The Interplay of Sleep, Cognitive Control and Brain Connectivity from a Graph Theoretical Perspective

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Summary

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Author statement: This thesis was an independent research project. The design was developed in collaboration with supervisor René Huster. Data collection was done by the author, two additional master students and an intern, all using different parts of the data. The idea, hypotheses, data processing, and analyses were developed and performed independently by the author.

Supervisor: René Huster

Co-supervisor: Christina Thunberg

Abstract: Sleep deprivation (SD) has severe negative effects on health and is a widespread problem in society. However, how it affects cognition, and in particular, cognitive control and the brain, is less well understood. This study sought to elucidate the interplay of sleep duration, cognitive control and brain connectivity. In order to investigate this, 17 participants underwent diffusion weighted imaging (DWI), performed a stop-signal task (SST) and wore actigraphs for two weeks. The DWIs were analysed with atlas-based deterministic tractography, and the obtained connectivity matrices were then analysed with a graph theoretical approach to assess brain connectivity. While it was predicted that short sleep duration would be positively correlated with attention, performance monitoring and global efficiency, no such correlations were identified. However, higher global efficiency was found to be associated with longer reaction times on go trials. Results further indicated a positive relationship between stop signal reaction times (SSRTs) and local efficiencies of right inferior frontal gyrus pars opercularis and right supplementary motor area/pre-supplementary motor area. Lastly, as predicted, post-error slowing and post-stop slowing were both found to positively correlate with local efficiency of left anterior cingulate cortex. The somewhat unexpected results can be explained by the small, homogenous sample, although the latter results and the identified small-worldness implies that the analysis itself was successfully applied. Thus, this study provides useful insight into how a graph theoretical approach can be applied in order to assess sleep, cognitive control and brain connectivity in a healthy sample and encourages further research with a comparable approach.

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1 Introduction

Sleep deprivation (SD), or sleep loss, is known to have severe negative effects on health and has been linked to negative health outcomes like increased weight, blood pressure and risk of heart attacks (Cappuccio et al., 2008; Krittanawong et al., 2019; Medic et al., 2017; Schwartz et al., 1998). While SD can be acute, it can also relate to shortened sleep durations for prolonged periods of time. Insufficient sleep is regarded a global public health problem as it is estimated that nearly 30% of adolescents and adults sleep less than six hours per night (Bellesi, 2019; Honn et al., 2019). Furthermore, SD is also considered the cause of several accidents, medical errors and increased mortality in work accidents (Åkerstedt et al., 2002; Flatley et al., 2004; Institute of Medicine (US) Committee on Sleep Medicine and Research, 2006). Hence, there is no doubt about the negative physical consequences of sleep deprivation; however, the cognitive impairment following sleep loss is less clear (Lim & Dinges, 2010). The brain's networks, synapses, neuronal membrane properties and even gene transcription involved in synaptic plasticity and cellular stress are extremely susceptible to sleep loss (Bellesi, 2019; Tononi & Cirelli, 2014). Thus, it is of utmost importance to study the brain and cognitive decline following habitual short sleep, as it can have detrimental effects on society, whether it be in the emergency room or in the board meeting (Whitney et al., 2017).

The present study is the first to assess how sleep can affect cognitive control and how this relates to brain structure from a graph theoretical perspective. First, previous studies will be reviewed in which cognitive control as a construct and how it is measured will be addressed. Then it will be discussed how sleep may have an impact on cognitive control and how it all traces back to the brain.

1.1 Cognitive Control

Previous studies have found SD to impair cognitive control (Lowe et al., 2017; Whitney et al., 2017). Cognitive control, in the literature often also referred to as executive control or executive functions (EFs), is considered an umbrella term for the ability to regulate thoughts and behaviours in relation to internal plans or goals (Koechlin et al., 2003; Verbruggen, McLaren, et al., 2014). This includes planning, attentional control, reasoning, monitoring, adaptation and organisation of lower level processes like perception and motor programming (Botvinick et al., 2001; Burgess & Stuss, 2017; Koechlin et al., 2003; Verbruggen, McLaren,

et al., 2014). Goal-adaptive behaviour thus relies on maintaining and using internal goals to manipulate various ongoing processes (Friedman & Miyake, 2017).

1.1.2 Measuring Cognitive Control

There are several tasks that can be utilised to measure cognitive control, for instance, the n-Back task for Updating, a task-switch paradigm for Shifting and the go/no-go task (GNGT) or stop-signal task (SST) for Inhibition (Friedman & Miyake, 2017). Updating, Shifting and Inhibition represent different factors that EF tasks load on to (Miyake et al., 2000). Here, Updating refers to updating working memory, Shifting involves flexible shift of attention or tasks and inhibition is the ability to suppress a prepotent behaviour (Friedman & Miyake, 2017; Verbruggen & Logan, 2009). While the GNGT and the SST are both used to measure inhibition, the GNGT measures action restraint, while the SST measures action cancellation which rely on separate brain activations (Swick et al., 2011). As this paper focuses on the SST, the other tasks will not be further elaborated on. The SST involves a go stimulus and a stop stimulus (Logan & Cowan, 1984). The go stimulus requires a fast response while the occasional stop stimulus on a subset of trials following the 'go', requires the participant to withhold their response. SST performance is popularly modelled as a horse race between the go process triggered by the go stimulus and the stop process triggered by the stop stimulus (Logan & Cowan, 1984; Verbruggen, Best, et al., 2014). The time between the go and stop signals is called the stop-signal delay (SSD). Performance on the SST is typically measured computationally by the stop signal reaction time (SSRT) which is a measure of the latency of the stop process (Logan & Cowan, 1984). Simply put, in cases of an average stop accuracy of 50% and a normal distribution of reaction times in go trials (goRTs), the SSRT is given by subtracting the mean SSD from the mean goRT. However, the integration method for SSRT calculation is generally preferred and considered the more reliable estimation of the SSRT (Verbruggen et al., 2019). With the integration method, the mean SSD is subtracted from the *n*th goRT in the goRT distribution, where n is the number of RTs multiplied by the probability of an unsuccessful stop (Verbruggen & Logan, 2009).

1.1.3 The Complexity of the SST

It is important to appreciate the complexity of a relatively simple task such as the SST. First, the primary task is to respond to go stimuli, which requires sustained attention or task engagement as it can be a rather monotonous and simple task (Kusztor et al., 2019). This can be assessed by looking at goRTs and the amount of omission errors (i.e. trials with no response) and go errors (i.e. go trials with an incorrect response). Second, there is the inhibition aspect, initiated by the stop stimulus and measured by the SSRT. In traditional

versions of the SST, inhibition is triggered by the appearance of a stop-stimulus, thus relying largely on bottom-up processing and may be activated without the need for effortful control (Verbruggen, Best, et al., 2014). This is often considered the predominant aspect of the task. Third, the SST also involves behavioural adjustment, for instance, in response to errors or unexpected events like an infrequent stop signal (Kusztor et al., 2019). In both cases, participants tend to slow down on the following trial, known as post-error slowing (PES) and post-stop slowing (PSS) respectively (Bissett & Logan, 2012a, 2012b; Danielmeier & Ullsperger, 2011). PES and PSS represent behavioural adaptation following neural signalling of need for adjustment, which is considered both reflexive and strategic. The signalling itself is more automatic while the behavioural adjustment, relying on explicit task and context information, is more strategic (Bissett & Logan, 2012b; Dutilh et al., 2012). In other words, the SST can be used to assess multiple aspects of cognitive control.

1.2 Sleep Deprivation and Cognition

In the literature, it seems SD most consistently impairs sustained attention (de Bruin et al., 2017; Lim & Dinges, 2010; Lowe et al., 2017). In view of the mentioned negative health outcomes, this is not unexpected, as sleep loss is associated with decreased arousal in the central nervous system (CNS; Cote et al., 2009). This has further been associated with impaired cognitive flexibility as observed when participants fail to follow feedback (feedback blunting) and appears to stem from a general problem with dynamic allocation of attentional resources (Honn et al., 2019).

In a meta-analytic review, Lowe and colleagues (2017) consistently found attentional lapses and impaired inhibitory control across studies, both of which point to trouble with sustained attention. However, the literature is highly inconsistent in relation to higher order functions like inhibition (de Bruin et al., 2017), possibly because most research in the field so far has utilised the GNGT rather than the SST (Kusztor et al., 2019). In two studies looking at SST performance following SD, Zhao et al. (2018) found prolonged SSRTs following SD while Kusztor and colleagues (2019), did not. However, as Zhao and colleagues (2018) report no RTs, it is hard to tell whether the observed effect reflects prolonged RTs rather than impaired inhibition. On the other hand, as they did apply an SSD tracking, the RTs should not influence the SSRT to such an extent. Yet, the researchers also fail to report the maximum SSD, and as such it is unclear if potential prolonged RTs could push the SSD to a high limit. This could prevent proper tracking, potentially affecting accuracies, which in turn can impact the SSRT. Considering that other studies have, in fact, found increased RTs on vigilance

tasks and the GNGT following SD (Chua et al., 2017; Honn et al., 2020; Vivo & Bellesi, 2019), it is possible that Zhao et al.'s (2018) findings reflect impaired sustained attention rather than inhibition. Related to impaired sustained attention, SD has also been found to impair accuracies in the GNGT (Chua et al., 2017; Honn et al., 2020; Renn & Cote, 2013) and the SST (Kusztor et al., 2019).

In relation to the more higher order cognitive control functions, Chua et al. (2017) argue that cognitive impairment due to SD can be explained by task load, such that performance decreases in demanding tasks, for instance in multitasking paradigms where divided attention is needed. Whitney et al. (2017) explained this as cognitive flexibility or flexible shifting of attentional control being impaired. In their study, they found that when task demands change, SD individuals fail to prevent errors when dealing with competing responses. Further, when errors occur, they elicit altered event-related potentials (ERPs) on the electroencephalogram (EEG; Kusztor et al., 2019; Whitney et al., 2017). Additionally, this is consistent with findings from Gevers et al. (2015) who investigated the effects of SD on cognitive control and found that conflict adaptation, a top-down mechanism, was impaired following SD. Although PES and PSS did not behaviourally show any change following SD in the study by Kusztor et al. (2019), that might be due to the study inducing acute SD. But, as studies have found SD impairments to be dose-dependent (i.e. the impairments accumulate over days), it is possible that PES and PSS show effects in relation to habitual short sleep (Jin et al., 2015; Khalsa et al., 2017; Krause et al., 2017; Lowe et al., 2017; Vivo & Bellesi, 2019). In sum, SD seems to impair top-down attentional control related to performance monitoring.

