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**TOO TIRED TO TALK?
SLEEP, FATIGUE, AND SOCIAL
FUNCTIONING**

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Too tired to talk? Sleep, fatigue, and social functioning.
THESIS FOR DOCTORAL DEGREE (Ph.D.)

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“You want to know how to paint a perfect painting? It’s easy.
Make yourself perfect and then just paint naturally.”
- *Robert M. Pirsig, Zen and the Art of Motorcycle Maintenance*

ABSTRACT

Sleep has been shown to have many health promoting functions, and is vital for the maintenance of physiological, cognitive, and emotional well-being. Much of what we know about sleep derives from studies showing what happens when individuals do not obtain sufficient sleep. A number of such studies have shown that sleep may also be vital for one of the key drivers of human dominance - our ability to be social. The overall aim of this thesis is to advance our knowledge of the relationship between sleep and social functioning, specifically focusing on the short-term effects of insufficient sleep, poor sleep quality, and related states such as sleepiness and fatigue, on our ability to perform a number of socially vital behaviours and functions.

Paper I longitudinally investigated potential bidirectional relationships between sleepiness/sleep and the amount of social activity individuals engage in. This paper followed 681 participants who completed a time-use questionnaire over three weeks requiring individuals to report their activity every 30 minutes. Participants also completed the Karolinska Sleepiness Scale (KSS) six times per day and the Karolinska Sleep Diary (KSD) each morning. Activity categorised as ‘social activity’ was counted and its association to sleepiness and sleep duration was analysed. We observed that higher sleepiness predicted a decrease in probability of conducting social activity in the near future and a decrease in the duration of social activity. Sleep duration did not predict next day social activity. In the opposite direction, we found that social activity moderated the association between time-of-day and sleepiness. Additionally, an increase in the total amount of socialising per day predicted that individuals would sleep less subsequently. The study has implications for understanding the dynamic role of sleep in human social behaviour and suggests that sleepiness, likely due to decreased social motivation, may hinder the maintenance of a healthy social life.

Paper II employed an experimental sleep deprivation paradigm to investigate the effect of acute sleep loss on communication ability. Participants were randomised to either one night of total sleep deprivation (N = 91) or normal sleep (N = 92). The following day, communication ability was assessed via performance in two collaborative tasks with a partner (a model-building task and a word-description task). During these collaborative tasks, aspects of speech prosody were also measured (speaking duration, speaking volume, and speaking volume consistency). Participants additionally completed individual verbal fluency assessments. Performance on the model-building task was worse if the model-builder was sleep deprived, whereas the sleep deprivation appeared to boost performance in the instruction-giver. All other aspects measured seem unaffected by sleep loss. The results suggest that sleep deprivation leads to changes in communicative performance during longer instructive tasks, while simpler word-description tasks appear resilient.

Paper III assessed whether sleep deprivation leads to changes in facial appearance. Subjects (same data collection as Paper II; sleep deprived = 91, normal sleep = 90) were photographed and their skin tone was measured using a spectrophotometer. Using the photographs, the degree of eye-openness, mouth curvature, and periorbital darkness was calculated. A separate sample of raters (N = 63) judged the appearance of subjects using the facial photographs in three dimensions: paleness, fatigue, and healthiness. The results did not reveal any evidence of changes in facial appearance following sleep deprivation, in neither objective nor subjective measurements. However, decreased skin yellowness, less eye openness, downward mouth curvature, and periorbital darkness all predicted how fatigued individuals were rated by others. These results exemplify the difficulty of assessing fatigue from facial features alone.

Paper IV examined whether sleep was related to cognitive empathy ability. Study 1 (N = 291) investigates the effect of normal variation in sleep duration and sleep quality on our ability to recognise and categorise the emotional state of others. Study 2 (same data collection as Papers II and III; sleep deprived = 90, normal sleep = 91) investigated whether one night of total sleep deprivation impacted the ability to recognise and categorise the emotional state of others. Both studies tested performance on a multimodal forced-choice task of emotion recognition, where participants had to correctly categorise an actor-portrayed emotion on screen. Self-reported sleep duration/quality (Study 1), and sleep deprivation (Study 2) did not predict overall emotion recognition accuracy. Follow-up tests found no emotion-specific effects, apart from one positive association suggesting that greater self-reported sleep quality could predict more accurate recognition of disgust (Study 1). The combination of these studies suggests that the ability to accurately categorise the emotions of others is resilient to acute periods of insufficient sleep.

In summary, the work in this thesis has combined different study designs and data-sources to investigate the relationship between sleep and social functioning, as well as the influence of related states such as sleepiness and fatigue. We find evidence that social motivation and communication depends on aspects of sleep, while facial appearance and cognitive empathy appear resilient. This thesis therefore exemplifies the complex relationship between sleep and social functioning, while providing exciting directions for future research.

LIST OF SCIENTIFIC PAPERS

This doctoral thesis is compiled based on the following original papers, each being referred to by its roman numeral:

- I. **Holding, B. C.**, Sundelin, T., Schiller, H., Åkerstedt, T., Kecklund, G. & Axelsson, J. Sleepiness, sleep duration, and human social activity: An investigation into bidirectionality using longitudinal time-use data. *Manuscript*.
- II. **Holding, B. C.**, Sundelin, T., Lekander, M., & Axelsson, J. (2019). Sleep deprivation and its effects on communication during individual and collaborative tasks. *Scientific Reports*, 9(1), 3131.
- III. **Holding, B. C.**, Sundelin, T., Cairns, P., Perrett, D. I., & Axelsson, J. (2019). The effect of sleep deprivation on objective and subjective measures of facial appearance. *Journal of Sleep Research*, 28(6), e12860.
- IV. **Holding, B. C.**, Laukka, P., Fischer, H., Bänziger, T., Axelsson, J., & Sundelin, T. (2017). Multimodal emotion recognition Is resilient to insufficient sleep: Results from cross-sectional and experimental studies. *Sleep*, 40(11), zsx145.

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LIST OF ABBREVIATIONS

CPAP	Continuous positive airway pressure
CRP	C-reactive protein
DLPFC	Dorsolateral prefrontal cortex
DMN	Default mode network
EI	Emotional intelligence
ERAM	Emotion Recognition Assessment in multiple Modalities (task)
fMRI	Functional magnetic resonance imaging
IL-6	Interleukin 6
KSD	Karolinska Sleep Diary
KSS	Karolinska Sleepiness Scale
MDMA	Methylenedioxyamphetamine
mPFC	Medial prefrontal cortex
NREM	Non-rapid eye movement
OSA	Obstructive sleep apnea
PFC	Prefrontal cortex
PSG	Polysomnography
REM	Rapid eye movement
SCN	Suprachiasmatic nucleus
SD	Standard deviation
SleSI	Sleep and Social Interaction (data collection)
SSRI	Selective serotonin reuptake inhibitor
SWS	Slow wave sleep
TNF	Tumor necrosis factor
VMPFC	Ventromedial prefrontal cortex

1. HUMAN SOCIAL RELATIONSHIPS

*“Man is an animal that makes bargains: no other animal does
this - no dog exchanges bones with another”*
Adam Smith, *The Wealth of Nations*

Humans have been called *the* social animal. We have the superpower that allows us to work together like almost nothing else on earth. Anthropologists and others are still trying to work out exactly what happened, but humans have developed amazing ways in which we can pool our resources and brain power to achieve things that individually would have been impossible. Take writing this thesis for example, I'm sure you've seen in the acknowledgements (since that was probably the first thing you read) that the very book you're holding in your hand would not exist if it were not for me having (at least some) skills in communication and cooperation.

The possibility to use our social superpower is reliant on the fact that we can tap into our store of social capital. By this, it is meant that each person is encased in a social structure that includes access to family, friends, acquaintances, and a societal support structure which can be used to help ourselves and the entire social group. Not only can you think of it as a resource that can be used to maintain our health and wellbeing, in fact it's often the interactions with these groups of people that give our lives meaning. If for whatever reason we lose some of our social capital, we feel it deeply. Focusing on our more proximal social network (putting aside changes at the societal level), a decrease in the number or quality of relationships we have with family and friends around us is associated with lower happiness (Demir & Özdemir, 2010), increases in depression (Teo, Choi, & Valenstein, 2013), and poorer health outcomes (House, Landis, & Umberson, 1988). We as humans have a need to belong (Baumeister & Leary, 1995).

Given this, there is considerable concern whether we in developed countries are becoming too socially isolated and thus losing important social connections (Holt-Lunstad, 2017). Some have even called this the "loneliness epidemic" (Korrespondenterna, 2018). Whether we are becoming more socially isolated is difficult to know, though some research suggests that at least in the last few decades loneliness rates have been fairly stable (Dahlberg, Agahi, & Lennartsson, 2018). Nonetheless, there remains a substantial amount of loneliness reported across developed countries, and significant variation in how much social interaction members of the population engage in.

One could argue that it's not the sheer number of friends that matters, it's the quality of our interactions with others. It's our ability to have meaningful conversations and build strong social bonds. This is where things get trickier. What does it mean to be social and how does one have successful conversations? How would we even go about measuring that? Social psychology, a discipline one century old but with sentiments going back significantly further, is where we can look for some answers.

Recent studies highlight that our brains go into overdrive as soon as we see another person. Within the first seconds, if not milliseconds, once we see another person we are already making judgments (and forming impressions) regarding traits such as healthiness (Axelsson et al., 2018), attractiveness (Zebrowitz & Montepare, 2008), and even more complex social constructs such as trustworthiness (Todorov, Baron, & Oosterhof, 2008). In fact, it has been

suggested that the so called Default Mode Network (DMN) of the brain, an observable pattern of activity and connectivity between certain brain regions when at rest, is actually a state which is poised to pick up social information over almost anything else (Li, Mai, & Liu, 2014). One could therefore argue that the default state of the brain is to be social.

Focusing on non-verbal cues, perhaps one of the most salient things we can tell about a person is their mood or emotional state. Though the process for which we can assess this is more complex than many would expect. Research suggests that there are dissociable forms of person-to-person mood inference (Shamay-Tsoory, Aharon-Peretz, & Perry, 2009). Firstly, we have what is called cognitive empathy when we try to recognise and deduce a person's mood state. This is similar to perspective-taking or theory of mind (though there are differences between these). The second form is emotional empathy, which underlines the capacity of emotion to act as contagion. By observing someone displaying an emotion, the brain tends to invoke oneself to feel the observed mood. For best emotional (and social) functioning, we need both of these systems working together.

While assimilating the non-verbal emotional cues, often their meaning is accompanied by a further source of social information. Once we start talking, a whole new world of social cues is unleashed. Just the way that someone speaks can have significant impacts on how we perceive, interpret, and judge the speaker. For example, pitch and other aspects of voice prosody have been shown to influence others (Ponsot, Burred, Belin, & Aucouturier, 2018). The main course however is the substance of the dialogue. What are you talking about, does it make sense? Perhaps if it's just a general chitchat, these language things might not play such a large role in your future. But what if it's a politician talking? The stumbling discourse of a leader may mean losing an election. On the other hand, a smooth-talking car salesperson may result in you coming away with a new car. Effective communication, incorporates and leans on many different cognitive and behavioural functions (Sperber & Wilson, 1987). This ranges from basic cognitive functioning to higher functions such as language ability (Littlemore & Low, 2006). Of course, the exact cognitive skills involved likely depends on the desired outcome, which in the case of the car salesperson is persuading you to give out your bank details. But it could equally be surgical success in a medical setting or seamlessly instructing airplanes in a transport setting.

Not all people are created equally when it comes to socialising. A total unanimity of social skill would not only make the world a boring place, but probably would lead to inefficiencies in our social system. Some people struggle in areas of communication while other people thrive. As Edward Thorndike, one of the early influencers in psychology stated "the best mechanic in the factory may fail as a foreman for lack of social intelligence" (Thorndike, 1920). Personality research has shown that there are certain stable differences in how people report behaving in social situations. The most well-known is the introversion-extraversion dimension (McCabe & Fleeson, 2012), mostly related with how much drive an individual has towards social interaction. As a more broad predictor of social skills, Goleman reimaged social intelligence as a distinct skillset (Goleman, 2007), building on his popular emotional

intelligence (EI) concept which has had large impacts on work-organisational psychology (Zeidner, Roberts, & Matthews, 2008).

