

It is important to keep in mind that all of these effects on the P300 occurred in the absence of any significant changes in response time due to sleepiness. In terms of behavioural measures alone, the participants were performing essentially at baseline levels even though they had been awake over 20 hours during testing. Thus, these differences in ERP patterns were not due to behavioural differences associated with experimental conditions, but rather they reflect electrocortical patterns known to relate to attentional resources. In the context of simple repetitive tasks, sleepy participants may be at risk of poor and possible dangerous performance should these resources be required.

Performance (Error) Monitoring

The ability to correct errors is, by definition, contingent on the detection of these errors. The error-negativity (Ne/ERN) and error-positivity (Pe) are good indices of these processes. In Chapter 4 and 5, there was no significant decrease in Ne/ERN amplitude based on sleepiness, yet there was a large decrease in the amplitude of the Pe. The Ne/ERN has been associated with error-detection (Coles et al., 2001) and possibly the response conflict associated with response slips (van Veen & Carter, 2002); however, recent evidence appears to indicate that the Ne/ERN is more closely related to some error-detection process than simply motor conflict generated by an attempt to correct the response (Masaki & Segalowitz, 2004). The Pe has been hypothesized to reflect error evaluation (Falkenstein, 2004). However, this may also be compatible with research suggesting that the Pe could actually be the electrophysiological marker for conscious recognition of the error (Nieuwenhuis et al., 2001).

Reductions in the Ne/ERN and CNV have been reported during mental fatigue (Boksem, Meijman, & Lorist, 2006). In these tasks, participants had to complete very long testing paradigms (2+ hours) but in the current studies the tasks were typically between 5 and 12 minutes with rests between each, so the effects noted were more likely due to sleepiness as opposed to on-task fatigue. Also, because the two CNV tasks were conducted in the same order each time (non-incentive followed by incentive) it could be argued that the increases observed were a result of participants becoming more familiar with the tasks, or the effect of some sort of learning. However, Boksem et al. (2006) noted decreases in the amplitude of the CNV during their long testing sessions that returned to normal when participants were

motivated, indicating that the decreases in CNV amplitude were more dependent on motivation than learning or fatigue. Therefore, the addition of a Go/NoGo condition proved to be an important manipulation in order to demonstrate the apparent diminished ability to differentiate between important and unimportant stimuli when participants are sleepy, which a standard CNV task (one without a NoGo condition) would not have detected.

Importance of ERP measures

The apparent discrepancy between the results of this thesis and previous research, which found little or no effect on performance and cognitive measures after less than 24 hours of sleep deprivation, demonstrates the importance and utility of ERP measures. By utilizing ERP measures I could clearly demonstrate some of the subtle effects in electrocortical activity and cognitive processing not observable in behaviour. This may influence how we view mild sleep deprivation and whether sleepy individuals are actually able to perform tasks effectively and competently. Sleepiness degrades cognitive performance. The consistent results in this thesis clearly demonstrate that. Behaviour, as measured by simple tasks, was typically not affected, yet across all tasks and motivation levels there were significant changes in these various ERPs that can be attributed to sleepiness.

Sleepiness and Motivation

One factor in performance cited in previous examples of sleep deprivation research is that with sufficient motivation, performance can be maintained. In this research, behavioural performance (response time) improvements were noted, but in spite of these improvements,

the ERPs were still altered by sleepiness. The CNV and P300 in chapter 3 showed that stimulus discrimination was impaired, even under conditions of higher motivation and maintenance of performance.

Limitations

Despite the significant findings of this study, there were several limitations, which could be examined in future research. The most apparent drawback is that only females participated in this study and results may not be able to be generalizable to everyone. Therefore, future research should be conducted to examine possible gender differences in cognitive responses to sleep and attentional impairments. A larger sample size would also increase the reliability of the results and allow for an individual-differences analysis. Another major limitation is that only those with regular sleeping patterns were assessed. Future research may include those more prone to sleep deprivation, such as shift-workers, to see if they may be less affected by the lack of sleep. Also, comparisons of attentional impairments between normal samples and those with attentional disorders could be examined to see how these participants' cognitive processes differ from one another. There are many other contexts in which this type of neurophysiological investigation could be employed in order to gain more advanced knowledge of how individuals' cognitive processes function.

Practical Applications

There are two main implications that speak to practical issues. The first is that this series of studies has demonstrated that there are subtle electrocortical effects on attention and performance monitoring associated with sleep deprivation that occur earlier than has been

previously thought and that cannot be readily documented with purely behavioural measures. The fact that these effects can be demonstrated electrophysiologically indicates that cortical resources are at risk with sleep deprivation during the simple (and somewhat tedious) tasks used, tasks that are often not so different from seemingly safe but repetitive activities required in many walks of life. However, electrophysiological measures normally show large individual differences across individuals, and therefore repeated-measures designs, such as were employed in the present thesis, are needed to capture these effects reliably.

The second practical result is that this research indicates that there is a need for continued and perhaps closer examination of performance after mild sleep deprivation to determine just how long people can adequately continue to perform repetitive tasks under these conditions. The common admonition that complex tasks become impossible after sleep deprivation may be misplaced; it is in the context of repetitive and not-very-interesting tasks that sleep deprivation affects attentional and performance capacity so that the introduction of sudden challenges may cause a risk for performance failure. The subtle changes reported in this paper may represent the early signals of a system at risk for performance decline or failure. However, a demonstration of these electrophysiological measures actually predicting performance failures is a task for another day.

References

- Akerstedt, T. (1991) Sleepiness at work: Effects of irregular work hours. In T. H. Monk (Ed.) *Sleep, Sleepiness and Performance*. (pp. 129-154) Chichester: Wiley.
- Akerstedt, T., & Folkard, S. (1994) Prediction of intentional and unintentional sleep onset. In R. D. Ogilvie and J. R. Harsh (Eds.), *Sleep onset: Normal and Abnormal Processes*. (pp. 73-88). Washington: American Psychological Association.
- Akerstedt, T., & Gillberg, M. (1990) Subjective and objective sleepiness in the active individual. *International Journal of Neuroscience*, *52*, 29-37.
- Arnedt, J. T., Owens, J., Crouch, M., Stahl, J., & Carskadon, M. A. (2005). Neurobehavioral performance of residents after heavy night call vs after alcohol ingestion. *Jama*, *294*(9), 1025-1033.
- Bares, M., & Rektor, I. (2001). Basal ganglia involvement in sensory and cognitive processing. A depth electrode CNV study in human subjects. *Clin Neurophysiol*, *112*(11), 2022-2030.
- Basile, L. F. H., Brunder, D. G., Tarkka, I. M., & Papanicolaou, A. C. (1997). Magnetic fields from human prefrontal cortex differ during two recognition tasks. *International Journal of Psychophysiology*, *27*(1), 29-41.
- Bendak, S., 12-h workdays: Current knowledge and future directions. *Work Stress*, 2003, *17*(4): 321-336.