However, there are some conflicting findings that warrant further discussion (de Bruin et al., 2017; Honn et al., 2019; Kusztor et al., 2019; Lim & Dinges, 2010). For instance, Zitser and colleagues (2020) found no effects of SD on cognition in adolescents and Sexton et al. (2017) also found null results in older adults. Furthermore, Gevers et al. (2015) found that automatic responses on congruent trials in a Stroop task (related to go-trials in an SST) remained stable regardless of SD or rested wakefulness. There can be several reasons for the inconsistencies. First, cognitive tasks aimed at measuring top-down mechanisms are often more engaging, thus introducing confounds like motivation, task complexity and difficulty (Kusztor et al., 2019; Lim & Dinges, 2010). Second, some of the findings can also be explained by bottom-up pathway-dependent mechanisms; for instance more response variability observed in sleep deprived individuals potentially indicating reduced engagement driven by local sleep (i.e. sleep-like states occurring locally at tightly interconnected neuronal assemblies such as in cortical columns; Hudson et al., 2020; Krueger et al., 2008; Rector et

al., 2005). Despite this, impaired sustained and divided attention are highly consistent findings and can explain increased RTs, decreased accuracies, more errors and inconsistent findings through cognitive instability (Chua et al., 2017; Honn et al., 2020).

1.3 About DTI

Early lesion studies showed that EFs are impaired in patients with frontal lobe damage, and the prefrontal cortex (PFC) was eventually seen as the loci for EFs (Burgess & Stuss, 2017). However, over the years, it became apparent that patients with other lesions, could also show impaired executive functioning. Thus, when neuroimaging studies showed that the PFC has a large amount of connections to subcortical, limbic, cerebellar and cortical areas, cognitive neuroscientists started to look at brain circuits rather than focusing just on brain regions (Burgess & Stuss, 2017; Johansen-Berg, 2010). To map the circuits of the brain, diffusion tensor imaging (DTI) can be used as it utilises the motion or diffusion of water molecules (Beaulieu, 2002). This is highly influenced by biological properties (i.e. myelin, cell membranes, microtubules, etc.). For instance, in white matter, which mostly consists of nerve fibres, there is anisotropy, meaning that water molecules diffuse more rapidly along the length of the fibre as opposed to across the width (Huettel et al., 2009). Diffusion can be quantified with several different parameters of which the most commonly used is fractional anisotropy (FA), which is considered a measure of microstructural integrity. Other parameters include mean diffusivity (MD), a measure of membrane density or molecular diffusion rate, and axial and radial diffusivity (AD and RD), measures of the diffusion rate along the main and transverse diffusion axis, respectively (Alexander et al., 2011; Soares et al., 2013). It should be mentioned that although these scalars represent different biological characteristics, they also often correlate.

A more advanced analysis that builds on DTI, is tractography (Huettel et al., 2009). Put simply, per voxel one can find the direction in which diffusion is preferred and use this to track fibres between associated brain regions. By following the preferred diffusion direction, images or maps of structurally connected regions can be created. As the efficiency of the connections is decided by the underlying white matter properties, the abovementioned diffusion parameters are used to indicate the strength of the connections within identified tracts (Fields, 2008).

1.4 Attention and the Brain

As discussed above, SD appears to consistently affect top-down processes, including attention. This can be linked to findings that sleep loss is associated with widespread reduced FA (Elvsåshagen et al., 2015; Mulder et al., 2019; Rocklage et al., 2009). In detail, the corona radiata, which spreads like a fan from the brainstem to the cortex, has been found to have decreased FA in SD (Khalsa et al., 2017). The anterior portion of this structure is strongly related to thalamocortical relays and reduced FA can indicate a disruption of these connections. Both the corona radiata and the thalamus are linked to attention, and in studies on SD this becomes more apparent (Krause et al., 2017). Sustained thalamic activation during task performance is related to maintained attention, while reduced activation is associated with lapses in attention. It is thus proposed that the thalamus works as a gating hub through which arousal signals from the brainstem ascend to the cortex via the corona radiata.

More specifically, while maintained attention is associated with sustained thalamic activity, attentional failure has been linked to the dorsolateral prefrontal cortex (dlPFC; Krause et al., 2017). The dlPFC is consistently reported as altered following sleep loss (Thomas et al., 2000) and has been found to correlate with resistance to SD (Cui et al., 2015). In other words, individuals who showed little change in task performance on a working memory task following sleep loss, were found to have higher FA in tracts to the dlPFC. As most tasks require attention for successful performance, it is natural that this points back to the role of the dlPFC in sustained and directed attention (Krause et al., 2017).

Furthermore, Khalsa and colleagues (2017) found sleep duration to correlate with FA of the orbitofrontal regions. Activation in this area has also been found to negatively correlate with reaction times, which is considered an attentional marker (Kong et al., 2018). Khalsa et al. (2017) also links changes in the region to attentional and other cognitive impairments, although they remain non-specific. They also suggest that it is connected to cortical areas forming part of the salience network (i.e. a network including the anterior insula and anterior cingulate, responsible for initiating and maintaining task-set; Dosenbach et al., 2006; Seeley, 2019). However, as is apparent, more research is needed in relation to the orbitofrontal regions.

1.5 Inhibition and the Brain

Inhibition, the predominant part of the SST, has been consistently found to rely on a right-lateralised ensemble of brain regions including the right inferior frontal gyrus pars opercularis (rIFGop), right supplementary motor area/pre-supplementary motor area (rSMA/pre-SMA),

primary motor cortex (M1) and basal ganglia structures (e.g. thalamus, subthalamic nucleus (STN), pallidum and caudate; Aron et al., 2014; Cai et al., 2014; Hampshire, 2015; Levy & Wagner, 2011). Lesion studies, both induced by TMS and in patients with frontal lobe damage, have shown that disruption of the rIFG impairs response inhibition (Aron et al., 2003; Chambers et al., 2007). The region is also commonly active in stopping tasks (Aron et al., 2007; Chevrier et al., 2007; Rubia et al., 2003). The SMA/pre-SMA has also been related to stopping both in fMRI and lesion studies (Aron et al., 2004; Derrfuss et al., 2004; Nachev et al., 2007). In relation to basal ganglia structures, their involvement is based on the direct, indirect and hyperdirect motor pathways of the basal ganglia (see Aron & Poldrack, 2006; Verbruggen, Best, et al., 2014; Zandbelt & Vink, 2010 for details). In short, the basal ganglia structures work together to execute motor control via different pathways through which eventually the inhibition or excitation of the thalamus affects the M1.

1.6 Performance Monitoring and the Brain

The SST also involves performance monitoring, which is often measured with PES and PSS. Behavioural adaptations to optimise performance rely on a wide range of frontal, parietal and subcortical brain regions including motor-limbic connections (Ullsperger et al., 2014). Considering that studies have found error-related ERPs to be altered and consistently so throughout a task in sleep deprived individuals, SD might lead to a perseverance of errors as the amplitudes of these ERPs tend to attenuate throughout the task in non-SD participants (Kusztor et al., 2019; Renn & Cote, 2013). Because performance monitoring engages widespread brain regions, it is not surprising that some of these areas, like the anterior midcingulate cortex (aMCC), the anterior cingulate cortex (ACC), the medial frontal cortex (MFC) and the dlPFC, are involved in attention shifting, performance and conflict monitoring and visual and motoric adaptive processes (Brown, 2013; Danielmeier et al., 2011; Sheth et al., 2012). This suggests that these regions play a role in top-down attentional shift towards task relevant stimulus features which leads to improved accuracy and prolonged RTs on post error trials (Danielmeier et al., 2011; Danielmeier & Ullsperger, 2011). In support of this, regions closely connected to the MFC involves the pre-SMA, aMCC and ACC which in turn communicate with the rIFG and STN, i.e. vital parts of the inhibition network, suggesting that PES is closely related to inhibition (Danielmeier et al., 2011; Molenberghs et al., 2009; Ullsperger et al., 2014; Wessel & Aron, 2017). In other words, inhibition regions are also active in other tasks which makes it consistent with a multi-demand cortex (MDC) theory. In the MDC framework, regions like the IFG and pre-SMA are considered crucial for successful

inhibition, but they are also recruited as a multifunctional network involved in other EFs like decision making, task rule maintenance and performance monitoring (Chambers et al., 2009; Swick et al., 2011). IFC subregions have been argued to form spatially distributed networks that are activated by infrequent stimuli and novel tasks whether they are inhibition related or not (Erika-Florence et al., 2014). Furthermore, Wessel and Aron (2017) found similar brain activation for unexpected outcomes, unexpected events and action stopping. They argue that it all relies on a fronto-BG network involving the pre-SMA, rIFC and STN in which ongoing motor- and cognitive representations are interrupted and suppressed to free up resources in order to deal with unexpected events. This emphasises how performance on the SST does not only rely on stopping, but rather on a wide range of functions that might rely on the same brain regions.

1.7 Graph Theory in Brain Connectivity

As is apparent from the literature summarised above, SD affects the brain rather globally, yet previous research has mainly focused on brain regions of interest or conventional MRI measures such as whole brain mean FA/MD or total white matter volume (Caeyenberghs et al., 2014). The same is also true for cognitive control research, but, as EFs and attention likely depend on widespread brain regions integrating information, such analyses might be deficient (Bressler & Menon, 2010; Caeyenberghs et al., 2014). Rather, network-based approaches could be more informative as they consider separate regions as parts of a global unit rather than individual entities (Caeyenberghs et al., 2014). Brain connectivity is considered highly important for brain functioning, particularly for information processing speed and EFs, and may therefore be a good alternative for analyses (Reijmer, Leemans, Caeyenberghs, et al., 2013). In recent years, graph theoretical approaches have been suggested to quantitatively characterise the white matter networks of the brain (see Bullmore & Sporns, 2009 for review).

In graph theory, a network is defined as a set of nodes and edges (Bullmore & Sporns, 2009). In case of the brain, the nodes are commonly denoting brain regions while the edges denote structural white-matter connections between the brain regions or nodes. The network reconstruction is performed by the tractography analysis and can be used to derive topological metrics of the network. Some of the most used metrics to investigate network integration is path length (i.e., average fewest edges between all pairs of nodes, see figure 1) and global efficiency (i.e., average inverse shortest path in the network; Rubinov & Sporns, 2010). On the other hand, to investigate network segregation, the metrics clustering

coefficient (i.e., fraction of a node's neighbours that are also neighbours, i.e. forming triangles, see figure 1) and local efficiency (i.e., global efficiency computed for node neighbourhoods) are commonly used. However, a well-designed network like the brain uses both segregation and integration, both of which can be captured by small-worldness (i.e., a network with greater clustering than a random network but equal to random path length). Another measure that captures both integration and segregation is betweenness centrality (i.e., the fraction of shortest paths in a network that pass through a given node) as it facilitates integration while also enabling links between anatomically unconnected regions.