However, while we may have a roughly stable average ability in different social domains, humans are also distinctly inconsistent. From month-to-month, day-to-day, and in some cases hour-to-hour we can have noticeable shifts in our social abilities, behaviour, and motivations. Perhaps the most noticeable acute changes in social functioning has been observed following drug use. Pharmacological interventions such as following consumption of methylenedioxymethamphetamine (MDMA; Bershad, Miller, Baggott, & De Wit, 2016), alcohol (Dolder et al., 2017), and even caffeine (Smith, Lawrence, Diukova, Wise, & Rogers, 2012) have been shown to impact our social cognitive and behavioural functioning. There are also less abrupt changes in everyday human physiological states which are associated with changes in how we comprehend and behave during social situations. You might have heard of being ‘hangry’, which is when you are being disagreeable to others because you feel hungry (MacCormack & Lindquist, 2019). Similarly, if you feel sick, you might end up with what’s known as sickness behaviour where you avoid others, and generally become a bit withdrawn (Hennessy, Deak, & Schiml, 2014). And then there are feelings of sleepiness or fatigue. But before we talk more about that, we need to go over some sleep basics.

2. SLEEP

“When we wake up in bed on Monday morning and think of the various hurdles we’ve got to jump that day, immediately we feel sad, bored, and bothered. Whereas, actually, we’re just lying in bed.”
Alan Watts, *The Philosophies of Asia*

The rest-activity cycle is ubiquitous across the planet. Indeed the entire animal kingdom seems to have adapted to the 24-hour cycle of the earth’s rotation (Merrow, Spoelstra, & Roenneberg, 2005). The universality of sleep must mean that it is important. Humans spend one third of their lives asleep – roughly 20-30 years. Perhaps therefore it is no wonder that sleep has been found to play a vital role in the maintenance of human health. Research over the last 100 years has revealed how sleep regulates many aspects of human functioning. Some of the main theories regarding why we sleep include regulating synaptic plasticity to avoid energy loss (Tononi & Cirelli, 2014), providing time for the brain to consolidate memories to long(er) term storage (Grosmark & Buzsaki, 2016; Kaida, Niki, & Born, 2015), and even removing neurotoxic metabolic waste products such as beta-amyloid from the brain (Xie et al., 2013).

There are two different biological processes¹ going on in humans that need to be explained in order to understand sleep (see Figure 1).

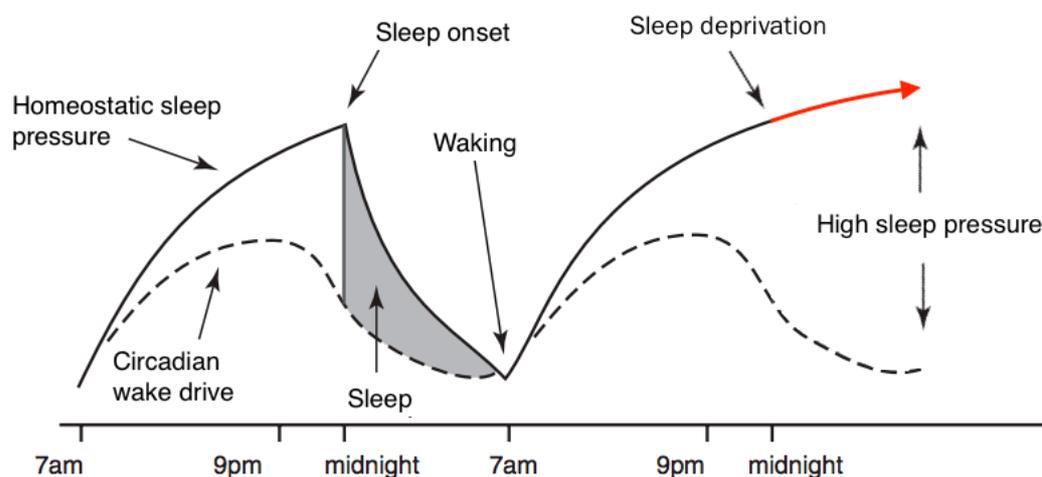


Figure 1. The two-process model of sleep-wake regulation, showing the relationships between the two processes under normal sleep and under sleep deprivation. Adapted from Muza (2018) with permission from the publisher.

First is the body's internal 24-hour clock. Most cells tested appear to have a clock, all synchronised to the timing of the suprachiasmatic nucleus (SCN) in the hypothalamus (Wright et al., 2013). As the earth takes 24 hours to turn on its axis, so too takes the brain 24 hours to run through its cycle. Though not precisely 24 hours, evolution has allowed some play in the system. This is why this internal oscillation has become known as the circadian (i.e. circa one day) rhythm. Our circadian rhythm acts to ensure that we appropriately cycle through a day-night rhythm, feeling alert or sleepy at the correct time of day. It also influences

¹ The so-called two process model of sleep-wake regulation was meant for describing sleep timing, rather than sleep functioning. To understand the process of moving from wake to sleep and back to wake, other models exist. For example the Phillips and Robinson model (Phillips & Robinson, 2007)

our nutritional intake, our emotions, core body temperature, our immune functioning, and many other processes.

So who sets the time on our internal clock? Well that would be the sun. We often think of the effect of sunlight being something that only botanists would consider, but this is a mistake. We as humans have specific cells, melanopsin cells (Güler et al., 2008), that respond only to the presence of light, sending signals to regions such as the SCN. Release of the hormone melatonin from the pineal gland, an internal messenger regulating the sleep-wake cycle, is directly dependent on signals (or actually lack of signals) from these light specific cells (Prayag, Najjar, & Gronfier, 2019). And just like plants, if we don't get sunlight we can become quite unwell. For example, because blind people do not get the light cues, they often show irregular sleep-wake patterns (Hartley, Dauvilliers, & Quera-Salva, 2018), which is in turn associated with multiple negative health outcomes (Baron & Reid, 2014).

We're not all ticking to the same beat though. Instead, you, the reader, will follow your own idiosyncratic pattern of peaks and troughs within the circadian waveform. For some people, the peak of wakefulness occurs earlier in the morning, leaving them to feel also sleepier early. There will be others whose circadian clock sends the signals of wakefulness very late in the evening. And then there is everything in between (Roenneberg, 2012).

Now let's talk about the second process, sleep homeostasis. The body has a method of assessing how long you have been awake, which is proposed to relate to the build-up of adenosine (Holst & Landolt, 2015). According to this theory, the concentration of adenosine increases minute by minute, and just like a dam filling up with water, the result is a greater and greater amount of pressure. The higher the sleep pressure, the harder it is to stay awake. The pressure will not decrease until you sleep and even then, it takes a full night of sleep (7-9 hours in an average adult) for the pressure to be back to baseline. This is what is meant by sleep homeostasis, sleep is the body's mechanism for keeping sleep pressure regulated.

Largely for the sake of simplicity, these two processes can be thought of as running in sync but also independently. This means that while the two systems are usually aligned, a sudden change in the running of one system should not necessitate a change in the running of the other system. However, there is some limited evidence suggesting that there may be a continuous interaction between the two processes. One review highlights that circadian phase modulation of cognitive performance is moderated by the amount of sleep pressure (Deboer, 2018), more specifically suggesting that time of day may have less of an impact on individuals who are sleep deprived.

Nonetheless, it is the relative positioning of the two processes regulating the sleep-wake cycle that is the key to assessing how strong the drive to sleep is. As is illustrated in Figure 1, a greater relative distance between between sleep drive and the circadian wake drive causes individuals to want to go to sleep. In both common and scientific parlance, this phenomenological motivation to sleep is known as sleepiness.

Typically, during a normal day, the circadian system acts as a wake-drive becoming the counterweight to the ever-increasing creep of sleep pressure. Especially, in the hours before bed when sleep pressure is highest, the body keeps feelings of sleepiness at bay by entering the “wake-maintenance zone”. It is as this wears off that our feeling of sleepiness becomes noticeable, the urge to sleep becomes strong, and we usually go to bed. However, the urge to sleep can become stronger. Much stronger. If we do not go to bed like our physiology is insisting, then sleep pressure will continue to build. And as I explain in the next chapters, this can lead to many changes in the cognitive and behavioural functioning of humans.

So what do we mean when we talk about sleep? One needs to realise that sleep is essentially an umbrella word comprising of different events. Similar to when we are awake, we are doing different things at different times during the night. In humans, our sleep is a repetition of (approximately) 90-minute cycles, where we move through the four stages of sleep. There are two broad categories of sleep that we obtain during each cycle – non-rapid eye movement (NREM, which is further divided into stage 1, stage 2, and stage 3 depending on the measured characteristics of brain waves) and rapid eye movement (REM). In the first half of the night, we typically get more NREM sleep, but this swaps round slowly during the night. NREM appears to be more vital for the performance of the functions set out at the beginning of this chapter, since humans can continue to perform well even when REM sleep is specifically deprived, such as in those taking selective serotonin reuptake inhibitors (SSRI; McCarthy et al., 2016). The actual function of REM sleep is not established, but likely revolves around consolidation of specific types of memories (Boyce, Glasgow, Williams, & Adamantidis, 2016).

In order to determine what the brain is doing while sleeping, we need to be able to measure inside the skull. Luckily, we have a method to do that. By recording electrical activity on the scalp representing brainwave activity, alongside eye movement and muscle activity, we can use these multiple signals to create a graph of the sleep, a method known as polysomnography (PSG). Different stages of sleep are defined by specific characteristics of the PSG signal. For example, NREM stage 3, is characterised by brain wave oscillations between 0.5-4hertz, commonly referred to as delta waves or slow-wave sleep (SWS).

PSG, while providing the best window into the sleeping brain that we currently have, does have a number of downsides. This includes the impracticality of needing trained technicians to wire up each person per night, which also comes with significant expense. Other methods of assessing sleep, that are more practical for longer term measurement, also exist

Actigraphy, which calculates sleep patterns by measuring the body’s physical activity, is a commonly used method of measuring sleep in ambulatory situations, with less need for experimenter intervention. Many studies that wish to quantify day-to-day changes in more rudimentary sleep parameters such as total sleep duration and timing will use actigraphy as the main method of accurately and reliably assessing sleep. It has been shown to be accurate compared to the ‘gold standard’ PSG, while being relatively easy to administer (Sadeh,

2011). Another method of quantifying sleep is by simply asking participants. Questionnaires such as sleep diaries can be used each morning with participants reporting how long they slept for and other similar questions. This is commonly used and the data often stands up well when compared to PSG (Zinkhan et al., 2014), however this method is at greater risk for subjective response biases.

We also have the ability to manipulate sleep in both directions. That is, we can restrict (or entirely remove) the sleep of participants. It is also possible to extend sleep, especially in populations that are at high risk of not getting enough sleep normally, such as in adolescent groups. In these ways we can have total control over sleep length. Additionally, there are methods to disturb sleep so that sleep quality is decreased, and some methods can even be used to target and disturb specific sleep stages only. Finally, new innovations may mean that it is possible to improve sleep quality. An exciting development, but one which needs significantly more research, is that of 'pink noise'. In essence, this is the delivery of an audio-cue timed to be in sync with the waves of the brain during SWS. Initial investigations suggests that this can enhance the amplitude of these slow waves, which researchers believe will lead to improved sleep efficiency (Papalambros et al., 2017).

Moving away from sleep, we can look at the symptoms we would expect if someone hadn't slept enough. While there is some evidence suggesting that the effects of sleep loss can be observed in the blood (Moller-Levet et al., 2013), the most salient symptom is if participants report feeling sleepy (Lo et al., 2012). Sleepiness is a physiological state where greater sleepiness makes it more and more difficult to force oneself to stay awake. It is also a phenomenological state where one increasingly desires sleep. On one hand, measuring sleepiness is less precise than measuring sleep duration or quality directly since sleepiness not only reflects the build-up of sleep pressure, but also pools the influence of the circadian phase, motivation, and environmental stimuli. On the other hand, while sleepiness may be a broader construct, this can also be a strength since it likely makes sleepiness a better predictor of how any given individual may perform or act at that moment.

3. THE PHYSIOLOGICAL EFFECTS OF SLEEP LOSS

Q: "I've been entirely preoccupied by a most frightening experience of my own. A couple of hours ago, I realised that my body was no longer functioning properly. I felt weak, I could no longer stand. The life was oozing out of me. I lost consciousness."

Capt. Picard: *"You fell asleep."*

Q: *"Terrifying. How can you stand it day after day?"*

Capt. Picard: *"You get used to it."*

Star Trek: The Next Generation, Déjà Q

On top of the loneliness epidemic mentioned in Chapter 1, we are also apparently in the midst of a global epidemic of sleeplessness (Huffington, 2016; Walker, 2019). One poll (Jones, 2013) found that compared to the number of hours we were sleeping in 1942 (approximately 8 hours per night on average) we now manage significantly less (approximately 6 hours 30 minutes on average). Others maintain that this is nothing more than a great headline, and that in the last one hundred years (at least) we are sleeping as much as ever (Hoyos, Glozier, & Marshall, 2015; Youngstedt et al., 2016). Either way, we've all experience not getting enough sleep at least once, and some of us experience it with regularity. No matter where you stand on that spectrum it isn't good – the effects of sleep loss run deep.