- Binks, P. G., Waters, W. F., & Hurry, M. (1999). Short-term total sleep deprivations does not selectively impair higher cortical functioning. *Sleep*, 22(3), 328-334.
- Bocca, M. L., & Denise, P. (2006). Total sleep deprivation effect on disengagement of spatial attention as assessed by saccadic eye movements. *Clinical Neurophysiology*, 117(4), 894-899.
- Boksem, M. A. S., Meijman, T. F., & Lorist, M. M. (2006). Mental fatigue, motivation, and action monitoring. *Biological Psychology*, 72, 123-132.
- Bonnet M, H. & Arand, D. L. (2003). Clinical effects of sleep fragmentation versus sleep deprivation. *Sleep Medicine Reviews*, 7, 297-310.
- Braver, T. S., Barch, D. M., Gray J. R., Molfese, D. L., & Snyder, A. (2001). Anterior cingulate cortex and response conflict: Effects of frequency, inhibition and errors. *Cerebral Cortex*, 11, 825-836.
- Cajochen, C., Foy, R., & Dijk, D. J. (1999). Frontal predominance of a relative increase in sleep delta and theta EEG activity after sleep loss in humans. *Sleep Research Online*, 2(3), 65-69.
- Campbell, K. B., & Colrain, I. M. (2002). Event-related potential measures of the inhibition of information processing: II. The sleep onset period. *International Journal of Psychophysiology*, 46(3), 197-214.
- Campbell, K. B., Suffield, J. B., & Deacon, D. L. (1990). Electrophysiological assessment of cognitive disorder in closed head-injured outpatients. *Electroencephalography and Clinical Neurophysiology, Supplement*, 41, 202-215.

- Carrillo-de-la-Pena, M. T. & Cadaveira, F. (2000). The effect of motivational instructions on P300 amplitude. *Clinical Neurophysiology*, 30(4), 232-239.
- Coles, M. G. H., Scheffers, M. K. & Holroyd, C. B. (2001). Why is there an ERN/Ne on correct trials? Response representations, stimulus-related components, and the theory of error-processing. *Biol Psychol*, 56:173-189.
- Corsi-Cabrera, M., Arce, C., Del Rio-Portilla, I. Y., Perez-Garci, E., & Guevara, M. A. (1999). Amplitude reduction in visual event-related potentials as a function of sleep deprivation. *Sleep*, 22(2), 181-189.
- Cote, K. A. (2002). Probing awareness during sleep with the auditory odd-ball paradigm. *International Journal of Psychophysiology*, 46(3), 227-241.
- Cote, K. A., De Lugt, D. R., & Campbell, K. B. (2002). Changes in the scalp topography of event-related potentials and behavioral responses during the sleep onset period. *Psychophysiology*, 39(1), 29-37.
- Daan, S., Beersma, D., & Borbely, A. (1984). Timing of human sleep: Recovery process gated by a circadian pacemaker. *American Journal of Physiology*, 246, R161-R178.
- Davies, P. L., & Segalowitz, S. J. (2000). Motivational effect on CNV. *Psychophysiology*, 37, S34.
- Davies, P. L., Segalowitz, S. J., Dywan, J., & Pailing, P. E. (2001). Error-related negativity and positivity as they relate to other ERP indices of attentional control and stimulus processing. *Biological Psychology*, 56, 191-206.

- Dikman, Z.V. and Allen, J.J.B., (2000). Error monitoring during reward and avoidance learning in high- and low-socialized individuals. *Psychophysiology*, 37(1): 43-54.
- Dinges, D. F., Pack, F., Williams, K., Gillen, K. A., Powell, J. W., Ott, G. E., et al. (1997). Cumulative sleepiness, mood disturbance, and psychomotor vigilance performance decrements during a week of sleep restricted to 4-5 hours per night. *Sleep*, 20(4), 267-277.
- Donchin, E. (1981). Surprise!.....Surprise?. *Psychophysiology*, 18, 493-513.
- Donchin, E., Karis, D., Bashore, T., Coles, M. Gratton, G. (1986). Cognitive psychophysiology and human information processing. In M. Coles, E Donchin, & S Porges (Eds.) *Psychophysiology Systems, Processes and Applications*. pp. 244-267. Guilford Press: New York.
- Drummond, S. P., & Brown, G. G. (2001). The effects of total sleep deprivation on cerebral responses to cognitive performance. *Neuropsychopharmacology*, 25, S1, S68-S73.
- Drummond, S, P., Brown, G. G., Gillin, J. C., Striker, J. L., Wong, E. C., & Buxton, R. B. (2000). Altered brain responses to verbal learning following sleep deprivation. *Nature*, 403, 655-657.
- Drummond, S. P. Brown, G. G., Stricker, J. L., Buxton, R. B. Wong, E. C., Gillian, J. C., & Janigro, D. (1999). Sleep deprivation-induced reduction in cortical functional response to serial subtraction. *Neuroreport: For Rapid Communication of Neuroscience Research*, 10, 18, 3745-3748.

- Drummond, S. P., Gillin, J. C., & Brown, G. G. (2001). Increased cerebral response during a divided attention task following sleep deprivation. *J. of Sleep Research, 10*(2), 85-92.
- Drummond, S. P., Meloy, M. J., Yanagi, M. A., Orff, H. J., & Brown, G. G. (2005). Compensatory recruitment after sleep deprivation and the relationship with performance. *Psychiatry Res, 140*(3), 211-223.
- Dywan, J., Mathewson, K. J., & Segalowitz, S. J. (2004). Error related ERP components and source monitoring in older and younger adults. In M. Ullsperger & M. Falkenstein (Eds.), *Errors, conflicts, and the brain: Current Opinions on Performance Monitoring*. Leipzig: Max Planck Institute for Cognition and Neuroscience, pp. 184-191.
- Dywan, J., Segalowitz, S. J., & Williamson, L. (1994). Source monitoring during name recognition in older adults: Psychometric and electrophysiological correlates. *Psychology and Aging, 9*, 568-577.
- Eimer, M. (1993). Effects of attention and stimulus probability on ERPs in a Go/Nogo task. *Biological Psychology, 35*, 123-138.
- Elbert, T., Ulrich, R., Rockstroh, B., & Lutzenberger, W. (1991). The processing of temporal intervals reflected by CNV-like brain potentials. *Psychophysiology, 28*(6), 648-655.
- Endrass, T., Franke, C., & Kathmann, N. (2005). Error awareness in a saccade countermanding task. *Journal of Psychophysiology, 19*, 275-280.
- Eriksen, B.A. and Eriksen, C.W. (1974). Effects of noise letters upon the identification of a target letter in a nonsearch task. *Percept. Psychophys., 16*(1): 143-149.

- Everling, S. & Fisher, B. (1998). The anti-saccade: A review of basic research and clinical studies. *Neuropsychologia*, 36, 885-899.
- Falkenstein, M. (2004). ERP correlates of erroneous performance. In M. Ullsperger & M. Falkenstein (Eds.), *Errors, conflicts, and the brain Current Opinions on Performance Monitoring*. pp.5-13. Leipzig: Max-Planck-Institut
- Falkenstein, M., Hohnsbein, J., Hoormann, J., & Blanke, L. (1991). Effects of crossmodal divided attention on late ERP components. II. Error processing in choice reaction tasks. *Electroencephalogr Clin Neurophysiol*, 78(6), 447-455.
- Folkard, S., & Akerstedt, T. (1991) A three process model of the regulation of alertness and sleep. In R. Broughton & R. Ogilvie (Eds.) *Sleep, Arousal and Performance*. (pp. 11-26). Cambridge: Birkhauser
- Fuster, J. (1999). Cognitive functions of the frontal lobes. In B. L. Miller & J. L. Cummings (Eds.). *The human frontal lobes: Functions and disorders* (pp. 187-195). New York: Guilford.
- Garcia-Larrea, L., Perchet, C., Perrin, F., & Amenedo, E. (2001). Interference of cellular phone conversations with visuomotor tasks: An ERP study. *Journal of Psychophysiology*, 15, 14-21.
- Gauthier, P., & Gottesmann, C. (1983). Influence of total sleep deprivation on event-related potentials in man. *Psychophysiology*, 20(3), 351-355.
- Gehring, W. J., Goss, B., Coles, M. G. H., Meyer, D. E., & Donchin, E. (1993). A neural system for error detection and compensation. *Psychological Science*, 4, 385-390.