Small-worldness is generally used as a measure of principal network organisation as it per definition represents the presence of segregated modules, having functional specialisation, with integrating links of a significant number (Rubinov & Sporns, 2010). Thus, small-worldness should be found in all well-designed anatomical networks (Caeyenberghs et al., 2014; Reijmer et al., 2015; Reijmer, Leemans, Brundel, et al., 2013; Reijmer, Leemans, Caeyenberghs, et al., 2013).

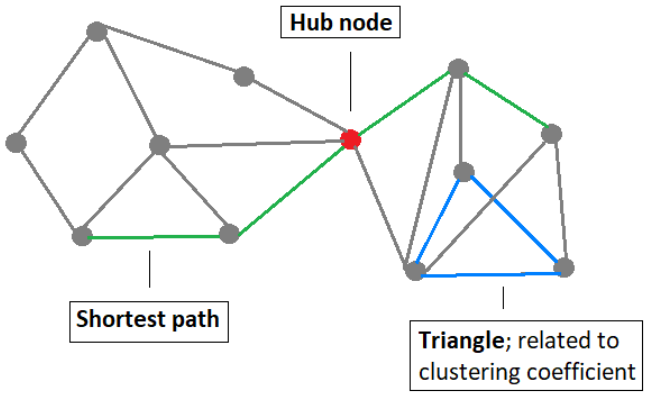

Figure 1. Measures of brain connectivity. An illustration of some central network measures. For instance, triangles (blue) are used in measures of segregation, while path length (green) is involved in calculation of betweenness centrality and other measures of integration. Hub nodes (red) are nodes involved in many shortest paths and thus have a high betweenness centrality.

1.7.1 Global and Local Efficiency

As implied above, connectivity analyses involve many different variables that are closely related (Rubinov & Sporns, 2010). For instance, in order to measure small-worldness, the clustering coefficient and characteristic path length must be known both from the network and from a random network that needs to be constructed. So, in an attempt to capture small-

worldness in one variable, Latora and Marchiori (2001) proposed global efficiency. This variable captures a system (e.g. the brain) in which information is exchanged in a parallel system and all nodes communicate via shortest paths (Achard & Bullmore, 2007).

Global efficiency is the graph theoretical metric that has been most consistently related to EFs (Caeyenberghs et al., 2014; Reijmer, Leemans, Caeyenberghs, et al., 2013; Reijmer et al., 2015). However, most research to date have focused on clinical samples like in traumatic brain injury (TBI; Caeyenberghs et al., 2014), Alzheimer's disease (AD; Reijmer, Leemans, Caeyenberghs, et al., 2013), cerebral amyloid angiopathy (CAA; Reijmer et al., 2015) and type 2 diabetes (Reijmer, Leemans, Brundel, et al., 2013). In these studies, reduced global efficiency has been associated to decreased memory performance (Reijmer, Leemans, Caeyenberghs, et al., 2013), lower performance in switching tasks (Caeyenberghs et al., 2014), slower processing and performance (Caeyenberghs et al., 2014; Reijmer et al., 2015) and impaired EFs, and then specifically divided attention and response inhibition (Reijmer, Leemans, Caeyenberghs, et al., 2013; Reijmer et al., 2015).

However, global efficiency alone does not capture the efficiency of the brain, hence local efficiency has been proposed to further capture the brain's hierarchical organisation (Latora & Marchiori, 2001). Local efficiency is related to the clustering coefficient in that it considers the connectedness of a node's neighbours (Cohen & D'Esposito, 2016; Fornito et al., 2016). But it differs in that local efficiency considers each individual node's direct and indirect connections without the initial node, thus computing the fault tolerance, i.e. the efficiency of a node neighbourhood after disruption of a node (Achard & Bullmore, 2007; Latora & Marchiori, 2003). A network that is both globally and locally efficient can be considered small-world as it implies an efficient integration of information on several levels, thus giving rise to a cost-efficient organisation.

1.8 Summary and Conclusion

Sleep deprivation has severe negative effects on health, but the cognitive impairment is less well understood. Reviews and meta-analyses have consistently found impaired sustained attention and problems allocating attentional resources. This leads to trouble with cognitive flexibility and conflict adaptation or performance monitoring, both of which are related to EFs. EFs include a range of processes and in order to investigate several of them simultaneously, the SST can be utilised. It is monotonous and simple enough to measure sustained attention, performance monitoring and inhibition without introducing confounds like task difficulty. Additionally, it allows the investigation of both top-down (e.g.

performance monitoring measured by PES and PSS) and bottom-up (e.g. inhibition measured by SSRTs) processes simultaneously.

However, the findings and methodologies in the literature are highly inconsistent. Most studies have looked at manipulated SD in which participants have been kept awake for an extended period in the lab. But, as several studies have found SD decrements to be dose-dependent, meaning that the impairments accumulate over days, it might be more informative to investigate habitual sleep (Jin et al., 2015; Khalsa et al., 2017; Krause et al., 2017; Lowe et al., 2017; Vivo & Bellesi, 2019). Previous work has also mainly focused on brain regions or tracts of interest, mean diffusion parameters or conventional MRI markers. An alternative approach that might be more fruitful in the analysis of the effects of SD on brain connectivity and its relation to cognition, is graph theory. In this framework, the brain regions are considered a unity rather than separate entities. Studies using a graph theoretical approach to brain connectivity have linked measures like global efficiency to performance on cognitive tasks, especially related to speed, accuracy and attention. Of note, studies adopting a graph theoretical approach in relation to EFs so far, have mainly focused on a clinical sample and, as implied before, different tasks measure different aspects of inhibition (i.e. GNGT versus SST), and clinical research often use different tasks than cognitive science (MacLeod et al., 2003). Thus, it is of interest to see how these measures behave in a sample of healthy, young adults.

1.9 The Present Study

Based on the summary above, the current study sought to investigate how habitual sleep duration, global efficiency and local efficiencies are related to sustained attention, performance monitoring and inhibition. While the literature mainly suggests that sleep selectively affects top-down control mechanisms, there are also other possible explanations. However, it is challenging to get a clear explanation as the field is riddled with task impurity and different methodologies. Therefore, an SST paradigm is here utilised as it allows the investigation of both top-down (performance monitoring and attention) and bottom-up (response inhibition) processes without introducing confounds like task difficulty. Sustained attention was assessed with goRTs, go errors (goErr) and go omissions (goOm), performance monitoring was measured with slowing (PES and PSS), and inhibition was computed with the SSRT. PES and PSS are included here as previous studies argue that sleep affect top-down mechanisms. Even though for instance Kusztor et al. (2019) did not find prolonged PES and PSS following sleep deprivation, they did find altered top-down related

electrophysiological responses. The present study could be able to clarify this as the behavioural effects of sleep may be more pronounced in habitual sleep.

The following hypotheses were formulated:

Shorter sleepers will:

1) have more errors (goErr and goOm) as a reflection of impaired sustained attention.

2) have longer goRTs, PES and PSS, as the first measure represents sustained attention and the latter two, performance monitoring.

3) have lower global efficiency as sleep affects the brain on a global level.

Additionally,

4) higher global efficiency will be related to faster goRTs as an efficient brain in which information is quickly integrated will have shorter reaction times.

In relation to local efficiencies:

5) Shorter SSRTs will be related to higher local efficiency of the inhibition network: rIFGop, rSMA/pre-SMA and bilateral M1.

6) More slowing (PES and PSS) will be associated with higher efficiency in the inhibition network (rIFGop, rSMA/pre-SMA), but also in regions associated with performance monitoring (bilateral ACC, bilateral MCC and bilateral dlPFC).

7) Attention (goRT, goOm and goErr) will be negatively correlated with local efficiency of bilateral orbitofrontal regions, bilateral thalamus and bilateral dlPFC.

2 Materials and Methods

2.1 Participants

A total of 28 participants were recruited from posters at the University of Oslo and online via social media. Due to the covid-19 pandemic, only 22 participants completed all sessions. Out of these, three were excluded due to faulty actigraphy watches, one from the behavioural analysis due to a too high stop accuracy (stop accuracy > 75%; Verbruggen et al., 2019), and one for deviating more than three standard deviations (SDs) from the mean on goErr. Thus, the total sample consisted of 17 participants (11 females, age range: 20-35 (mean: 26.88, SD: 3.41)). All participants reported no current or previous psychological or neurological disorders, were right-handed and suited for MRI scanning. Additionally, all but one participant had normal or corrected to normal vision but as the one participant did not deviate on any of the measures, the person was included in the analysis. On the first session, all participants received information about the experiment and the procedures and gave their written consent to participate in the study according to the Helsinki declaration. The participants were compensated with a universal gift card of 500 NOK for their participation on the last session. The study was approved by the internal ethics committee at the Department of Psychology at the University of Oslo.

2.2 Design

The full study consisted of three sessions: two EEG recordings with cognitive control tasks and questionnaires and one separate session in the MR scanner. This paper focuses on the SST behavioural performance, actigraphy and DWI. SST performance was analysed from session two in order to better correspond to the objective sleep duration measure from the actigraphy data which was collected in the two weeks between session one and session two. This correlation study investigated how sleep and brain connectivity correspond to SST performance. The included predictor variables were sleep duration, global efficiency and local efficiencies, while the outcome variables were goRTs, PES, PSS, goErr, goOm, SSRTs and global efficiency.

2.3 Materials

2.3.1 Setup

The stop signal task was presented using a Dell Precision T5500 computer (Dell, Inc., Texas, USA) with Windows 10. The participants were seated approximately 70 cm from the Eizo

FlexScan S2411W monitor (EIZO, Inc.) with a resolution of 1920x1200 and a refresh rate of 60 Hz. Stimuli was presented using the Psychophysics Toolbox (version 3.0.16; Brainard, 1997; Pelli, 1997; Kleiner et al., 2007) running in MATLAB R2019a (The MathWorks, Inc., Massachusetts, USA). Responses were given on a Cedrus RB-740 response pad (Cedrus corporation, San Pedro, CA, USA).

2.3.2 Task

The participants completed a visual stop signal task where they responded to coloured arrows (figure 2). The arrows pointed left or right, indicating which hand the participants should use to respond (i.e. if the arrow pointed to the left, the participants should press the left-most button). On 24% of the trials, the arrow was followed by another in a different colour indicating a stop-signal. The arrows were blue and orange, one colour for the go-arrows and the other for the stop-arrows. The colours were counterbalanced between the participants.

