The Impact of Sleep on Perceptual Learning and Attention

Zhishan Liu

A thesis submitted for the degree of
Doctor of Philosophy

Cardiff University

April 2025

Thesis Summary

This thesis examines the complicated relationship between learning and brain plasticity, as well as the human brain's unique ability to learn and adapt. Building on previous research, the thesis aimed to examine online, offline wake, and offline sleep learning. The objective is to advance our knowledge of this complex relationship. The effects of sleep on learning consolidation, its role in modifying cognitive abilities, and the inter-individual variability in these processes are still not completely understood in the literature today. Our research aims to fill these gaps, with the hope that it will have a positive impact on training and therapy approaches, thereby enhancing cognitive and learning capacities.

The first empirical chapter provides an in-depth exploration of a backward masking task, a learning task that integrates online learning with sleep. Our findings shed new perspectives into the process of learning and the possible brain mechanism involved in the backward masking learning by indicating a sleep-dependent component. This work contributes by outlining the brain mechanisms underpinning sleep-dependant learning, a topic that has previously received little attention in the literature.

Using a method comparable to backward masking learning, our next chapter explores the effect of sleep on selective attention. The aim is to clarify the state-dependent components essential for optimal task performance by contrasting the sleep response to both learning tasks. This section builds on the knowledge gap by expanding our understanding of how sleep impacts learning and cognition.

In Chapter 4, the thesis delves into the analysis of inter-individual differences, aiming to uncover the links between learning variability and discrepancies in brain structure, particularly in the domains of perceptual and motor learning.

This thesis examines the potential benefits of incorporating sleep-in learning consolidation in detail. The aim is to advance knowledge of the adaptive learning capacity of the human brain and to open up opportunities for new treatments and educational approaches that improve cognitive and learning skills.

Declaration and Statements

DECLARATION

This work has not been submitted in substance for any other degree or award at this or any other university or place of learning, nor is it being submitted concurrently for any other degree or award (outside of any formal collaboration agreement between the University and a partner organisation).

Signed: Date: 17th April 2025

STATEMENT 1

This thesis is being submitted in partial fulfilment of the requirements for the degree of PhD.

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STATEMENT 2

This thesis is the result of my own independent work/investigation, except where otherwise stated, and the views expressed are my own. Other sources are acknowledged by explicit references. The thesis has not been edited by a third party beyond what is permitted by Cardiff University's Use of Third-Party Editors by Research Degree Students Procedure.

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STATEMENT 3

I hereby give consent for my thesis, if accepted, to be available in the University's Open Access repository (or, where approved, to be available in the University's library and for inter-library loan), and for the title and summary to be made available to outside organisations, subject to the expiry of a University-approved bar on access if applicable.

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WORD COUNT: 49,577

(Excluding summary, acknowledgements, declarations, contents pages, appendices, tables, diagrams and figures, references, bibliography, footnotes and endnotes)

Acknowledgements

This thesis would not have been possible without the support, advice, friendship, commitment, and love of many individuals, and I am grateful for everything they have done. A variety of individuals have been important in the completion of this thesis, and the few words I have written here cannot reasonably thank them all.

First and foremost, I would like to express my deepest gratitude to my lead supervisor, Dr Chen Song, for her enthusiasm, advice, and experience during the years we worked together. I am thankful to her for providing me with the incredible opportunity to study at the Cardiff University Brain Research Imaging Centre (CUBRIC), and for making my doctoral studies an experience that was far beyond my expectations.

Additionally, I would like to thank Mark Johansen, who co-supervised me and provided numerous expert theoretical insights into my research topic. I also express my gratitude to Dr Matthias Gruber, who reviewed sections of my thesis and provided numerous helpful suggestions to enhance the work and writing of this thesis.

In Dr Chen Song's lab, both past and present, gave me invaluable assistance and companionship. In practice, I gained a great deal from the encouragement and friendship of several of my CUBRIC and School of Psychology colleagues. I am highly appreciative of the opportunity to learn from you. A special thanks must go to my fellow graduate students, research assistants, internship students, and placement students, who have joined our lab and have been invaluable in all aspects of my studies, while fostering a pleasant and dynamic working atmosphere.

Finally, I would like to extend my personal thanks to my family. Both of my parents have been unwavering in their support and reassuring me when I was struggling. Thank you for your ongoing encouragement and understanding while I undertake my research and write up my thesis. Without their continuous support, I would not have been able to complete my PhD path.

Glossary

The following abbreviations are used throughout the thesis:

AC	Attentional Capture
CSF	Cerebrospinal Fluid
CS	Conditioned Stimulus
DV	Dependent Variable
DWI	Diffusion-Weighted Imaging
EEG	Electroencephalogram
ERP	Visual Evoke Potential
FEFT	Finding Embedded Figures Test

fMRI	Functional Magnetic Resonance Imaging
GM	Grey Matter
IV	Independent Variable
LL	Lower Left
MPRAGE	Magnetization-Prepared Rapid Acquisition Gradient-Echo
MRI	Magnetic Resonance Imaging
NMR	Nuclear Magnetic Resonance
NREM	Non-rapid Eye Movement
REM	Rapid Eye Movement

RF	Radio Frequency
ROI	Region of Interest
RT	Reaction Time
SD	Sleep Deprivation
SHY	Synaptic Homeostasis Hypothesis
SNR	Signal-to-Noise Ratio
SPM	Statistical Parametric Mapping
SWS	Slow Wave Sleep
TDT	Texture Discrimination Task
US	Unconditioned Stimulus

UR	Upper Right
VBM	Voxel-Based Morphometry
VPL	Visual Perceptual Learning
VS	Visual Search
WM	White Matter

Contents

CHAPTER 1:

Introduction

1.1. General Introduction

In the field of psychology, the definition of "learning" has been a broad subject of controversy and is currently being debated due to the potential ambiguity of the term. From a behaviourist perspective, however, "learning" is generally understood as changes in behaviour or knowledge brought about by experience that have lasting effects (De Houwer et al., 2013). From a cognitivist perspective, however, "learning" is not just a behavioural influence; instead, it refers to skills acquired through mental processes. Thus, cognitive psychologists define "learning" as understanding memory and the mechanisms of problem solving and memory (Sweller, 1988). Furthermore, in the field of neuroscience literature, learning is highly related to the discussion of plasticity, which is the brain’s ability to change the structure and function in response to learning (Kolb & Gibb, 2011).

A related concept lies within this broad field is perceptual learning, which is the long-term improvement in perceptual skills through practice or experience. Perceptual learning in contrast to general learning, represents an increased sensitivity to visual, auditory or other sensory stimuli, typically achieved through the repetition of complex tasks (Ahissar & Hochstein, 1997; Kahalani-Hodedany et al., 2024; Su et al., 2014). These definitions provide the theoretical foundation for understanding the interplay between learning and perceptual processes. This is a crucial concept central to this thesis, which examines how sleep facilitates the consolidation of perceptual and attentional learning.

Building on from this theoretical understanding, advances in neuroscience provided critical insights into the complex and dynamic neural structures that comprise the human brain. It is widely accepted in the literature that the human brain is not a static organ; instead, it is constantly changing in response to both external and internal factors throughout a person's lifespan (Draganski & May, 2008; Kolb & Gibb, 2011; Pascual-Leone et al., 2005). Studies relating to brain development, learning, memory, and sleep have shed light on the ways in which the brain's multiple structures adjust to and anticipate changes in their external surroundings (Klinzing et al., 2019; Tamaki et al., 2020a).

Plasticity itself is a central construct for this thesis. Within the literature, it is well established that as people age, the connection and development of the brain become 'fixed' or less flexible, which means that learning new things or adapting to change becomes more difficult. Children, for instance, were expected to learn a new language more easily because their brains were still growing, while for adults, their brain paths were already 'set in place' (Hartshorne et al., 2018). However, the ability for the adult brain to change and adapt does not disappear. Recent research has demonstrated that learning may alter the brain and that many social and cognitive skills persist throughout adulthood (Hertzog et al., 2008; Kempermann et al., 2018; Kwok et al., 2011). Higher-level cognitive skills, including working memory, logical thinking, and attentional control, remain flexible well into adulthood, with plasticity possibly intensifying during adolescence (Bang et al., 2023; Sampaio-Baptista et al., 2018; Selemon, 2013; Watanabe & Sasaki, 2015). The main evidence supporting this theory comes from studies on visual perceptual learning (Bang et al., 2023; Hofer et al., 2006) and visual deprivation trials (Q. S. Fischer et al., 2007; Sato & Stryker, 2008), which include both temporary and permanent blindness. These studies demonstrated that life events and environmental pressures, such as performing visual tasks or insufficient visual information, can lead to alterations in the visual system. Synaptic alterations, such as changes in synaptic density and the features of receptor fields, along with wider brain network changes that extend beyond distinct sensory pathways, are examples of the types of changes that can occur at many different levels (Karmarkar & Dan, 2006). This evidence from previous research has demonstrated that learning is not limited to one area; instead, it has long been proposed with a multifaceted idea. Many review papers generally propose that learning is viewed as a dynamic process that spreads across many domains, including perceptual, cognitive and motor, emphasising its capacity for change and implementation (Craik & Bialystok, 2006; Green & Bavelier, 2008).

The term "brain plasticity" is commonly used in the fields of both psychology and neuroscience to describe the outstanding ability of the brain to reorganise itself in response to new challenges and experiences. The concept goes beyond changes in the structure of the brain (structural plasticity), but also functional plasticity, which is referring to modifications in the way the brain process, as highlighted in the review by Pascual-Leone et al. (2005). Empirical evidence supporting the idea of plasticity was provided by Draganski et al. (2004) in their longitudinal study, which found that individuals who learned a juggling task showed changes in grey matter (GM) within the motion-sensitive visual areas. More recent research has extended these findings to white matter (WM) adaptations. For instance, research using diffusion tensor imaging (DTI) and functional magnetic resonance imaging (fMRI) to assess WM neuroplasticity in healthy adults before and after exercise training. It focuses specifically on non-dominant hands, as it can observe neuroplasticity changes in the corpus callosum and internal capsule. The results showed that changes in DTI fraction anisotropy and low-frequency oscillation (LFO) in both WM regions were associated with improved behaviour of the non-dominant hand (Frizzell et al., 2022). The findings from this study provide additional information on the structural and functional aspects of WM changes following learning.

According to the previous research, the brain has the ability to adapt and modify itself in response to demands and challenges, which can lead to the development of new skills, behaviours, and memories (Draganski et al., 2004; Kolb & Gibb, 2011). One of the factors believed to influence brain plasticity and learning is sleep (Dang-Vu et al., 2006; Nissen et al., 2021; Ruch et al., 2021). The intricate connection between sleep and these processes plays a role in facilitating sleep functions. Previous reviews have synthesised evidence into the systems consolidation framework, showing correlation between sleep and the development of changes in the human brain (Krueger et al., 1995; Walker, 2005). This frameworks proposed that during sleep, acquired information is first being processed, then integrated, followed by consolidation under some circumstances., thereby enhancing its potential for long-term retention in memory (Diekelmann & Born, 2010; Ngo et al., 2020).

Although sleep is indeed influential, it does not work in isolation and there are other factors that also contribute to learning and brain plasticity, such as individual's feelings, cognitive difficulties, and stimuli from the environment (Tyng et al., 2017; Wiest et al., 2022). Although there is a lot of research that links sleep, learning, and plasticity, there are still gaps in our understanding of when sleep results in gains that are only useful in one place compared to those that can be used in many places. Some studies indicate greater specificity. For instance, enhancements in the TDT are often restricted to the training visual position and orientation (Karni & Sagi, 1991; Schwartz et al., 2002). However, under different task conditions or extensive training, partial transfer across visual field locations has been observed (Xiao et al., 2008). Similarly, motor learning tasks exhibit both local consolidations, associated with the training sequence, and, in specific contexts, generalisation to untrained sequences or effectors (Korman et al., 2003). It is, therefore, an open and important subject to figure out what conditions sleep contributes to that help with this generalisation. Further investigation is still needed in order to build a complete picture of the complex connections that are present between sleep and other factors that could possibly influence brain development. The development of better methods to enhance memory and learning in individuals will be dependent on the development of comprehensive approaches that include all these interconnected factors. The insight and findings provided in this thesis have an opportunity to help with the development of more efficient learning styles that take advantage of the brain's natural ability for adaptation in several domains, including sleep.

Gaining insight into the relationship between learning, brain plasticity, and sleep plays an important role in the field of psychology. The main goal of this thesis is to further develop our comprehension of the relationship among these three components and aims to address the gap mentioned in the previous section. Understanding these links is crucial, as they serve as the basis for investigating fundamental concepts, research findings, and the consequences of this linked interaction. The interplay among these elements is complex, and encompasses characteristics that continuously evolve over time. A good example of this would be the fact that the process of learning may be directly influenced by both how much sleep and the quality of sleep, and this in turn has an effect on the ability of the brain to change and adapt. The degree of plasticity in our brains may also have an influence on how individuals learn as well as how sleep operates in the body. This is in addition to the fact that the opposite is also true. When it comes to learning initiatives, methods of treatment for brain injuries, and therapies for sleep-related cognitive difficulties, it is crucial to have a deeper understanding of this recurrent link since it has substantial implications. It is important to note that all of these consequences are interdependent and interrelated.

Although the empirical chapters in this thesis do not involve direct brain measurements, the thesis supports a psychobiological perspective. In other words, behavioural outcomes are understood through psychological models, such as attentional and cognitive explanations of perceptual learning (Mitchell & Hall, 2014), as well as neurobiological frameworks, such as restructuring models and systems consolidation. Improvements seen offline after sleep are seen as behavioural proof that consolidation processes are effective, while gains that happen immediately after learning are seen as support for local reorganisation.

The rationale for the thesis, therefore, leads to three interconnected objectives. First, to investigate the degree to which perceptual and attentional learning is specific to the trained stimuli and locations instead of applying to untrained stimuli. Second, to determine if sleep enhances offline enhancements in contrast with comparable periods of wakefulness. Third, to determine whether these behavioural consequences are more effectively explained by behavioural focus models or neurologically based consolidation theories, thus explaining the mechanisms that underlie consolidation and generalisation. In trying to accomplish these objectives, the current chapter offers a theoretically grounded and empirically validated explanation of the role of sleep in regulating the appearance of plasticity in learning. Starting with a comprehensive evaluation of each characteristic that is being addressed on its own in order to first build a concrete understanding of the basic concepts. Next, will look into previous research studies, reviews, and conceptual frameworks that indicate how neuroplastic changes within the brain contribute to the process of learning, as well as how these processes are influenced by the potential influence of sleep.

1.2. Learning and Brain Plasticity

1.2.1. Brain Plasticity

Reviews often associate the term "plasticity" with the nervous system. However, it is not often defined and usually refers to changes in neural structure and function that are commonly classified as "brain remodelling" (Merzenich et al., 2014). According to the review article published by Innocenti (2022), neuroplasticity is fundamental to the existence of the nervous system because it transforms environmental inputs into behavioural outputs, at the same time it goes beyond simple reflexes to allow the nervous system to be actively shaped and modified by these environmental inputs. In the late 19th century, scientists proposed that the individual brain adapts in a specific way, which sparked interest in these phenomena (Denes, 2015). This concept was revolutionary because at the time the structure of the brain was static. Moving forward, more and more researchers, such as Cai et al. (2014) and Zatorre et al. (2012), have described that the nervous system has the ability to change the structure and organisation of structures, as well as their functions in response to experience, trauma, or learning, suggesting that the human brain is not unchangeable or static. In the current decade, researchers have developed new approaches and perspectives on the plasticity of the brain after exploring the concept more and more. Merzenich et al. (2014) argued that researchers once thought that plasticity could only happen during the pregnancy stage and the first few years of development. Multiple studies from the 20th century and more current research indicate that the brain is still plastic at any age (Erickson et al., 2013; Lövdén et al., 2013; May, 2011; Schmidt et al., 2021).