- Gehring, W. J., Himle, J. and Nisenson, L. G. (2000). Action-monitoring dysfunction on obsessive-compulsive disorder. *Psychol Sci*, *11*:1-6
- Geisler, M. W. & Polich, J. (1990). P300 and time of day: Circadian rhythms, food intake, and body temperature. *Biological Psychology*, *31*, 117-136.
- Gosselin, A., De Koninck, J., & Campbell, K. B. (2005). Total sleep deprivation and novelty processing: implications for frontal lobe functioning. *Clinical Neurophysiology*, *116*(1), 211-222.
- Hajcak, G., McDonald, N. & Simons, R. F. (2003). To err is autonomic: Error-related brain potentials, ANS activity, and post-error compensatory behavior. *Psychophysiology*, *40*:895-903.
- Hajcak, g., Vidal, F., & Simons, R. F. (2004). Difficulties with easy tasks: ERN/Ne and stimulus component overlap. In M. Ullsperger & M. Falkenstein (Eds), *Errors, conflicts, and the brain. Current opinions on performance monitoring* (pp. 204-211). Leipzig: Max Planck Institute for Human Cognitive and Brian Sciences
- Harrison, Y, & Horne, J. A. (2000). The impact of sleep deprivation on decision making: A review. *Journal of Experimental Psychology: Applied*, *6*, 236-249.
- Hoffman, L. D. & Polich, J. (1998). EEG, ERPs and food consumption. *Biological Psychology*, *48*, 139-151.
- Holroyd, C. B., & Coles, M. G. H. (2002). The neural basis of human error processing: reinforcement learning, dopamine, and the error-related negativity. *Psychological Review*, *109*, 679-709.

- Holroyd, C.B., Coles, M.G.H. and Nieuwenhuis, S.. Medial prefrontal cortex and error potentials. *Science*, 2002, 296(5573): 1610-1611.
- Holroyd, C., Dien, J. & Coles, M. (1998). Error-related scalp potentials elicited by hand and foot movements: Evidence for an output-independent error-processing system in humans. *Neuroscience Letters*, 242, 65-68.
- Horne, J. A. (1991). Dimensions to sleepiness. In T. H. Monk (Ed.) *Sleep, sleepiness and performance* (pp. 169-196). Oxford: Wiley & Sons.
- Horne, J. A. (1993). Human sleep, sleep loss and behaviour: Implications for the prefrontal cortex and psychiatric disorders. *British Journal of Psychiatry*, 162, 413-419.
- Horne, J. A. & Ostberg, O., A self-assessment questionnaire to determine morningness - eveningness in human circadian rhythms. *Int. J. of Chron.*, 1976 4: 97-100.
- Horne, J. A., & Pettitt, A. N. (1985). High incentive effects on vigilance performance during 72 hours of total sleep deprivation. *Acta Psychologica*, 58(2), 123-139.
- Jolicoeur, P., & Dell'Acqua, R. (1999). Attentional and structural constraints on visual encoding. *Psychological Research*, 62, 154-164.
- John, M. W. A new method for measuring daytime sleepiness: The Epworth sleepiness scale. *Sleep*, 1991, 14: 540-545.
- Jones, K, & Harrison, Y. (2001). Frontal lobe function, sleep loss, fragmented sleep. *Sleep Medicine Reviews*, 5, 463-475.
- Killgore, W. D., Balkin, T. J., & Wesensten, N. J. (2006). Impaired decision making following 49 h of sleep deprivation. *Journal of Sleep Research*, 15(1), 7-13.

- Kleitman, N. (1963). *Sleep and Wakefulness* rev ed. Chicago: University of Chicago Press.
- Klein, C. & Berg, P. (2001). Four-week test-retest stability of individual differences in the saccadic CNV, two saccade task parameters, and selected neuropsychological tests. *Psychophysiology*, 38, 704-711.
- Knight, R. T. (1984). Decreased response to novel stimuli after prefrontal lesions in man. *Electroencephalogr Clin Neurophysiol*, 59(1), 9-20.
- Kok, A. (2001). On the utility of P3 amplitude as a measure of processing capacity. *Psychophysiology*, 38, 557-577.
- Koslowsky, M and Babkoff, H. (1992). Meta-analysis of the relationship between total sleep deprivation and performance. *Chronobio. Int.*, 9:132-136
- Lee, H. J., Kim, L., Kim, Y. K., Suh, K. Y., Han, J., Park, M. K., et al. (2004). Auditory event-related potentials and psychological changes during sleep deprivation. *Neuropsychobiology*, 50(1), 1-5.
- Lee, H. J., Kim, L., & Suh, K. Y. (2003). Cognitive deterioration and changes of P300 during total sleep deprivation. *Psychiatry & Clinical Neurosciences*, 57(5), 490-496.
- Leger, D. (1994). The cost of sleep related accidents: A report for the national commission on sleep disorders research. *Sleep*, 17, 84-93.
- Lieberman, H. R., Tharion, W. J., Shukitt-Hale, B., Speckman, K. L., & Tulley, R. (2002). Effects of caffeine, sleep loss, and stress on cognitive performance and mood during U.S. Navy SEAL training. Sea-Air-Land. *Psychopharmacology*, 164(3), 250-261.

- Loh, S., Lamond, N., Dorrian, J., Roach, G., & Dawson, D. (2004). The validity of psychomotor vigilance tasks of less than 10 minute duration. *Behavior Research Methods, Instruments & Computers*, 32, 339-346.
- Lubin, A. Performance under sleep loss and fatigue. In S. S. Kety, E. V. Evarts and H. L. Willimas (Eds) *Sleep and Altered States of Consciousness*. Williams and Wilkins, Baltimore, 1967: 506-513.
- Luu, P., Collins, P., & Tucker, D. M. (2000). Mood, personality, and self-monitoring: negative affect and emotionality in relation to frontal lobe mechanisms of error monitoring. *J Exp Psychol Gen*, 129(1), 43-60.
- Makeig, S., & Jung, T. P. (1996). Tonic, phasic, and transient EEG correlates of auditory awareness in drowsiness. *Cognitive Brain Research*, 4, 15-25,
- Malone, S. & Iacono, W. (2002). Error rate on the antisaccade task: Heritability and developmental change in performance among preadolescent and late-adolescent female twin youth. *Psychophysiology*, 39, 664-673.
- Masaki, H., & Segalowitz, S. J. (2004). Error negativity: A test of the response conflict versus error detection hypotheses. In M. Ullsperger & M. Falkenstein (Eds.), *Errors, conflicts, and the brain Current Opinions on Performance Monitoring*. pp.76-83. Leipzig: Max-Planck-Institut.
- McCarthy, M. E. and Waters, W. F. (1997). Decreased attentional responsitivity during sleep deprivation: Orienting response latency, amplitude and habituation. *Sleep*, 20:114-123.

- McCartt, A. T., Pack, A. M., Walsleben, J. A., Hammer, M. C., & Pack, A. I. (1995). Scope of the problem of sleepiness and vehicular crashes: A population survey approach. *Sleep Research, 24*, 449.
- Mitchell, R.J. and Williamson, A.M. Evaluation of an 8 hour versus a 12 hour shift roster on employees at a power station. *Appl. Ergon.*, 2000, 31(1): 83-93.
- Mitler, M.M., Carskadon, M.A, Czeisler, C.A, Dement, W.C, Dinges, D.F, Graeber, R.C. (1988). Catastrophes, sleep, and public policy: Consensus report. *Sleep, 11*, 100-109.
- Morris, T. L., & Miller, J. C. (1996). Electrooculographic and performance indices of fatigue during simulated flight. *Biological Psychology, 42*(3), 343-360.
- Muller-Gass, A., & Campbell, K. (2002). Event-related potential measures of the inhibition of information processing: I. Selective attention in the waking state.[erratum appears in Int J Psychophysiol. 2003 Feb;47(2):185]. *International Journal of Psychophysiology, 46*(3), 177-195.
- Murphy, T. I., Richard, M., Masaki, H., & Segalowitz, S. J. (2006). The effect of sleepiness on performance monitoring: I know what I am doing, but do I care? *Journal of Sleep Research, 15*, 11-15.
- Nakano, T, Araki, K., Michimori, A., Inbe, H., Hagiwara, H. & Koyama, E. (2000). Temporal order of sleepiness, performance and physiological indices during 19-h sleep deprivation. *Psychiatry and Clinical Neurosciences, 54*, 280-282.
- Nash, A. J., & Fernandez, M. (1996). P300 and allocation of attention in dual-tasks. *International Journal of Psychophysiology, 23*, 171-180.