The task consisted of five blocks lasting approximately two and a half minutes, adding up to a total duration of about 13 minutes. In total, the participants completed 450 trials (340 go trials and 110 stop trials) in random order. Each block started with a black fixation cross centred on a grey background lasting between 700 and 1200ms. The stimulus was presented for 100ms and responses were collected throughout the trial. The duration between the go- and stop stimulus (the SSD) varied according to performance and ranged from 100ms to 600ms starting at 250ms. For each successful stop trial, the SSD increased with 50ms, and for each unsuccessful stop trial, it decreased with 50ms. This tracking procedure was used to achieve an overall stop accuracy of 50% and is generally recommended for stop signal paradigms (Verbruggen et al., 2019).

After each block, the participants received some short feedback on the screen and had a self-paced pause while seated in the chamber and without the experimenters coming in. The feedback was either “Be faster!” if the average goRT was longer than 600ms, “Be more accurate!” if the average stop accuracy was less than 40%, “Be faster and more accurate” if the goRT was longer than 600ms and the accuracy on stop trials was less than 40%, or otherwise “Well done!”. The feedback was block-based and not influenced by previous blocks.

Before the main task started, the participants practiced the task for about a minute in order to make sure they understood the task. The training consisted of 20 trials in random order and the participants got “Correct!” or “Incorrect!” feedback after each trial.

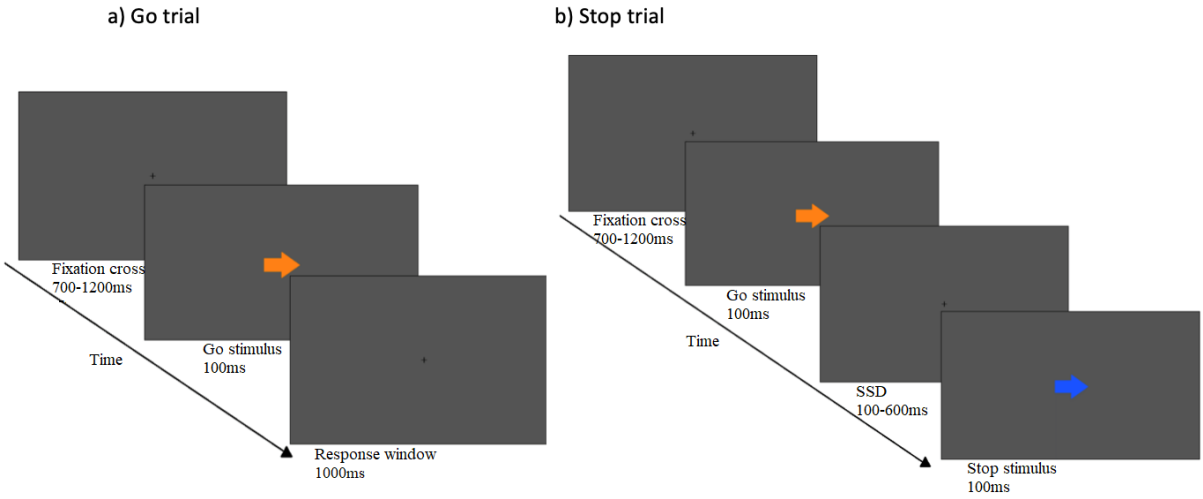

Figure 2. The stop signal paradigm utilised. A, an example go trial. B, an example stop trial. The colours were counterbalanced between participants.

SSD = stop signal delay, ms = milliseconds.

2.3.3 Actigraphy

The actiwatch spectrum plus wrist actigraphs (Actiwatch Spectrum Plus, Philips Respironics Inc, Murrysville, PA, USA) were set to fifteen seconds epochs and recorded bedtime, get-up time, hours spent in bed, hours spent asleep, sleep latency, sleep efficiency, number of awakenings and total duration of the awakenings based on light and activity levels. Actigraphs have been reported to be in close agreement with polysomnography (PSG) in several instances (Scott et al., 2020; Walia & Mehra, 2019) and similar watches have been used in related studies (Khalsa et al., 2017).

2.3.4 MRI Data Acquisition

The MRI session took place at the Intervention Centre at Oslo University Hospital on a 3.0 Tesla Philips Ingenia whole-body scanner (Philips Medical Systems, Best, Netherlands) with a 32-channel head coil. T1 images were acquired with echo time (TE) = 2.3, repetition time (TR) = 5.1, field of view (FOV) = 256 x 256 x 184, matrix = 256 x 254 x 184, voxel size = 1.0 x 1.0 x 1.0 mm. The duration of the T1 scan was 06.29 min. The DWIs were acquired with a single-shot echo planar imaging (EPI) sequence, one b0 image and the diffusion weighting was distributed across 32 non-collinear directions with a b-value = 1000s/mm2, flip angle = 90 degrees, TR = 13.45s, TE = 62ms, FOV = 224 x 224 x 120 and matrix = 96 x 94 x 60. The acquired voxel size (2.33 x 2.38 x 2.0mm) was reconstructed to 2.0mm isotropic voxels. The total duration of the DWI acquisition was 09.51 min.

2.4 Procedure

The complete study consisted of three sessions: two EEG recordings with cognitive control tasks and questionnaires and one separate session in the MR scanner. Prior to participation, participants were given information about the study and asked to carefully read through the inclusion criteria. On the first day in the EEG laboratory, all participants signed a written informed consent form after going through the inclusion criteria checklist. After the paperwork was completed, the EEG cap and electromyography (EMG) electrodes were placed on the participant. Then, the participants were given the instructions for the SST before they completed a short training session for about one minute to make sure they understood the task. Next, they performed the main task which lasted about 13 minutes. Following the SST, the participants performed a task-switch task, a Stroop task, an n-Back task and a resting state task, in that order. The total duration of the EEG preparation and tasks were about two and a half hours. Afterwards, the participants got to wash the EEG gel out of their hair before they completed six questionnaires: Pittsburgh Sleep Quality Index (PSQI; Buysse et al., 1989), Epworth Sleepiness Scale (ESS; Johns, 1991), the positive and negative affect scales (PANAS; Watson et al., 1988), Achenbach System of Empirically Based Assessment Adult Self-Report (ASEBA-ASR; Achenbach & Rescorla, 2003), emotion regulation questionnaire (ERQ; Gross & John, 2003) and a dietary/health questionnaire (Turconi et al., 2003) which took about 30-40 minutes to complete. Finally, the participants were given the wrist actigraph (Actiwatch Spectrum Plus, Philips Respironics Inc, Murrysville, PA, USA) and a sleep diary (Carney et al., 2012). The experimenters emphasised that the watch should be worn every night and preferably as much as possible during the day as well. After 13-15 days, the participants came back to the laboratory to repeat the session. On this session, the experimenters collected the actigraphs and the diaries and the participants were offered to view their own actigraphy data at the end of the session.

During or after these two weeks, the participants underwent the third session. This was an MRI scan consisting of a T1, DWI and resting state fMRI. The experimenters sent out a specific screening list prior to scanning provided by the Intervention Centre at Oslo University Hospital. On the day of the scanning, the experimenters went through said screening list with the participant to make sure it was safe for the person to be in the MR scanner. After the list was filled out, the experimenters followed the participant into the scanner room and explained the procedure of the scanning; the person was to lie as still as possible without falling asleep. All participants wore double set of ear protection and held an alarm button in case they experienced any discomfort during the scanning. No tasks were

performed in the scanner, but the participants were offered to watch Mr. Bean or Charlie Chaplin while listening to the radio for entertainment during the T1 and DWIs. For the resting state fMRI, the participants looked at a fixation cross without radio or movies for entertainment. The MRI session lasted for about 40 minutes.

2.5 Analyses

2.5.1 Behavioural Data

Task performance on the SST was evaluated by computing the reaction time between go stimulus and response (goRT), the SSRT, the accuracy on go trials (goErr and goOm) and slowing after stop trials and error trials (PSS and PES, respectively) in an in-house MATLAB R2019a (The MathWorks, Inc., Massachusetts, USA) script. Trials with RTs exceeding 1000ms were considered go omissions. The SSRTs were calculated using the integration method as recommended by Verbruggen et al. (2019). Calculating PES and PSS consist of subtracting the measure of pre-stop RTs from a measure of post-stop RTs. Pre-stop RTs were defined as the average RT of the third valid go trial in a sequence of at least four valid got trials (Danielmeier & Ullsperger, 2011). Post-stop RTs were defined as the average RT for valid go trials following a successful or unsuccessful stop trial for PSS and PES, respectively.

2.5.2 Sleep Analyses

To objectively assess sleep duration, the mean sleep duration from the actigraphs were used. For six participants the actigraphy data were spurious. Thus, three members of the project team reviewed these datasets and corrected potentially erroneous entries based on their inter-rater agreement to ensure quality. The sleep durations from the actigraphs were given in the hh:mm format and was converted to hours in decimals (e.g. 7:30 was converted to 7.50).

2.5.3 DWI Analysis

The raw DWI and T1 image DICOM files were converted into NiFTI format using dcm2niix implemented in MRIcroGL (version 1.2.2; http://www.cabiatl.com/mricrogl/; Li et al., 2016) The DWI analysis was performed with ExploreDTI v4.8.6 (Leemans et al., 2009). The preprocessing included artefact inspection to check for excessive motion, eddy current-induced distortions- and motion correction with a non-DWI as reference, EPI correction with high resolution T1 images and transformation of the data into 1 mm isotropic voxels for diffusion tractography analysis (see figure 3 for processing flow chart).

Tractography. A deterministic tractography analysis was performed on the whole brain and with every voxel as seed point. The parameters were set to a seed point resolution of 1.0 x 1.0 x 1.0 mm, FA threshold of 0.2 and an angle threshold of 45°. In other words, the

tractography analysis terminated if a voxel reached an FA value of less than 0.2 or if it contained an angular turn exceeding 45°. Next, a connectivity analysis was carried out based on the AAL atlas (Tzourio-Mazoyer et al., 2002) which contains masks for brain regions and parameters are computed for the pair-wise connections between the regions. This led to a 90-by-90 square connectivity matrix containing the averaged FA values along each tract and a 90-by-90 binary connectivity matrix. The connectivity analysis gives two matrices for each diffusion parameter to separate between pass and end tracts, however as this analysis focus on the END tracts based on previous research (Reijmer, Leemans, Caeyenberghs, et al., 2013; Reijmer, Leemans, Brundel, et al., 2013; Reijmer et al., 2015), the PASS connections will not be further elaborated on. The columns in the matrices represent the seeding region, while the rows represent the regions the tract terminates in. Streamline tractography can occasionally result in false positive tracts, thus identified tracts usually need to meet a set criterion in order to be deemed reliable. As there is no consensus in the literature about the inclusion criteria of a tract, the current study included those present in at least 50 % of the participants, as this is used in several studies with similar design (Leh et al., 2007; Orr et al., 2015; Reijmer, Leemans, Brundel, et al., 2013; Vik et al., 2015). The DWI processing steps are visualised in figure 3.