In an animal study conducted by Yang et al. (2014), they found that the performance of those who slept after completing a motor learning exercise increased, and their brain activity patterns changed, demonstrating the plasticity of their brains. The researchers employed a technique known as two-photon imaging to observe the formation of dendritic cell spines in the motor region of mice after they learnt new motor skills. According to their research, sleep after learning significantly increased the number of new dendritic spines that were generated compared to wake. They discovered that sleep plays a role in increasing the number of these dendrite spines compared to wakefulness. The findings from this study showcased the brain's ability to also adapt in adulthood, highlighting the importance of sleep for promoting changes following learning. In another experiment conducted by Anguera et al. (2013), older individuals between the ages of 60 and 85 were engaged in a designed video game to improve their control, particularly multitasking abilities. Participants in the study practiced the video game at home over a one-month period. The results showed that individuals not only improved gaming skills but also progression in other cognitive functions like sustained attention and working memory was also observed. Remarkably, these enhancements persisted for six months without any further learning, indicating that the game had a lasting impact on their cognitive abilities. Additionally, the prefrontal cortex (PFC), which is a region of the brain linked to cognitive control, was more active when the individuals were playing the game. This showed that learning influenced the patterns of brain activity in addition to improving cognitive function. This study highlights that the ageing brain remains capable of plastic changes, which was one of the first to offer causal evidence that playing video games might help older individuals' cognition. Again, suggesting the idea that the ability for the brain to change due to learning is not only available during a young developmental age, but the brain remains plastic even in a mature age.

At a cellular level, neuroplasticity is the result of the interaction of several molecular and synaptic mechanisms that both remodel existing neural networks and create new ones (Citri & Malenka, 2008; Hogan et al., 2020). Synaptic plasticity refers to the ability of synapses, which are the connections between neurons, to vary in size (Magee & Grienberger, 2020). The phenomenon of synaptic plasticity was initially seen in the hippocampus demonstrated by Bliss and Lomo (1973), who reported pre- and post-synaptic neurons were repeatedly and nearly simultaneously activated, it led to an enhancement of synaptic inputs at the stimulated junctions. This phenomenon being discussed is known as long-term potentiation (LTP). LTP works by strengthening the connection between neurons when they are consistently activated together, which enhances their communication (Bliss & Lomo, 1973). According to Bliss and Collingridge (1993), LTP serves as a process for memory and learning because it demonstrates the brain's ability to adapt to experiences. For instance, when an individual repeatedly practices specific sequences while learning to play the piano, the synaptic connections between the neurons involved in that motor activity become stronger. Over time, these connections become more robust, allowing for more finger movements without conscious effort (Pascual-Leone et al., 1995). This phenomenon were further expanded by Levy and Steward (1983), and subsequent research found that established that LTP functions as a universal process across several brain areas (Caporale & Dan, 2008; Malenka & Bear, 2004; Nicoll, 2017). In contrast, long-term depression (LTD), has been investigated in many different regions of the brain which emphasis on the continuing decreases in synaptic strengths, believed to be essential to forgetting, pruning, and reorganisation (Lovinger & Abrahao, 2018). The functional importance of LTP and LTD is evident in skill learning studies. For instance, Pascual-Leone et al. (1995) demonstrated, using transcranial magnetic stimulation (TMS) mapping, that piano practice in new learners altered motor cortical representations of finger movements, corresponding with the LTP-induced enhancement of motor circuits. On the other hand, LTD ensures that connections that are not working as well are weakened, making room for new learning to occur. These processes together demonstrate how alterations in synapses are responsible for forming memories, learning new skills, and changing behaviour. Overall, LTP and LTD work together simultaneously to control the strength of synaptic connections within the human, where LTP strengthens the connections, allowing for the improvement of forming memories. LTD weakens the less active connections, leading the brain to clear out information that is not in use, which allows spaces for new learning, highlighting the idea that, through this cycle of process, the brain can learn, adapt, and optimise learning.

Synaptic plasticity is also facilitated by the growth and contraction of dendrites, the lengthening of neurons that receive communications from other neurons, and the formation and destruction of synapses (Hotulainen & Hoogenraad, 2010; Kirchner et al., 2025). Therefore, the brain is capable of adapting to new knowledge and experiences because of this structural remodelling of neuronal circuits that may occur from learning (May, 2011). Cai et al. (2014) characterised neuroplasticity as "an innate property or ability for active lifetime learning and relearning." This point of view emphasises the concept that the brain can adapt and evolve over the course of an individual's entire life, not just in early childhood but at any age. The authors emphasise that the flexibility of the brain is not limited by age but that it may peak during a particular stage of early development. This view supports the growing body of evidence that suggests that the adult brain remains plastic and capable of change in response to experience and learning.

1.2.2. Connection Between Plasticity and Learning

Learning involves changes in the brain's structure and function, going beyond merely cognitive processes. These changes, known as structural plasticity, highlight the brain's ability to alter its internal structure in response to learning experiences. An important body of research that supports the idea is Draganski et al.'s (2004) study, which was based on the hypothesis that repeated practice of a juggling motor task, which requires coordination skills, could cause changes in the GM volume within the human brain. This experiment utilised one learning group and one control group, and MRI techniques were employed to capture images of the brain. Participants were scanned at three different time points throughout the experiment: before learning, after three months of learning to juggle, and three months after completing the learning process. Results showed that juggling for three months, participants showed a significant increase in GM in the mid-temporal region of the brain that is believed to be responsible for processes of complex visual motion (Zeki et al., 1991). Furthermore, after a three-month break from juggling, the participants still showed some identifiable changes compared to pre-learning, but there was a clear reduction in GM volume. This study suggests that learning motor skills such as juggling may lead to an increase in the amount of GM in certain areas of the brain. However, while the study reported structural changes, it did not explore the relationship between these changes and long-term learning or behavioural gains. Furthermore, the study did not have a direct measure of the functional outcome (i.e., what changes were observed during the task while the participant learnt), so it is unclear how structural changes lead to improved behavioural performance.

Complementary evidence comes from studies of real-world expertise. Maguire et al. (2000) compared London taxi drivers with controls. The purpose of the study was to investigate potential effects of a high-intensity spatial navigation experience on brain structure, with a focus on the hippocampus, a region of the brain known to be involved in spatial memory. The researchers compared images of the brain anatomy of London taxi drivers who followed predetermined routes and those who often drove complex routes daily. Significant differences in posterior hippocampus size were found between taxi drivers and non-taxi drivers, suggesting that the cognitive demands of navigation may lead to structural changes in the brain. This study provides compelling evidence of the correlation between learning and brain plasticity. This finding supports the idea that the human brain undergoes structural changes in the aspect of performance experiences and environmental stress during learning. Mechelli et al. (2004) observed greater GM density in the lift inferior parietal cortex of bilinguals compared with monolinguals, suggesting structural changes resulting from proficiency in particular language. Gaser and Schlaug (2003) compared professionals (those who practice for at least an hour every day), amateur and non-musician groups. Findings shows that GM volume was greatest in professional musicians, moderate in amateur musicians, and lowest in non-musicians across a variety of brain areas related to creating music, including motor, auditory, and visual-spatial regions. These studies provide strong support for the idea of plastic alterations in connection to long-term motor learning, which fills the gaps in Draganski's study where no direct evidence of long-term outcome was provided.

Recent study has built on these findings by examining the effect of time. Leipold et al. (2021), investigated the long-term musical ability and its impact on extensive brain networks, both anatomical and functional. The evidence provided by this study indicated that those who started studying music later in life had much fewer connection patterns than those who started earlier. It also suggests that the brain can change its anatomical and functional components dramatically within a key window of time when it is highly receptive to musical input. All things considered, the study contributes to the growing corpus of evidence supporting neuroplasticity, the hypothesis that the brain may restructure itself in response to experiences and learning. It highlights how remarkable it is that, even in adulthood, the brain can change both physically and functionally to learning music. The idea of neuroplasticity as a whole is supported by the body of research that points to the possibility that learning alters the brain's structure and function, which leads to the enhancement of our behavioural ability. As well as empathising the fact that the brain may still reorganise itself in reaction to unfamiliar situations and extensive practice, even in the time of maturity.

However, while all the studies described above provide strong evidence that learning is associated with significant structural changes in the brain, they mostly concentrate on the online learning stages, which are those in which individuals are actively working on tasks. However, there is a knowledge gap in the literature when it comes to offline changes—those that take place during rest periods, such as sleep, that serve a major role in memory consolidation and ongoing skill development. For instance, although changes in brain structure during active learning and practice are shown by Maguire et al. and Gaser and Schlaug's study, they do not examine how brain structures change during offline periods during which learning is reinforced. A growing body of research indicates that consolidation processes that take place offline, especially during sleep, are crucial for stabilising and improving learnt material (Diekelmann & Born, 2010; Stickgold & Walker, 2013). As a result, this lack of focus represents a critical gap, and try to bridge this knowledge gap by merging neurological explanations for learning processes with behavioural models, thereby offering a more comprehensive comprehension of learning processes.

1.3. Learning

1.3.1. Factors Contributing to Learning

There is a large amount of evidence that demonstrates how various factors, such as environmental stimuli, cognitive commitment, and neurological changes, interact and influence the complex process of learning (Cheng et al., 2025; Song & Cai, 2024). Researchers in this field have emphasised the importance of the temporal component in relation to learning. It is not just determined by the time spent on an activity or task (online). The brain's capacity to reorganise neural networks and enable the consolidation and integration of recently acquired information into long-term memory systems depends on these offline times, especially sleep.

One of the conventional psychological models commonly used to explain online learning is the Rescorla-Wagner model (Recorla & Wagner, 1972). This model, originally developed to describe associative learning, posits that learning occurs when there is a discrepancy, or prediction error, between the expected outcome and the actual result. This model proposes that a person tends to learn more strongly when the prediction error is greater. One example of such an assumption comes from the idea of classical conditioning. Learn to associate a conditioned stimulus (CS), like a bell, with an unconditioned stimulus (US), like food. To start with, CS will not trigger any responses; however, when the CS is repeatedly paired with the US, it will begin to respond to the US based on the CS. Later, when the CS is presented without the accompaniment of the US, the prediction error becomes significant, and the expectation starts to change accordingly, thereby decreasing the prediction error over time. This means that when someone is frequently exposed to a stimulus, it will begin to lower their prediction error, which in turn will strengthen associative links and enhance perceptual skills within the context of perceptual learning. This model provides a strong foundation for comprehending online learning, which happens during active engagement with the learning stimuli. This model takes into account how real-time repetition, reinforcement and expectation violation influence learning. What this means in the PL context is that repeated exposure to specific inputs (e.g. visual features) can lead to a decrease in errors, which results in a refined sensitivity in perception. However, although the model can capture the online learning dynamics that occur during the learning session, it ignores offline activities that take place while an individual is asleep or is at rest, which are essential for integrating and consolidating what was learnt (Tucker et al., 2020; Wamsley, 2022). As a result, although the Rescorla-Wagner model sheds light on how learning occurs instantly during active learning, it is unable to adequately explain how learning and memory increase during times of inactivity.

Another intriguing model is the Mackintosh model (Mackintosh, 1975), which moves the emphasis from prediction error to selective attention, which is a complement to the Rescorla-Wagner model. The Mackintosh model posits that animals will give greater attention to stimuli that reliably predict significant events and disregard those that do not. This model focuses on how learning efficiency might be impacted by how one allocates attentional resources. The Mackintosh model states that the predictive ability of stimuli affects how much attention is dedicated to learning about them, in contrast to the Rescorla-Wagner model, which hypothesises that learning happens as long as prediction mistakes remain. For instance, when a stimulus reliably indicates a significant occurrence, it attracts a person's attention more, thereby promoting more efficient learning. Conversely, individuals disregard stimuli with poor predictive value, leading to a decrease in the amount of information they retain. One example of this event is drivers' behaviour at traffic lights; while driving, the driver often pays more attention to traffic lights because they have important indications on whether can go or need to stop. However, in contrast, an individual may not pay too much attention to a billboard on the side of the road, as this is often less relevant to us.

The theories mentioned above give a valuable framework for comprehending the concept of learning, but their underlying processes still differ. The Mackintosh model highlights how learners manage their attention by paying more attention to important stimuli, while the Rescorla-Wagner model is based on the idea of prediction error. Remarkably, neither model thoroughly considers the crucial role that offline consolidation processes—such as sleep—play in promoting long-term memory and adaptable application of newly learnt content. The previously mentioned difference emphasises the need for combining perspectives from psychological models of online learning with discoveries from neuroscience on offline consolidation.

The finding that significant improvements in the execution of tasks often follow periods of rest or sleep, even in the absence of further practice, provided an incentive for looking into offline learning mechanisms. The resulting theory asserts that the brain keeps processing and organising knowledge acquired during active involvement even during these offline times. It has been shown that learning offline, especially when sleeping, involves the reactivation of neuronal circuits used during learning, which aids in the reorganisation and reinforcement of synaptic connections (Stickgold & Walker, 2013). Based on various research approaches, including behavioural evaluations and polysomnography, these processes are thought to improve the integration and long-term retention of learnt content (Diekelmann & Born, 2010)

A fundamental study that investigates the importance of sleep in learning was carried out by Karni et al. (1994), which explored how perceptual learning skills are acquired during sleep. In this experiment, six young adults were trained on a texture discrimination task before and after a normal sleep period or disrupted sleep at either REM or SWS. The findings revealed that perceptual skills were better absorbed after a normal sleep period, with a decrease of 23 ms in reaction time (RT) to stimuli; however, this significant improvement was not found in the REM or SWS-deprived group, which instead led to a 19 ms gain in RT. This study demonstrated that different sleep stages, such as REM, are important for the consolidation of the learning task, as indicated by the improvement found in the non-sleep-deprived group. This study has notably provided information on isolating the effects of specific stages of sleep, giving strong support for the importance of REM in learning. This study also points to an important gap in the literature regarding the generalisability of the results to other types of learning tasks and long-term memory consolidation.

Diekelmann and Born (2010) expanded this area of research by conducting an extensive review to look at the ways in which different sleep stages affect memory consolidation for motor and cognitive skills. Their analysis summarises the results of several studies in the field, suggesting that different sleep stages, such as rapid eye movement sleep and slow-wave sleep (SWS), can have multiple functions during consolidation. Studies have shown that REM sleep is more important for the consolidation of procedural memories (such as motor abilities) and emotional memories, while SWS sleep is critical for the consolidation of declarative memories (such as factual information). However, this review highlights another important process of declarative memory consolidation which is system consolidation, which occurs when neural patterns generated during learning are again active during SWS. On the other hand, REM sleep primarily contributes to synaptic consolidation, a process that fortifies synaptic connections, particularly in the context of procedural learning. This difference shows the difficult process of memory consolidation and shows how sleep supports the different components of learning, depending on the nature of the task that was learnt, and the specific sleep stage involved. Overall, the review paper emphasises that sleep is an important component of learning that not only maintains but also improves and reconfigures memory, which promotes the integration of recently learnt material into the larger cognitive network.