- Naitoh, P., Johnson, L. C., & Lubin, A. (1971). Modification of surface negative slow potential (CNV) in the human brain after total sleep loss. *Electroencephalography and Clinical Neurophysiology*, 30, 17-22.
- Nieuwenhuis, S., Ridderinkhof, K. R., Blom, J., Band, G. P. H., & Kok, A. (2001). Error-related brain potentials are differentially related to awareness of response errors: Evidence from an antisaccade task. *Psychophysiology*, 38, 752-760.
- Nilsson, J. P., Soderstrom, M., Karlsson, A. U., Lekander, M., Akerstedt, T., Lindroth, N. E., et al. (2005). Less effective executive functioning after one night's sleep deprivation. *Journal of Sleep Research*, 14(1), 1-6.
- Ogilvie, R. D., Simons, I. A., Kuderian, R. H., MacDonald, T., & Rusternburg, J. (1991). Behavioral, event-related potential, and EEG/FFT changes at sleep onset. *Psychophysiology*, 28, 54-64.
- Overbeek, T. M. J., Nieuwenhuis, S., Ridderinkhof, K. R., (2005) Dissociable components of error processing: On the functional significance of the Pe vis-à-vis the ERN/Ne. *Journal of Psychophysiology*. 19, 319-329.
- Pack, A. M., Cucchiara, A., Schwab, W., Rodgman, E, & Pack, A. I. (1994) Characteristics of accidents attributed to the driver having fallen asleep. *Sleep Research*, 23, 141.
- Pack, A. M., Willis, D. K., & Pack, A. I. (1995). Variation in methods used by state police to identify a crash as being caused by a driver falling asleep at the wheel. *Sleep Research*, 24, 452.

- Pailing, P.E. and Segalowitz, S.J. (2004a). The effects of uncertainty in error monitoring on associated ERPs. *Brain Cognition.*, 56(2): 215-233.
- Pailing, P.E. and Segalowitz, S.J. (2004b). The error-related negativity as a state and trait measure: Motivation, personality, and ERPs in response to errors. *Psychophysiology*, 41(1): 84-95.
- Pailing, P.E., Segalowitz, S.J., Dywan, J. and Davies, P.L. (2002). Error negativity and response control. *Psychophysiology*, 39(2): 198-206.
- Patrick, G. T., and Gilbert, J. A. On the effects of loss of sleep. *Psychol. Rev.*, 1896, 3: 469-483.
- Polich, J. P300 development from auditory stimuli. (1986). *Psychophysiology*, 23(5): 590-597.
- Polich, J., & Criado, J. R. (2006). Neuropsychology and neuropharmacology of P3a and P3b. *Int J Psychophysiol*, 60(2), 172-185.
- Polli, F. E., Barton, J. J S; Vangel, M., Goff, D. C., Iguchi, L., Manoach, D. S. (2005). Schizophrenia patients show intact immediate error-related performance adjustments on an antisaccade task. *Schizophrenia Research*, 82, 191-201
- Ramirez, J., Bomba, M., Singhal, A., & Fowler, B. (2005). Influence of a visual spatial attention task on auditory early and late Nd and P300. *Biological Psychology*, 68, 121-134.
- Reyner, L. A. & Horne, J. A. (1997). Suppression of sleepiness in drivers: Combination of caffeine with a short nap. *Psychophysiology*, 34(6), 721-725.

- Ridderinkhof, R., De Vlugt, Y., Bramlage, A., Spaan, M., Elton, M., Snel, J. and Band, G.P.H. (2002). Alcohol consumption impairs detection of performance errors in mediofrontal cortex. *Science*, 298(5601): 2209-2211.
- Rosahl, S. K., & Knight, R. T. (1995). Role of prefrontal cortex in generation of the contingent negative variation. *Cerebral Cortex*, 5(2), 123-134.
- Santamaria, J, & Chiappa, K. H. (1987). The EEG of drowsiness in normal adults. *Journal of Clinical Neurophysiology*, 4, 327-382.
- Santesso, D. L., Segalowitz, S. J., & Schmidt, L. A. (2006). Error-related electrocortical responses are enhanced in children with obsessive-compulsive behaviors. *Dev Neuropsychol*, 29(3), 431-445..
- Segalowitz, S. J. (1999). ERPscore program: Peak and area analysis of event-related potentials. St Catharines, Ontario. Brock University.
- Segalowitz, S. J., & Barnes, K. L. (1993). The reliability of ERP components in the auditory oddball paradigm. *Psychophysiology*, 30(5), 451-459.
- Segalowitz, S. J., Unsal, A., & Dywan, J. (1992a). Cleverness and wisdom in 12-year-olds: Electrophysiological evidence for late maturation of the frontal lobe. *Developmental Neuropsychology*, 8, 279-298.

- Segalowitz, S. J., Unsal, A., & Dywan, J. (1992b). CNV Evidence for the Distinctiveness of Frontal and Posterior Neural Processes in a Traumatic Brain Injured (TBI) population. *Journal of Clinical and Experimental Neuropsychology*, *14*, 108-128.
- Segalowitz, S. J., Velikonja, D., & Storrie-Baker, J. (1994). Attentional allocation and capacity in waking arousal.. In R. D. Ogilvie and J. R. Harsh (Eds.) *Sleep onset: Normal and Abnormal Processes*. (pp. 351-368). Washington: American Psychological Association.
- Scheffers, M.K. and Coles, M.G.H. (2000). Performance monitoring in a confusing world: Error-related brain activity, judgments of response accuracy, and types of errors. *J. Exp. Psycho. Hum.*, *26*(1): 141-151.
- Scheffers, M., Humpfrey, D., Stanny, R. R., Kramer, A. F. & Coles, M. G. H. (1999). Error-related processing during a period of extended wakefulness. *Psychophysiology*, *36*, 149-157.
- Scott, J. P. R., McNaughton, L. R., & Polman, R. C. J., (2006). Effects of sleep deprivation and exercise on cognitive, motor performance and mood. *Physiology and Behavior*, *87*, 396-408.
- Shucard, D. W., Abara, J. P., McCabe, D. C., Benedict, R. B.H., & Shucard, J. L. (2004). The effects of covert attention and stimulus complexity on the P3 response during an

- auditory continuous performance task. *International Journal of Psychophysiology*, 54, 221-230.
- Smith, M. E., McEvoy, L. K., & Gevins, A. (2002). The impact of moderate sleep loss on neurophysiologic signals during working-memory task performance. *Sleep*, 25(7), 784-794.
- Stemmer, B., Segalowitz, S.J., Witzke, W. and Schönle, P.W.. (2003). Error detection in patients with lesions to the medial prefrontal cortex: An ERP study. *Neuropsychologia*, 42(1): 118-130.
- Sugerman, J., & Walsh, J. (1989) Physiological sleep tendency and ability to maintain alertness at night. *Sleep*, 12, 106-112.
- Tecce, J. J. (1972). Contingent negative variation (CNV) and psychological processes in man. *Psychological Bulletin*, 77(2), 73-108
- Tecce, J. J., & Cattanach, L. (1993). Contingent negative variation (CNV). In E. Niedermeyer & F. Lopes da Silva (Eds.), *Electroencephalography: Basic principles, clinical applications, and related fields* (3rd ed., pp. 887-910). Baltimore: Williams & Wilkins.
- Thomas, M., Sing, H., Belenky, G., Holcomb, H., Mayberg, H., Dannals, R., et al. (2000). Neural basis of alertness and cognitive performance impairments during sleepiness. I. Effects of 24 h of sleep deprivation on waking human regional brain activity. *Journal of Sleep Research*, 9(4), 335-352.