Connectivity. The connectivity analyses were performed using the Brain Connectivity Toolbox (Rubinov & Sporns, 2010; https://www.sites.google.com/a/brain-connectivity-toolbox.net/bct/) in which the clustering coefficient, characteristic shortest path length and global efficiency were extracted to investigate network architecture while local efficiencies were found for regions of interest (ROIs) in order to measure regional properties (see section 1.9 for a brief description of the different measures).

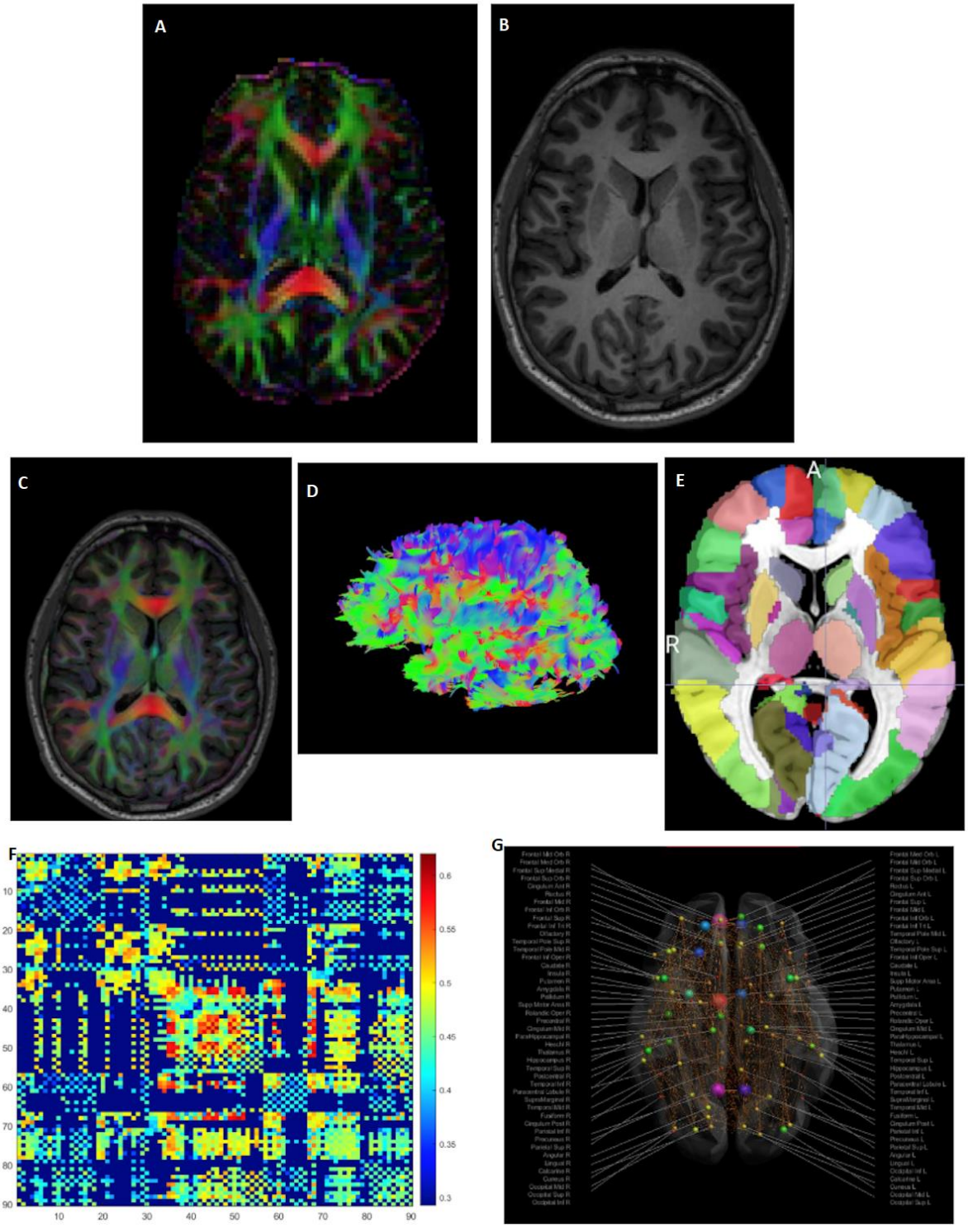

Figure 3. Flow chart of brain network reconstruction. The DWIs (A) were corrected for movements and distortions with the T1 and b0 image (B), which gave a corrected FEFA image (C). Deterministic tractography (D) and connectivity analyses based on the AAL (E) were performed and resulted in connectivity matrices for passing and ending tracts (F), visualised in G.

2.5.4 Statistical Analyses

All statistical analyses were performed in IBM SPSS Statistics for Windows, Version 26.0. Participants deviating more than three SDs from the mean of the variables were considered outliers and excluded from further analyses. This was true for one participant on goErr (z score: 3.73).

In order to test hypothesis 1 to 3, correlation analyses were performed between the sleep measure (duration) and the error measures (goOm and goErr), the reaction time measures (goRT, PES, PSS), and the global efficiency. To test hypothesis 4, global efficiencies were correlated with goRTs. Further, to test hypothesis 5, SSRTs were correlated with local efficiencies of rIFGop, rSMA/pre-SMA and bilateral M1. Hypothesis 6 was tested by correlating PES and PSS with local efficiencies of rIFGop, bilateral ACC, bilateral MCC and bilateral dlPFC. And finally, hypothesis 7 was tested in a correlation analysis with attention (goRT, goOm and goErr) and local efficiencies of orbitofrontal regions, thalamus and dlPFC, all of which were bilateral.

As all hypotheses were directed, the correlation analyses had a one-tailed significance level of .05. Further, linear associations were expected so Pearson's r was used as correlation coefficient despite slight non-normality of the data. For testing of hypotheses five, six and seven, a Benjamini and Hochberg (1995) procedure for false discovery rate (FDR) correction was performed.

All figures were made with StataSE 16 for Windows. Confidence intervals were calculated in MATLAB R2019a (The MathWorks, Inc., Massachusetts, USA) and with www.vassrastats.net/rho.html.

3 Results

Note that as the AAL atlas was used for connectivity analysis and for objective identification of brain regions, the names of the regions in the current analysis contain terms usually associated with grey matter (i.e. gyrus). However, the analysis is performed on white-matter and the names for the brain regions included in the current analysis, are used to comply with the atlas and hence to avoid any confusion in that regard. Additionally, it should be noted that as the utilised version of the AAL does not directly include the dlPFC, this region is here considered as the dorsolateral superior frontal gyrus (dlSFG) and the middle frontal gyrus (Rolls et al., 2015).

3.1 Behavioural Results

All participants' data met the assumptions of the horse race model (i.e. slower goRT relative to RT on unsuccessful stop trials) and all included participants had near 50% stop accuracy. Means and standard deviations (SDs) are reported in Table 1.

Table 1.

Descriptive Statistics: Means and Standard Deviations (SDs)

	Mean	*SDs*
Age	26.88	3.41
Sleep duration	7.48	.56
goRT (ms)	604.88	93.09
goOm (%)	.23	.38
goErr (%)	.24	.32
PES (ms)	45.89	38.81
PSS (ms)	52.45	36.48
SSRT (ms)	184.92	17.37
SSD (ms)	406.32	79.01
Go accuracy (%)	99.48	.46
Stop accuracy (%)	53.74	5.58
Global efficiency	.51	.02

goRT = Reaction time on go trials, goOm = go omission trials, goErr = wrong response on go trials, PES = post-error slowing, PSS = post-stop slowing, SSRT = stop signal reaction time, SSD = stop signal delay, ms = milliseconds

3.2 Brain Connectivity Analysis

All participants exhibited a small-world topology (clustering coefficient divided by clustering coefficient of random network > 1 and characteristic path length divided by characteristic path length of random network ≈ 1), thus demonstrating principal network properties and indicating successful network reconstruction.

3.3 Correlation Analyses

3.3.1 Hypothesis 1: Shorter sleepers will have more errors (goErr and goOm)

The one-tailed bivariate correlation analyses between sleep duration and goErr and between sleep duration and goOm revealed no significant relationships (r = -.34, p = .09, 95% CI [-.71, .17] and r = -.33, p = .10, 95% CI [-.70, .18], respectively).

3.3.2 Hypothesis 2: Shorter sleepers will have longer goRTs, PES and PSS

The one-tailed bivariate correlation analysis between sleep duration and goRTs was non-significant (r = .09, p = .37, 95% CI [-.41, .55]). Additionally, the one-tailed bivariate correlation analyses between sleep and PES and sleep and PSS were non-significant (r = -.12, p =.34, 95% CI [-.57, .38] and r = -.10, p =.35, 95% CI [-.55, .40], respectively).

3.3.3 Hypothesis 3: Shorter sleepers will have lower global efficiency

The one-tailed bivariate correlation analysis between sleep duration and global efficiency did not reach significance (r = -.005, p = .49, 95% CI [-.48, .48]).

3.3.4 Hypothesis 4: Lower global efficiency will be related to longer goRTs

The one-tailed bivariate correlation analysis between global efficiency and goRT yielded a significant positive association although a negative one was predicted (r = .50, p = .02, 95% CI [.03, .79]; see figure 4).

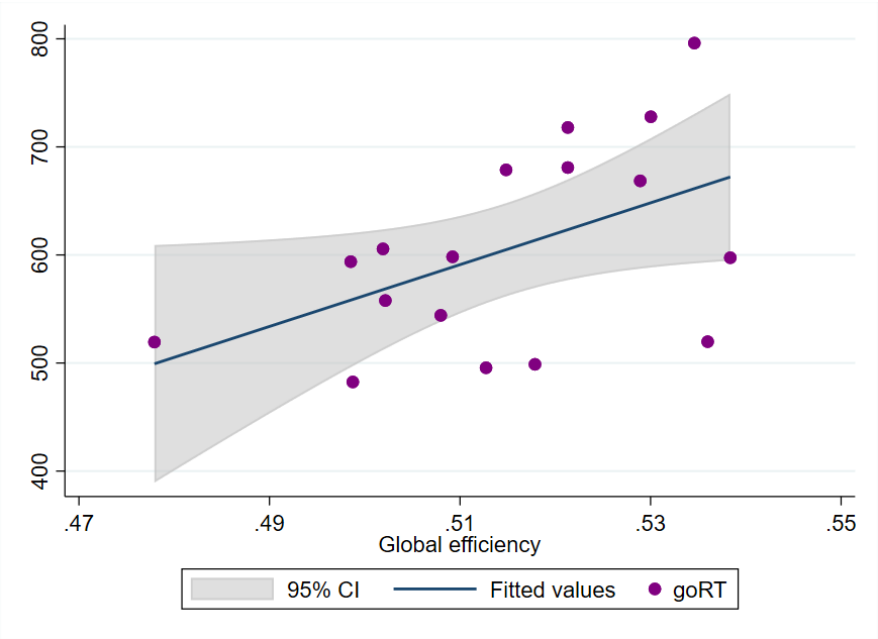

Figure 4. Scatterplot of goRTs by global efficiencies. 95% confidence intervals are indicated by the shaded grey area and the fitted values are shown (blue line).
CI = confidence interval, goRT = reaction times on go trials.