A note before we continue. Not all sleep loss is experienced the same. Many of the studies that are referenced from here forward use very heavy manipulations of total sleep deprivation for one or more nights. It is a reasonable argument to make that such levels of sleep loss happen fairly seldom to the average person. What is generally implied from the sleep deprivation studies, is that similar effects would also occur but to a smaller extent in lesser amounts of sleep loss. Another conjecture often made is that chronic sleep loss, for example getting 4 hours of sleep for a number of days, adds up over time leading at some point to a similar impairment seen in total sleep deprivation studies. While separate studies have shown that such assumptions are supported by the data (Belenky et al., 2003; Cote et al., 2009; Van Dongen, Maislin, Mullington, & Dinges, 2003), it cannot be stated with total certainty that chronic poor sleep quality, for example, would lead to the same changes in physiological functioning that is seen following sleep deprivation.

3.1 NEUROPHYSIOLOGICAL CHANGES

Starting with the brain, there are clear changes if we do not sleep. An exhaustive list of the neurophysiological changes that occur in relationship to sleep loss is beyond what I am going to go into here (See Krause et al., 2017). However, a broad overview can help understand the key changes that occur following sleep loss.

Even when at rest (i.e. not doing anything in particular), changes in the DMN are observed, such as decreased connectivity between distinct areas of the brain that make up the DMN (Yeo, Tandi, & Chee, 2015). This is particularly relevant for this thesis since the DMN has been associated with multiple skills related to theory of mind and mentalising (Li et al., 2014; Mars et al., 2012), both vital skills for social interaction.

When sleep deprived participants are asked to perform simple cognitive tasks, changes in activity have been observed using functional magnetic resonance imaging (fMRI). First of all, when engaged in a task, usually one observes a deactivation in the DMN. However in sleep deprived participants, the deactivation is not as noticeable (Gujar, Yoo, Hu, & Walker, 2010). Task specific brain activity also appears to show differences following sleep loss. For example, there are decreases in blood-oxygenation-level-dependent (BOLD) activity in the dorsolateral prefrontal cortex (DLPFC) and the intraparietal sulcus when performing

attentional or working-memory tasks (Krause et al., 2017). Additionally, the ability to consolidate memories is decreased, with studies showing specific impairments in learning and encoding activity within, for example, the hippocampus (Yoo, Hu, Gujar, Jolesz, & Walker, 2007).

There are also important changes in the reward system, which is responsible for driving human motivation and associative learning. For example, studies have shown amplified activation in the ventral striatum when exposed to reward (Greer, Goldstein, Knutson, & Walker, 2016; Mullin et al., 2013), which is a part of the mesolimbic reward pathway. Relatedly, the ventral striatum is regulated by areas of the prefrontal cortex (PFC), especially the medial prefrontal cortex (mPFC), and sleep deprivation has been shown to have an impact here by decreasing the functional connectivity between these regions (Gujar, Yoo, Hu, & Walker, 2011). A functional disconnect between the PFC and the amygdala has also been observed (Yoo, Gujar, Hu, Jolesz, & Walker, 2007), which appears to lead to reduced ability to regulate emotions and thus leads to amplified responses to emotionally salient stimuli. However, a larger study using a sleep restriction protocol did not replicate the disconnect between the amygdala and the PFC despite observing impaired emotional regulation (Tamm, Nilsson, et al., 2019), exemplifying that our understanding of the neurocorrelates of this relationship is still rather undeveloped.

3.2 METABOLIC, ENDOCRINE AND IMMUNOLOGICAL CHANGES

Sleep loss compromises the body's energy homeostasis via a triple-hit of impairment in glucose metabolism, changes in food intake, and changes in physical activity. Examples of changes in glucose metabolism are impaired glucose tolerance and decreased glucose uptake (Schmid, Hallschmid, & Schultes, 2015), giving a sleep deprived person a similar metabolic profile to that seen in those with type 2 diabetes. There is laboratory evidence that when sleep deprived, participants tend to overeat (Markwald et al., 2013), and other studies showing that physical activity is decreased in those who have not slept sufficiently (Schmid et al., 2009). The evidence for this final point is however mixed with some studies showing an increase in activity after sleep restriction (Brondel, Romer, Nougues, Touyarou, & Davenne, 2010). Nonetheless, these three changes would explain why individuals who have chronic sleep problems or bouts of short sleep tend to gain weight (Chaput, Després, Bouchard, & Tremblay, 2008; Markwald et al., 2013)

In terms of endocrine changes, sleep has a major influence on the levels of some hormones, while others are regulated by other biological systems. Decreases following sleep deprivation or sleep restriction have been reported in circulating testosterone, thyroid stimulating hormone, and growth hormone while circulating cortisol is elevated (Briançon-Marjollet et al., 2015; Mullington, Haack, Toth, Serrador, & Meier-Ewert, 2009).

Sleep loss has also been reported to elevate blood concentrations of inflammatory proteins, which may be reflective of impaired immune functioning and disease processes. There are

reported increases in white blood cells (leukocytes), and subsequent pro-inflammatory cytokines such as Interleukin-6 (IL-6) and tumor necrosis factor (TNF) alpha (Mullington, Simpson, Meier-Ewert, & Haack, 2010) However, a meta-analysis of the available literature did not observe a significant association between IL-6 or TNF-alpha and short sleep duration, though short sleep duration did show a relationship with a marker of inflammation - C-reactive protein (CRP; Irwin, Olmstead, & Carroll, 2016). There is also evidence that insufficient sleep leads to an impairment in the ability to ward off illness (S. Cohen, Doyle, Alper, Janicki-Deverts, & Turner, 2009; Prather, Janicki-Deverts, Hall, & Cohen, 2015).

4. SLEEP LOSS IN A SOCIAL WORLD

“Good grades, social life, enough sleep – choose two”

It is perhaps surprising in the context of this contemporary thesis, that scientists have been researching the social effects of sleep loss going back to some of the earliest experimental sleep studies. Between the late 1950's and early 1960's there was an initial flurry of research on this topic and already in 1940 there was a paper published investigating changes in aggressive behaviour and irritation following one night of sleep deprivation (Sears, Hovland, & Miller, 1940). Other important studies from this period include a paper that investigated how sleep deprivation led to changes in communication performance, finding a gradual decrease in the ability to receive and understand instructions (Schein, 1957), a study showing that sleep deprivation led to greater variability in social behaviours (Murray, Schein, Erikson, Hill, & Cohen, 1959), an investigation revealing changes in speech such as speaking more slowly (Morris, 1960), decreases in friendliness and taking social initiative (Laties, 1961), and a further study showing decreases in social competence, cooperation, and social interest (Pasnau, Naitoh, Stier, & Kollar, 1968). These studies being completed in the age of behaviourism, with its emphasis on understanding behaviour over all else, was likely why these early sleep researchers were interested in understanding how sleep related to our interpersonal functioning. However, the take-off of the cognitive revolution moved the interests of sleep researchers elsewhere. And it was not until social cognition became a research entity that slowly but surely sleep researchers started to be interested in human social lives once again.

The implications of these early studies on our current state of knowledge is difficult to gage, since the goalposts for acceptable practices within psychology have changed significantly. However, as later research has shown (as well as some of my own research) the studies were definitely asking the right questions. In this chapter, I will give an overview of the current state of the literature linking sleep to social behaviour. I will use the model illustrated in Figure 2 to highlight how sleep loss effects at the individual level can have social implications.

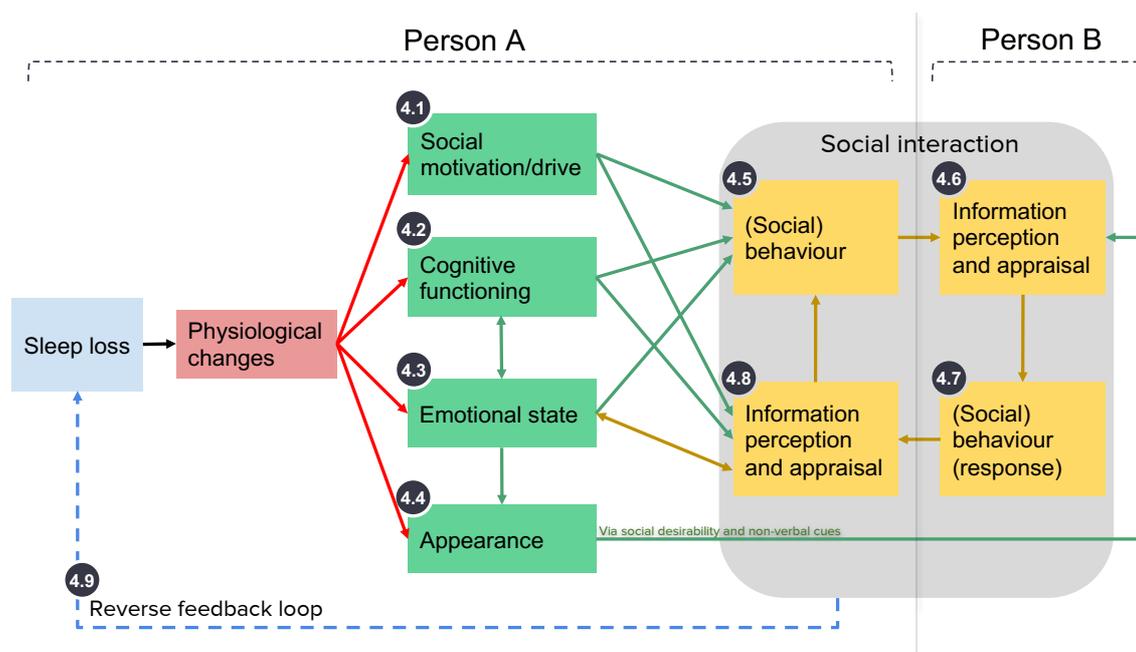


Figure 2. A model illustrating how sleep loss may impact human social interactions. Each number on the graph is represented with a respective subsection in this chapter.

4.1 THE EFFECT OF SLEEP LOSS ON SOCIAL MOTIVATION

As highlighted in Chapter 1, humans have a natural draw towards social activity. Though there are differences in how social one person may feel compared to another. To some extent our sociability is a stable personality trait (Cheek & Buss, 1981). But our desire for social contact can also change from day to day and even moment to moment. This change in the strength of how much we as humans are driven to engage in social interaction with others is referred to here as social motivation.

Building on the basic research into the reward system (Berridge, 1996), motivation has been split into incentive salience (“wanting”) and the hedonic impact of obtaining (“liking”) a prospective goal. Incentive salience orientates individuals towards something by it becoming more attractive and attention grabbing. The hedonic response refers to the extent of pleasure that one gains from obtaining that goal (Botvinick & Braver, 2014). Often reward research focuses on food to highlight the difference between these, with the “wanting” relating to craving food, and the “liking” being related to the pleasurable experience of eating. However, the system also applies to other potential goals, which may be a desired extrinsic reward (such as a new car) but it can equally refer to intrinsic rewards. Social interaction can be thought of as a kind of intrinsic reward.

By thinking of social interaction as an intrinsic reward, the motivation to socialise can also be conceptualised using a similar two-dimensional framework. The first dimension is extent that we seek out other people. This can be thought of as an approach-avoidance dimension accounting for the extent to which we orientate ourselves towards social situations and thus come into social contact with others. For example, a low incentive salience towards social

contact could lead the way to social passiveness and subsequent social withdrawal. This social ‘wanting’ system, has been proposed to be impaired in Autism (Kohls, Chevallier, Troiani, & Schultz, 2012). Conversely, not getting the amount of social interaction that we desire can lead to feelings of loneliness (Peplau & Perlman, 1979). The second dimension is the amount of enjoyment we get out of social interaction. It may be that when we engage in social interaction we also do not find any enjoyment in the interactions or perhaps even actively dislike them. In the case where an individual wouldn’t get pleasure out of a social interaction, it could be said to be a state of social anhedonia. This is something that is often reported in schizophrenia disorder (Silvia & Kwapil, 2011). An individual without any hedonic rewards from social interaction, may initiate conversations equally often with other people, but end up spending significantly less time in the interactions since they do not find much pleasure in the social activity.