- Travis, F., & Tecce, J. J. (1998). Effects of distracting stimuli on CNV amplitude and reaction time. *International Journal of Psychophysiology*, *31*, 45-50.
- Tsai, L., Young, H., Hsieh, S., & Lee, C. (2005). Impairment of error monitoring following sleep deprivation. *Sleep*, *28*, 707-713.
- Ullsperger, M. and Szymanowski F. ERP correlates of error relevance. In M. Ullsperger & M. Falkenstein (Eds.), *Errors, conflicts, and the brain: Current Opinions on Performance Monitoring*. Leipzig: Max Planck Institute for Cognition and Neuroscience, 2004: 171-177.
- van Dongen, H. P., Baynard, M. D., Maislin, G., & Dinges, D. F. (2004). Systematic interindividual differences in neurobehavioral impairment from sleep loss: evidence of trait-like differential vulnerability. *Sleep*, *27*(3), 423-433.
- van Dongen, H. P., Maislin, G., Mullington J. M. and Dinges, D. F. (2003). The cumulative cost of additional wakefulness: Dose-response effects on neurobehavioral functions and sleep physiology from chronic sleep restriction and total sleep deprivation. *Sleep*, *26*, 117-126.
- van Veen, V., & Carter, C. S. (2002). The timing of action-monitoring processes in the anterior cingulate cortex. *J Cogn Neurosci*, *14*(4), 593-602.
- Verleger, R., Jaskowski, P., & Wascher, E. (2005). Evidence for an integrative role of P3b in linking reaction to perception. *Journal of Psychophysiology*, *19*, 165-181.
- Walter, W. G., Cooper, R., Aldridge, V. J., McCallum, W. C., & Winter, A. L. (1964). Contingent Negative Variation: an electrical sign of sensori-motor association and

- expectancy of the brain brain. *Nature*, 203, 380-384.
- Webb, W. B. (1995). The cost of sleep-related accidents: A reanalysis. *Sleep*, 18, 276-280.
- Wu, J., Buchsbaum, M. S., Gillin, J. C., Tang, C., Cadwell, S., Wiegand, M., et al. (1999). Prediction of antidepressant effects of sleep deprivation by metabolic rates in the ventral anterior cingulate and medial prefrontal cortex. *Am J Psychiatry*, 156(8), 1149-1158.
- Yamamoto, T., Saito, Y., & Endo, S. (1984). Effects of disturbed sleep on contingent negative variation. *Sleep*, 7(4), 331-338.
- Yeung, N., Botvinick, M.M. and Cohen, J.D. (2004). The Neural Basis of Error Detection: Conflict Monitoring and the Error-Related Negativity. *Psych. Rev*, 111(4): 931-959.

Appendix A

HEALTH AND HISTORY QUESTIONNAIRE

Name: _____ Date: _____

Name of Interviewer: _____

First, I would like to get some general background information:

Age: _____

D.O.B.: _____

Handedness: _____

Current Address: _____ Permanent: _____

Phone: _____

Phone: _____

Marital Status: _____

Current Living Arrangements (with family, friends, alone ?)

Currently Employed? _____ Describe type of work hours/ duties/ etc Last employed?

Education to Date? (Grades completed? Special Training?)

In general how would you describe yourself as a student? (A B C)

Best Subjects?

Worst Subjects?

Ever fail a grade? Circumstances?

Major Hobbies? Current/Past?

Now I would like to ask you some questions about your health. Have you had any

- Serious childhood diseases?
- Injuries, falls, broken bones?
- Sports Injuries?
- High Fevers
- Serious Infections?
- Diabetes?
- Liver Problems?
- Kidney Problems?
- Problems with arteries?
- Stroke?
- Seizures?
- Hypertension?
- Heart Problems? Angina?
- Blood Problems?
- Breathing problems?
- Asthma? Emphysema?
- Tuberculosis
- Skin Disorders?
- Serious Allergies?
- Cancer? Treatment?
- Surgery?
- Psychiatric Problems?
- Anxiety or Depression?
- Problems with vision?
- Hearing problems?
- Paralysis or numbness?
- Fainting or dizziness?
- Serious Headaches?
- Blurred vision?
- Serious viral/immune disorders? Treatment?
- Stomach Problems? Digestion? Ulcers?
- Bowel or bladder problems?
- Movement problems, arthritis, sore joints?

If YES to any of the above, please explain. When, how serious, long term effects?

Nature of treatment (e.g chemo therapy)

Are you taking any prescribed over-the-counter medications? Which Ones? Purpose?

Using the terms none, mild, moderate or heavy, how would you describe your use of caffeine _____, alcohol _____, other recreational drugs _____

Current/Past? Changes?

Appendix B

SUBJECT SCREENING QUESTIONNAIRE

Name: _____ Age: _____

Telephone: _____ Sex: _____

Please circle the best response for each question or fill in the blank if required.

1. How many hours do you routinely sleep each night?

less than 5 5 6 7 8 9 10 more than 10 **Does this vary much?** yes no

How long does it typically take you to fall asleep?

Less than 5 min. 5 to 10 min. 10 to 20 min over 20 min.

What time do you typically go to bed _____ Does this vary much? yes no

2. Do you smoke? Yes No **Have you ever smoked?** Yes No

How long has it been since you quit? _____

3. How many cups of coffee or tea do you drink in an average day? _____

4. How many sodas/pops do you drink in an average day? _____

5. How many alcoholic drinks do you consume in a week? _____

6. Are you taking any prescribed or non-prescribed drugs (including recreational drugs) OTHER THAN birth control pills? Yes No

7. Have you ever had a head injury? Yes No

8. Do you have any neurological disorders (seizures, etc)? Yes No

9. Have you ever been on medication for a long period of time? Yes No

10. How many times per month do you stay up until 3 or 4 a.m.

11. How well do you feel you can function after being awake for 20-24 hrs (i.e. in the middle of an "all nighter") compared to your usual daytime ability? Circle one.

Much worse Worse Slightly worse About the same Slightly better Better Much better

Appendix C

Circadian Rhythm Questionnaire

J. A. Horne and O. Ostberg

Instructions

1. Please read each question very carefully before answering.
2. Answer ALL questions.
3. Answer questions in numerical order.
4. Each question should be answered independently of the others. Do NOT go back and check your answers.
5. All questions have a selection of answers. For each question place a cross alongside ONE answer only. Some questions have a scale instead of a selection of answers. Place a cross at the appropriate point along the scale.
6. Please answer each question as honestly as possible. Both your answers and the results will be kept in strict confidence.
7. Please feel free to make any comments in the section provided below each question.

Please supply the information requested below.