Stickgold and Walker (Stickgold & Walker, 2005, 2013), have further advanced our understanding of sleep-dependent memory consolidation, which supports the above-mentioned viewpoints. Their findings suggest that sleep both stabilises memory and modifies it, enabling newly learnt content to be generalised and integrated into the framework of existing knowledge. In one study, participants were taught procedural (visual discrimination) and declarative (word learning) tasks. Following the training, participants were divided into two groups, with one group remaining awake and the other allowed to sleep. The results showed that sleep had a significant positive effect on participants' ability to complete the task, especially the procedural skills critical to REM sleep. According to Walker and Stickgold, sleep reorganises and consolidates memory traces, increasing the flexibility and adaptability of what is learnt for future use. This process greatly improves the effectiveness of learning in daily life. This finding highlights that sleep is not so much a passive state but is more of an active state that directly supports learning, memory, and cognitive performance.

Beyond sleep, another factor that contributes to learning is the different types of learning tasks, such as motor, perceptual, and attentional learning. It is believed that these types of learning tasks engage distinct neural networks and strongly depend on the task and the content (Yotsumoto et al., 2008). This suggests that task-dependency portraits the plasticity and adaptability of the learning process, where the nature of the task itself can affect specific brain regions and processes that are involved. Furthermore, individual differences also contribute to an important role in the outcome of learning. Cognitive abilities, biological makeup, and structural and functional differences in the human brain all contribute to one's learning ability and the speed at which the learning occurs. For example, Kanai and Rees (2011) carried out a study with the purpose of examining the connection that exists between the anatomy of the brain and one's cognitive capabilities. The researchers concluded that individual variations in brain anatomy, particularly in the PFC, appeared linked to differences in cognitive abilities such as learning. Similarly, in a study conducted by May (2011) reviewed evidence relating to the impact of the brain's ability to adapt on learning. The review provided insights into how differences in brain plasticity could affect the speed and effectiveness of the learning process, with factors such as age, genetics, and prior experience shaping these outcomes.

Furthermore, Takeuchi et al. (2011) expand this idea by exploring the relationship between differences in working memory (WM) function and more extensive cognitive abilities. They employed an fMRI n-back WM task and an alternative cognitive test to see if brain activity during WM could predict creativity. The research indicated that higher creativity scores were correlated with diminished task-induced deactivation in the precuneus, a component of the default mode network (DMN) that is generally inhibited during challenging cognitive tasks (Mayer et al., 2009; Utevsky et al., 2014). This pattern suggests that individuals with higher creativity might have a broader attentional distribution, rather than completely suppressing DMN activity during a WM task. These results explain the influence of neuronal dynamics on WM and more complex cognitive tasks, emphasising the significance of inter-individual variability in shaping learning outcomes.

Taken together, the findings from these studies provide credibility to the idea that different aspects of one's environment might affect one's ability to learn. The timing of learning, the individual variation of learning ability, and the ability to change the brain are all key aspects that play a part in the development of the learning process. Developing an understanding of these aspects can help optimise educational tactics and interventions to promote learning that is both effective and personalised.

1.3.2. Time of the Learning

Building on the understanding of the ways in which different contributors may influence skill learning, it is necessary to address a very fundamental component relating to learning, which is the time that learning occurs. This temporal characteristic influences the ability of an individual to take in, maintain, and use knowledge in different settings (Joiner & Smith, 2008). Broadly, learning can occur in two forms: online learning and offline. In this thesis, online learning is identified as the information participants pick up about the task while performing the activity. For the quick acquisition and development of new skills and information, this type of learning is essential (Doyon & Benali, 2005). Online learning is often related to real-time brain activity, such as the cortex, which has an important role in the development of skills (Doyon et al., 2009). For instance, Bavelier and Green (2019) carried out a study to look at how playing video games can influence cognitive functions, especially in attention and working memory. The participants in the study were split into two groups, where one group played action video games and the other group played non-action games. Cognitive performances were assessed before and after the sessions using some unrelated tasks, such as tests for attention and memory. The findings from the study highlighted that those who are in the testing group developed better cognitive flexibility, working memory, and attentional skills, with these benefits extending beyond gaming to other cognitive domains. This study supports the idea that engaging in action video games can enhance brain plasticity and cognitive function, facilitating cross-domain transfer of learnt skills. However, the long-term persistence of these effects remains uncertain, and further research is needed to explore their underlying neural mechanisms and applicability to other age groups.

On the other hand, offline learning is identified as activities that take place after acquisition and during sleep or during wakefulness when participants are not doing the learning task (Tucker et al., 2020). The periods when an individual are awake but not actively working are known as offline wake periods. During these periods, information acquired during learning may be involuntarily reactivated, reorganised, and integrated into long-term memory networks (Tambini & Davachi, 2019). Dewar et al. (2012) investigated this idea by evaluating the acquisition of new verbal memory in their study. Seven days following the learning session, they discovered that memory performance had significantly improved. They concluded that an offline wake period following learning allowed new memory traces to be more thoroughly integrated and, as a result, to be retained for a significantly more extended period. Similar findings from Craig and Dewar (2018) were observed, where they found that participants were much better at differentiating newly encoded target images from similar lure images when the learning took place following a 10-minute offline wake period. This finding emphasises that our cognitive state during consolidation not only influences our memory retention but also affects the level of detail in our new memories. Both studies suggest a strong connection between the offline wake period and learning, as it helps prevent the loss of memories.

Furthermore, Schlichting and Preston (2015) extended these findings by examining the effect of offline periods on learning generalisation. They trained individuals on a task that required them to associate specific stimuli with specific responses, followed by an offline interval. They found that the length of the offline period was positively correlated with individuals' ability to apply newly learnt skills to novel stimuli, suggesting the idea that the longer the offline interval, the better the learning and the more it can be consolidated and generalised. However, one of the limitations of this study is that it only focuses on one type of task, and it is not possible to conclude whether, if a different task were used, it would lead to a similar finding.

When combined, these results provide compelling evidence that learning occurs throughout both online and offline phases. However, gaps remain relating to the specific brain processes that offline learning uses to combine different kinds of information, especially when it comes to complex real-world tasks. Filling up these gaps will help us develop a more sophisticated understanding of the roles that wakefulness and sleep play in the development and maintenance of skills.

1.3.3. Transfer of Learning

Transfer of learning refers to how information or specific skills acquired in one context can be used in another context (Haskell, 2001). This concept has been extensively studied in the fields of psychology and education because it helps us understand how individual acquire and remember knowledge and skills (Schubert et al., 2014; Vleugels et al., 2020). This idea has strong applications in several fields and different aspects of our daily lives. For instance, the concept that driving a car can facilitate learning to drive a truck relies on the transference of motor skills between these two situations. Essentially, the ability to apply what have been learnt in situations enhances our learning process and adaptability. The transfer of learning encompasses aspects such as positive or negative transfer and near or far transfer. Positive transfer occurs when knowledge gained in one area positively affects performance in a related field (Müssgens & Ullén, 2015). Language learning is an intriguing example of this positive transfer because research have shown that learning one language may make learning a second language easier, especially if the two languages have similar linguistic characteristics (Abrahamse et al., 2013; Ortega, 2008). In skill domains, action-video-game learning has also resulted in cross-task attentional benefits compared to non-action controls (Bavelier et al., 2012; Green & Bavelier, 2003), which supports the idea that learning can provide measurable performance improvements beyond the specific task learnt. Language learning is a interesting scenario, as it is natural to assume that learning one language may facilitate the learning of a second, particularly if the two languages share similar grammatical features. In fact, this form of transfer strengthens general learning and can speed up learning new skills based on what one already knows. In the perceptual domain, task design may limit or facilitate transfer: fundamental research indicates an important specificity of enhancement to trained features/areas, although “double-training” can promote transfer to untrained retinal locations (Xiao et al., 2008).

In contrast, negative transfer occurs when the information hinders the performance of a future, related activity from the prior one. An example of such a transfer is when two tasks superficially resemble each other but differ in critical functioning aspects. In this case, the inappropriate transfer of rules or methods impairs the performance of the novel task (Bandura & Locke, 2003; Ni et al., 2023). According to Perkins & Salomon (2012), negative transfer comes into view during instances when the previously gained skills interfere with the process of learning something new. This interference often illustrates the critical problem that exists within the process of learning, whereby prior knowledge needs to be inhibited or changed as one learns something different.

This then led into the discussion of another crucial element relating to the degree of transfer, which can be classified as either a near or far transfer of learning. When the new learning activity is quite comparable to the old one, near transfer occurs, facilitating an effortless transfer of skills (Wirth et al., 2025). Far transfer involves the process of adapting information or skills in situations that are very dissimilar from the initial learning environment (Barnett & Ceci, 2002). While near transfer is prevalent, far transfer offers greater challenges but offers the capacity to enhance innovation and problem-solving abilities in unfamiliar contexts. Empirical evidence of far transfer is uncommon; however it has been documented following intensive training or when tasks display shared latent processes (Green & Bavelier, 2003; Xiao et al., 2008).

As stated by the work of Torrey et al. (2010), the ability to transfer is crucial to enhancing learning efficiency, as it allows one to apply prior knowledge, thus reducing the requirement to relearn what has previously been learnt. The function of learning transfer is important; without the ability to transfer, all learning would be situation-specific, and significant repetition of previously learnt materials would be required, which is not an efficient way to learn. As a result, learning transfer is a critical component of human learning, and its study is essential for designing effective learning environments. From a psychobiological standpoint relevant to this thesis, the process of transfer could depend on the consolidation of learning: offline processes, particularly sleep, can stabilise or reorganise representations, potentially facilitating generalisation under certain conditions (Borin et al., 2024; Conessa et al., 2023; Drouin et al., 2023a; LaBonte-Clark et al., 2025). The study of learning transfer extends beyond the straightforward application of acquired information or skills in psychology. This highlights the value of understanding the transfer of learning and the process that additionally speeds up the learning process, but also helps individuals become more skilled at tackling complicated problems. The importance of learning transfer should not be overstated, as it is essential to how effectively individuals learn If the ability to transfer knowledge were absent, the acquisition of knowledge would be limited to specific situations, also requiring the process of repetitive relearning of previously acquired information in every new setting.

1.3.4. Individual Differences in Learning and Transfer

These studies, in general, demonstrate that differences in the brain's structure and function result in measurable differences in learning behaviours. For example, those who have stronger brain connections tend to be less likely to get mentally tired (van der Linden et al., 2003), better at doing more than one thing concurrently (Strobach et al., 2012), and learn motor skills faster (Ericsson et al., 1993). Understanding such difference in individuals is important for learning, professional training, and therapy. Individualised methods that use an individual's cognitive abilities may be more successful than standardised approaches (Gkintoni et al., 2025).

Furthermore, these inter-individual differences also influence the behaviour of perceptual and attentional learning. On insightful review by Kanai and Rees (2011), provides meaningful evaluation into how structural differences in the PFC may predict individual differences in cognitive skills, especially in relation to learning and memory. The review suggests that differences in behaviour and cognition are linked to differences in anatomical traits such GM volume, and WM integrity, and cortical thickness. They also demonstrated that brain anatomy differences are not only external noise. Instead, they are a systematic contributor to individual differences in the effectiveness of learning, including recall and attentional control. Although Karni and Rees's review provided a significant theoretical framework, it mainly synthesises correlational findings, indicating that causal mechanisms require examination through focused empirical studies.

Gur et al. (2020) carried out research to examine if differences in GM volume could predict cognitive skills. Using structural MRI, they demonstrated that differences in GM across frontal and parietal regions was significantly correlated with cognitive ability and working memory capacity. This research offered substantial evidence for the "parieto-frontal integration theory" of intelligence, indicating that individuals who have enhanced anatomical resources in these areas are more successful at acquiring and applying knowledge. However, given that it uses a correlational design, it was unable to determine if GM differences were intrinsic or it was a result of previous learning experiences. Takeuchi et al. (2011) provided additional evidence by examining the potential of working memory learning for producing functional and structural changes in the brain. Their participants underwent intense mental calculation training during MRI scanning. The findings shows that learning can improve mental calculation significantly which was accompanied by increase in GM volume within the PFC and parietal region, as well as leading to stronger connectivity between these areas. This study expanded beyond correlational methods and demonstrated that learning can induce changes within the brain and providing a potential mechanism for the development of individual difference over time.

Verghese et al. (2016) went beyond this work to examine the relationship between PFC structure and multitasking skill. Conclusive results showed that individuals who had larger volumes of the PFC were able to reach much higher degrees of cognitive flexibility and multitasking at post-training. This study aimed to identify how changes in the structure of the PFC affect not only base levels of cognition but also the ability to continuously learn. The researcher quantified PFC volume using MRI. The results showed that the larger the PFC, the greater the improvement in multitasking skills after training. These findings are particularly important at the behavioural level in that the enlarged PFCs would suggest that individuals may respond well to certain cognitive training, such as multitasking or shifting-attention kinds of tasks. This emphasises the importance for research to take into consideration individual differences in the development of interventions for cognitive training. It suggests here that cognitive training should be performed in relation to the structural capacity of the learner's brain, rather than assuming a one-size-fits-all approach for higher efficacy of the intervention.

In fact, Scholz et al. (2009) examined the WM change due to training as the predictor of gains in cognitive performance. They investigated the possibility that WM plasticity resulting from training can predict improvements in learning performance. DTI scanning was done to create images for participants both prior to and following their learning regarding the visuospatial and motor tasks. Scholz et al found that there was a significant change in WM organisation, especially within the posterior intraparietal sulcus, which was associated with task performance improvement. Individuals showing more efficient WM connectivity after training performed better in both visuospatial and motor tasks, indicating that WM reorganisation might be an important sign in learning and memory. This finding reinforces the importance of understanding neural plasticity in relation to both cognitive psychology and informing strategies in behavioural training, such as in skill acquisition within sports or rehabilitation, for example. These WM changes underline the fact that the timing and structure of the programs are important for maximum cognitive improvements, suggesting that frequent and well-structured practice sessions may improve learning outcomes.

Together, these studies show that individual differences in brain structure and function are important to the field of psychology at the behavioural level because these neurological differences translate into real-world differences in learning behaviours. For instance, individuals with higher neural connectivity show resistance to cognitive fatigue, multitasking ability, and an increase in the rate of motor skill learning. With this realisation, educational psychologists and trainers can construct personalised approaches that leverage the cognitive strengths and weaknesses that an individual possesses. An approach like that gives way to neurological research into actionable strategies that affect behaviour—through academic settings, through professional training, and through therapeutic intervention.

This research enables the field of behavioural psychology to recognise that differences in learning are not just about the content being learned but are also about how the brain processes and consolidates that information. Behavioural interventions that take such neurological underpinnings into account will likely result in successful learning. While all the above-mentioned studies in this section provide insights into the neuroanatomical basis of individual differences in learning, the true importance of these studies lies in their implications for behaviour. These findings bridge neurological and behavioural levels, providing practical application to how to understand, teach, and train individuals. In other words, it should be recognised that learning cognitive tasks involves differences and complexity in individuals. This thesis adds to the existing literature by investigating the behavioural manifestations of these differences, with a particular focus on online and offline learning processes. Comprehending these differences may facilitate targeted interventions that enhance learning outcomes, especially for individuals encountering difficulties in skill acquisition.