Evidence shows that sleep loss may lead to changes in social motivation in both of the mentioned dimensions. Axelsson and colleagues (in review) showed that sleepiness changes the motivational goals whereby the desire to be alone increases, suggesting that the salience of social contact is decreased. Similarly, an experience sampling study found that decreased sleep duration measured over 14 days was associated with an increased motivation to be alone (Totterdell, Reynolds, Parkinson, & Briner, 1994). Sleep restriction of 4 hours sleep per night for 12 days has also been shown to lead to continuous decreases in an ‘optimism-sociability’ factor, consisting of items such as friendly, sociable, trusting, and helpful, but also with less-relevant items such as optimistic, clearheaded, and creative (Haack & Mullington, 2005). Therefore, the construction of this factor makes it difficult to ascertain whether it is the sociability part, or the optimism part which is driving the effect. Nonetheless, these studies parallel findings from within neuroscience showing that sleep deprivation leads to decreased activity within the ventromedial prefrontal cortex (VMPFC), an area representing social reward valuation (Libedinsky et al., 2011).

There also exists evidence that sleep loss and related states lead to less enjoyment (less positive emotional response) to social interaction. Within romantic couples, worse sleep leads to less positivity and more negativity during conflict-discussions (Gordon & Chen, 2014a; S. J. Wilson et al., 2017), as well as decreased marital satisfaction (Cottrell & Khan, 2005). There is evidence of increased negative emotional responses to social situations in older adolescents, though this factor includes a measurement of withdrawal so it is difficult to separate this from the social salience effect of sleep loss (McMakin et al., 2016). In an upcoming paper (Sundelin, Holding, Koslov, Stellar, Mendes, & Page-Gould, in prep), two studies showed that feeling physically tired was associated with decreased liking of a stranger after a short interaction. Interestingly, a further study found that being sleep deprived did not reduce how upset participants felt when experiencing social ostracism presented through a computer task (Liu, Mulick, & Chee, 2014), suggesting that even sleepy people feel hurt when socially excluded.

If we do have a decrease in the orientation motivation towards social interaction, and potentially a change in how much we like those interactions, how does this manifest behaviourally? This has also been shown in a study where participants showed behaviour representative of social withdrawal (Ben Simon & Walker, 2018), for example keeping a greater physical distance from others. A further, though significantly smaller, study followed 11 participants over two weeks and observed that the amount of time spent in SWS was associated with an increase in the amount of time participants spent with other people (as objectively measured using a wearable device) (Butt, Ouarda, Quan, Pentland, & Khayal, 2015). In elderly adults, a cross-sectional study showed that an increase in daytime sleepiness was associated with less social engagement (Lee et al., 2013). Overall, the initial evidence appears to suggest that sleep is predictive of both the desire to socialise as well as how much individuals enjoy social interactions.

In the model presented in Figure 2, there is also a link between changes in social motivation and how one perceives and appraises incoming (especially social) stimuli. This is because evidence from cognitive neuroscience has shown that motivation can have meaningful impacts on how we perceive and interpret incoming information (e.g. Maksimenko et al., 2017). If such lower cognitive functioning is altered, it is likely that social skills that depend on these will also be compromised.

4.2 THE EFFECT OF SLEEP LOSS ON COGNITIVE FUNCTIONING

In the previous chapter, it was described how the brain undergoes a multitude of physiological changes, including changes in baseline activity, reactivity, and connectivity, in response to sleep loss. Moving to a higher level of explanation, these physiological changes are the main cause of significant changes in our cognitive performance. The literature investigating the relationship between various types of sleep loss/disturbance and cognitive performance is vast. From basic cognitive skills, such as perception and attention, to more complex executive tasks such as creativity (divergent thinking), sleep loss and sleepiness tend to affect it (Jackson & Van Dongen, 2011; Killgore, 2010; Wickens, Hutchins, Laux, & Sebok, 2015). Comparisons of cognitive performance following sleep loss, suggest that it is more basic cognitive performance that consistently shows impairments, while for more complex tasks, the evidence is less robust (Wickens et al., 2015). One aspect to keep in mind, is that it is not only the average performance that decreases in such tasks, but that performance becomes much more variable, representing state-instability of the brain where waking performance is becoming increasingly intruded on by micro-sleeps (Doran, Van Dongen, & Dinges, 2001).

It is our thoughts that drive our behaviour which is why our cognitive state is so important for predicting changes in social behaviour. Studies in other domains have shown that specific cognitive impairments are associated with alterations in social abilities in different ways. For example, cognitive impairment in areas such as working-memory has been associated with social functioning in schizophrenia (A. S. Cohen, Forbes, Mann, & Blanchard, 2006; Liddle,

2000), attention ability and processing speed predicts social skills 18 years later (Sarapas, Shankman, Harrow, & Faull, 2013), brain injury leading to impairments in executive functioning leads to impaired conversational skills (Godfrey & Shum, 2000), and aging-related deficits in executive control lead to increases in social inappropriateness (Henry, von Hippel, & Baynes, 2009). These studies highlight the real possibility that decreased cognitive functioning could have impacts on social skills. Indeed, the effect of sleep loss on memory consolidation, especially episodic memory, has been exemplified as a cognitive impairment observed following disturbed sleep that may have direct effects on our social lives. This is because a decrease in being able to recall social knowledge could hinder communication and the building of social relationships (Diekelmann, Paulus, & Krach, 2018).

In recent years research into how cognition is related to social interaction has become somewhat of a sub-discipline called ‘social cognition’. Social cognition suggests that there are distinguishable cognitive abilities, that have developed specifically for the use within social interaction. Similar to basic cognitive functioning, many of these have also been shown to be impaired following sleep loss, which theoretically would lead to noticeable changes in how an individual performs within social situations. Examples of such social cognitive abilities would be face recognition, social working memory, and different forms of empathy. The effect of sleep loss on some of these will be discussed further later.

4.3 THE EFFECT OF SLEEP LOSS ON EMOTIONAL FUNCTIONING

While studied less intensively than cognition, the science relating sleep loss to emotional functioning also has a large literature to draw on. Studies now show that insufficient sleep has important implications for how we feel and react emotionally (Beattie, Kyle, Espie, & Biello, 2015; Deliens, Gilson, & Peigneux, 2014). Sleep loss causes individuals to feel less positive emotions, and (though evidence is less consistent) more negative emotions (Ritchie, Knauer, Guerin, Stothard, & Wright, 2018; Schwarz et al., 2018; Talbot, McGlinchey, Kaplan, Dahl, & Harvey, 2010). Reactivity to emotional stimuli also changes, with some studies showing this is only in response to positive-valence stimuli (Pilcher, Callan, & Posey, 2015), while others also observe it for negative-valence stimuli (Yoo, Gujar, et al., 2007). An inability to control emotional responses can have major implications for our behaviour in social situations (Eisenberg & Fabes, 1992).

The relationship between sleep disturbance and emotions has been hypothesised as why sleep problems are often found to precede the onset of mood disorders such as depression (Perils, Giles, Buysse, Tu, & Kupfer, 1997) and symptom severity in bipolar disorder (Plante & Winkelman, 2008), as well as increased anxiety (Batterham, Glozier, & Christensen, 2012; Gillin, 1998). Conversely, changes in our emotional state and emotional reactivity does not only have to be a bad thing. This manipulation of emotional functioning by sleep deprivation has also been put to use for treatment of clinical depression. By breaking the pattern of emotional flattening, a characteristic of depression, a night of sleep deprivation has been shown to have strong possibilities as a form of treatment for depression (Boland et al., 2017).

This potential of sleep deprivation as a therapy would seem to be counter-intuitive, since sleep disturbances can also be a prodrome of depression, highlighting the complexity of the relationship between sleep and emotions.

In addition to the overall effects of sleep loss on emotion, the model in Figure 2 highlights its influence on cognitive ability, as well as the appraisal of social cues. This is because of evidence that one's emotional state can moderate performance in certain cognitive tasks, sometimes referred to as the difference between hot cognition (when cognition can be influenced by emotional state) and cold cognition (cognitive performance that is not influenced by emotion) (Smilek & Frischen, 2013). Examples of sleep loss leading to changes in hot cognition include one study that found sleep deprivation caused valence-specific performance changes in an emotional working-memory task (Gerhardsson et al., 2019). Another example comes from the effects of sleep loss on emotionally dependent decision making tasks (Pace-Schott, Nave, Morgan, & Spencer, 2012).

4.4 THE EFFECT OF SLEEP LOSS ON APPEARANCE

It is not so controversial to state that our current health status affects how we look. People who are sick, will look sick. This might include features such as changes in skin colour, loss of muscle mass, dull eyes, skin blemishes, and changes to the way we move (empirically supported by Axelsson et al., 2018). But perhaps it is a larger leap to assume that sleep can impact the way we look?

Having said that, in English the term 'beauty sleep' is well known and so is the sentiment. Studies show that people at least believe that we can tell if someone is tired. Lay people use facial features such as drooping eyelids and dark circles under the eyes to identify signs of fatigue (Sundelin et al., 2013), a tradition that continues all the way to ancient Chinese medicine (Chen, Liu, Zhang, Yan, & Zeng, 2015).

Science also supports that sleep loss has impacts on our appearance. When participants were photographed after 8 hours of sleep and after 31 hours of wakefulness, others rated the sleep deprived faces as looking more tired, less healthy, and less attractive (Axelsson et al., 2010; Sundelin, Lekander, Sorjonen, & Axelsson, 2017). A follow-up study suggested that the visual cues of an individual's fatigue were hanging eyelids, red eyes, swollen eyes, dark circles under the eyes, pale skin, wrinkles/fine lines, and droopy corners of the mouth (Sundelin et al., 2013).

Further evidence for changes in our appearance can also be seen in non-experimental manipulations of sleep. Patients with obstructive sleep apnea (OSA) when treated with continuous positive airway pressure (CPAP) were rated as appearing more youthful, attractive, and alert two months after beginning treatment (Chervin et al., 2013). A conceptual replication in another sample of patients with severe OSA found that patients were rated as looking younger after treatment (Yagihara, Lorenzi-Filho, & Santos-Silva, 2019). Both of

these studies make it difficult to know what the mechanism of effect is though, since the changes in appearance may not relate to sleep but rather a general improvement in health. However, the importance of sleep is further reinforced by a study showing that chronic poor sleep quality is associated with greater appearance of skin aging (Oyetakin-White et al., 2015).

There is of course more to appearance than static images of our face, and researchers are increasingly highlighting that more attention should be paid to more ecologically valid stimuli (Risko, Laidlaw, Freeth, Foulsham, & Kingstone, 2012). One example of visual cues that can be observed by others is the responsiveness of one's face to emotional stimuli. When sleep deprived participants were shown "emotionally provocative" film clips, compared to well-rested control participants, the sleepy participants showed less facial expressiveness (Minkel, Htaik, Banks, & Dinges, 2011). Similarly, when making a facial expression, sleep deprived participants do this slower than well-rested individuals (Schwarz et al., 2013). In a conversational setting, this could lead to important impacts in how one is perceived by others.

4.5 THE EFFECT OF SLEEP LOSS ON SOCIAL BEHAVIOUR

Sleepy people behave in different ways than they do when well-rested. On top of the changes in social approach/avoidance discussed in Section 4.1, another of the key changes that occurs to sleep deprived people is that there appears to be a significant decrease in the ability to self-regulate behaviours (similar to the reduced ability to regulate emotions). This loss of self-regulatory ability has been suggested to increase propensity for hostility and social-norm violating behaviours (Christian & Ellis, 2011). Relatedly, there is an increase in putting blame on others and accepting less blame (Kahn-Greene, Lipizzi, Conrad, Kamimori, & Killgore, 2006), reductions in trust toward others and changes in bargaining approaches (Anderson & Dickinson, 2010) and impaired integration of emotional and cognitive skills to make moral judgements (Killgore et al., 2007).

There also appear to be important changes in the way we verbally communicate our opinions. At a more basic level, sleep deprivation has been found to lead to changes in both voice prosody and language use. One study showed that post sleep-deprivation, individuals spoke with a lower pitch, used fewer words, and used relatively fewer positive words (McGlinchey et al., 2011). Backing up these findings, an earlier study found that sleep deprived individuals used less appropriate intonation and sounded more fatigued when reading children's stories (Harrison & Horne, 1997). A number of studies have found that verbal fluency, a widely used assessment to explore broad changes in language ability, is impaired after sleep deprivation (Harrison & Horne, 1997; Horne, 1988). However, studies of the relationship between sleep and verbal fluency have been inconsistent with some studies not finding this effect (Binks, Waters, & Hurry, 1999; Tucker, Whitney, Belenky, Hinson, & Van Dongen, 2010). At a more abstract level – appreciation of humour has been shown to be decreased in sleep deprived participants (Killgore, McBride, Killgore, & Balkin, 2006). Overall, these studies

appear to provide a conceptual replication of the communicative changes that were first observed 60 years ago (Morris, 1960).