Name:

Sex: Male Female

Age: ____ years

1. Considering your own "feeling best" rhythm, at what time would you get up if you were free to plan your day?

		-+-		-+-		-+-		-+-		-+-		-+-		
a.m.	5		6		7		8		9		10		11	12

2. Considering your own "feeling best" rhythm, at what time would you go to bed if you were free to plan your evening?

		-+-		-+-		-+-		-+-		-+-		-+-		-+-	
p.m.	8		9		10		11		12	a.m.	1		2	3	

- | | | |
|----|---|--|
| 3. | If there is a specific time at which you have to get up in the morning, to what extent are you dependent on being woken up by an alarm clock? | Not at all dependent _
Slightly dependent _
Fairly dependent _
Very dependent _ |
|----|---|--|

- | | | |
|----|---|--|
| 4. | Assuming adequate environmental conditions, how easy do you find getting up in the morning? | Not at all easy _
Not very easy _
Fairly easy _
Very easy _ |
|----|---|--|

- | | | |
|----|---|--|
| 5. | How alert do you feel during the first half hour after having woken in the morning? | Not at all alert _
Slightly alert _
Fairly alert _
Very alert _ |
|----|---|--|

- | | | |
|----|--|--|
| 6. | How is your appetite during the first half hour after having woken in the morning? | Very poor _
Fairly poor _
Fairly good _
Very good _ |
|----|--|--|

- | | | |
|----|--|--|
| 7. | During the first half hour after having woken in the morning, how tired do you feel? | Very tired _
Fairly tired _
Fairly refreshed _
Very refreshed _ |
|----|--|--|

- | | | |
|----|--|---|
| 8. | When you have no commitments the next day, at what time do you go to bed compared to your usual bedtime? | Seldom or never later _
Less than one hour later _
1-2 hours later _
More than 2 hours later _ |
|----|--|---|

9. You have decided to engage in some physical exercise. A friend suggests that you do this one hour twice a week and the best time for him/her is between 7:00 - 8:00 a.m. Bearing in mind nothing else but your own "feeling best" rhythm, how do you think you would perform?

Would be in good form _
 Would be in reasonable form _
 Would find it difficult _
 Would find it very difficult _

10. At what time in the evening do you feel tired and as a result in need of sleep?

p.m. 8 | - + - | - + - | - + - | - + - | - + - | - + - | - + - |
 9 10 11 12 a.m. 1 2 3

11. You wish to be at peak performance for a test which you know is going to be mentally exhausting and lasting for two hours. You are entirely free to plan your day and considering only your own "feeling best" rhythm which ONE of the four testing times would you choose?

8:00 - 10:00 a.m. _
 11:00 a.m. - 1:00 p.m. _
 3:00 - 5:00 p.m. _
 7:00 - 9:00 p.m. _

12. If you went to bed at 11:00 p.m. at what level of tiredness would you be?

Not at all tired _
 A little tired _
 Fairly Tired _
 Very Tired _

13. For some reason you have gone to bed several hours later than usual, but there is no need to get up at any particular time the next morning.

Which ONE of the following events are you most likely to experience?

Will wake up at usual time and will NOT fall asleep . . . _
 Will wake up at usual time and will doze thereafter . . . _
 Will wake up at usual time but will fall asleep again . . . _
 Will NOT wake up until later than usual _

14. One night you have to remain awake between 4:00 - 6:00 a.m. in order to carry out a night watch. You have no commitments the next day. Which ONE of the following alternatives will suit you best?

Would NOT go to bed until watch was over _
 Would take a nap before and sleep after _
 Would get a good sleep before and a nap after _
 Would take ALL sleep before watch _

15. You have to do two hours of hard physical work. You are entirely free to plan your day and considering only your own "feeling best" rhythm which ONE of the following times would you choose?

- 8:00 - 10:00 a.m. _
- 11:00 a.m. - 1:00 p.m. . . . _
- 3:00 - 5:00 p.m. _
- 7:00 - 9:00 p.m. _

16. You have decided to engage in hard physical exercise. A friend suggests that you do this one hour twice a week and the best time for him/her is between 10:00 - 11:00 p.m. Bearing in mind nothing else but your own "feeling best" rhythm, how do you think you would perform?

- Would be in good form _
- Would be in reasonable form _
- Would find it difficult _
- Would find it very difficult _

17. Suppose that you can choose your own work hours. Assume that you worked a FIVE hour day (including breaks) and that your job was interesting and paid by results. Which FIVE consecutive hours would you select?

12	1	2	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5	6	7	8	9	10	11	
12												12												11
Midnight												Noon												Midnight

18. At what time of day do you think that you reach your "feeling best" peak?

12	1	2	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5	6	7	8	9	10	11	
12												12												11
Midnight												Noon												Midnight

19. One hears about "morning" and "evening" types of people. Which ONE of these types do you consider yourself to be?

- Definitely a "morning" type _
- Rather more a "morning" than an "evening" type _
- Rather more an "evening" than a "morning" type _
- Definitely an "evening" type _

Circadian Rhythm Questionnaire Scoring Sheet

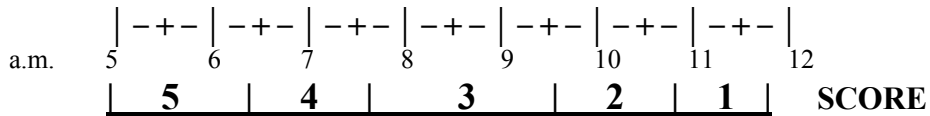
J. A. Horne and O. Ostberg

Scoring Instructions

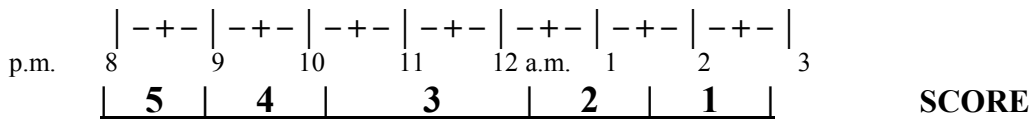
1. Each question receives only one score.
2. For questions which have a choice of four answers (#'s 3, 4, 5, 6, 7, 8, 9, 11, 12, 13, 14, 15, 16, 19) the score is shown on the right beside each choice.
3. For questions which require one mark on a continuous scale (#'s 1, 2, 10) the ranges which indicate the score to be assigned are shown below the scale.
4. For questions 17 and 18 assign the score which falls at the midpoint of the five hour period they have indicated.
5. Mark the score beside each question on the **original** questionnaire. **DO NOT** mark on this score sheet!
6. Add up all scores.
7. Use the table shown below to determine the category.
8. Mark the score and category on the cover of the **original** questionnaire.

Definite Morning	70-86
Moderate Morning	59-69
Neither	42-58
Moderate evening	31-41
Definite evening	16-30

1. Considering your own "feeling best" rhythm, at what time would you get up if you were free to plan your day?



2. Considering your own "feeling best" rhythm, at what time would you go to bed if you were free to plan your evening?



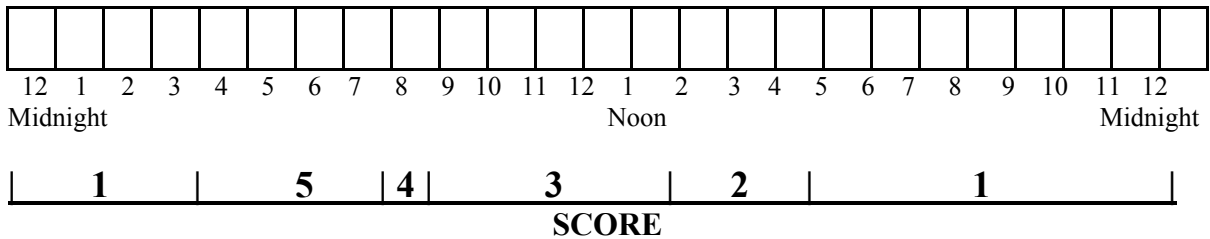
- | | | |
|----|---|--|
| 3. | If there is a specific time at which you have to get up in the morning, to what extent are you dependent on being woken up by an alarm clock? | Not at all dependent 4
Slightly dependent 3
Fairly dependent 2
Very dependent 1 |
| 4. | Assuming adequate environmental conditions, how easy do you find getting up in the morning? | Not at all easy 1
Not very easy 2
Fairly easy 3
Very easy 4 |
| 5. | How alert do you feel during the first half hour after having woken in the morning? | Not at all alert 1
Slightly alert 2
Fairly alert 3
Very alert 4 |
| 6. | How is your appetite during the first half hour after having woken in the morning? | Very poor 1
Fairly poor 2
Fairly good 3
Very good 4 |