1.4. Role of Sleep in Learning and Plasticity

The field of sleep research commonly uses the electroencephalogram (EEG), a tool that analyses brain electrical activity. EEG works by capturing brain wave frequencies and provides insights into how the brain functions (I. G. Campbell, 2009). Generally, researchers use EEG data to identify patterns of brain activity that change as an individual transition from being awake to falling asleep. During wakefulness, the EEG readings primarily consist of frequency brainwaves with amplitudes indicating an alert and focused cognitive state. However, when approaching sleep, these brainwave oscillations undergo shifts (Hori, 1985). Usually, at the beginning of each sleep cycle, there is a decrease in head wave frequencies. The sleep cycle consists of five phases that repeat four to five times throughout the night and serve purposes in restoring and rejuvenating our bodies. These phases involve coordination between systems and are crucial for overall health and well-being. A typical sleep cycle goes back and forth between non-rapid eye movement (NREM) and rapid eye movement (REM) sleep four to five times a night (Patel et al., 2025). Each cycle supports different physical and mental functions (Sazgar & Young, 2019).

NREM and REM are two states that occur during sleep (Le Bon, 2020). NREM light sleep corresponds to the first stage of the sleep cycle. During this stage, characterised by alpha waves with a frequency of 8-13 Hz and high amplitude, you transition between being awake and asleep. As you enter stage two, sleep spindles emerge, which refer to bursts of repetitive brain wave activity at 10-12 Hz (Dotto, 1996). NREM stages three and four are sometimes referred to as "slow-wave sleep" (SWS). During this time, low frequency (up to 4 Hz) and high amplitude delta waves will characterise the reduced spindle production. REM sleep, in contrast, is the fifth stage and is distinguished by atonia and rapid eye movement (Spencer, 2013). The stage of sleep known as REM is when people dream, and the brain activity related to this period is relatively similar to that of waking individuals. REM sleep also causes the paralysis of all bodily muscles, except those necessary for breathing and circulation. REM sleep can also be referred to as paradoxical sleep, due to its unique combination of enhanced cerebral activity and decreased muscle tonicity (Luppi, 2018). Despite the idea that there are still many theoretical disagreements regarding the significance of both REM and NREM sleep for learning and memory (Siegel, 2001), REM sleep has been proposed to be a unique state that may support learning, memory-related functions and plasticity (Colten & Altevogt, 2006).

While there is ongoing discussion regarding the different roles of NREM and REM sleep in memory processes, growing research indicates that they may offer complementary contributions. Wagner et al. (2001) offered direct empirical data demonstrating that REM-rich sleep explicitly improves the consolidation of emotional memories. Participants studied both emotional and neutral text passages and were then assessed following intervals of either early sleep (marked by SWS), late sleep (marked by REM), or equivalent wake periods. Recall was considerably better post-sleep compared to wakefulness; notably, late sleep enhanced in REM preferentially improved memory for emotional texts relative to neutral ones. These findings indicate that REM sleep facilitates the processing of emotionally significant information, presumably through amygdala–hippocampal connections, although the study was limited to spoken materials. More recently, Shuster et al. (2024), discovered new REM electrophysiological signatures related to cognitive processing in humans, strengthening the idea of connection between REM activity and memory integration.

Given the diverse roles that the various phases of sleep play, understanding how sleep influences brain plasticity and learning can be challenging. Specifically, SWS has been linked to the retrieval of memory, which involves recalling events and information. Diekelmann and Born (2010), in a comprehensive review, suggest that during SWS, there is a replay within the hippocampal-neocortical dialogue of the learning-related events in the brain, leading to memory consolidation and strengthened connections. On the other hand, REM sleep is believed to be crucial for consolidating information, often accompanied by vivid dreaming (Stickgold, 2005). Animal research supports this model: Wilson and McNaughton (1994) examined hippocampal place cells in rats navigating a maze and observed that the same activation patterns were reactivated during subsequent SWS period, indicating a replay mechanism for memory consolidation.

Furthermore, the review conducted by Rasch and Born (2013) highlighted the important function of stage N2 sleep spindles in NREM sleep. It has been suggested that these brief bursts of brain activity, called spindles, may serve an informational transfer function from the hippocampus—a brain structure described as the centre for encoding information in short-term storage—through to the neocortex—the brain structure responsible for storing information in long-term storage. Maybe one important indication of the occurrence of spindles during sleep plays a critical role in the effective consolidation of memories, further highlighting how stages of sleep interact with cognitive functions.

These findings together show that sleep is not a passive state but an active biological event that promotes memory consolidation, plasticity, and the transfer of learning. SWS seems to play a role in hippocampus replay and consolidating declarative and emotionally important information, while REM plays a role in synaptic consolidation and learning procedural skills. Sleep spindles, mainly when observed in clusters, have been recognised as a biomarker for both consolidation and transfer between different types of sleep. These results align with psychobiological concepts, especially systems consolidation theory, and provide a framework to evaluate the role of sleep for promoting task-specific consolidation compared to broader generalisation. The significance of sleep in perceptual and attentional learning is particularly relevant to this thesis. REM-dependent consolidation may facilitate improvements in perceptual discriminating tasks, but NREM spindle activity may play a role in attentional control and the transfer of skills across contexts. The psychological and biological models of sleep-dependent consolidation offer a justification and theoretical framework for the subsequent empirical chapters that follow, which investigate the impact of sleep on the specificity and transfer of perceptual and attentional learning.

1.4.1. The Need of Sleep

The usual sleeping pattern is typically characterised by a reduction in responses and sensitivity to external stimuli, which may rapidly return to normal, as sleep has a decreased capacity to respond to external stimuli, unlike hibernation or coma (Cirelli & Tononi, 2008). The two major processes responsible for driving the sleep regulatory process include a circadian rhythm and a homeostatic drive. The circadian rhythm synchronises the sleep-wake cycle with the external day-night pattern to ensure that rest is obtained at night and alertness during the day (Borbély et al., 2016). In contrast, the homeostatic drive increases the need for sleep depending on the duration of wakefulness and cognitive or physical demands throughout the day (Deboer, 2018). Together, these two processes work together to ensure a very delicate balance in the body between the rest period and the active period, highly critical for maintaining cognitive functions related to attention and decision-making.

Research has extensively indicated that sleep serves a range of purposes, such as promoting growth (Papatriantafyllou et al., 2022), conserving energy (Roth et al., 2010), enhancing performance (Aeschbach et al., 2008; Alain et al., 2015; Debarnot et al., 2013; McDevitt et al., 2018; Tucker & Fishbein, 2008), and influencing psychological well-being (Lo Martire et al., 2020; Vadnie & McClung, 2017). These studies into different benefits of sleep suggest that it is unrealistic to view sleep as having one purpose (Zielinski et al., 2016). Comprehensive reviews have highlighted the idea of cross-species assessments offer additional evidence, which demonstrated that empirical research has found variables such as age, body size, and ecological niche significantly affect sleep duration and architecture in mammals (Siegel, 2005). One particular theory known as Energy Conservation Theory are commonly used to explain this, which suggests that sleep may have evolved as a mechanism to conserve energy and regulate behaviour over a 24-hour cycle. According to this theory, the primary role of sleep is to reduce energy expenditure during periods throughout the day and night. This hypothesis is supported by evidence indicating that our body temperature and calorie needs decrease when asleep, but increase once an individual wakes up (Northeast et al., 2020). However, sleep does more than just save energy. Sleep also plays a role in maintaining brain function, which is widely recognised as one of its significant benefits. It is commonly understood that getting sleep is essential for memory retention and cognitive abilities (Graveline & Wamsley, 2017; Tucker et al., 2020).

Research on behaviour has linked sleep deprivation (SD) to difficulties in tasks requiring attention, such as filtering out irrelevant visual stimuli from a set of memories. For example, Blagrove et al. (1995) used the Finding Embedded Figures Test (FEFT), which is a test of the ability to filter out irrelevant stimuli. The finding showed that SD adversely impacts the neurological filtering mechanism, thereby decreasing performance. The decrease in task performance with SD is particularly troubling for those individuals operating under high-stress conditions where great attention to detail and speed of decision-making are critical (Killgore et al., 2006). Sleep deprivation has also been associated with impaired cognitive performance in tasks entailing higher-order performance, such as cognitive flexibility, creative thinking, and language skills. The longer the period of SD, the more severe the cognitive impairments become; hence, sleep continues to be not only integral for learning but also for maintaining overall cognitive function. Similarly, research has also shown that SD can impact performance in other domains involving memory recall (Frenda et al., 2014; Martínez-Cancino et al., 2015), creative thinking (Harrison & Horne, 1999), language skills (Harrison & Horne, 1997), and decision-making (Killgore et al., 2006; Schnyer et al., 2009)(Killgore et al., 2006; Schnyer et al., 2009).

The general body of research underlines the indispensable role of sleep both for physiological and cognitive aspects and expresses the need to understand and exploit all of the potential of sleep in cognitive rehabilitation, education, and mental health. From a psychobiological standpoint, these effects are effectively explained through systems consolidation theory, which suggests that sleep facilitates the reactivation and transfer of newly preserved memories from temporary storage in the hippocampus to enduring networks in the neocortex (Diekelmann & Born, 2010), which the thesis will go into more detail in the next section. However, for the current thesis, which examines the stabilisation and transfer of perceptual and attentional learning, understanding the role of sleep in maintaining cognitive performance is a fundamental basis for support. Lack of sleep not only interferes with attentional processing and decision-making but also interferes with the consolidation processes essential for learning generalisation.

1.5. Sleep and Cognition

1.5.1. Learning, Memory and Sleep

The correlation between memory consolidation and sleep is an important research area in psychological research, especially in the field of learning (Griessenberger et al., 2012; Schäfer et al., 2020; Talamini et al., 2008). The exact mechanism by which sleep promotes memory consolidation remains unclear, but there is solid evidence that sleep has cognitive advantages. A fundamental study conducted by Wagner et al. (2006) examined the effects of sleep on emotional memory. In this experiment, participants were asked to memories passages containing strong emotions. Participants' memory ability significantly improved after a brief three hours of sleep. The impact showed remarkable persistence for a duration of up to four years, therefore highlighting the crucial significance of short-term sleep in the process of long-term memory consolidation. The study underscores the significance of sleep in effectively stabilising and retaining acquired knowledge, hence facilitating its long-term retention and retrieval. Nevertheless, despite these discoveries, the underlying mechanisms by which sleep increases learning and memory remain inadequately comprehended. The research conducted by Wagner et al. provides a fundamental understanding of the mechanisms by which memory consolidation may function in wider domains, such as perceptual learning. The methodology used in their study, which involved assessing memory retention following a brief period of sleep, may be modified to examine if comparable consolidation processes take place with non-emotional memories or perceptual learning operations. This work establishes a strong foundation to suggest that the processes controlling the consolidation of emotional memories may be similar to those involved in other types of memory, such as perceptual or procedural memory. Existing gaps in the literature, such as the impact of various sleep stages or durations on these cognitive processes, provide important avenues for future research.

Further support for the role of sleep in consolidation comes from research using motor sequence learning tasks. Fischer and Born (2009), for example, trained participants on finger-tapping sequences and compared groups tested after sleep versus wakefulness. They found a significant improvement in motor function following 12 hours of rest. This finding provides additional evidence to the notion that there is a consistent improvement in performance for motor sequence tasks associated with sleep. Similarly, Albouy et al. (2013) used motor sequence tasks where participants were required to enter a specified number sequence as quickly and precisely as they can (for example, 4-1-3-2-4 or 2-4-1-3-2), at the same time using fMRI to examine the benefit of sleep on performance. They demonstrated that post-sleep improvements were accompanied by increased activity in the hippocampus and medial PFC in the sleep group compared to the SD group. After learning SD group performance only stabilised and did not improve. These findings suggest that explicit motor task learning consolidation occurs exclusively after adequate sleep since only the sleep group displayed reorganisation of the hippocampal-neocortical networks, underpinning the principle of system consolidation (Diekelmann & Born, 2010).

There are two main categories of long-term memory: declarative and procedural memory (Cohen & Squire, 1980; Squire, 2004). Declarative memory encompasses the ability to store factual information, whereas procedural memory is concerned with the recall of learnt responses based on prior experience in response to relevant stimuli. Diekelmann and Born (2010) emphasise that the state of encoding significantly impacts whether memories for learning have access to sleep-dependent consolidation. While the encoding for procedural memories might entail both implicit and explicit processes, the encoding for declarative tasks is often explicit. This explicit declarative memory processes also appear to be sensitively dependant to sleep (Fattinger et al., 2017; Korman et al., 2003; Walker et al., 2002; Wilhelm et al., 2008). For example, the study conducted by Tucker et al. (2006), showed that a short period of nap containing only NREM sleep would improve declarative memory performance on a paired association task, although the procedural benefits in the study was less consistent. This study adds to the current evidence which suggests that certain types of sleep stage might be more important than other stages. Such that the finding suggests the role of SWS in supporting declarative memories through the hippocampal–neocortical transfer, while REM is more relevant with procedural and emotional memory (Rasch & Born, 2013; Walker & Stickgold, 2004).

Furthermore, several studies have also pointed out other potential factors that might be responsible for the sleep-dependent benefit in learning. One of these is how much and when sleep occurs (Korman et al., 2007; Payne et al., 2012). A review examining the patterns across studies has commonly demonstrated that, after a night of sleep, performance generally improves significantly, and this impact is frequently observed after 8 hours of sleep (Diekelmann & Born, 2010). However, recent studies have emphasised that having a quick nap after sleep can help individuals remember the content they have learnt (McDevitt et al., 2018). In the learning of perceptual discrimination tasks, for example, Mednick et al. (2003a) discovered that sleep-dependent learning might be completed with a brief (60-90 minute) napping time. In terms of amplitude, dependence on sleep stages, and retinotopic specificity, this nap-dependent learning was highly similar to that previously described for an 8-hour sleep period. Although it appears that even a short amount of sleep is sufficient to help with consolidating learning, and longer sleep durations result in an even greater benefit (Gais et al., 2000; Lo et al., 2014; Tucker et al., 2020).

While the reviewed research in this chapter provides robust evidence for sleep-dependent consolidation across memory systems, notable gaps remain. One noticeable gap is that much of those studies concentrate on emotional memories and motor learning, leaving the question of whether perceptual and attentional domains operate under similar mechanisms unclear. This directly fits with the aims of the current thesis: to investigate whether sleep enhances consolidation in perceptual and attentional learning tasks, and to evaluate if the observed offline benefits indicate system-level processes aligned with consolidation theories. The thesis aims to address these unanswered questions by synthesising behavioural paradigms with psychobiological models, aiming to determine if the concepts exhibited in declarative and procedural memory extend to other modalities of learning.

1.5.2. The Synaptic Homeostasis Theory

Researchers have made contributions to several theoretical frameworks across the sleep literature in an attempt to better explain the evidence on the effect of sleep on memory consolidation. One widely acknowledged theory in the literature claims that sleep fosters the circumstances necessary for brain plasticity. The capacity of the brain to change and adapt as a result of experience is known as plasticity (Ribeiro, 2012), as previously mentioned. The synaptic homeostasis hypothesis (SHY) continues to be one of the most organised hypotheses that explains most of the data reported in the literature and has been well documented in reviews (Tononi & Cirelli, 2003, 2006, 2014). SHY hypothesised that while awake, the brain actively picks up information from its surroundings by strengthening synaptic connections between highly active brain areas. The sensory-motor detachment from the environment causes the brain to substitute more minor, less active synaptic contacts during sleep (Tononi & Cirelli, 2014). It is believed that the brain processes and coordinates newly learnt responses more effectively when routinely active synaptic connections are strengthened, and less frequently active synaptic connections are weakened. In the cortex and hippocampus of rats, indices of synaptic strength are shown to rise during the day and fall during the night, according to research by Vyazovskiy et al. (2008). This study provides credence to the notion that synaptic downscaling occurs during sleep. Further evidence was provided by Liu et al. (2010), who discovered that synaptic potentiation in the frontal cortex of rats was enhanced after waking and reduced after sleep. Again, this work offers factual data emphasising the idea that sleep is beneficial for maintaining synaptic homeostasis. Therefore, maintaining synaptic homeostasis is the critical objective of sleep. Sleep improves neural sensitivity and learning capacity by lowering synaptic strength, enabling the consolidation and integration of new information while boosting the signal-to-noise ratio (SNR) (Figure 1.1).