4.6 JUDGEMENTS OF A SLEEPY PERSON

If we behave differently and show clear signs of sleep loss, how does this change how we are perceived by others? Evidence shows that sleep loss leads to a number of different changes in how our dispositions and personality are judged by others. At a purely static visual inspection using pictures, sleep loss causes a decrease in how socially appealing we are (Sundelin et al., 2017). In a further study, 18 participants were interviewed both when well-rested and again when sleep deprived. The study found that when videos of these interviews were observed by others, the sleep deprived participants were judged as less socially appealing (Ben Simon & Walker, 2018). Another set of perceived changes is in leadership judgements. Within a military setting, five days of sleep restriction in naval officers led to their leadership behaviour being rated as more passive-avoidant (Olsen, Pallesen, Torsheim, & Espevik, 2016). Similar changes in leadership has been observed in other situations (Barnes, Guarana, Nauman, & Kong, 2016).

4.7 INTERACTIONS WITH A SLEEPY PERSON

Morris (1960, p. 453) made an insightful statement when he wrote that “the subjective experiences of sleep-deprived subjects must be evaluated in the context of the total environment; a purely intrapsychic view is insufficient if not misleading”. Simply focusing on individual effects of sleep loss is not enough. We need to understand more about how changes due to sleep loss affect social relationships and take account of the dynamic manner in which information passes between individuals. If we know that behaviour is changed, and also that judgements of sleep deprived people are affected, what does this mean for behavioural outcomes of social interactions?

One of the closest social relationships humans have is often with their partner or spouse, and a number of studies have shown that sleep disturbances in one partner can have an impact on the relationship. If one partner experiences acute poor sleep, it can lead to a shift towards a more negative mood not only in the sleepy individual but also in their partner (Gordon & Chen, 2014a). Another study found a similar effect whereby an increase in one partner’s sleep time was associated with their partner reporting more positive behaviours/events relating to their relationship (Yorgason et al., 2016). There also appears to be a meaningful interaction between the sleep of partners, with one study finding that sleep only predicted greater emotional response to conflict when both partners had obtained insufficient sleep, suggesting that sufficient sleep in one partner was enough to protect the couple from conflict (S. J. Wilson et al., 2017).

In the workplace, there are also changes in performance that relate to the sleep of an individual (Barnes & Hollenbeck, 2009; Barnes, Lucianetti, Bhave, & Christian, 2014). For

example, police end up being less able to deescalate volatile encounters when tired (James, James, & Vila, 2018). One particularly important theory paper highlights that while sleep deprivation could impair an individual's performance, it may not necessary be the case that group performance is impaired, proposing that others can take up the slack to some extent (Faber, Häusser, & Kerr, 2017), which would match the evidence from romantic couples (S. J. Wilson et al., 2017). Nonetheless, evidence shows that increased overall fatigue within a workplace does lead to decreases in whole-team functioning (Banks et al., 2019).

4.8 THE EFFECT OF SLEEP LOSS ON SOCIAL PERCEPTION

4.8.1 Face perception

One of the most important sources of social information comes from visual cues originating from faces. Unfortunately for sleep deprived people, there is evidence showing that sleepy people struggle with face perception. In participants who slept less than 6.5 hours per night for three nights, tasks revealed that recalling and differentiating faces from memory was worse than in those who slept 7 hours or more (Beattie et al., 2016). Other evidence derives from insomnia research, which is difficult to compare to short or insufficient sleep, since many of the symptoms often stem from comorbid psychiatric problems such as anxiety or depression (Benamins et al., 2017). However, they still are relevant since the main complaint in insomnia, is difficulty in sleeping. Those with insomnia have been found to have selective attention towards facial attributes that signal tiredness, including the eye-region, and spend longer looking at faces that appear tired (Akram, Robson, & Ypsilanti, 2018). However, another small study observed the opposite; that insomniacs focused less on the eyes and more on the mouth and nose area when determining emotions (Zhang, Chan, Lau, & Hsiao, 2019). Insomniacs also tend to perceive tired people around them as looking less tired (Akram, Sharman, & Newman, 2017).

4.8.2 Recognising emotions and intentions

But what about non-static, and even non-verbal social cues? Being able to understand, and potentially empathise or sympathise with, the emotions of other people is one of the key elements of successful social interactions (Parr, Waller, & Fugate, 2005). There have been a number of studies showing that sleep deprivation impacts our ability to correctly infer the emotional state of others. For example, one found that after being kept awake for almost two and a half days, participants reported having lower emotional intelligence and empathy towards others (Killgore et al., 2008). Following this initial study, further research has used a variety of sleep-loss paradigms and empathy tasks to investigate what the actual effect of sleep was on emotion categorisation. This has produced many conflicting results (Beattie, 2018). For example, one study only found an effect of sleep loss on recognising sadness (Cote, Mondloch, Sergeeva, Taylor, & Semplonius, 2014), while another only within women when recognising anger and happiness (van der Helm, Gujar, & Walker, 2010). A further study found that the discrimination of social threat was impaired in participants who were

sleep deprived (Goldstein-Piekarski, Greer, Saletin, & Walker, 2015). In a more real-to-life setting, a study found that in romantic couples, self-reported sleep in one person was predictive of how able individuals could assess their partners emotional state (Gordon & Chen, 2014b).

However, it may be that cognitive accuracy is not impaired, but rather other aspects. For example, a study found that while insomnia symptoms were not related to emotion recognition accuracy, people with these symptoms rated the facial features of others as appearing less intense (Kyle, Beattie, Spiegelhalder, Rogers, & Espie, 2014), potentially stemming from impaired emotional empathy. It could also be that it just takes longer to make an accurate inference of emotional state. One study investigating changes in sarcasm detection following sleep deprivation found that sleep deprived participants were equally accurate, it just took them slightly longer to come to the conclusion (Deliens et al., 2015).

It also appears that visual perspective taking during a socially-relevant task is impaired in individuals that haven't slept sufficiently (Deliens et al., 2017). If such perspective taking is truly impaired, then it would be no wonder that sleep deprived people have difficulty assessing the intentions of others, since they find it difficult to understand at least one aspect of the viewpoint of others. This could lead to an overall decrease in cognitive empathy.

4.8.3 Stereotypes and trust

Our attitudes and the dispositional judgements we make about others also change relating to our sleep. Evidence shows that stereotypical thinking and cognitive short-cuts are increased when people are in a hurry or cognitively tired (Webster, Richter, & Kruglanski, 1996). Therefore, it makes sense that a number of studies have shown that different types of sleep disturbance lead to increases in the tendency to engage in these types of cognitive shortcuts. Chronic sleep restriction leads to increased implicit biases and greater weighting of stereotypically negative facial features when deciding if someone is dangerous (Alkozei et al., 2018, 2017). This effect also appears in practice, with one study showing that racial bias in police is increased when officers were sleeping less (James, 2018). Another study in a more applied setting found that increased sleepiness when evaluating potential employee résumé led to an increase in the amount of stereotypes used to describe a member of an outgroup, and a more positive evaluation of applicants within the in-group (Ghumman & Barnes, 2013). It's possible the reason for that is that it takes cognitive effort to overcome such biases, and when sleepy we simply don't have the energy anymore. For a similar reason it may be why sleep deprived individuals are more willing to take advice from other people (Häusser, Leder, Ketturat, Dresler, & Faber, 2016). On the other hand, studies have also shown that sleep deprivation leads to less trust of others, at least when tested on economic games (Anderson & Dickinson, 2010; Dickinson & McElroy, 2017).

4.8.4 Other social cues

We may simply miss parts of a particular social interaction, due to lapses in attention (Jung, Ronda, Czeisler, & Wright, 2011), which can impact one's ability to be a "good group member" (Heatherton, 2011). This was found to occur in nurses, with sleep loss not only preceding making more errors themselves, but also being less likely to catch the errors of colleagues (Dorrian et al., 2006). Such an ability to monitor behaviours from others is a vital part of successful teamwork (Marks & Panzer, 2004).

4.9 REVERSE FEEDBACK LOOP

This thesis focuses on the effect that sleep loss has on our social functioning. However, there is a fair amount of research also showing that different aspects of our social lives can have impacts on our sleep. In this way, the relationship between sleep and the social world should be thought of as a dynamic two-way interaction. Examples of the reverse effect of social activity can be seen in a number of studies. Recent social rejection has been shown to precede shorter-sleep durations (Gordon, Del Rosario, Flores, Mendes, & Prather, 2019). Relatedly, discrimination has been linked to poorer sleep quality in a number of studies. Chronic exposure to discrimination was found to link to poorer objective and subjective indices of sleep (Lewis et al., 2013). Perceived discrimination was a partial mediator of ethnic differences in sleep architecture as assessed via PSG (Tomfohr, Pung, Edwards, & Dimsdale, 2012). Couple conflict the previous day was associated with subsequent sleep disruption (Hicks & Diamond, 2011). Individuals that report themselves to be lonely have been found to show poorer sleep efficiency and more night-time awakenings as measured through PSG (Cacioppo et al., 2002). In younger participants, social media use before bed has been shown to decrease sleep duration and quality (Hale, Li, Hartstein, & LeBourgeois, 2019). A general fact is that since many of the studies are cross-sectional, the direction of effects cannot be determined and therefore it could equally be the case that the sleep disturbances came before these changes. However, it is likely that there are at least some effects in the reverse direction, which hypothetically could act to lead individuals into a pattern of negative reinforcement.

5. PSYCHOLOGY IN THE WAKE OF THE REPLICATION CRISIS

“If you torture the data long enough, it will confess”
Darrell Hull, How to Lie with Statistics

“The roof is leaking and won’t keep out the rain for much longer. Monsters live in the dungeon” (Chambers, 2017, p. ix). This is an example of how some are currently describing the state of psychological science. What has become widely known as the Replication Crisis is not exclusive to psychology, scientists from other fields were also observing problems on the horizon (Ioannidis, 2005), but the replication crisis has hit psychology especially hard.

The appearance of the “monsters” was first noticed in 2011 in relation to a paper entitled “Feeling the Future” (Bem, 2011), which purported to be evidence for human precognition (i.e. that humans could see into the future). When the article was published, a large academic uproar ensued, with researchers across the discipline asking how evidence could be collected for such an extremely unlikely theory, and why it was allowed to be published. Making matters worse it was published in one of psychology's most prestigious journals, which then refused to publish a non-significant replication attempt, providing a clear track for amplifying positive publication bias. The key concern was that if this study can slip through the peer-review net, how many other published psychology studies are also of dubious merit?

So enters a coalition of psychology researchers across the world with their attempt to answer this question, by undertaking to replicate 100 previously well-regarded and trusted studies in psychology. The results made clear that the monsters had truly settled in. Only 39% of studies were reported by the authors as being successfully replicated (Open Science Collaboration, 2015). If taken to be the truth and then generalised, then the majority of the science that experimental psychologists have pushed onto the world is untrue.

This crisis has been met with a strong response, with many believing that our analytical techniques are where we’ve gone wrong, especially the over reliance on the p-value. Taken to the extreme, some are demanding that researchers “abandon statistical significance” (McShane, Gal, Gelman, Robert, & Tackett, 2019). Some have focused on bad research practices including “cherry picking” and reporting only significant findings, data massaging, excessive flexibility in methodology, p-harking (deciding the hypotheses after running the analysis), no controls for model overfitting, and underpowered samples. Others believe that we focus far too much on individual studies and pay too little attention to theory. “Darwin ran exactly ZERO controlled experiments” tweeted Moshe Hoffman, a researcher at MIT, “Darwin DID have a unifying theoretical framework” (Hoffman, 2017). In addition, there has often been a lack of transparency and openness, as well as publishing incentive systems that reward researchers for reporting positive significant findings only, therefore encouraging them to leave their non-significant studies forgotten “in the file drawer”.

The influence of this debate has no doubt had an impact on this thesis. From the larger sample sizes, newly popularised statistical methods, replication attempts, as well as using computer techniques and programs associated with the larger ‘open science’ movement. The debate is evolving psychology at an astonishing rate, and I am certain that the psychology of the future will be very different from the subject that I started studying in 2006.

6. AIMS AND OBJECTIVES

In the previous five chapters I highlighted the current state of knowledge regarding our understanding of the link between sleep and our social lives. Using the model set out in Figure 2 as an initial guide to the expected pathways of effects, this thesis acts as a broad inquiry into the socially relevant cognitive, behavioural, and physiological impacts that sleep loss, and related states such as sleepiness and fatigue, has on humans.