3.3.5 Hypothesis 5: Shorter SSRTs will be related to higher efficiency of rIFG, rSMA/pre-SMA and M1

The one-tailed bivariate correlation analyses between SSRTs and the local efficiencies of rIFGop, rSMA/pre-SMA and M1 were all predicted to be negatively correlated, however, they revealed that SSRTs positively correlate with rIFGop local efficiency (r = .57, p =.008, 95% CI [.12, .82]; figure 5) and with rSMA/pre-SMA local efficiency (r = .57, p =.009, 95% CI [.12, .82]; figure 6). These correlations remained significant after FDR-correction.

The one-tailed bivariate correlations between SSRTs and bilateral M1 were both non-significant (see table 2).

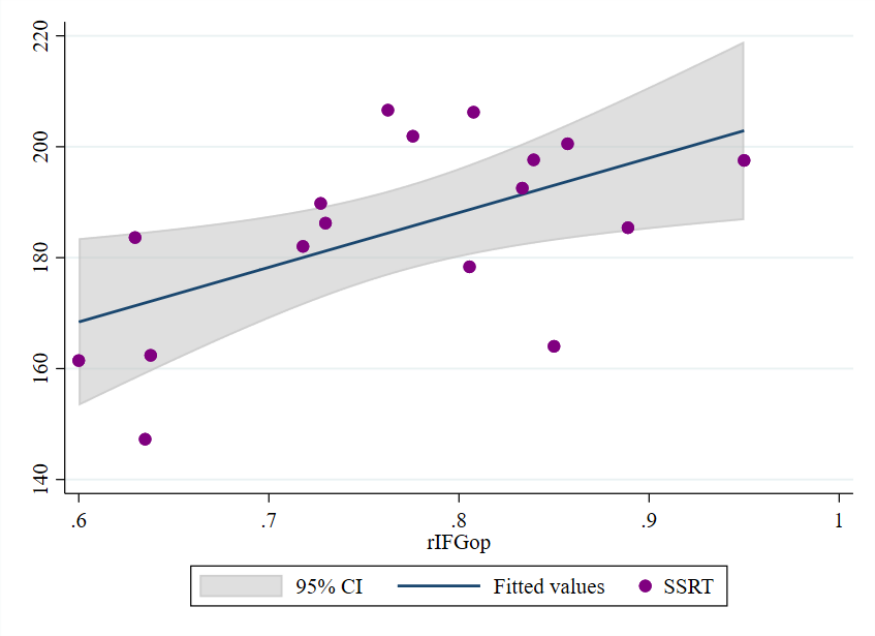

Figure 5. Scatterplot of SSRTs by rIFGop local efficiencies. 95% confidence intervals are indicated by the shaded grey area and the fitted values are shown (blue line).

CI = confidence interval, rIFGop = right inferior frontal gyrus pars opercularis,

SSRT = stop signal reaction time.

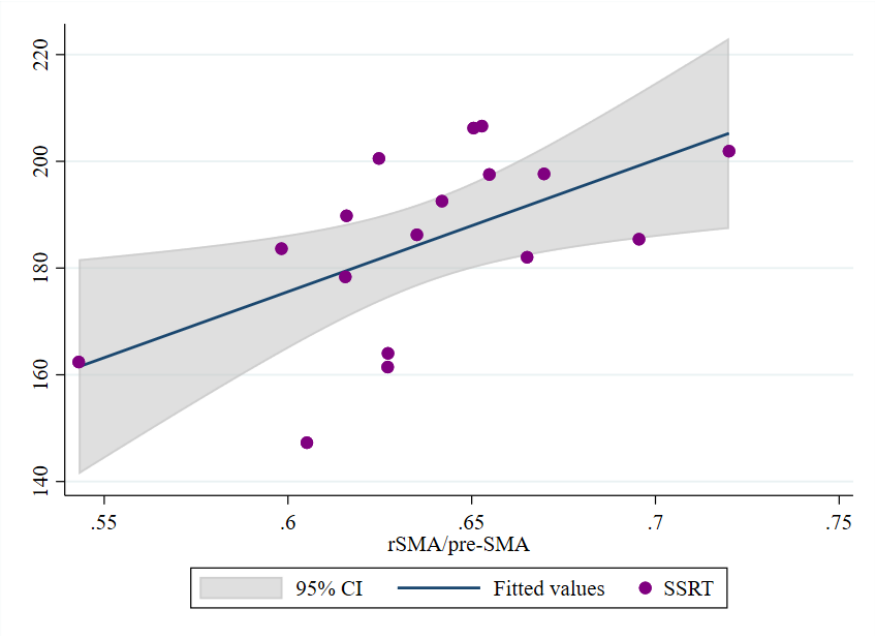

Figure 6. Scatterplot of SSRTs by rSMA/pre-SMA local efficiencies. 95% confidence intervals are indicated by the shaded grey area and the fitted values are shown (blue line).

CI = confidence interval, rSMA/pre-SMA = right supplementary motor area/pre-supplementary motor area, SSRT = stop signal reaction time

Table 2.

Non-significant correlations with SSRTs: Correlation coefficients, p-values and confidence intervals.

	SSRT		
	Pearson's *r*	*p*	95% CI
lM1	.03	.46	-.46, .50
rM1	-.07	.40	-.53, .42

CI = confidence interval, lM1 = left primary motor cortex, rM1 = right primary motor cortex

3.3.6 Hypothesis 6: More slowing (PES and PSS) will be associated with higher local efficiency in rIFG, rSMA/pre-SMA, bilateral ACC, bilateral MCC and bilateral dlPFC

After FDR-correction, PES positively correlated with the left ACC local efficiency in a one-tailed bivariate analysis (r = .71, p = .001, 95% CI [.35, .89]; figure 7). However, PES did not significantly correlate with local efficiencies of rIFGop, right SMA/pre-SMA, right ACC, left or right MCC and left or right dlPFC (see table 3).

Furthermore, after FDR-correction, PSS positively correlated with left ACC local efficiency (r = .62, p = .004, 95% CI [.20, .85]; figure 8) in a one-tailed bivariate correlation. However, PSS did not significantly correlate with local efficiencies of rIFGop, right SMA/pre-SMA, right ACC, left or right MCC and left or right dlPFC (see table 3).

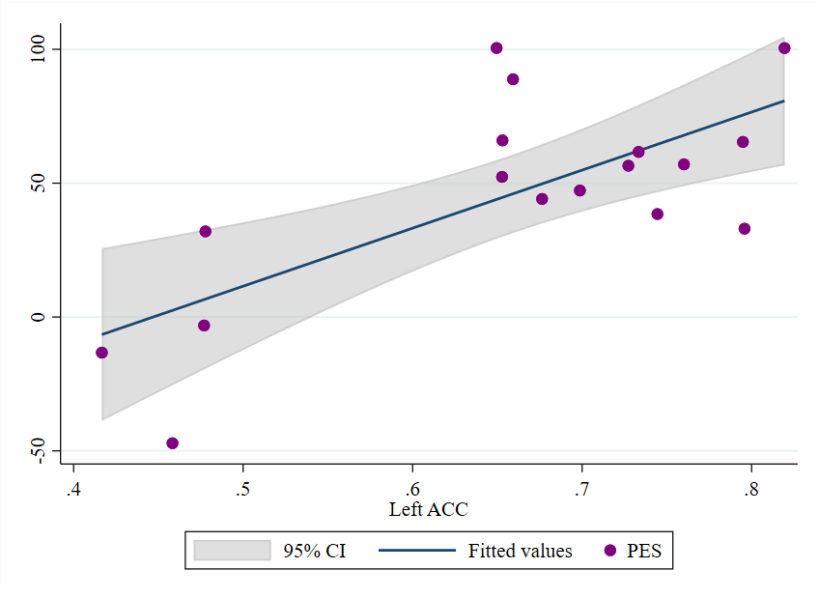

Figure 7. Scatterplot of PES by left ACC local efficiencies. 95% confidence intervals are indicated by the shaded grey area and the fitted values are shown (blue line).

CI = confidence interval, ACC = anterior cingulate cortex, PES = post-error slowing

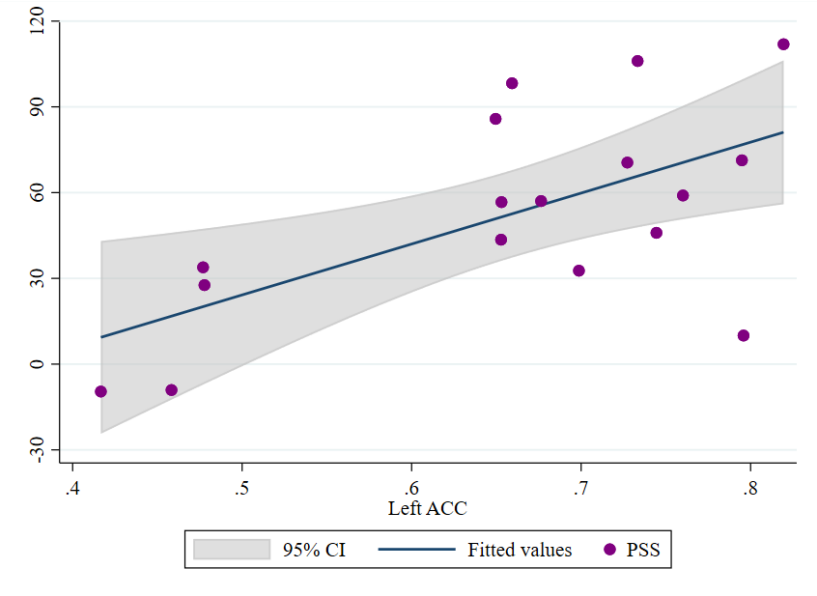

Figure 8. Scatterplot of PSS by left ACC local efficiencies. 95% confidence intervals are indicated by the shaded grey area and the fitted values are shown (blue line).