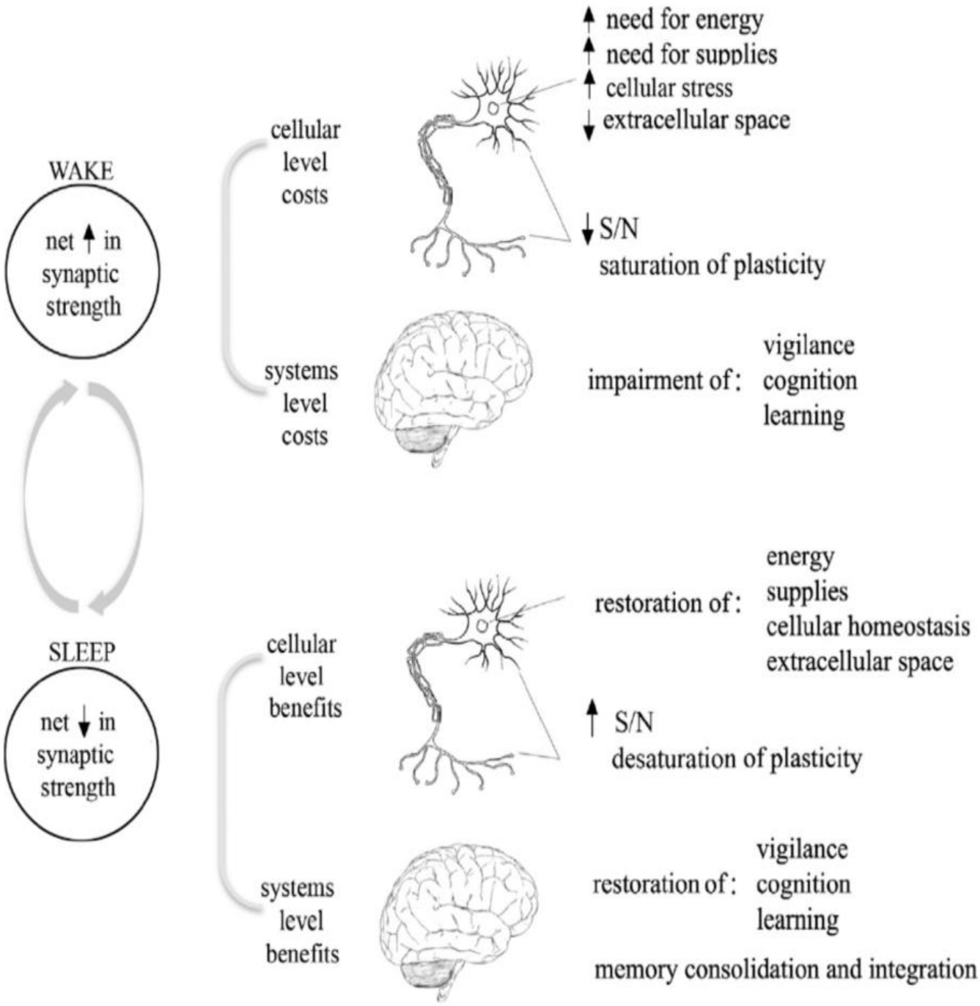

Figure 1.1. *The Synaptic Homeostasis Hypothesis: Signal to noise ratio. (Retrieved from Tononi & Cirelli, 2014). Figure demonstrating a net increase in synaptic strength during wake, enhancing learning but at the cost of higher energy demand, cellular stress, reduce extracellular space. Whereas sleep restores the balances by downscaling synaptic strength.*

It has been demonstrated that the synaptic homeostasis system affects several components of learning and memory, including the capacity to gather newly learned information, consolidate it (by up-scaling stronger synapses and decreasing SNR), and eventually integrate it with previously taught schemas (Tononi & Cirelli, 2014). The capacity to learn new memories is one benefit of sleep for memory processing, and SHY claims that one of the most apparent advantages of sleep is the restoration of learning ability. For instance, Chee and Chuah (2007) observed that the decline in performance accuracy was positively correlated with the 24-hour SD that followed the acquisition of a visual memory task. Similar to this, Yoo et al (2007) discovered that only one night of SD is enough to cause a severe loss in the capacity to encode episodic memory. These findings highlight the fact that insufficient sleep significantly affects our capacity to form lasting memories of new experiences. It implies that having enough sleep before learning is crucial for enabling the brain to build memories. A further advantageous effect of sleep on memory is the activity-dependent down-selection of synapses, which is frequently used to explain many aspects of memory consolidation. As an illustration, in the paired-associate learning paradigm Nere et al (2013), discovered through computer simulations that increasing the activation of a particular memory during the down-selection process result in a selective enhancement of that memory. This is consistent with the findings by Antony et al (2012), who observed that being cued while sleeping enhances memory stability following learning.

SHY does not, however, come without criticism. Although refined, others argue that the idea may oversimplify the complex relationships underlying sleep, learning, and plasticity. In the review by Rasch and Born (2013), they stated that the model fails to effectively take into consideration REM sleep's contribution to memory consolidation. The basic idea of the hypothesis, which suggests that sleep-dependent synaptic downscaling occurs, is mainly supported by indirect data, requiring more empirical validation.

1.5.3. Active System Consolidation Theory

The active system consolidation theory during sleep draws attention to many crucial ideas. Firstly, this idea assumes that memories are reactivated and strengthened when asleep. Second, it implies that not all learning may be strengthened while sleeping and that consolidation occurs only in some learning domains. Finally, the idea emphasises that memories undergo qualitative modifications as they are transferred to long-term memory storage (Born & Wilhelm, 2012). With regard to sleep-dependent memory and learning, consolidation, and integration, this appealing hypothesis has been able to correctly anticipate and explain a number of behavioural, physiological, and neuroimaging findings (Rasch & Born, 2013).

According to this concept (Figure 1.2), information is first processed simultaneously in the hippocampus and neocortical networks when a person is awake. During the sleep cycles, especially SWS, the newly developed memory traces are consistently reactivated and gradually restructured. This process leads to memory representations and improves synaptic connections within the neocortex, as explained in the review by Born and Wilhelm (2012). Several studies have also found a connection between sleep spindles, learning, and cognitive abilities and that both procedural and declarative memory consolidation has been linked to activity after post-learning sleep (Antony et al., 2019; Fogel & Smith, 2006; Laventure et al., 2016; Schabus et al., 2004). For example, Cowan et al. (2020)identified that spindles observed during sleep are associated with modifications in memory traces. These modifications include increased connectivity in hippocampal cortical networks and enhanced pattern resemblance in cortical memories. The findings provide evidence suggesting that spindles may serve as a mechanism for reorganising neuronal memory traces during nighttime sleep. Additionally, studies have shown that spindles are also related to abilities such as attentional skills and perceptual learning, domains that are directly relevant to this thesis. Nishida and Walker (2007), showed that more spindle activity was linked to better performance on a visual discrimination task, which means that spindles have an association with learning perceptual skills. In contrast, Bergmann et al. (2012), demonstrated that spindles encourage hippocampal-neocortical communication essential for both declarative and non-declarative memory consolidation. These studies emphasise the significance of the ASC framework in comprehending the consolidation of perceptual and attentional learning processes. However, the strength of this hypothesis lies in its inability to address and clarify these facts related to spindles.

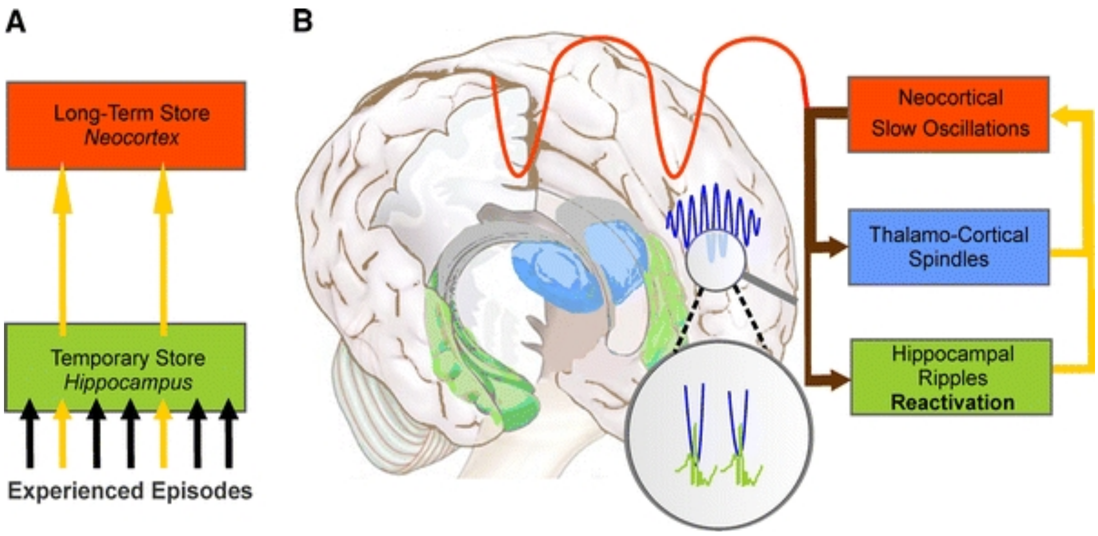

Figure 1.2. Sleep is the consolidation of active processes. The hippocampus serves as a temporary storage location for recently acquired memories, which are then reallocated to the neocortex, the long-term store, during slow-wave sleep (SWS). ***B*** *The link between the neocortex and the hippocampus, which is controlled from the top to the bottom by the neocortical slow oscillation (red), forms the foundation for system consolidation during SWS. Depolarising up phases of the slow oscillations cause sharp-wave ripples (green) in the thalamocortical spindles and the hippocampal memory traces (blue) to reactivate repeatedly. Sharp-wave ripples coil into single peaks of a spindle together with matching awakened memory information. (image adapted from Born & Wilhelm, 2011).*

However, this theory is also not without debate. There is ongoing discussion over the precise function of REM sleep in memory consolidation, some research suggested that SWS—rather than REM sleep—is more important for memory consolidation (Marshall & Born, 2007). Furthermore, the hypothesis mostly overlooks the significance of other sleep phases for learning and plasticity due to its concentration on REM sleep. Notwithstanding these problems, the Active System Consolidation Theory has greatly influenced how researchers perceive the dynamic interactions among sleep, memory, and learning. To explain the specific processes at play and resolve the roles of various sleep phases in memory consolidation, further study is required.

1.5.4. Comparison Between SHY and Active System Consolidation Theory

The theories of the SHY and the Active System Consolidation Theory have been extensively studied to gain insights into how learning is consolidated during sleep. These theories recognise the role that sleep plays in memory and learning. They propose different mechanisms for this process. Both the active system consolidation hypothesis and the SHY theory emphasise the importance of brain oscillations occurring during SWS in memory consolidation. Both ideas, however, offer different viewpoints on how sleep-dependent memories are encoded and consolidated.

In contrast to the SHY hypothesis, which suggests that sleep improves learning and memory by bringing synapses to their baseline level, the active systems model proposes that memories are actively strengthened and reorganised during sleep (Liu et al., 2024). The active systems model takes into account the mnemonic effects of subcortical structures like the hippocampus (Duan et al., 2025). The active systems model takes into account the mnemonic effects of subcortical structures such as the hippocampus. Furthermore, according to the SHY theory, any disruption in the rhythm of slow-wave SWS could potentially reduce its impact on memory functions during sleep (Tononi & Cirelli, 2003). However, recent research has demonstrated that external stimulation of oscillations enhances memory rather than diminishes it (Ngo et al., 2020). Nevertheless, there are still some aspects in understanding how post-learning sleep specifically enhances networks associated with acquired memory traces (Diekelmann & Born, 2010).

In summary, research has shown that incorporating information into long-term memory and selectively preserving existing information are the key elements of the memory consolidation process (Paller et al., 2021). A recent theory suggests that this process influences how information is stored in networks through interactions between the neocortex and hippocampal regions, which are essential for consolidation (Moscovitch et al., 2016). Advanced technology has shed light on how sleep impacts our learning abilities. While these two theories propose various mechanisms, they complement each other. The Active System Consolidation Theory explains how sleep aids in consolidating memories, while the SHY theory suggests that sleep plays a role in preparing us for learning. Recent studies using neuroimaging techniques have helped unravel the interaction between these systems (Klinzing et al., 2019). However, further research is still needed to comprehend the processes and integrate these hypotheses into a comprehensive framework for sleep-dependent learning and memory consolidation.

Although the focus of this thesis is not to test these models directly, the models can provide a conceptual framework that informs the research question in this thesis. The thesis uses these models as indicators for investigating the differential consolidation of perceptual and attentional learning across wakefulness and sleep, as well as to determine if these processes are signs of domain-general or domain-specific mechanisms. By contextualising the empirical research within these psychobiological frameworks, the thesis enhances the understanding of the interplay between sleep and learning processes, especially in the absence of direct examination of the brain substrates defined by SHY or ASC theory.

1.6. Summary and Thesis Outline

The main goal of this thesis is to conduct a thorough investigation to examine how wakefulness and sleep together shape the balance between specificity and generalisation in human learning, with a particular focus perceptual and attentional learning, as well as looking at whether there are any shared or distinct mechanisms. The aim proposed in this thesis is informed by both psychobiological models of memory consolidation (e.g., the SHY, which emphasises the role of sleep in downscaling and restoring the capacity to learn, and the ASC, which highlights hippocampal–neocortical interactions during slow-wave sleep) and behavioural models of learning (e.g., the Rescorla-Wagner model, which conceptualises learning as reducing the amount of prediction error, and the Mackintosh model, which highlights selective attention to predictive stimuli). These models collectively establish a theoretical framework for interpreting the behavioural outputs of sleep-dependent learning as indirect markers to examine whether sleep facilitates the transfer of learning beyond task-specific improvement.

Chapter 2 focuses on the backward masking task, a classic paradigm used to investigate the sleep-dependent components of online and offline perceptual learning. The chapter is informed by research indicating that online perceptual learning is significantly unique to the learnt visual features, spatial location, and task (Ahissar & Hochstein, 1997; Crist et al., 1997; Karni & Sagi, 1991), potentially constraining the ability to adapt. Psychobiological theories, on the other hand, suggest that sleep helps learning by restructuring traces of memory (Gais et al., 2000). Chapter 2, therefore, explores how sleep contributes to the generalisation in the backward masking task beyond the specificity typically observed during wakefulness. The study aims to determine if sleep changes the way the brain stores information to help transfer perceptual skills by comparing online learning while awake with offline consolidation while sleeping.

Chapter 3 extends this rationale to examines the impact of sleep on selective attention. Posner and Peterson (1990) in their review mentioned that attentional control serves as an essential for identifying relevant from irrelevant information, however, the role of sleep in the consolidation of attentional information remains largely unexplored. Previous studies in the perceptual learning literature have shown that sleep enhances performance on challenging visual tasks (Albouy et al., 2013; Mednick et al., 2003a), which raises questions about whether attentional improvements post-sleep signify a generalisation of fundamental control processes or if they are limited to specific tasks. Chapter 3 investigates this by contrasting attentional enhancements following sleep and wakefulness, and by evaluating whether the mechanisms align with or differ from those identified in backward masking.