Paper I. *Holding, B. C., Sundelin, T., Schiller, H., Åkerstedt, T., Kecklund, G. & Axelsson, J. Sleepiness, sleep duration, and human social activity: An investigation into bidirectionality using longitudinal time-use data. Manuscript.*

In Paper I, we studied the link between sleepiness/sleep and the amount of social interaction, acting as an investigation into whether sleepiness/sleep could be impacting our drive for social connection.

Paper II. *Holding, B. C., Sundelin, T., Lekander, M., & Axelsson, J. (2019). Sleep deprivation and its effects on communication during individual and collaborative tasks. Scientific Reports, 9(1), 3131.*

In Paper II, we investigated the effect of sleep deprivation on individuals performance when engaged in paired tasks requiring collaboration and communication. We were particularly interested in how individuals' ability to communicate varies and whether this is task dependent.

Paper III. *Holding, B. C., Sundelin, T., Cairns, P., Perrett, D. I., & Axelsson, J. (2019). The effect of sleep deprivation on objective and subjective measures of facial appearance. Journal of Sleep Research, 28(6), e12860.*

In Paper III, using the same participants as Paper II, this article investigated how facial appearance was objectively impacted by sleep deprivation and whether the sleep loss effect had an impact on the subjective judgements of external raters. The article also investigated what facial features were used when individuals are asked to make judgements about the fatigue state of someone else.

Paper IV. *Holding, B. C., Laukka, P., Fischer, H., Bänziger, T., Axelsson, J., & Sundelin, T. (2017). Multimodal emotion recognition is resilient to insufficient sleep: Results from cross-sectional and experimental studies. Sleep, 40(11), zsx145.*

In Paper IV, using the same participants as Papers II and III, as well as a separate cross-sectional sample, I investigated whether one specific aspect of social information appraisal – cognitive empathy – was related to sleep duration or quality.

7. THE PAPERS: METHODS, RESULTS, AND CONCLUSIONS

In this section the method and results of each of the papers will be described in turn. Since papers II, III, and IV largely result from a single data collection, there is significant methodological overlap. However, important specifics vary between papers (for example task). Table 1 provides an overview of the methodological elements for each of the papers.

Table 1. Overview of the papers included in this thesis

	Paper I	Paper II	Paper III	Paper IV
Title	Sleepiness, sleep duration, and human social activity: An investigation into bidirectionality using longitudinal time-use data	Sleep deprivation and its effects on communication during individual and collaborative tasks	The effect of sleep deprivation on objective and subjective measures of facial appearance	Multimodal Emotion Recognition Is Resilient to Insufficient Sleep: Results From Cross-Sectional and Experimental Studies
Relevant Chapter 4 subsection	4.1	4.5	4.4	4.8
Design	Longitudinal	Experimental	Experimental	Study 1. Cross-sectional Study 2. Experimental
Sample	681 participants (mean age = 44 years, SD = 11).	183 participants (well-rested = 92, sleep deprived = 91; mean age = 25 years, SD = 7).	Subjects: 181 subjects (well-rested = 90, sleep deprived = 91; mean age = 25 years, SD = 7). Raters: 63 raters (mean age = 23 years, SD = 4)	Study 1. 291 participants (mean age = 23 years, SD = 3) Study 2. 181 participants (well-rested = 91, sleep deprived = 90; mean age = 25 years, SD = 7)
Outcome of interest	1) Time-use survey a) Social activity incidence (socialising yes/no) per given time-frame (3 hourly or daily) b) Social activity duration (summed amount of social activity) per given time-frame (3 hourly or daily)	1) Verbal fluency a) Score b) Errors 2) Model building task a) Builder performance b) Describer performance 3) Taboo card game a) Speaker performance b) Guesser performance 4) Voice characteristics a) Speaking duration b) Volume c) Volume consistency	1) Rater judgements a) Fatigue b) Health c) Paleness 2) Objective measurements a) Skin colour b) Eye-openness c) Periorbital darkness d) Mouth curvature	1) Emotion recognition a) Accuracy b) Speed
Predictor	Self-reported sleep duration, sleepiness, time-of-day	Sleep deprivation	Sleep deprivation, self-reported sleepiness	Study 1. Self-reported sleep duration and sleep quality Study 2. Sleep deprivation
Statistical method	Generalised additive mixed-effect models	Bayesian mixed-effect models	Bayesian mixed-effect models	Frequentist / Bayesian mixed-effect models
Data/code Access	To be published with manuscript	doi.org/10.5281/zenodo.1239717	doi.org/10.5281/zenodo.1414101	Available on request

7.1 PAPER I: SLEEPINESS, SLEEP DURATION, AND HUMAN SOCIAL ACTIVITY: AN INVESTIGATION INTO BIDIRECTIONALITY USING LONGITUDINAL TIME-USE DATA

7.1.1 Specific aims and hypotheses

The primary aim of this paper was to investigate whether subjective sleepiness and/or sleep duration had an effect on near-future social activity. Following the predictions set out in Figure 2 suggesting that sleep loss would cause decreased social motivation, we hypothesised that both greater sleepiness and shortened sleep duration would precede a decrease in social activity. We further explored, without any strong hypothesis, whether the effect of sleepiness on social activity changed depending on time-of-day. Our secondary aim was to investigate whether a relationship in the opposite direction was observable, such that social activity predicted subsequent sleepiness and/or sleep duration. Given the small amount of existing evidence, this question was analysed in an exploratory manner.

7.1.2 Methods

The sample was 681 participants (mean age = 44 years, standard deviation (SD) = 11 years; women = 537). This paper uses data collected in 2005-2006 during a study of the health impacts of reducing work hours by 25% (Bildt, 2007). Data were collected at three timepoints: 1) baseline (1-2 months before the reduced working hours), 2) 9 months after reduced working hours, 3) and 18 months after reduced working hours.

Each day participants completed a time-use questionnaire in which they reported their primary activity every 30 minutes. Participants selected from 13 predefined activities for each time-interval: work, work performed at home, household work, care of own children, care of others, personal care, mealtime, sleep, rest, freetime, social activity, own time, and other. Participants additionally completed the single-item Karolinska Sleepiness Scale (KSS) sleepiness assessment (Åkerstedt & Gillberg, 1990) six times per day (07:00, 10:00, 13:00, 16:00, 19:00, and 22:00) and the Karolinska Sleep Diary (KSD; Åkerstedt, Hume, Minors, & Waterhouse, 1994) each morning when they awoke.

To get a finer grained understanding of the relationship between sleepiness and social activity, we looked at the effect of sleepiness at different times of day. We combined 30-minute intervals to create a total of six chunked periods representing 3 hours each. For each of these chunks, the number of 30-minute intervals with reported social activity was added together, creating a value between 0 (zero social activity) and 6 (constant social activity). Each chunk immediately followed the sleepiness ratings and included the times as follows: early morning (7:00-09:59), late morning (10:00-12:59), early afternoon (13:00-15:59), late afternoon (16:00-18:59), early evening (19:00-21:59), and late evening (22:00-00:59). For investigating the reverse association, each chunk was used to predict the subsequent

measurement of sleepiness (apart from the first sleepiness rating of the day at 07:00, since there was no previous social activity reported).

We considered the social activity data as made up of two components: 1) a process where individuals choose to engage or not engage in any social activity during the specific time-frame, and if a person engages in social activity then 2) a process where individuals choose the extent of time they are socially active. Therefore, we analysed 1) the incidence of social activity (yes/no) and 2) the extent of social activity (within a 3-hour period this could be between 1-6 periods, for a whole day this could be between 1-39 periods). This helped circumvent statistical problems due to zero-inflated data.

Since we were interested in the effect of within-subject changes in sleepiness and sleep duration, we split within-subjects variance from between-subjects variance using the recommended technique of within-subjects centering (van de Pol & Wright, 2009). Therefore, when sleepiness and sleep duration are mentioned this value refers to changes within-subject compared to the participant's own average level.

To analyse the data, we used generalised additive mixed-effects models. The main benefit of this technique is that the shape of the association between outcome and predictor variables are not constrained to be only linear, but are determined from the data itself. In the context of this paper, this means that the relationship between sleepiness or sleep duration with social activity does not have to change at an equal pace, thus allowing for the potentiality of specific regions within the association where the relationship may be stronger or weaker.

7.1.3 Results and conclusions

The results showed that increased sleepiness predicted a decreased probability of engaging in future social activity, and if engaged, the duration of social activity became shorter. The effect of sleepiness also depended on the time of day, with sleepiness appearing to have a greater impact at times when the probability of socialising was typically the greatest – the late afternoon and early evening. We observed a similar moderating effect of *type* of day, where free days (days where individuals do not work) showed the strongest effect of sleepiness on the probability of engaging in social activity, likely because individuals had greater freedom to choose their activity, thereby causing changes in social motivation to become more apparent. In the reverse direction, time-of-day was found to predict how sleepy participants felt, and the amount of social activity was found to moderate the relationship of time-of-day with sleepiness.

Interestingly, we did not observe that within-subject sleep duration had any association with social activity the following day. This is in contrast to our hypothesis, which specified that we expected decreased sleep duration to predict less social activity. We did however observe that having more social contact was predictive of shorter sleep duration the following night.

In a broader context, this research can help us understand one of the drivers of human well-being. Humans are distinctly social animals, and regular social interaction is vital for our wellbeing (Kawachi & Berkman, 2001). While sleepiness may only predict a fraction (in our analysis approximately up to 4%) of social activity, by understanding the many additive causes of social contact we can create more accurate guidance and innovations to avoid social isolation and thereby support mental well-being.

To summarise, variations in the state of sleepiness predict measurable changes in the amount of social activity people take part in. Over time, it is plausible that repeated episodes of high sleepiness may lead people to become deprived of social interaction, a behavioural process vital for the well-being of humans.

7.2 PAPER II: SLEEP DEPRIVATION AND ITS EFFECTS ON COMMUNICATION DURING INDIVIDUAL AND COLLABORATIVE TASKS

7.2.1 Specific aims and hypotheses

This study investigated how one night of total sleep deprivation affected performance during different tasks intended to test verbal communication. The primary aim was to determine whether sleep loss impairs the ability of individuals to communicate, specifically during dyadic interactions. Based primarily on the studies highlighted in Section 4.5, we hypothesised that sleep deprivation would lead to a decrease in dyadic task performance. We also aimed to replicate effects on verbal fluency noted in previous studies as well as explore whether the characteristics of people's speech were different following sleep deprivation.

7.2.2 Methods

183 healthy participants (104 women; mean age = 25.36 years, SD = 6.49 years) were randomised to either one night of total sleep deprivation (N = 91) or a night of normal sleep with 8-9 suggested hours in bed (N = 92). The following day, participants completed individual verbal fluency tasks and two dyadic tasks together with another participant: a model-building task and a word-description task.

Verbal fluency was assessed with the FAS Swedish Letter Task and the Swedish Verb Task (Tallberg, Ivachova, Jones Tinghag, & Östberg, 2008). The FAS task required participants to say as many words as possible that begin with a given letter (F, A, and S). The verb task required participants to say as many verbs as possible. Words could not be names or just minor adjustments to previously mentioned words. Participants had 60 seconds for each letter in the FAS task, and 60 seconds for the verb task. The number of accepted words was summed, with a greater total score representing better verbal fluency. The number of rule-breaking errors were also counted.

The first of the dyadic tasks was a model-building task. In pairs, participants were assigned a role as either a 'describer' or a 'builder'. Participants sat at opposite ends of a table and the

describer was instructed to turn their chair around so that participants were no longer sitting face-to-face. The describer was then handed (without letting the builder see) an abstractly shaped model built from Lego (Lego Group, Billund, Denmark) bricks and asked to instruct their partner to build an identical model. The main outcomes for this task were the pair's score (number of bricks correctly placed), the time taken to complete the task (in seconds, max 600), and a standardised z-score of efficiency (score/time taken to complete task).

The second of the dyadic tasks was for participants to play the word-description game Taboo (Hasbro, Pawtucket, Rhode Island, USA). During this task, participants attempted to describe as many target words as possible to their partner in 60 seconds but without saying the target word or five related words, while their partner had to try and correctly guess the word. Each participant took three turns as the speaker and three turns as the guesser. The outcome variable was the total score for each of the six rounds.

During these tasks (and an additional task not reported here), each participant wore a Sociometric Badge (Sociometric Solutions Inc., Boston, MA, USA) while interacting with their partner. These devices provide a non-intrusive and objective method to measure speech patterns of the wearer. The total time that participants were wearing the badge was approximately 40 minutes, though this varied depending on the time it took each pair to complete all tasks. The outcome values for each participant are the total speaking duration (in seconds, including overlapping speech), mean volume, and mean volume consistency.

7.2.3 Results and conclusions

Sleep deprivation did not have an effect on the verbal fluency tasks, neither in terms of number of words produced nor number of errors.