SCORE

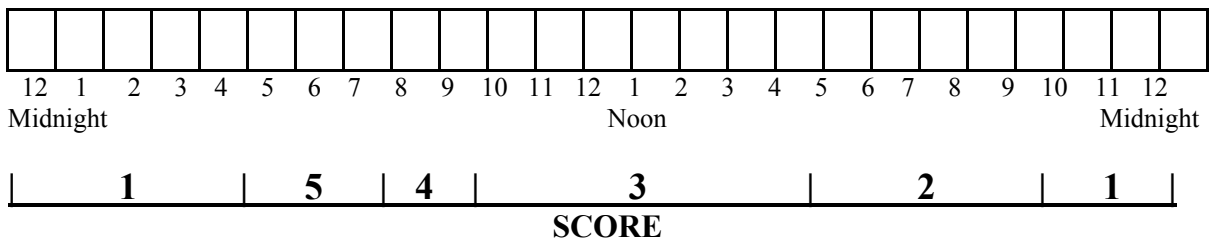
16. You have decided to engage in hard physical exercise. A friend suggests that you do this one hour twice a week and the best time for him/her is between 10:00 - 11:00 p.m. Bearing in mind nothing else but your own "feeling best" rhythm, how do you think you would perform?

- Would be in good form 1
- Would be in reasonable form 2
- Would find it difficult 3
- Would find it very difficult 4

17. Suppose that you can choose your own work hours. Assume that you worked a FIVE hour day (including breaks) and that your job was interesting and paid by results. Which FIVE consecutive hours would you select?



18. At what time of day do you think that you reach your "feeling best" peak?



SCORE

19. One hears about "morning" and "evening" types of people. Which ONE of these types do you consider yourself to be?

- Definitely a "morning" type 6
- Rather more a "morning" than an "evening" type . . . 4
- Rather more an "evening" than a "morning" type . . . 2
- Definitely an "evening" type 0

Appendix E

THE EPWORTH SLEEPINESS SCALE

(morning version) How likely are you to doze off or fall asleep in the following situations, in contrast to feeling just tired? Even if you have not done some of these things recently try to work out how they would have affected you. Use the following scale to choose the most appropriate number for each situation: **Please answer this as if it were approximately 2-4 hours after you woke up in the morning (i.e. about 10-11 a.m.)**

0 = no chance of dozing
1 = slight chance of dozing
2 = moderate chance of dozing
3 = high chance of dozing

SITUATION	CHANCE OF DOZING
Sitting and reading (at 10 a.m.)	_____
Watching TV (at 10 a.m.)	_____
Sitting inactive in a public place such as a theater or a meeting	_____
As a passenger in a car for an hour without a break (at 10 a.m.)	_____
Lying down to rest (at 10 a.m.)	_____
Sitting and talking to someone (at 10 a.m.)	_____
Sitting quietly after a meal without alcohol (at 10 a.m.)	_____
In a car, while stopped for a few minutes in traffic (at 10 a.m.)	_____

THE EPWORTH SLEEPINESS SCALE (Evening Version)

How likely are you to doze off or fall asleep in the following situations, in contrast to feeling just tired? Even if you have not done some of these things recently try to work out how they would have affected you. Use the following scale to choose the most appropriate number for each situation: **Please answer this as if it were approximately 4 hours after you would normally have gone to bed (i.e. about 3-4 a.m.)**

0 = no chance of dozing
1 = slight chance of dozing
2 = moderate chance of dozing
3 = high chance of dozing

SITUATION	CHANCE OF DOZING
Sitting and reading (at 4 a.m.)	_____
Watching TV (at 4 a.m.)	_____
Sitting inactive in a public place such as a theater or a meeting	_____
As a passenger in a car for an hour without a break (at 4 a.m.)	_____
Lying down to rest (at 4 a.m.)	_____
Sitting and talking to someone (at 4 a.m.)	_____
Sitting quietly after a meal without alcohol (at 4 a.m.)	_____
In a car, while stopped for a few minutes in traffic (at 4 a.m.)	_____

Appendix F

THE EPWORTH SLEEPINESS SCALE SCORING KEY

1 - 6	Congratulations, you are getting enough sleep!
7 - 8	Your score is average
9 and up	Seek the advice of a sleep specialist without delay

Other scoring from web

Epworth Sleepiness Scores (ESS) by Diagnosis

Diagnosis	Epworth Sleepiness Score	Range
Normal Controls	5.9 $\pm\pm$ 2.2	2 - 10
Primary Snoring	6.5 $\pm\pm$ 3.0	0 - 11
OSA	11.7 $\pm\pm$ 4.6	4 - 23
Narcolepsy	17.5 $\pm\pm$ 3.5	13 - 23
Idiopathic hypersomnia	17.9 $\pm\pm$ 3.1	12 - 24
Insomnia	2.2 $\pm\pm$ 2.0	0 - 6
PLMD	9.2 $\pm\pm$ 4.0	2 - 16

In OSA, ESS > 16 was only seen in patients with moderate to severe disease.

Appendix H

Objective Sleepiness

The Alpha Attenuation Test (AAT) (ref) was used as an electrophysiological (objective) measure of sleepiness. Participants are instructed to look at a fixation point on the computer. They will be prompted (by the computer) to alternately open and close their eyes each 30 seconds for 6 minutes. The Alpha Attenuation Co-efficient (AAC) is calculated as the ratio of eyes open to eyes closed alpha power (8-12 Hz measured at O2) during this task.

Auditory Oddball (P300) Task

A Standard (easy) Oddball consisting of 40 targets and 160 non-targets was used. The target tones will be 800 Hz tone and the non target tones 1000 Hz. All tones were 100 ms in duration with a rise/fall time of 5ms. The ISI varied between 1.3 and 1.6 seconds (mean 1.45 seconds). Participants were required to press the space bar each time they detected a target tone.

Working Memory Tasks

Working memory (WM) were assessed using the N-back task. Participants were required to complete two versions of this task. An “easy” version (1-back) and a “challenging” version (2 back). In both tests, 10 letters (both upper and lower case) were presented one at a time, at the center of the computer monitor for 250 ms. A total of 180 trials were presented with an ITI of 1750 msec. These were divided into three blocks of 60 trials with a 30 second break between the first and second blocks as well as the second and third blocks. For each version of this task, targets appear on 30% of the trials (18 targets per block) and each of the 10 letters appeared 15 times total (5 times per block).

In the 1-back condition, participants were required to respond if the letter that appeared was identical to the one that appeared immediately before it (regardless of case). For example if the sequence was X . . y . . r . . R . . , the participant would respond to the “R”. In the 2 back condition, participants were required to respond if the letter that appeared was identical to the one that had appeared 2 trials previously regardless of case (e.g. X F R f respond).