CI = confidence interval, ACC = anterior cingulate cortex, PSS = post-stop slowing

Table 3.

Correlations with PES and PSS: Correlation coefficients, p-values and confidence intervals.

	PES			PSS		
	Pearson's *r*	*p*	95% CI	Pearson's *r*	*p*	95% CI
rIFGop	.52	.02	.05, .80	.55	.01	.10, .82
rSMA/pre-SMA	.25	.17	-.26, .65	.06	.41	-.43, .53
rACC	.08	.39	-.42, .54	-.13	.31	-.57, .37
lMCC	.17	.25	-.34, .60	.32	.11	-.19, .69
rMCC	-.15	.28	-.59, .36	-.08	.38	-.54, 42
ldlSFG	.23	.19	-.28, .64	.25	.17	-.26, .65
rdlSFG	.20	.23	-.31, .62	.09	.36	-.41, .55
lMFC	-.30	.12	-.68, .21	-.44	.04	-.76, .05
rMFC	.22	.20	-.29, .63	.30	.12	-.21, .68

rIFG op = right inferior frontal gyrus pars opercularis, rSMA/pre-SMA = right supplementary motor area/pre-supplementary motor area, rACC = right anterior cingulate cortex, lMCC = left midcingulate cortex, rMCC = right midcingulate cortex, ldlSFG = left dorsolateral superior frontal gyrus, rdlSFG = right dorsolateral superior frontal gyrus, lMFC = left middle frontal cortex, rMFC = right middle frontal cortex, CI = confidence interval

3.3.7 Hypothesis 7: Attention (goRT, goOm and goErr) will be negatively correlated with local efficiency of bilateral orbitofrontal regions, bilateral thalamus and bilateral dlPFC

The one-tailed bivariate correlation analyses between goRT and local efficiencies of bilateral orbitofrontal regions, bilateral thalamus and bilateral dlPFC revealed no significant relationships after FDR correction. Further, the one-tailed bivariate correlation analyses between goOm and local efficiencies of bilateral orbitofrontal regions, bilateral thalamus and bilateral dlPFC revealed no significant relationships after FDR correction. And lastly, the one-tailed bivariate correlation analysis between goErr and local efficiencies of bilateral orbitofrontal regions, bilateral thalamus and bilateral dlPFC revealed no significant relationships after FDR correction. See table 4 for correlation coefficients, p-values and confidence intervals.

Table 4.

Correlations with goRT, goOm and goErr: Correlation coefficients, p-values and confidence intervals.

	goRT			goOm			goErr		
	Pearson's *r*	*p*	95% CI	Pearson's *r*	*p*	95% CI	Pearson's *r*	*p*	95%CI
lsOFC	.21	.20	-.30, .63	.25	.17	-.26, .65	.04	.45	-.45, .51
rsOFC	.06	.41	-.43, .53	.18	.25	-.33, .61	.10	.35	-.40, .55
lmOFC	.37	.07	-.13, .72	.51	.02	-.04, .80	.08	.38	-.42, .54
rmOFC	.16	.28	-.35, .59	.09	.37	-.41, .55	-.11	.34	-.56, .39
lsmOFC	-.18	.25	-.61, .33	.11	.34	-.39, .56	.11	.34	-.39, .56
rsmOFC	.20	.23	-.31, .62	.39	.06	-.11, .73	.15	.29	-.36, .59
lTha	-.04	.45	-.51, .45	.17	.26	-.34, .60	-.07	.40	-.53, .42
rTha	.10	.35	-.40, .55	.07	.40	-.42, .53	.14	.30	-.37, .58
ldlSFG	.05	.43	-.44, .52	-.03	.46	-.50, .46	-.31	.11	-.69, .20
rdlSFG	.27	.15	-.24, .66	.14	.30	-.37, .58	.33	.10	-.18, .70
lMFC	.46	.03	-.03, .77	.32	.10	-.19, .69	-.04	.44	-.51, .45
rMFC	.18	.24	-.33, .61	.20	.22	-.31, .62	.23	.19	-.28, .64

lsOFC = left superior orbitofrontal cortex, rsOFC = right superior orbitofrontal cortex, lmOFC = right middle orbitofrontal cortex, rmOFC = right middle orbitofrontal cortex, lsmOFC = left superior medial orbitforntal cortex, rsmOFC = right superior medial orbitofrontal cortex, lTha = left thalamus, rTha = right thalamus, ldlSFG = left dorsolateral superior frontal gyrus, rdlSFG = right

dorsolateral superior frontal gyrus, lMFC = left middle frontal cortex, rMFC = right middle frontal cortex, CI = confidence intervals

4 Discussion

The aim of this study was to investigate how sleep, cognitive control and brain connectivity interact by using actigraphy, a stop-signal task and a graph theoretical approach to brain connectivity. Based on previous research it was hypothesised that shorter sleep would be associated with more errors, slower responses, more slowing in response to errors and stop signals and lower global efficiency. Additionally, it was predicted that global efficiency would negatively correlate with reaction times on go trials. In relation to local efficiencies, it was hypothesised that shorter SSRTs would be associated with higher local efficiency in rIFGop, rSMA/pre-SMA and bilateral M1. It was also predicted that more slowing (PES and PSS) would be associated with higher efficiency in rIFGop, bilateral ACC, bilateral MCC and bilateral dlPFC. And lastly, a negative correlation was predicted between the attention measures (goRT, goOm and goErr) and local efficiency of bilateral orbitofrontal regions, bilateral thalamus and bilateral dlPFC.

Contrary to previous research, the current study did not find sleep duration to correlate with cognitive control or brain connectivity. However, global efficiency positively correlated with goRTs, which is the opposite relationship of what was predicted. Furthermore, in relation to the local efficiencies, it was found a positive association between SSRTs and rIFGop and between SSRT and rSMA/pre-SMA, which was also contrary to the predicted negative relationship. Lastly, and as predicted, the correlations between PES and lACC and between PSS and lACC yielded significant positive associations.

4.1 Sleep, Behavioural Findings and Global Efficiency

In relation to sleep, it was hypothesised that shorter average sleep duration would correlate with impairments in top-down and strategic control, here operationalised as more errors and omissions on go trials, longer goRTs, and more slowing (i.e. more PES and PSS). However, the current study did not find any significant results in relation to sleep at all. Although unexpected, this might have several reasons; one possible explanation is the small and homogenous sample in relation to sleep duration. Most previous findings come from studies in which sleep was manipulated and participants were kept awake for an extended period of time in order to ensure sleep deprivation. However, in this sample the mean sleep duration was 7.48 hours with a standard deviation of .56. In other words, all participants were well-rested. It may thus have been beneficial to incorporate sleep quality as a measure in the analyses, as other studies found sleep quality to impact neural networks associated with

cognitive control (Khalsa et al., 2017). However, others again have reported null findings by incorporating sleep quality into their study; Zitser and colleagues (2020) for instance, did not find sleep duration to have an impact on cognition or brain structure when taking sleep quality into account. Interestingly, they used similar analysis methods as Khalsa et al. (2017), and as such their null findings should not be disregarded. Thus, the current results might not be clarified by simply additionally investigating sleep quality. Yet another option would be to also consider sleepiness as measured by the Epworth Sleepiness Scale (ESS; Johns, 1991). A study by Lo et al. (2016) found subjective sleepiness to not return to baseline even after two nights of recovery sleep following a night of restricted sleep. This indicates that sleepiness potentially is of high interest in the case of habitual sleep; if the brain is not given enough time to recover from prolonged short sleep, sleepiness might accumulate over time, consequently introducing possible cognitive decline. Moreover, sleepiness is not commonly added in sleep studies looking at cognitive control and could thus be of interest for future studies.

Furthermore, contrary to the hypothesis, global efficiency was found to be positively correlated with goRTs. This is a rather unexpected finding as higher global efficiency should, in theory, result in faster RTs. This because global efficiency measures parallel information exchange and integration in the network via shortest communication routes, and as such the stimulus would be interpreted and a response generated faster. Previous studies have found global efficiency to be positively related to divided attention, response inhibition, memory, processing speed and overall performance on EF tasks in clinical samples (Caeyenberghs et al., 2014; Reijmer, Leemans, Caeyenberghs, et al., 2013; Reijmer et al., 2015). However, one of the studies found no correlation between EFs and global efficiency in their healthy control group (Caeyenberghs et al., 2014). This could indicate that global efficiency might not be sensitive enough to capture small effects and variations as is often observed in healthy adult populations.

On the other hand, this does not fully explain why the current results indicate an inverse relationship of what was expected with an RT slowing in response to higher global efficiency. In this study, RTs are considered to be related to processing speed, attention and top-down control of task behaviour. However, although somewhat speculative, one can argue that RTs are more strategic in that the participant might choose slower responses in order to increase their stop accuracy (Leotti & Wager, 2010). In relation to global efficiency and EFs, this could indicate that participants with high global efficiency, lean more towards an accuracy bias in the speed-accuracy trade-off that is found in the SST. In view of this, goRTs

become strategic and related to improved task performance. Considering how previous studies found performance, as measured by accuracy, to positively correlate with global efficiencies (Caeyenberghs et al., 2014; Reijmer, Leemans, Brundel, et al., 2013), it is then not surprising that global efficiency here positively correlated with goRTs. However, this warrants further investigation in which a task not manipulating performance should be used, or alternatively, strategy should be considered as a variable if using the SST paradigm.

4.2 Local Efficiency and Inhibition, Performance Monitoring and Attention

While it was hypothesised that SSRTs would be negatively correlated with local efficiency of the rIFGop, the rSMA/pre-SMA and the bilateral M1, the results indicate strong positive relationships with the rIFGop and rSMA/pre-SMA. This is rather unexpected as all literature points to the opposite relationship. This is because higher efficiency is related to information transfer and, as with global efficiency, if external stimuli is integrated and interpreted quickly, the appropriate response can be executed faster. And as the rIFGop and rSMA/pre-SMA are considered initial nodes in the inhibition network (Vergani et al., 2014), their local efficiency should be related to shorter SSRTs. As such, the positive correlation is a highly interesting finding which warrants further research. Especially when considering how graph theoretical metrics can be applied to many different types of data. For instance, Cohen and D'Esposito (2016) used the approach to analyse functional connectivity at rest relative to during task performance. They reported that during tasks, local efficiency decreased in task-active regions. This decrease was related to improved accuracy in a 3-back task and more stable performance in a finger tapping task. They argue that this might reflect a pruning of the connections that are not necessary for optimal task performance. In relation to the current findings, this could invalidate the results as the local efficiency of the rIFGop, for example, at rest, may not be representative of the efficiency during task performance. Thus, it might be more beneficial to investigate local efficiencies of the inhibition network on a functional connectivity dataset collected during task performance rather than based on structural neuroimaging.