Sleep deprivation did have role-specific effects on the model-building task. Focusing on the predictors of overall pair performance (number of bricks correctly placed), the data suggested that sleep deprivation in the builders caused a decrease of 1.18 (13%) in task score. Sleep deprivation in the describer was associated with an increase of 0.87 (10%) in task score (see Figure 3). No interactions were added to the models as this decreased model fit. Sleep deprivation did not predict time taken to complete the task. However, we observed that sleep deprivation in builders was found to decrease task efficiency (score/time-taken), while this was not significant in describers.

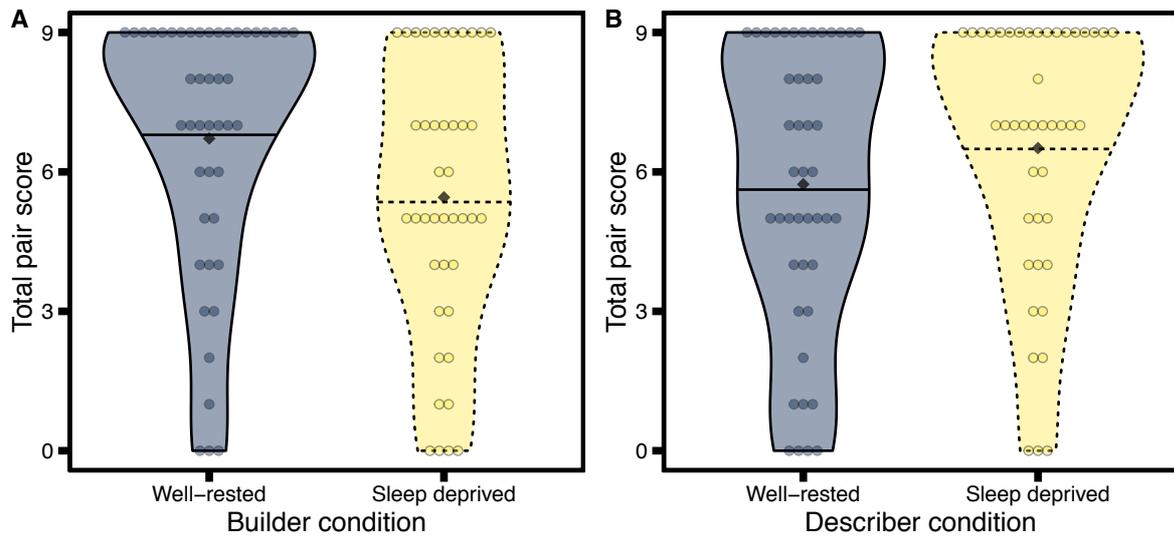


Figure 3. Performance on the model-building task split for the two main effects. The black diamond within each violin represents the mean. The middle line represents the median of the density function. Other dots represent the final score (raw data) of the pair.

Sleep deprivation was not found to have an impact in the word-description task. We additionally did not observe any difference between conditions in any of the speech characteristics.

Overall, the effects of sleep deprivation on communication ability are inconsistent. The changes in the builder performance in the model building task follows previous research suggesting that verbal perception and linguistic comprehension are decreased after sleep loss. The improvement in model-building score if the describer was sleep deprived was unexpected (though some speculation around this effect can be read in the full paper). Compared to the model-building task, the word-description task allows for full attention to be directed at the speaker, rather than being split between the speaker and the building bricks which may explain the different outcomes as sleep deprived people have impaired attentional abilities. Furthermore, the brevity of the word-description task may make it less susceptible to failures in attention.

More broadly, it is difficult to quantify communication ability, since the definition of performance depends heavily on the situation. In this study, we have aimed to address this issue by investigating the effect on sleep deprivation on communication in different ways, specifically using the performance on three verbal tasks as a marker for communicative ability. Since many occupations rely on the ability to quickly understand and act on instructions, it is important for future studies to clarify the mechanisms behind the changes we observed in the model-building task. An impairment in successfully following instructions could have important implications for a wide range of work environments such as on-call medical staff or air transport, where sleep loss is common.

7.3 PAPER III: THE EFFECT OF SLEEP DEPRIVATION ON OBJECTIVE AND SUBJECTIVE MEASURES OF FACIAL APPEARANCE

7.3.1 Specific aims and hypotheses

The aim of this study was to assess what the effects of sleep deprivation were on facial appearance, both subjectively and using computerised analysis tools. Objective features that we were interested in was skin colour, eye openness, mouth curvature, and periorbital darkness. Subjective changes we were interested in was how the faces of sleep deprived people were perceived in terms of health, paleness, and fatigue. We were also interested in understanding what facial features others used when making such judgments. Based on the previous research highlighted in Section 4.4, we hypothesised that sleep deprivation would lead to increased facial paleness, decreased eye openness, increased periorbital darkness, and negative mouth curvature (more droopy corners of the mouth). Since the studies had previously found effects of sleep loss on subjective ratings of health, fatigue, and paleness, we expected to replicate those findings. The utilisation of objective cues by external raters to make subjective judgements about an individual's level of fatigue was examined in an exploratory manner.

7.3.2 Methods

181 Subjects (103 female; mean age = 25.39 years, SD = 6.49 years) were randomised to one night of total sleep deprivation (N = 91) or a night of normal sleep (N = 90). The following day at approximately 14:00 facial photographs were taken. Subjects were not permitted to wear makeup, jewellery, or glasses. Participants also reported their subjective level of current sleepiness using the KSS.

After taking the photographs, skin colour was measured at different locations on the faces of participants (left cheek, right cheek, and forehead) using a spectrophotometer (CM-700d, Konica Minolta Inc, Tokyo, Japan). This could only be done for 141 subjects because of a delay in obtaining the equipment. Colour was assessed according to the CIELAB colour dimensions: dark-light, green-red, and blue-yellow. Higher values represent greater intensity of the second specified colour (i.e., higher green-red value indicates greater skin redness).

The photographs were computer analysed to assess systematic changes in facial features. The degree of eye-openness was measured by dividing the distance between the pupil and top eyelid by the width between the inner and outer canthus. Higher values represent greater eye openness. Mouth curvature was measured by subtracting the height of the mouth's centre from the mean height of the left and right corners of the mouth and then dividing by the width of the mouth. Periorbital darkness was measured using the photographs and analysing the lightness of cropped patches from below the left and right eyes. Since we were interested in the difference relative to the subject's skin colour, we subtracted this value from the lightness

of the forehead region. A higher value means that the periorbital area is darker relative to the forehead.

On a later occasion, a separate set of 63 raters (32 female; mean age = 23.37 years, SD = 3.95 years) rated the faces on seven-point scales pertaining to fatigue (in Swedish trötthet; “How fatigued is this person?”, 1 = very fatigued to 7 = very alert), health (in Swedish hälsa; “How is this person's health?”, 1 = very bad health to 7 = very good health), and paleness (in Swedish blek hud; “How pale is this person's skin?”, 1 = not pale at all to 7 = very pale).

7.3.3 Results and conclusions

The results showed that neither sleep deprivation nor subjective sleepiness had any discernible effect on the appearance variables measured. This includes the objective measurements such as skin-colour, mouth curvature, eye openness, and periorbital darkness. This also includes the subjective ratings of fatigue, health, and paleness. Nonetheless, many of these variables were found to predict fatigue judgements (regardless of the true fatigue of the subjects). Less eye openness, less facial yellowness, more downturned lips, and greater periorbital darkness, all predicted increases in how fatigued the faces were rated on average.

Overall, the subjective and the objective data both consistently showed that the effects of sleep deprivation could not be observed through the use of the appearance variables measured. An interesting aspect is that despite the features evaluated apparently having low cue validity, these features simultaneously have significant cue utilisation by raters. Outside observers clearly used these cues to evaluate fatigue (at least in photographs). The results have implications for computerised fatigue detection applications, by highlighting that accurate classification of fatigue and sleep loss through a single static image is problematic. We suggest that automatic recognition systems that focus on detecting sleep deprivation or fatigue should use data on changes within individuals.

7.4 PAPER IV: MULTIMODAL EMOTION RECOGNITION IS RESILIENT TO INSUFFICIENT SLEEP: RESULTS FROM CROSS-SECTIONAL AND EXPERIMENTAL STUDIES

7.4.1 Specific aims and hypotheses

This paper consists of the results from two separate studies. The overall aim was to address methodological drawbacks of previous studies into the effect of sleep loss on emotion recognition, by introducing a new emotion recognition task. In Study 1, we aimed to establish whether impairments in emotion recognition were associated with normal variations in sleep patterns. Based on the previous literature, it was predicted that: (1) shorter sleep duration would be related to a decrease in overall emotional recognition accuracy and (2) poorer self-reported sleep quality would be related to a decrease in overall emotional recognition accuracy. The effects of these sleep variables were also investigated for each emotion without

specific predictions. In Study 2, we used an experimental paradigm to investigate whether a night of total sleep deprivation would affect emotion recognition the following day. It was predicted that sleep deprived participants would show a decrease in overall emotion recognition accuracy. The effect of sleep deprivation was also investigated for each emotion without specific predictions.

7.4.2 Methods

Study 1 used a cross-sectional design consisting of 291 participants (182 women, mean age = 22.95 years, SD = 3.23 years). Participants completed a number of items taken from the KSD to assess sleep duration and sleep quality the previous night.

Study 2 used an experimental design with 181 individuals (103 women, mean age = 25.32 years, SD = 6.51). Participants were quasi-randomised into either a sleep-deprivation (N = 90) or a well-rested sleep-control (N = 91) condition.

Both studies used the same forced-choice emotion recognition task (the ERAM task; Laukka et al., 2015). In this task, participants were presented with a sequence of 72 short clips where actors portray different emotion states. These clips show one of 12 emotions (anxiety, despair, disgust, hot anger, interest, irritation, happiness, panic fear, pleasure, pride, relief, and sadness), and after each stimulus presentation participants were required to select which emotion best represented the stimulus from a list shown on the screen. Each clip shows frontal views of the actor's face and upper torso and provides facial, auditory, and bodily cues of emotion. The items were presented in three conditions: 24 visual-only, 24 audio-only, and 24 audio-visual. Furthermore, each stimulus was either easy or hard to recognise based on standardised accuracy scores. The outcome was whether the participant made a correct selection (incorrect/correct).

The analysis was similar in both studies, using generalised linear mixed effects models to investigate the relationship between accurate emotion recognition, self-reported sleep quality/duration (Study 1), sleep deprivation (Study 2), modality, and difficulty. The interaction between self-reported sleep quality/duration (Study 1), sleep deprivation (Study 2), and emotion-specific accuracy was followed up with planned contrasts. Bayes Factors were also estimated providing a likelihood ratio for the null hypothesis against the alternative hypothesis.

7.4.3 Results and conclusions

In Study 1 there were no main effects of self-reported sleep duration or sleep quality on emotion recognition accuracy. Sleep quality showed a significant interaction effect with emotion-specific accuracy, and planned contrasts found that sleep quality was positively associated with accuracy of recognising disgust. No other emotions showed significant associations, and no interaction was found between sleep duration and emotion-specific

accuracy. Bayesian analysis followed a similar pattern of results, supporting conclusions that sleep duration and sleep quality are unlikely to have an effect on emotion recognition.

In Study 2 there was no main effect of sleep deprivation on emotion recognition ability. A significant interaction was found between sleep deprivation and emotion-specific accuracy. However, no individual emotions showed a significant change in recognition rates as a result of sleep deprivation. Bayesian analysis again showed a similar pattern of results, with the data generally supporting the null hypothesis that there is no difference between the sleep deprivation and normal sleep conditions in emotion recognition ability.

Overall, in these two studies we found that variations in recent sleep duration, either natural or experimental, have no effect on emotion recognition accuracy. Subjectively rated sleep quality was also generally unrelated to emotion recognition ability, though a positive association was found with the recognition of disgust. This specific relationship is a novel finding, though intensity ratings of facial disgust have been shown to be decreased after sleep deprivation (Ginani, Pradella-Hallinan, & Pompéia, 2015). However, we did not find that sleep duration or sleep deprivation was associated with impairment in recognising disgust and therefore it may be that other aspects related to poor self-reported sleep quality could lead to this impairment. For example, depression has been linked to both decreased sleep quality (Nutt, Wilson, & Paterson, 2008) and deficits in recognising facial expressions of disgust (Douglas & Porter, 2010). The studies presented here involve considerably larger samples than previous studies and the results support the null hypotheses. Therefore, we suggest that the ability to accurately categorise the emotions of others is not associated with short-term sleep duration or sleep quality and is resilient to acute periods of insufficient sleep.