In conclusion, this thesis delves into the capacity of how one continuously learns and evolves, by connecting behavioural theories of perceptual and attentional learning with psychobiological models of memory consolidation. This thesis seeks to improve theoretical comprehension and practical applications for enhancing learning and cognitive performance by examining the role of sleep in facilitating generalisation across perceptual and attentional domains.

CHAPTER 2:

Balancing Specificity and Generalisation in Learning: The Critical Role of Sleep and Wakefulness

2.1. Abstract

Learning a visual task can lead to significant improvements in visual performance, a phenomenon known as visual perceptual learning (VPL). Notably, these improvements emerge not only during the "online" phase—when individuals are actively engaged in training—but also during the "offline" phase, particularly during sleep, which is when the consolidation processes occur. Although increasing evidence shows the importance of both phases, the processes by which wake, and sleep interact to balance the generalisability against specificity in VPL remain unknown.

This chapter demonstrated how sleep and wakefulness operate in conjunction to modify the characteristics of perceptual learning. Due to localised neuronal plasticity and specificity, visual enhancements during wakefulness were limited to the precise visual elements and spatial locations used during learning. Sleep, on the other hand, supported the abstraction and redistribution of the effects of learning by enabling learning to generalise to untrained visual features and visual field locations.

The findings lead to a dynamic framework where sleep encourages the integration and adaptability of learnt skills across larger domains, while waking refines task-specific representations to maximise accuracy. These procedures work together to support visual learning's consolidation and flexibility. Understanding plasticity based on experience and creating focused therapies to improve perceptual learning in clinical and practical contexts are both significantly impacted by this chapter.

2.2. Introduction

Visual signals are fundamental to our interaction with the external environment, enabling us to perform a wide range of tasks essential for survival and thriving, which include regulating circadian rhythm, navigating through complex surroundings, identifying objects, and understanding social signs. Visual perceptual learning (VPL), the process of improving visual skills through training, shows how flexible and able the brain is to handle new information (Ahissar & Hochstein, 1997; Seitz & Watanabe, 2005). VPL corresponds to the improvement of an individual's capacity to recognise, analyse, and comprehend visual stimuli due to repeated practice or experience (Dosher & Lu, 2017; Goldstone, 1998). Studies indicate that these enhancements occur not just during the "online" period, during which individuals actively interact with the visual stimuli, but also during the "offline" phase, especially during sleep (Mednick et al., 2003b; Stickgold et al., 2000). The precise processes via which online and offline learning stages influence the specificity and generalisation of acquired visual tasks are not well understood.

This chapter aims to examine how wakefulness and sleep differentially affect visual perceptual learning. The hypothesis is that the online and offline learning stages in VPL fulfil complementary functions, including discrete but interrelated neural mechanisms that improve task-specific performance and generalisation. During the online phase, marked by active interaction with certain visual stimuli, it is expected to enhance localised neuronal plasticity in the visual cortices, resulting in focused performance enhancements (Chen et al., 2016; Fiorentini & Berardi, 1980). On the other hand, in the offline phase which mainly occurs during sleep time, it is believed to support widespread balancing of synaptic connections, which can enhance the benefits of localised learning by extending it to a broader range of perceptual skills across various visual fields (Buffalo et al., 2006; Tononi & Cirelli, 2006).

During the online phase, neurons in the visual cortices show stimulus selectivity during awake, in which individual neurons react to a restricted set of visual properties and a limited range of locations in the visual field (Hubel & Wiesel, 1968; Kamitani & Tong, 2005). Neurons located in regions such as the primary visual cortex (V1) and higher-order areas like V4 show selective responses to specific visual inputs. For example, in previous studies, V1 are found to be precisely calibrated to specific orientations and spatial positions, preferentially reacting to visual stimuli that align with their favourite characteristics (Hubel & Wiesel, 1968; A. Schoups et al., 2001). Hubel and Wiesel's pioneering study on the striate cortex of non-human primates demonstrated that neurons in V1 region exhibit notable selectivity for visual characteristics, including orientation, spatial frequency, and motion direction. They show that V1 is structured into orientation and ocular dominance columns, with distinct layers dedicated to processing from simple to complex visual stimuli. This study provides valuable insights into how the brain processes visual information and responds to specific frequencies. This helps us understand how neural circuits change during VPL. In addition, their findings regarding hierarchical and columnar organisations remain important in contemporary neuroscience, providing a framework to investigate how experience-dependent plasticity enhances neural pathways during VPL and facilitates learning specificity.

Building on this foundation, Jehee et al. (2012) examined how perceptual learning influences specific neural responses, particularly in the representation of orientation. Their study showed that PL improves the specificity of orientation representations in early visual regions, including V1. Using functional magnetic resonance imaging (fMRI), they found that learning to distinguish subtle orientation variations especially improves neural tuning for the acquired orientation. This result aligns with Hubel and Wiesel's findings, as it corroborates the notion that V1 neurons are both specialised and capable of refinement through learning. Their results showed that training improves the brain's ability to detect small changes in orientation differences, which supports the idea that selectivity is what enables task-specific improvements. This research indicates that VPL changes established cortical mechanisms via localised synaptic modifications, thereby strengthening circuits immediately associated with the learned feature.

While the brain is connected to and responsive to sensory inputs during wakefulness, in contrast, sleep is characterised by a sensory disconnection between the brain and the environment (Türker et al., 2023), which promotes the reorganisation and integration of newly learnt perceptual abilities into global neural networks, equilibrating neuronal excitability and connection throughout the brain (Tononi & Cirelli, 2006). This offline phrase is unique for facilitating larger generalisation of learning via homeostatic plasticity, which serves as a stabiliser of neural networks in the brain (G. Wang et al., 2011). For instance, sleep may decrease differences in excitability between neurones that are activated frequently and those that are not, thereby helping the transfer of skills to new locations or stimuli (Salehinejad et al., 2022). This approach is crucial for reinforcing learning beyond the attributes acquired during the online phase.

As indicated across a variety of domains of perceptual and motor tasks, extensive research supports the vital function that sleep plays in enhancing brain plasticity and consolidating learning processes (Karni & Sagi, 1991; Mednick et al., 2003; Stickgold et al., 2000; Yotsumoto et al., 2008). Sleep enhances neuronal and behavioural indicators of memory consolidation across different paradigms, notably in visual (Censor et al., 2006; Pourtois et al., 2008) and motor learning (Makino et al., 2017; Vyas et al., 2018). For instance, Censor et al. (2016) conducted particularly noteworthy research, as it shed light on the connection between the degree of learner adaptability and the efficiency of sleep-dependent consolidation. According to their findings, the number of learning trials completed during the learning phase had a substantial impact on both the execution of the task and the success of subsequent learning. In particular, it was demonstrated that the optimal number of repetitions enhanced learning and discrimination, whereas excessive trials had the opposite effect, most likely due to adaptation-induced saturation. However, the study did not explicitly report the correct number of trials. Further, Censor et al. hypothesised that the optimal amount of sleep consolidation occurs when the brain reaches an adaptable state during learning sessions. This condition reflects the integration of newly acquired information. This study suggests that the extent to which sleep helps consolidate memories is determined by the degree to which neuronal circuits are plastic during the learning period. At the same time, these results highlight the interaction between active engagement during training and the restorative effect of sleep; they also give vital insights into a more comprehensive understanding of brain adaptation during learning.

There is a continuous interest in the role of sleep in perceptual learning, in particular, the relationship to memory consolidation and neural plasticity (MacDonald & Cote, 2021; Stickgold et al., 2000). Sleep seems to dynamically influence the neuronal mechanisms associated with perceptual learning by promoting adaptability, reorganising brain connections, and enhancing perceptual and discriminative capabilities over time (Capone et al., 2019; Reis et al., 2023). Tasks such as the backward masking task provide a solid foundation for examining these processes. The backward masking requires participants to recognise a fixing letter and determine the orientation of the target array presented in a designated visual field position (horizontal or vertical alignment). This task has emerged as a well-recognised instrument for examining VPL and clarifying the brain processes linked to learning (Karni & Sagi, 1991; Ofen et al., 2007).

Studies have shown that performance, in backward masking significantly gets better after a night's sleep, especially right after learning (Gais et al., 2000; Karni, 1995; Matarazzo et al., 2008). These improvements persist over time, suggesting that sleep plays a role in solidifying learning and enabling long lasting changes in brain structure. However, these enhancements mostly apply in situations and are limited to the characteristics and location of the trained stimulus (Crist et al., 1997; Karni & Sagi, 1991; Poggio et al., 1992; Yotsumoto et al., 2009). The specificity of these impacts aligns with findings from studies conducted in areas like V1, known for the precise tuning to orientation and spatial positioning (Bang et al., 2014; Hua et al., 2010). However, there are still questions concerning the circumstances that lead to generalisation. Certain studies indicate that transfer between retinal sites is constrained (Yotsumoto et al., 2009) although others have identified partial generalisation when stimuli possess shared characteristics (J.-Y. Zhang et al., 2008). Whether learnt perceptual skills can be reliably transferred to new stimuli or locations and the brain mechanisms involved in facilitating this transfer remains as an open question.

Studying brain activity through Electroencephalogram (EEG) helps provide further insight into the mechanisms behind perceptual learning by examining the brains functions. For instance, research has demonstrated that training, with a backward masking task such as the Texture Discrimination Task (TDT) can alter both processing areas such as C1 and later stages, like P3 (Ahmadi et al., 2018; Dove et al., 2000). The changes found highlight the fact that perceptual learning includes both initial and further processing phases in the brain. However, difficulties persist in understanding how these hierarchical processes interact during sleep, which encourages this generalisation. In addition, research have reported that early cortical regions like V1 and mid-level regions like V4 are important for perceptual learning effects (Kosai et al., 2014; Raiguel et al., 2006), but less is known about how higher-order regions, including the prefrontal cortex, facilitate learning, particularly in enhancing generalisation (Kwon et al., 2015; Rahnev et al., 2011).

Several studies have investigated the potential for perceptual learning to generalise beyond the training stimulus. Dosher et al. (2013) and Mastropasqua et al. (2015) showed that generalisation can occur in some situations, notably when there is considerable similarity between learnt and unlearnt stimuli. This implies that transfer effects may need the engagement of superior cortical areas accountable for attentional regulation and the execution of intricate task requirements. More research is needed to figure out how sleep-dependent mechanisms interact with these top-down processes, and whether they use the same or different brain processes as those that help with task-specific learning.

Studies using magnetic resonance imaging (MRI) have further improved our knowledge of how sleep affects perceptual learning by allowing non-invasive tracking and evaluation of structural and functional alterations in the brain. For instance, Tamaki et al. (2013) used fMRI to investigate brain activity after sleep in the backward masking TDT tasks. The finding shows that sleep following learning resulted in increased activity within the cortex, which is intimately involved in visual processing. According to these findings, sleep may help reinforce what was learned about perception by increasing brain activity in areas related to the task at hand, thereby improving the neural pathways that facilitate the task. In a similar vein, Yotsumoto et al. (2008) distinguished two stages of PL: a first period marked by increased brain activity in V1 (visual region), which corresponds to the taught region, and a second phase where activation declines but performance gains continue. The evidence suggests that training leads to an increase in synaptic connections or their strength within the local network in V1, which enhances performance. However, after this initial phase, the activation increases in V1 disappeared, while the performance enhancement was still maintained. Ditye et al. (2013) research investigated whether changes in brain structure could predict the extent of improvement following perceptual learning. They found that following training, GM volume in the posterior superior temporal sulcus increased and that the degree of changes will predict task improvement. Based on the given findings, perceptual learning involves both neuronal circuits strengthening as well as improvement, highlighting the idea that perceptual learning involves distinct neural processes that occur over time.

Previous research has laid the groundwork for our understanding, but it also has the potential to fail in capturing the complexities of the most recent developments in neuroscience. Therefore, while sleep has been recognised as essential for consolidating learning on specific tasks and facilitating transfer to untrained tasks, its impact on generalised learning remains largely unknown. Therefore, further research is needed to explore whether sleep promotes or limits generalisation and to identify the specific features of generalisation that can be attained. In fact, examining the question can help scientists gain a deeper understanding of how neuroplasticity works and how memory systems function in general, making an important contribution to the field of cognitive neuroscience.

This chapter primarily aims to investigate the role of wakefulness and sleep in shaping the specificity and generalisability of VPL. While learning a visual task often leads to significant improvement in overall performance, as mentioned above, the mechanisms through which these enhancements become either narrowly task-specific or generalisable across conditions remain unclear within the literature. Whether benefits obtained through learning specific visual features, spatial locations, or tasks can transfer to untrained situations, and whether such generalisation is mostly supported during wakefulness or sleep, is a fundamental discussion in this chapter. Generalisation is a fundamental aspect of perceptual learning, as it is linked to the capacity to transfer learnt skills to novel tasks, environments, or elements. This chapter assessed whether the enhancement in visual performance gained from learning specific features, spatial locations, or tasks may extend to untrained features, locations, or tasks. The study also further examined whether this generalisation occurred mainly during wake or sleep.

The main hypothesis of this Chapter is that generalisation in learning is contingent upon certain qualities and situations, with sleep acting as a crucial facilitator of this process. It also examined whether this generalisation usually took place during awareness or sleep. By balancing this specificity and generalisation, the sleep-wake cycle ensures both the accuracy in visual processing and adaptability in the task that was learned. This study also aims to gain a deeper understanding of how perceptual learning develops from task-specific improvements to more general abilities by evaluating these characteristics.

This Chapter, therefore, explores the distinction between two stages of learning: online learning takes place when one is actively engaged in a task, while offline learning occurs during periods of rest or sleep when one is inactive. Shifting from processing to consolidation and generalisation during sleep poses challenges, in understanding these transitions can enhance our knowledge on how procedural learning operates. How sleep impacts generalisation processes. This thorough strategy provides perspectives on how alertness and sleep influence effective and adaptable learning methods.

2.3. Methods

2.3.1. General Design

Two sub-studies (Experiment 1 and Experiment 2) was conducted to examine whether improvements in visual performance could generalise across visual field locations, visual features, or visual tasks, and whether this generalisation occurred during wakefulness or sleep. Specifically, the experiments tested whether improvements from the trained visual field location (lower-left visual field), visual feature (orientation in Experiment 1, luminance in Experiment 2), and visual task (backward masking) would generalise to the untrained visual field location (upper-right visual field), visual feature (luminance in Experiment 1, orientation in Experiment 2), and visual tasks (orientation discrimination, luminance discrimination, temporal discrimination).

To minimise overlap between the groups of visual cortical neurons activated by the trained and untrained visual field locations, our experiment selected the lower-left and upper-right visual fields as the trained and untrained locations, respectively. Similarly, to minimise overlap between the groups of neurons activated by the trained and untrained visual features, orientation (a spatial feature) and luminance (a non-spatial feature) was chosen in this senario. To ensure that the trained and untrained tasks activated similar groups of visual cortical neurons but distinct groups of prefrontal cortical neurons, the tasks were designed to involve the exact visual field locations and visual features, but different task rules.