Nevertheless, as predicted, PES and PSS were found to strongly and positively correlate with local efficiency of the left ACC. This hypothesis was based on the role of the ACC in behavioural adaptations and conflict monitoring of which PES and PSS are behavioural markers (Brown, 2013; Sheth et al., 2012). However, when considering the mean PES and PSS of the sample, both of which were around 50ms, and how the correlations with the lACC are near identical, it is worth considering that the goRT could heavily influence this

relationship. First and foremost because both PES and PSS are difference measures that are both calculated based on the same goRT estimation. And further, as discussed above, goRTs can have a strategic nature, in which the participant slows down their responses in order to improve the accuracy. This can also be in line with a positive correlation with the lACC local efficiency as the ACC has also been proposed to be involved in prediction and evaluation of potential outcomes of a behaviour (Brown, 2013). In other words, individuals with high local efficiency of the lACC might better predict that faster RTs decrease the chance of accuracy and therefore choose to slow down their responses.

Furthermore, PES and PSS were not found to positively correlate with local efficiencies of rIFGop, rSMA/pre-SMA, MCC or dlPFC. Previous literature found the white-matter integrity of the inhibition network to be associated with PES (Danielmeier et al., 2011). Specifically, Danielmeier and Ullsperger (2011) and Danielmeier and colleagues (2011) found pre-SMA, IFC and STN of the right hemisphere to be crucial for PES. The authors discuss that post-error adjustments appear to be triggered by the pre-SMA, although they also discuss this function in relation to the ACC. Considering how the SMA/pre-SMA and rIFGop have been viewed as early agents in the motor system and responsible for planning and preparing movements, they may be more indirect parts of slowing (Vergani et al., 2014). It is therefore possible that the rIFGop and rSMA/pre-SMA are more functionally active (i.e. during a task) and structural imaging may not be able to capture its full involvement.

Nonetheless, the ACC is frequently found to be involved in conflict monitoring, which is an important aspect of cognitive control and in particular when there is an interference between the stop and go process (Larson et al., 2014; Verbruggen, Best, et al., 2014). However, the ACC is often described with different names in the literature which makes it challenging to know if the same region is actually being referred to (Wessel & Aron, 2017). For instance, the literature often refers to the MCC or anterior MCC as involved in performance monitoring (Danielmeier et al., 2011). It is therefore possible that the current study had null findings in relation to the MCC as it was considered one region, rather than being parcellated into anterior and posterior portions.

In relation to the observed null findings between PES and PSS and the dlPFC, there can be several explanations. For one, the dlPFC has been found to be more active in the GNGT relative to the SST and may therefore be less applicable in this study (Swick et al., 2011). However, as the region is considered to be involved in attentional processes, it should still be related to PES and PSS (Chambers et al., 2009). Yet again, this can point back to the

homogenous sample, as the null findings can be explained by the lack of variance in the data. It is also important to acknowledge the complexity of the dlPFC as it is a region involved in many cognitive functions and may therefore not yield significant results when considered as one independent region (Duncan & Owen, 2000).

Unexpectedly, the current study found no significant results in the analyses of the attention measures (goRT, goOm and goErr) and bilateral orbitofrontal regions, bilateral thalamus and bilateral dlPFC. There could be several reasons for this; firstly, previous studies have found sleep deprived participants to have longer RTs and to make more errors or omissions (Chua et al., 2017; Honn et al., 2020; Whitney et al., 2017). However, as mentioned above, the present sample did not show any tendencies for habitual shortened sleep. In relation to this, the error- and omission rates were very low, and the data overall was rather unvaried. Because of this, the goRT, goOm and goErr may not be sensitive enough to measure fine attentional variance in a homogenous sample.

Furthermore, and as mentioned above, there are some limitations to using the AAL atlas, which are also applicable here. The dlPFC and orbitofrontal regions are highly diverse areas with connections to widespread brain regions and are, as such, involved in a wide range of functions (Leh et al., 2007; W. Li et al., 2013). Based on this, it may not be applicable to assess these regions as ROIs in a healthy sample where neural communication should, in theory, run optimally. Relatedly, the thalamus is also a complex region and many of the studies of which the current hypothesis was based on, reported attentional measures in correlation with the thalamus in sleep deprived individuals (Khalsa et al., 2017; Krause et al., 2017). Again, considering the current sample and how complex the effects of sleep deprivation appears to be on the brain, the thalamus, dlPFC and orbitofrontal regions may not necessarily correlate with attentional measures in a non-sleep deprived, healthy sample. Rather, they might drive a more global network involved in attentional mechanisms (Khalsa et al., 2017).

4.3 Limitations and Future Research

There are some limitations to this study that should be addressed. First, due to the covid-19 pandemic, the number of participants who completed all three sessions was limited. Furthermore, in relation to sleep duration, it appears to have been a rather homogenous group as most slept between seven and eight hours on average in the two weeks that sleep data was collected. It is possible that a larger sample would demonstrate a wider range of sleep durations and as such provide a better impression of how sleep affects the brain and

behaviour. As the participants additionally filled out sleep diaries in the two weeks of data collection, they might have been made more aware of their own sleeping patterns which further could inspire them to change their behaviours. Previous studies have used sleep diaries as a means of therapy for patients with sleep disorders to track their own sleep habits and map their improvement (Riemann et al., 2017). Thus, it is possible that the participants in the current study, adjusted their sleep over the two weeks resulting in a mean sleep duration reflecting what is widely recommended (Institute of Medicine (US) Committee on Sleep Medicine and Research, 2006). It could therefore be of interest to see how much the diary influenced the sleep in a separate study.

Further, to enrich the analyses of sleep, future research should consider incorporating sleep quality and sleepiness into their analysis. Sleep is a very complex concept which can have widespread effects both on health and cognition. Therefore, in order to broaden our understanding of its full implications, it could be of interest to look at several aspects combined.

Secondly, in order to obtain graph theoretical measures to analyse brain connectivity, a deterministic tractography approach (Basser et al., 2000; Mori et al., 1999) was used to get connectivity matrices. But, deterministic tractography algorithms are highly sensitive to noise and poor imaging resolution and may thus terminate in instances where no clear diffusion direction is found, for example near grey matter (Mori & Zijl, 2002) or in case of "crossing fibres" (i.e. brain regions with a more complex fibre architecture; Jeurissen et al., 2011; Tournier et al., 2011) thus running the risk of missing out on existing fibres. To avoid this issue, other tractography approaches based on more complex diffusion models could have been considered, like for instance diffusion spectrum magnetic resonance imaging (DSI; Wedeen et al., 2008; Wedeen et al., 2005) or high angular resolution imaging (HARDI) with a Q-ball reconstruction of multiple fibre orientations (Hess et al., 2006; Jeurissen et al., 2011; Tuch, 2004). Other tracking procedures more sensitive to uncertain fibre orientations could also have been considered, like probabilistic tractography in which it can also be established a confidence of connections from a seed point to the whole brain (Behrens et al., 2007; Descoteaux et al., 2009; Jeurissen et al., 2011).

The potential limitations of graph theoretical measures should also be discussed as they for instance assume that neural signals propagate in brain networks via shortest paths (Fornito et al., 2016). While this may be true, our current understanding of signal transmission within the brain is not yet at the point where this assumption can be made with certainty.

In addition, the current study revealed some surprising findings, for example in relation to goRTs, which warrants further investigations. Especially in relation to how RTs are conceptualised; are they automatic in response to a simple go stimulus? Or are they driven by a more strategic error aversion? In relation to this, it could be interesting to ask participants after task completion to report their task strategy, and potentially also use a different task in which performance is not manipulated.

Additionally, a function-structure comparison should be investigated with regards to graph theoretical metrics. It would be highly interesting to analyse the changes in local and global efficiency between rest and task performance. This could potentially help clarify the unexpected positive correlations observed in the current study. In addition, it could also contribute to the current understanding of structural and functional networks.

Lastly, future studies should consider using a larger atlas for analysing brain connectivity in cognitive control. The atlas-based approach helps avoid user-bias when analysing specific regions and contributes to consistent naming in the literature. However, some of the regions are diverse and should therefore be segregated into smaller parcels or regions for instance by employing a different atlas.

4.4 Implications

This study is highly original, and it provides valuable insights into how graph theoretical metrics can be applied to investigate sleep and cognitive control in a healthy population. It shows that a graph theoretical approach can be applied in a field troubled with conflicting findings and methodologies in an attempt to clarify the inconsistencies. While this study supports previous findings of a relationship between global efficiency and reaction times, further research into the nature and direction of this relationship appears to be warranted. In view of this, the unexpected findings should not be disregarded but rather considered motivation for further investigations into the field of sleep and cognitive control using graph theoretical metrics for brain connectivity. Previous research using a similar methodological approach has focused on clinical samples, but the current study argue that the graph theoretical metrics can be applied to healthy samples as well, with the potential of broadening our understanding of brain connectivity in sleep, cognitive control and potentially also other fields.

4.5 Concluding Remarks

The current study investigated the interplay of sleep duration, cognitive control and brain connectivity from a graph theoretical approach. Sleep duration was calculated as the mean over two weeks based on actigraphy watches. Cognitive control was here divided into attention (goRT, goOm, goErr), inhibition (SSRT) and performance monitoring (PES, PSS) of which inhibition was considered a bottom-up driven process, and attention and performance monitoring being more top-down in nature. The results indicate, unexpectedly, that global efficiency of the brain is positively correlated with goRTs. Further, contrary to hypotheses, no associations between sleep duration and goRTs, goErr, goOm, PES, PSS or global efficiency were identified.

From the analyses of the local efficiencies it was found, as predicted, that PES and PSS positively correlate with efficiency of the lACC. However, it was also found that SSRTs positively correlate with efficiencies of rIFGop and rSMA/pre-SMA, although the opposite relationship was expected. This warrants further investigation, preferably with a larger, less homogenous sample. In such a sample it may also be found further associations in relation to sleep and also between SSRTs and M1, PES/PSS and SMA/pre-SMA and dlPFC-regions, and between attention measures and orbitofrontal regions, thalamus and dlPFC-areas.

The null findings should not be disregarded though, as most of the identified findings are somewhat in line with previous literature despite the use of a novel method. Rather, the unexpected findings should be seen as an inspiration for future research using a graph theoretical approach to investigate neural networks in relation to sleep and cognitive control.

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