8. GENERAL DISCUSSION

8.1 OVERALL FINDINGS

In Chapter 6 I set out the goal of increasing our knowledge regarding the relationship between sleep (specifically the effects of not getting enough of it) and social functioning. I aimed to test different pathways to understand potential mechanisms by which sleep, and related states such as sleepiness and fatigue, may cause changes in how humans behave in social situations. The results indicate that, despite the many strong conclusions made by other researchers over the past years, the effects of sleep on social functioning remain difficult to pin down.

In Paper I we observed that when individuals reported being more sleepy they also appeared to become slightly less social, following the pattern of expected behaviour given the model in Figure 2. This matches the predictions made by a previous study, showing that as sleepiness increases so does a desire to be alone (Axelsson et al., in review). But given this evidence, it is surprising that we did not observe shorter sleep duration leading to the same effect since this is a primary pathway that drives individuals to feel more sleepy (Dinges, 1989), and has been shown to impact social contact previously in a small study (Butt et al., 2015). Something to investigate in future work is how the effect of changing sleep duration depends on how much one usually sleeps. If you are sleeping 9 hours a night, perhaps the effects of losing an hour of sleep is not the same as if you usually slept only 6 hours. In the current analysis, no matter how much a participant normally slept, the effect of losing an hour of sleep has the same weighting in the model. Another aspect to take account of, is that sleepiness is not only the effect of increasing sleep pressure. It also takes into account circadian rhythmicity, contextual environmental influences such as light or noise, and changes in state physiology such as emotional state, sickness, or self-medication with, for example, caffeine. Therefore, it makes intuitive sense that sleepiness would be a better predictor of how individuals behave over sleep duration.

Paper I was also unique within this thesis since I investigated how social activity relates to subsequent sleepiness and sleep duration. Here we observed that sleepiness appears to interact with the time-of-day effect to predict future social activity, apparently having different relationships depending on whether the social activity was occurring earlier or later in the day. The nature of the study design makes it difficult to know the aetiology of such a relationship, but one potential theory is that the alerting impact of social interaction on sleepiness (as shown previously, Eriksen, Åkerstedt, Kecklund, & Åkerstedt, 2005) is different depending on the time of day. According to our data, it appears that high social activity acts to reduce the daily variation in sleepiness, with participants less likely to feel very sleepy in the evenings, but feeling more sleepy during the middle of the day. Perhaps easier to interpret is that sleep duration was found to be decreased following a day with a greater amount of social activity. This may be because individuals steal time from sleeping to socialise (supported by previous evidence, Basner et al., 2007), and/or the process of being socially active makes individuals feel less sleepy (which our own data supports).

In Paper II, we observed that despite the many studies in the past that have shown that language ability and related cognitive functions are impaired following sleep deprivation (e.g. McGlinchey et al., 2011; Morris, 1960; Pilcher, Jennings, Phillips, & McCubbin, 2016), only one of the many variables measured in our study showed an impairment. We found evidence that performance during a model-building task requiring one to pay attention, understand, and act on verbal instructions was decreased following sleep loss. Unexpectedly, we also observed that sleep deprivation predicted an increase in model-building performance when in a role requiring individuals to give procedural instructions. With this mixed bag of findings, it is difficult to make strong conclusions about the relationship between sleep and communicative ability. Perhaps the most important impact that this paper can have is that it acts as a springboard for future studies to investigate how sleep loss is related to communicative performance, using our findings to frame hypotheses around. A particular avenue of interest is studies that test communicative performance during longer tasks, since the effects of sleep loss were only observed on the longest of the tasks performed. This additionally fits well with the evidence from the cognitive domain that sustained attention is one of the main consequences of sleep insufficiency (Lim & Dinges, 2010). If one loses focus while listening to instructions, it makes sense that performance would be impaired.

Paper III again provided an interesting and unexpected set of results. In previous (smaller) studies, the data has shown fairly consistent evidence that sleep loss leads to changes in facial appearance, specifically relating to skin colour and various facial features such as the eye-region (Axelsson et al., 2010; Chervin et al., 2013; Oyetakin-White et al., 2015; Sundelin et al., 2013; Talamas, Mavor, Axelsson, Sundelin, & Perrett, 2016). By contrast in Paper III, using both objective and subjective methodology, we observed no impact of one night of sleep deprivation on the variables measured. Therefore, this study appears to suggest that sleep deprivation in fact does not change how we look. However, there are some key methodological details that differentiate this study from the previous literature, which may explain the diverging evidence. The individual variation in the sample was substantial, with a mix of ages between 18-45 and different ethnicities. Additionally, we only analysed one image per person using a between-subjects study design. Since the expected effects have been shown to be of small to medium size, it is possible that effects can only be easily extracted through more homogenous or repeated-measures datasets. Nonetheless, if the effects of sleep loss on appearance are so difficult to notice even with a strong sleep deprivation paradigm, questions could be asked about the social relevance of the cues in the general population where sleep loss is likely to be much less.

Finally, in Paper IV, we have a fairly comprehensive refutation of our original hypotheses. In two separate studies using different study designs we found no effect of sleep loss on emotion recognition. This paper has substantial advantages over previous papers, such as a improved emotion recognition task, helping to triangulate the answer to whether sleep loss impacts our ability to cognitively empathise with others. However, the null findings of this paper do not make this the end of the story. Cognitive empathy is only one part of our

empathic ability. This study says nothing about the spread of emotions between people (emotional contagion /emotional empathy), nor does it say anything about how sleepy people act on the emotional cues that they perceive. In fact, a study from Stockholm University's Stress Research Institute found that emotional contagion was indeed decreased following sleep deprivation, though only following the presentation of happy faces and not angry faces (Tamm, Schwarz, et al., 2019). Being simply able to recognise emotions is only one aspect of a social tool-kit which is needed for social success.

8.2 METHODOLOGY IN FOCUS

One key strength of this thesis, is the use of different designs and technical methodology to understand the effects. For example, we use study designs ranging from experimental to longitudinal, with both self-report measurements as well as novel objectively measured outcomes such as skin colour measured via spectrophotometry. Experimental sleep deprivation is a useful tool that allows for researchers to experimentally assess the impact of restricting or removing sleep while keeping as many other parameters as possible equal. The SleSI study from which data in papers II-IV was at least partly taken, had strict criteria for who could possibly take part, and approximately 700 potential participants were not included because they didn't meet the screening criteria including sleep or health problems. Methods such as this, remove (as much as possible) the influence of potential confounding variables that may change or mask the effect of sleep loss. We could also keep aspects of the environment stable (such as temperature and light level) to remove similar confounding effects. While experimental studies remain the best way to assess causal effects, they are also notoriously difficult to generalise to outside of the lab. One of the main issues, as presented in Chapter 3, is that individuals are rarely totally deprived of sleep in their daily lives. By complementing the experimental data, with other study designs, we get a more accurate picture of the relationship of sleep as a whole and its relationship to the outcome of interest – in the case of this thesis, social functioning. Though, this can also be problematic, as the more dissimilarity between studies, the more difficult it becomes to elucidate what causes the differences in findings. For example, if effects are seen for sleepiness but not for experimental sleep duration, does this mean that the effect is not robust or that there is a meaningful difference in effect between the two constructs?

A related problem derives from Brandolini's Law – the amount of energy needed to refute bullshit is an order of magnitude bigger than to produce it (Brandolini, 2013; Williamson, 2016). Many sleep studies have the problem of using small samples (including a fair few referenced in this kappa). Small samples lead to an increased likelihood of finding spurious "significant" results. This combined with the positive publication bias in science, means that likely some of the effects we have been told exist in the past are nothing but mirages. At what point do we have enough evidence to decide that an effect doesn't actually exist, despite there being a well-cited peer-reviewed paper showing it? Ultimately, this comes down to the difficulty of running true replications in sleep studies, where data collection takes a long time and is very costly. Hopefully, by running some relatively close replications along the way

(such as investigating the effect of sleep deprivation on verbal fluency in Paper II), this thesis can help future reviews of the literature come to conclusions that more accurately align with the truth.

One further methodological issue is rather semantic. What are the differences between the following terms: sleepiness, fatigue, tiredness, and drowsiness? While being commonly interchanged by the majority of the population (including in clinical environments), the difference in meaning of these English terms has actually been the source of a fair amount of controversy within the sleep field (Shen, Barbera, & Shapiro, 2006). This thesis uses the definitions defined by previous work in the Swedish context (Sundelin, 2015), concluding that fatigue is similar to tiredness and the Swedish word “trötthet”. Sleepiness on the other hand is more related to drowsiness and the likelihood of actually falling asleep, focused around the Swedish word “sömnighet”. Study III uses fatigue as a concept, investigating whether participants looked more fatigued after sleep loss (as rated by external judges) and/or whether specific aspects of the different facial cues measured predicted how fatigued faces appeared to others.

8.3 THE THESIS IN A LARGER CONTEXT

All the hypotheses in this thesis has been based on previous research, the majority of it mentioned in Chapter 4. However, the fact that not all hypotheses set out in the individual papers were supported, suggests that there remain aspects of the relationship between sleep and social functioning that are unknown. In the two previous published reviews of this literature, rather strong conclusions have been made. One review paper stated that sleep has “far-reaching effects on social processes from basic social cognitions to complicated social interactions” (Gordon, Mendes, & Prather, 2017). The issue is that both sleep and social functioning are very broad areas, and therefore there is significant room for over-interpretation of findings. And as the studies in this thesis suggest, the effects of even heavy sleep deprivation appear to be quite specific rather than far-reaching. An earlier review takes a more nuanced approach stating that “the relationships between sleep, emotion, and social functioning are complex, and the specific outcome measures (e.g. subjective/objective, behavioural, physiological, brain) could also affect reported results” (Beattie et al., 2015). This is a viewpoint that aligns more closely with what this thesis has observed. But it also implicitly emphasises the non-trivial problem of the huge amount of researcher degrees of freedom we have. Perhaps the field would be better suited by a significantly greater emphasis on the mechanisms of the effects, rather than simply following the significant results that are published down the rabbit hole. This is a scientific habit that is far easier said than done.

8.4 FUTURE DIRECTIONS

There are a lot of meaningful and exciting directions for future research. I suggest that further research should go into understanding how transient states (like sleepiness or fatigue) can predict how humans react in social situations. The power of these states has been shown in

previous studies, and the impact of sleepiness was highlighted in Paper I. Could sleepiness say more about how we will behave than our own personality traits? Or perhaps how sleepy we tend to feel in fact drives our reported personality? It may also be that sleepiness has a role to play in explaining fluctuations in state personality (R. E. Wilson, Thompson, & Vazire, 2017). Another interesting project would be to investigate the benefits of sleep extension, sleep treatment in individuals with insomnia, or pharmacological intervention to reduce sleepiness such as nicotine or caffeine, and assess whether this has any beneficial effects on social skills, and whether such effects are mediated by a reduction in sleepiness.

There are also paper-specific limitations that future research would do well to address. In Paper I, all data came from self-reported sources, which while often accurate does come with a number of downsides. The availability of consumer sleep trackers, the development of devices that can provide objective measures of social interaction (e.g. sociometric badges as used in Paper II), as well as fatigue detection systems using eye-blink (or similar), now make a similar study using only objective measurements a feasible prospect in the near future. In Paper II, the communication tasks were generally short in duration (maximum 10 minutes), therefore a future study could be made to test the hypothesis that the effects of sleep deprivation become more obvious as the last length increases. Building on Paper III, follow-up studies would benefit from investigating the relationship between sleep and non-static aspects of appearance, for example body-movement and changes in eye-openness over time.

Finally, as the amount of research connecting sleep to the social world increases, so does the importance of incorporating the existing evidence in a cohesive and theoretically grounded manner. Therefore, future research should emphasise not only the effects, but also the mechanisms. Bringing together the existing findings in a way that can be used to predict changes in social functioning is important for the findings in this thesis and similar works to be moved from simply an academic curiosity into having a positive impact on people's lives. In words commonly attributed (I couldn't find a primary source, but I like the sentiment) to Nikola Tesla: "Science is but a perversion of itself unless it has as its ultimate goal the betterment of humanity".

8.5 IN CONCLUSION

Does sleep loss lead to changes in social functioning? The results of this thesis highlight the pitfalls of simply stating yes. Instead, the studies exemplify that the relationship between these things are complex, dynamic, and dependent on many internal and external factors. Of course, one thesis is never enough to truly understand a concept, and luckily there is an increasing group of researchers focused on understanding this phenomenon. Hopefully, this work can act as a part of that, and provide some guidance and momentum towards a true understanding of the relationship between sleep, fatigue, and social functioning.

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