Dual Tasks

The dual task was simply the combination of the same auditory oddball task described above with a visual working memory task performed simultaneously. In the working memory task, the participant was presented with a series of numbers presented sequentially on the computer screen and was required to respond with their left hand each time three consecutive odd (e.g. 2, 3, 5, 1 respond), increasing (e.g. 3, 2, 3, 4 respond) or decreasing (e.g., 4, 7, 6, 5, respond) numbers appeared.

Saccade Tasks

The saccade/anti-saccade tasks were administered in two sections. In the first section the participant was required to attend to the focus point in the center of the computer monitor. A lower case o was presented for 250 ms either on the left or right side of the monitor (visual angle of 16°). The participant was instructed to look in the direction of the letter and then return their gaze to the central target as quickly as possible.

In the second phase the participant was instructed to look in the opposite direction to the letter (i.e. o flashes on left, look right) and then return to the target as quickly as possible. Each task consisted of 100 trials (randomly ordered, 50-right, 50-left) with an ISI of 1.5 seconds. In order to minimize head movements the participant placed her head on a chin rest

which was located 35 cm from the screen.

Flanker Task (Error Detection)

The Flanker Task required participants to respond to the central letter (S or H) embedded within 4 types of stimulus arrays. The stimuli will consist of HHHHHH or SSSSSS (80 of each) or SSHSS or HSHHH (160 times each). These are presented in the center of the computer screen for 250 ms with an ITI of 1 second. The keys used to respond will be counterbalanced, half the participants will press the D key with their left index finger when an H is the center letter and the K key with their right index finger when S is the center letter. The other participants will press D for S and K for H. Participants were instructed that accuracy is more important than speed but to respond quickly.

Contingent Negative Variation (CNV)

The CNV test will incorporate a Go/NoGo task. Participants received an initial warning stimulus in the center of the screen for 250 ms. This was either a red (NoGo) or green (Go) square. After a 2000 ms delay a target appeared on the screen. At this time the participant was to press the space bar if the warning stimulus was green, but to withhold any response if the stimulus was red. They were also instructed to wait for and then respond to the second stimulus and not attempt to anticipate it or “time” their responses. There were 30 “Go” and 30 “NoGo” trials. The ITI will vary randomly from 4 to 7 seconds (mean = 5.5).

This test had two conditions. The first condition (described above) was repeated with a financial incentive to illicit more effort. Participants earned \$0.10 for each appropriate response on Go trials with a response time of less than 250 ms and will be penalized for each response on a NoGo trial or response time of under 100 ms on a Go trial (indicating

inappropriate anticipation). Their reward was never negative however (i.e. they did not have to pay for bad performances)

Changing Oddball

The final ERP test will be a “changing” oddball (Murphy & Segalowitz, 2004). There were 16 blocks of trials. Each block consisted of between 7-10 targets and 21-30 non targets. Tones were 100 ms in length (5 ms rise/fall time) and were presented at 80 db from a speaker in front of the participant. The target and non-target tones differed by 700 Hz, ranged from 800 Hz to 2200 Hz, and were never repeated in subsequent blocks. The target was the higher tone for 8 blocks and the lower tone for the other 8 blocks. The inter-stimulus interval ranged from 1.2 to 1.6 seconds with a 7 second pause between blocks.

The instructions given to the participants were to listen to the first tone of each block, and then to respond by pressing the space bar on a keyboard as quickly as possible each time they heard a target tone, i.e., one that was different from the first tone. Participants were also instructed to fix their gaze on a focus point at the center of the computer monitor in front of them and minimize blinking during each block of trials.

The AAT was then repeated as the last test to assess the arousal level after testing has completed.

Appendix I

Subject ____ Date _____ Session 1 2 Condition A S

Please indicate how you feel by placing a mark on this line.

Very Sleepy _____ Very Alert

Please indicate how you feel by placing a mark on this line.

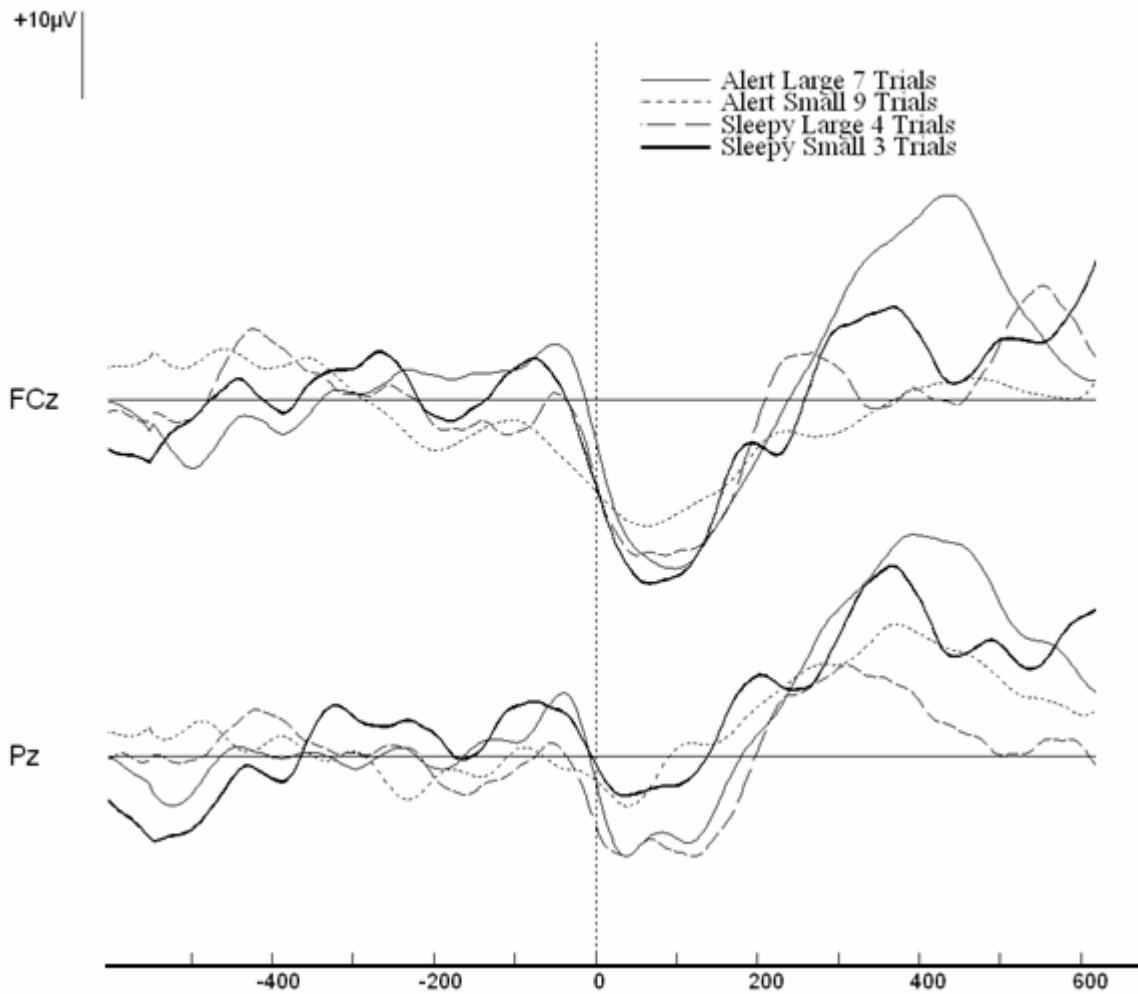
No Effort _____ Maximum Effort

Please indicate how well you think you performed on the previous task.

Very Poorly _____ Very Well

How many errors do you think you made _____.

Appendix J



These are event-related potentials (Ne/ERN/Pe) from each condition for one participant who had relatively few trials included in the average. This demonstrates that the Ne/ERN and Pe are both clearly identifiable even with fewer than 10 trials.