A well-established backward masking perceptual learning task were used in this current study (Berard et al., 2015; Harris & Sagi, 2018; Karni & Sagi, 1991; Kondat et al., 2023). A target stimulus - a nineteen-by-nineteen array of lines-was briefly presented for 10 ms, followed by a blank interval, and then a mask stimulus—a nineteen-by-nineteen array of randomly rotated crosses—was presented for 100 ms (Figure 1.1a and Figure 1.1b). The stimuli were displayed on a black background. Each cell in the nineteen-by-nineteen array measured 0.77 × 0.77 visual degrees; the line (length: 0.42 visual degrees) or the cross (size: 0.42 × 0.42 visual degrees) appeared at a random location within the cell but was constrained to be at least 0.09 visual degrees from the cell’s edge.

Within the target stimulus, three adjacent lines differed from the rest lines in either orientation (Experiment 1) or luminance (Experiment 2). Participants were instructed to identify these distinct lines and report whether they were vertically or horizontally aligned. The orientation or luminance difference between the three distinct lines and the rest lines remained constant across trials and was set well above the discrimination threshold to ensure participants could achieve 100% accuracy when the target stimulus was not followed by the mask. By contrast, the duration of the blank interval—that is, the interstimulus interval between the offset of the target stimulus and the onset of the mask—varied across trials according to a two-up-one-down staircase procedure to maintain task difficulty at each participant’s threshold level (Cornsweet, 1962; Levitt, 1971; P. Zhang et al., 2019). Two consecutive correct responds reduced the ISI by 7 ms, but one incorrect response increased ISI by 7 ms. This method targets the ISI time at which participants get 70.7% accuracy, facilitating effective threshold estimate without exposing stimuli much above or below the participant's threshold.

The learning process thus focused on improving the ability to extract task-relevant signals from the target stimulus before visual processing was disrupted by the mask, rather than enhancing sensitivity to subtle differences in orientation or luminance. In this sense, the trained task (backward masking) differed fundamentally from the untrained tasks (orientation, luminance, or temporal discrimination), which required participants to detect subtle differences in these features without interference from the mask. This design ensured that the trained and untrained tasks activated similar groups of visual cortical neurons but distinct groups of prefrontal cortical neurons, allowing us to disentangle the contributions of stimulus-related and task-related neural circuits to VPL.

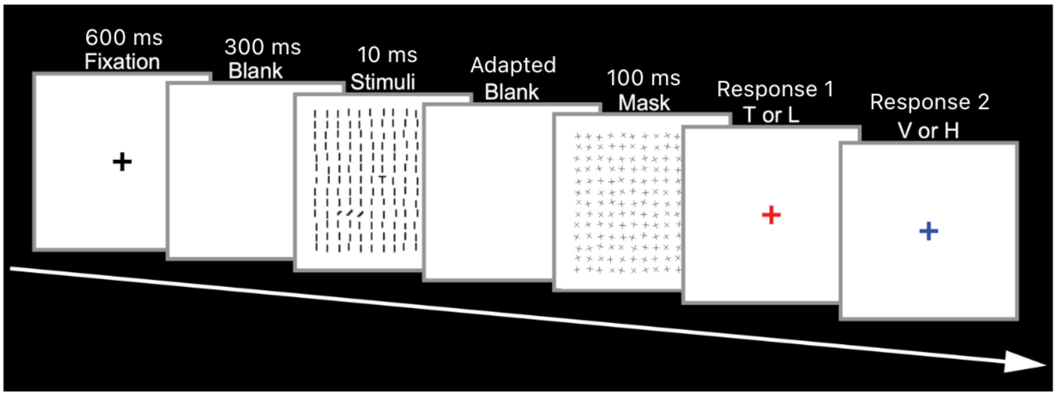

Figure 1.1a Trial structure for the Backward Masking Orientation Task. Each trial started with a fixation cross shown for 600 ms, then by a blank gap of 300 ms. The textural stimulus, including diagonal lines with a target characteristic (horizontal or vertical alignment), was shown for 10 ms. Following a modified blank period, a 100 ms mask was shown. Participants first reacted to the centre letter ("T" or "L") and then to the direction of the target lines (vertical or horizontal). This approach regulated fixation and ensured task involvement with both central and peripheral visual inputs.

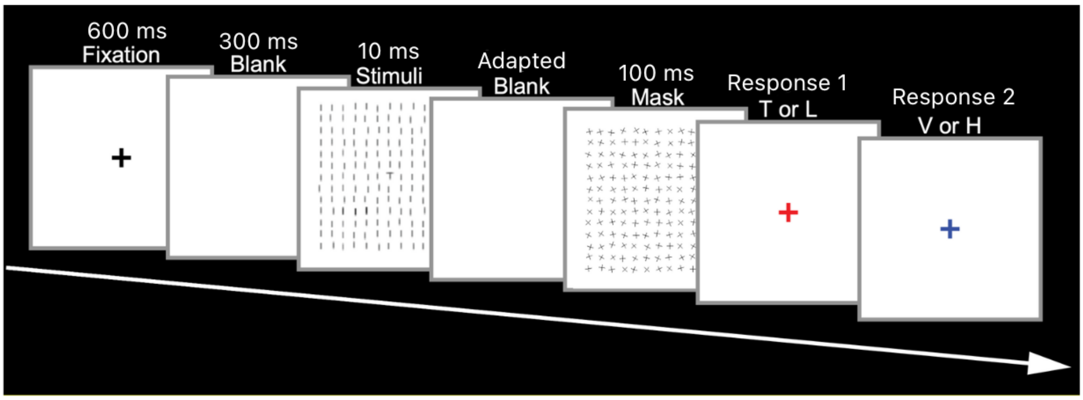

Figure 1.1b Trial structure for Backward Masking with a luminance difference in the lower-left (LL) visual field quadrant. This task element was not included in the core learning task but was included as an untrained task to assess the generalisation of perceptual learning. Participants first indicated the centre letter ("T" or "L") and then determined the direction of the target lines (vertical or horizontal). The trial sequence facilitated controlled fixation and task involvement while examining generalisation effects.

The learning session involved a backward masking task, focusing on either orientation (Experiment 1) or luminance (Experiment 2) in the lower-left visual field. Each test session included ten tasks:

- Task A: backward masking of orientation in the lower-left visual field
- Task B: backward masking of orientation in the upper-right visual field
- Task C: backward masking of luminance in the lower-left visual field
- Task D: backward masking of luminance in the upper-right visual field
- Task E: orientation discrimination in the lower-left visual field
- Task F: orientation discrimination in the upper-right visual field
- Task G: luminance discrimination in the lower-left visual field
- Task H: luminance discrimination in the upper-right visual field
- Task I: temporal discrimination in the lower-left visual field
- Task J: temporal discrimination in the upper-right visual field

Among these tasks, tasks A and C were identical to those used in the learning sessions of sub-study one and sub-study two, respectively. The remaining tasks differed from the learning session tasks in visual field location, visual feature, or task rule. Including tasks, A and C in the test sessions allowed us to assess local improvements in visual performance, while including the other tasks enabled us to evaluate generalised improvements. Performance in 10 tasks were assessed during five test sessions to determine whether learning improvements are specific to the trained settings or generalisable to other scenarios as well. Additionally, the morning and evening groups was compared to distinguish between the effects of the sleep-wake cycle and the passage of time and explored whether these advancements occur during wakefulness or sleep. The main idea is that sleep helps learning to transfer across features or tasks that were not previously practised, but when awake, learning focuses solely on what was learned, like visual aspects and locations. It is expected that although sleep encourages generalisation to untrained settings, improvements during wakefulness will be limited to trained conditions, thereby emphasising the complementary functions of wakefulness and sleep in balancing learning specificity and adaptability.

The independent variable (IV) was manipulated on two levels: the time of day when participants learned the backward masking task (morning or evening) for both experiments. Thus, the time that participants were retested was also manipulated. The dependent variables (DV) measured in this study were the discrimination threshold for individual participants to identify which aspects of learning can be generalised.

A conventional sleep study approach (Figure 1.2) was used to examine the roles of online learning, offline wakefulness, and sleep in VPL. The morning and evening groups adhered to an identical testing protocol and completed four test sessions: (I) a baseline test conducted immediately before the learning session, (II) a test conducted immediately after the learning session (0-hour), (III) a test conducted twelve hours after the learning session, (IV) test conducted twenty-four hours after the learning session. This strategy enabled direct comparisons between morning and evening cohorts to mitigate circadian influences and differentiate the impacts of awake and sleep on the specificity and generalisation of learning. Overall, participants committed approximately 5 hours across three experimental sessions.

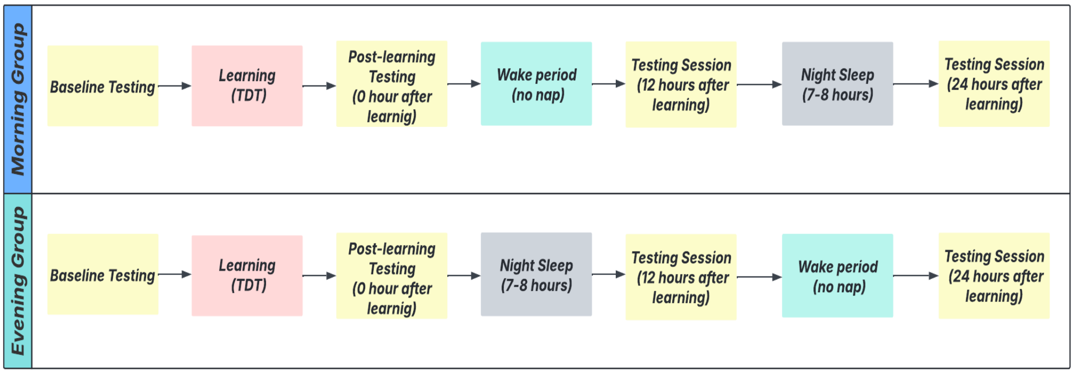

Figure 1.2 Experimental timeline demonstrating the protocol for the morning and evening groups. The morning group completed baseline testing, a learning session, and post-learning testing (0-hour), followed by 12-hour wake and 24-hour post-sleep testing. The evening group completed the same timeline in reverse, beginning with a night of sleep before the 12-hour wake period. This design outlines the effects of sleep and wakefulness on learning and generalisation.

2.4. Experiment 1: Materials and Methods

2.4.1. Participants

Thirty-two healthy volunteers with normal or corrected-to-normal vision, consistent bed and rise times, 7~8 hours of sleep per night, no history of sleep, medical, or psychiatric disorders, no daytime nap habit, and no excessive daytime sleepiness, were recruited to participate in the study. All participants provided written informed consent and were compensated for their time with either 24 course credits or £30. The study received approval from the research ethics committee at Cardiff University (EC.18.02.13.5226G). Participants were instructed to maintain their regular sleep patterns and refrain from consuming alcohol or caffeinated beverages from two weeks prior to the study's commencement until its conclusion. They received actigraphy wristwatches and sleep diaries to document their sleep-wake patterns. Two participants withdrew from the study and were excluded from the data analysis. Among the remaining participants, thirty (mean age = 21.17, SD = 2.55) took part in the experiment, fifteen in the morning group and fifteen in the evening group. The group assignments were randomised.

2.4.2. Experimental Procedures

The testing tasks included a backward masking orientation and luminance task, orientation discrimination, luminance-contrast discrimination, and flicker-fusion temporal discrimination. Each task was executed in both the trained (LL) and untrained (UR) visual field locations, enabling a comprehensive investigation of learning transfer across features, spatial locations, and tasks. All sessions took place in a dark experimental room, where stimuli were displayed on a high-resolution monitor (ASUS VG248QE, 1920 × 1080 pixels; refresh rate: 100 Hz for discrimination tasks, 144 Hz for flicker-fusion tests) with a viewing distance of 61.5 cm and a screen size of 54.3cm. Eye fixation was observed using an EyeLink 1000 Plus eye tracker, while stimulus presentation and data acquisition were conducted using MATLAB (MathWorks Inc., Natick, MA, USA) in conjunction with Psychtoolbox (Brainard, 1997).

2.4.3. Backward Masking Task

Both forms of backward masking tasks require participants to detect three diagonally aligned target lines arranged in either a horizontal or vertical arrangement inside a textured stimulus. In the target stimulus, three adjacent lines, located in the lower-left visual field (tasks A and C) or upper-right visual field (tasks B and D), differed from the other lines in either orientation (tasks A and B) or luminance (tasks C and D). Specifically,

- In tasks A and B, the three distinct lines were tilted at 45 degrees, while the other lines were either all vertical or all horizontal. All lines were displayed at the monitor's maximum luminance.

- In tasks C and D, the three distinct lines were displayed at the monitor's maximum luminance, while the other lines were shown at 40% of the maximum luminance. All lines were either vertical or horizontal.

- In tasks A and C, the three distinct lines were located at an eccentricity of 5.45 visual degrees and a polar angle of 225 degrees.

- In tasks B and D, the three distinct lines were located at an eccentricity of 5.45 visual degrees and a polar angle of 45 degrees.

To ensure central fixation, a randomly rotating letter "T" or "L" was shown at the centre of the display during each trial, rotated by 0, 90, 180, or 270 degrees (Figure 1.3). Participants were first given the task of identifying the centre letter (T or L), which can be presented in different rotations, and then reporting the direction of the target lines (vertical or horizontal) via an assigned set of buttons on a response box.

<table>
<tr><th colspan="8">Answer1: whether the central fixation letter is T or L</th></tr>
<tr><td>Sample 1</td><td>Sample 2</td><td>Sample 3</td><td>Sample 4</td><td>Sample 5</td><td>Sample 6</td><td>Sample 7</td><td>Sample 8</td></tr>
<tr><td>⊤</td><td>⊥</td><td>⊢</td><td>⊣</td><td>└</td><td>┌</td><td>┘</td><td>┐</td></tr>
<tr><td colspan="4">left key (left hand keyboard)</td><td colspan="4">right key (left hand keyboard)</td></tr>
</table>

Figure 1.3. Example of the central fixation task used to ensure visual focus during the experiment. The central letter (either "T" or "L") was displayed at the centre of the screen and rotated. Participants were instructed to identify the letter at the centre and respond using the designated keys on the keyboard (left key for "T" and right key for "L"). The task aimed to maintain fixation and attention while subsequently reporting the arrangement of the target lines.

Participants were instructed to maintain fixation on the centre of the screen and to identify the three distinct lines before the mask stimulus disrupted visual processing of the target stimulus. After the offset of the mask stimulus, participants made two unspeeded forced-choice responses: first, they reported the identity of the fixation letter using the left-hand keypad (left key: T; right key: L), and second, they reported the alignment of the three distinct lines using the right-hand keypad (left key: vertical alignment; right key: horizontal alignment).

The blank interval (i.e., the interstimulus interval between the offset of the target stimulus and the onset of the mask stimulus) was the variable of interest. During both the training and test sessions, the timing was adjusted using a staircase method, where after every two consecutive correct trials, the interval decreased by one step. Conversely, one incorrect trial caused an increase by one step, starting at

250 ms with a 10 ms increment. A trial was classified as correct only if both the first response (fixation letter identity: T or L) and the second response (alignment of the three distinct lines: vertical or horizontal) were correct. The training session consisted of 576 trials, with breaks taken after every 96 trials. The test session included 96 trials and measured the threshold interstimulus interval at which accuracy converged to 70.7%. To assess learning effects, thresholds was compared across five test sessions (I~IV). A smaller threshold suggested a greater ability for extracting task-relevant information from the target stimulus prior to visual processing being disturbed by the mask.

2.4.4. Pure Discrimination Tasks

In addition to the backward masking task, each participant also completed a series of basic discrimination tasks. Which comprise of the following tasks:

(i) Orientation discrimination

Eight cardinally sinusoidal gratings are arranged in a circle around a central fixation cross within this discrimination task. The ISI remained 500 ms, and then another circular array of eight gratings was presented for 300 ms (Figure 2.1a). The gratings were displayed on a gray background at 50% of the monitor's maximum luminance. Each grating had a radius of 2.28 degrees and a spatial frequency of 2.2 cycles per degree. The eight gratings were positioned at an eccentricity of 5.45 visual degrees and polar angles of 0, 45, 90, 135, 180, 225, 270, and 315 degrees, respectively. The eight gratings were the same at one of the two presentation periods. One of the eight gratings in the other presentation was slightly different in orientation from the others. Participants were asked to determine which presentation included the pop-out grating for each trial (first or second presentation). There were two visual quadrants where the pop-out grating was kept in place (LL or UR). Using the standard 2-up-1-down staircase, the orientation difference between the pop-out grating and the other gratings was changed in order to determine the discriminating, the staircase began with an orientation difference of 8.5 degrees and had a step size of 0.5 degrees. Each task concluded after 31 staircase reversals (~100 trials), measuring the discrimination threshold at which accuracy converged to 70.7%. The purpose of this work is to evaluate the generalisability of learning lower-level visual characteristics from the backward masking task to the same low-level features in this task, as well as across other visual locations.

(ii) Contrast discrimination

This was a similar visual discrimination as to the orientation discrimination task. In this task, the pop-out grating differed from the other grating in terms of its contrast (Figure 2.1b). The pop-out grating was also maintained at two visual quadrants (LL or UR). The staircase for this task started with a luminance contrast difference of 34% and had a step size of 2%. This task was included in the study to assess the contrast features within the backward masking luminance task to maintain consistency. Each task concluded after 31 staircase reversals (~100 trials) of measuring discrimination threshold.

(iii) Temporal discrimination

The temporal task that was used in this study was commonly referred to as 'flicker fusion.' This task consists of a white circle displayed at a particular location (LL or UR) around a fixation cross. In each trial, a white circle was present once (one flash) or twice (two flashes). Participant would respond using a keypad whether they saw one or two white circles (Figure 2.1c). The circle had a radius of 1.61 visual degrees and a luminance set to 50% of the monitor's maximum. It was displayed on a black background at an eccentricity of 5.45 visual degrees and a polar angle of 225 degrees (LL visual field) or 45 degrees (UR visual field). The blank interval was the variable of interest. When the interval was long, participants could perceive it and thus recognised the two sequentially presented circles as temporally separate. When the interval was short, they could not perceive it and instead viewed the two circles as a single presentation (Brainard, 1997).

The standard 2-up-1-down staircase method was used to vary the ISI of the two-circle trial in order to determine the discriminating threshold that was reached when the accuracy settled to 70.7% correct. The staircase began with an interval of 70 ms and had a step size of 7 ms. Each session concluded after 31 staircase reversals (~100 trials), This task was used to assess whether the temporal need in the learned backward masking task may be generalised to the temporal need of a novel task.

Sample 1	Sample 2
First Presentation  Second Presentation 	First Presentation  Second Presentation 
Left Key (Right Hand Keyboard)	Right Key (Right Hand Keyboard)

Figure 2.1a. An array of gratings will appear twice on the screen. In one presentation all gratings will be identical. In the other presentation, one of the gratings will differ from the other gratings. [Left] Sample 1 shows pop-out grating (orientation difference) is presented in the first presentation in the LL quadrant. [Right] Sample 2 shows pop-out grating (orientation difference) is presented in the second presentation in the LL quadrant.

Sample 1	Sample 2
First Presentation  Second Presentation 	First Presentation  Second Presentation 
Left Key (Right Hand Keyboard)	Right Key (Right Hand Keyboard)

Figure 2.1b. An array of gratings will appear twice on the screen. In one presentation all gratings will be identical. In the other presentation, one of the gratings will differ from the other gratings. [Left] Sample 1 shows pop-out grating (contrast difference) is presented in the first presentation in the LL quadrant. [Right] Sample 2 shows pop-out grating (contrast difference) is presented in the second presentation in the LL quadrant.

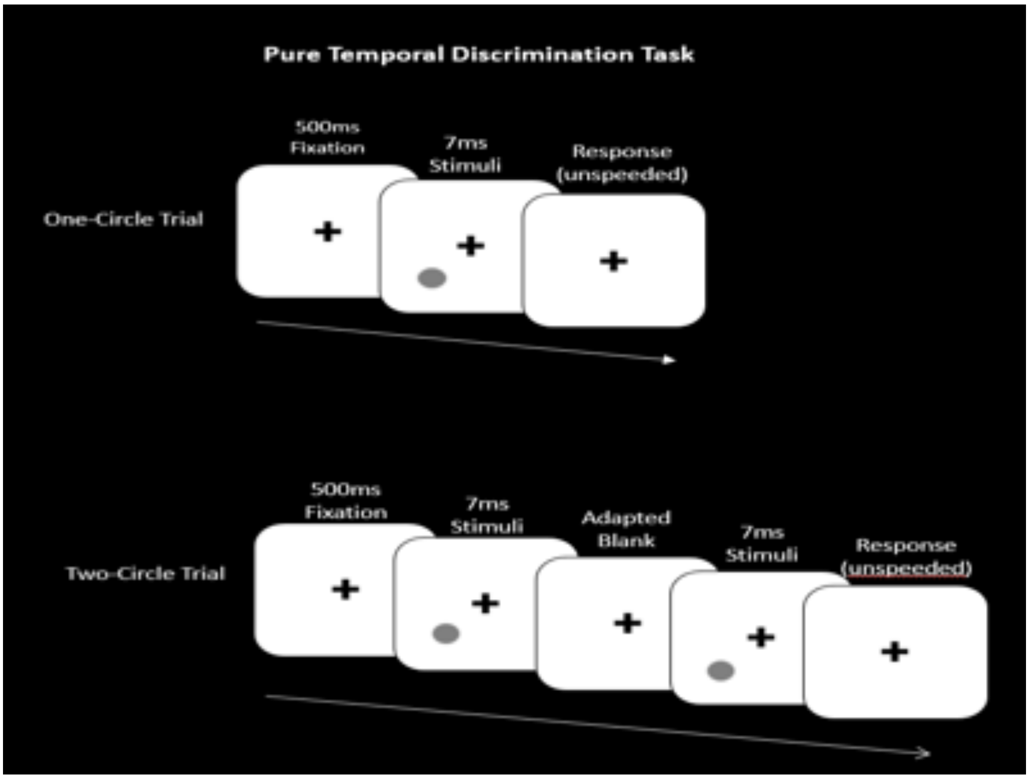

Figure 2.1c. Temporal discrimination (flicker fusion) task showing the possible one-circle and two-circle flashes that will appear on the screen. The stimuli will appear at different location on the screen (LL or UR).

The pure discrimination tasks used in this current study were modified from established psychophysical paradigms used to evaluate low-level visual sensitivity, including orientation discrimination (Edden et al., 2009; Mikhailova & Gerasimenko, 2023), contrast discrimination (Campbell & Green, 1965; Foley & Legge, 1981), and temporal flicker fusion paradigms (Dzn, 1958). The specific design of the stimuli (e.g., the number of gratings, eccentricity) varied slightly from that of prior experiments. However, the fundamental perceptual processes remained unchanged, which is to identify minor differences in orientation, contrast, or temporal intervals. These changes were made to make sure that the location in space and temporal parameters were the same for all activities, especially the backward masking paradigm, while still following the basic rules of psychophysics.

2.4.5. Data Pre-processing and Statistical Analysis

Using the discriminating threshold as the main dependent variable in this study, rather than other metrics such as reaction time, was a key methodological decision. In contrast to other measures that may be influenced by unrelated cognitive or motor processes, the discrimination threshold provides a clear and measurable indicator of perceptual sensitivity (B. A. Dosher & Lu, 1999; Gold et al., 1999). Discrimination thresholds are fundamentally linked to perception and learning, which can avoid artificially high or low responses in response to task difficulty, or reaction speed, which can be impacted by strategic changes in response selection (Levi et al., 1994)

To ensure that task difficulty remained adaptive and performance-sensitive, a staircase method was designed and employed to identify the perceptual limit of stimulus discrimination. The ISI between the stimuli was interactively adjusted employing a two-down, one-up staircase method, which targets the 70.7% accurate response threshold (Levitt, 1971). The staircase ISI will decrease after two successive correct responses and increase after an incorrect response. A reversal occurs when the direction of ISI adjustment changes (e.g., from decreasing to increasing or vice versa). The overall threshold was calculated as the average ISI of the final six reversals, as a previous study shows that focusing on later reversals rather than the full trial provides a more accurate and stable threshold estimate (García-Pérez, 1998; Levitt, 1971).

The difference between the mean discrimination thresholds at baseline and at later test sessions was used to assess how much learning-related progress was present. It is important to note that baseline values were calculated from the whole baseline block. This method is in line with how perceptual learning research is usually done, where performance gains are usually measured by differences in thresholds between complete baseline and post-training sessions instead of partial segments (Ahissar & Hochstein, 1997; Crist et al., 1997; Karni & Sagi, 1993; Yotsumoto et al., 2008). This method decreases the impact of early-trial variation and confounds such as unexpected changes in attention, warm-up, or fatigue during a session (Fahle & Edelman, 1993).

Thresholds for the pure discrimination tasks were determined as the mean of the stimulus differences at which participants met a specified accuracy. The differences were determined by a comparable staircase method, whereby the difficulty level (e.g., orientation or contrast) was adaptively changed based on participant responses. In the flicker fusion test, perceptual thresholds were established as the mean duration between two flickering stimuli at which participants could no longer consistently differentiate distinct flashes, in line with standard methods employed to assess temporal resolution in visual processing.

Statistical analyses were performed to evaluate changes in perceptual thresholds at four time points: baseline (0 Hours), 12 Hours, and 24 hours. A repeated-measures analysis of variance (ANOVA) was used to assess within-subject changes, considering correlations among repeated measurements: effect sizes (η^2) were reported for ANOVA results, and intervals of confidence were included if applicable. All statistical analyses were performed using SPSS (IBM, Version 29.0.1.0), with an alpha level set at 0.05.

2.5. Experimental 1: Result

2.5.1. Demographic Data

Following the exclusion of two participants due to misunderstanding task instructions and withdrawal, the final sample comprised 15 participants in the morning group (mean age = 20.53, SD = 1.67) and 15 participants in the evening group (mean age = 21.86, SD = 3.09). Actigraphy recordings indicated that the two groups' sleep during the night lengths were similar. Participants in the morning group reported sleeping for an average of 6 hours and 57 minutes, and those in the evening group slept for an average of 7 hours and 15 minutes.

2.5.2. Assumption Checks

Shapiro–Wilk tests were applied, along with Q–Q graphs for each time point and group, to check whether the data follow a normal distribution. While specific parameters (e.g., backward masking thresholds at 24 hours) showed minor deviations from normality, group sizes were consistent, violations were not severe, and repeated-measures ANOVA is robust to moderate non-normality (Blanca et al., 2017; Field, 2024). Consequently, parametric analyses were considered suitable.

2.5.3. Overall Group × Time Effects

To analyse the differences in learning trajectories over time. A 2 (Group: Morning, Evening) × 4 (Time: Baseline, 0 hr, 12 hr, 24 hr) mixed-design ANOVAs were performed for the main outcome measures which was the backward masking tasks. Time was considered a within-subjects variable, while Group was regarded as a between-subjects variable. Partial η^2 has been established as the effect size, aligning with conventional methodology in repeated-measures designs. Mauchly's test was used to check the assumption of sphericity because the within-subjects component Time includes four levels. When the assumption of sphericity was violated, which was true in this case, Greenhouse–Geisser adjustments were used on the degrees of freedom to reduce increased Type I error rates.

For the learned backward masking orientation at lower left (LL) condition, there was a significant main effect of Time, $F(1.71, 47.96) = 215.40$, $p < .001$, indicating a significant decrease in thresholds across sessions. The Group × Time interaction was also significant, $F(1.71, 47.96) = 6.52$, $p = .005$, indicating different learning pathways among the groups. For the unlearned tasks, backward masking luminance LL showed a significant main effect of Time, $F(2.50, 70.06) = 111.93$, $p < .001$, and a significant Group × Time interaction, $F(2.50, 70.06) = 22.94$, $p < .001$. Similarly, for the backward masking orientation at upper right (UR), there was a significant main effect of Time, $F(2.37, 66.33) = 135.16$, $p < .001$, and a significant Group × Time interaction, $F(2.37, 66.33) = 24.63$, $p < .001$. Finally, for the backward masking luminance UR, there was a significant main effect of Time, $F(2.44, 68.26) = 146.82$, $p < .001$, and a significant Group × Time interaction, $F(2.44, 68.26) = 32.65$, $p < .001$.

For all the pure discrimination tasks, mixed ANOVAs revealed no significant Time effects or Group × Time interactions for any measure (Table 2.1).

Table 2.1

Results of Mixed ANOVAs Examining the Effects of Time and Time × Group Interactions Across All Variables, with the Backward Orientation LL as the learned task

Dependent Variable	Effect	df_1	df_2	F	p	η^2
Backward Masking Orientation LL (ms)	Time	1.71	47.96	215.40	< .001	.89
	Time × Group	1.71	47.96	6.52	.005	.19
Backward Masking Luminance at LL (ms)	Time	2.50	70.06	111.93	< .001	.80
	Time × Group	2.50	70.06	22.94	< .001	.45
Backward Masking Orientation at UR (ms)	Time	2.37	66.33	135.16	< .001	.83
	Time × Group	2.37	66.33	24.63	< .001	.47
Backward Masking Luminance at UR (ms)	Time	2.44	68.26	146.82	< .001	.84
	Time × Group	2.44	68.26	32.65	< .001	.54
Contrast Discrimination at LL (%)	Time	2.56	71.60	.99	.39	.03
	Time × Group	2.56	71.60	.50	.66	.02
Orientation Discrimination at LL (degree)	Time	2.32	64.92	.68	.53	.02
	Time × Group	2.32	64.92	.24	.82	.01
Flicker Fusion at LL (ms)	Time	2.06	57.64	.71	.50	.03
	Time × Group	2.06	57.64	.06	.94	.002

Contrast Discrimination at UR (%)	Time	2.55	71.33	1.70	.18	.06
	Time × Group	2.55	71.33	.036	.75	.01
Orientation Discrimination at UR (degree)	Time	2.35	65.79	.10	.93	.003
	Time × Group	2.35	65.79	.30	.78	.01
Flicker Fusion at UR (ms)	Time	2.54	71.18	2.20	.11	.07
	Time × Group	2.54	71.18	.80	.48	.03

Note. df_1 = numerator degrees of freedom (effect), df_2 = denominator degrees of freedom (error). Greenhouse–Geisser corrected values are reported where Mauchly's test indicated violations of sphericity.

2.5.4. Between-Group Comparisons

Follow-up from the mixed-ANOVA results, independent-samples t-tests were carried out to determine when the groups start to differ. This enabled us to identify if the Morning and Evening groups displayed differences at baseline and identify the specific time points at which group trajectories changed.

For the learned backward masking orientation LL task, there were no significant differences between groups at Baseline, $t(28) = 0.83$, $p = .413$, $d = 0.30$, or at 0 hr, $t(27.56) = -1.17$, $p = .254$, $d = -0.41$. A significant between-group difference was identified at 12 hr, $t(19.29) = 3.54$, $p = .002$, $d = 1.26$, with the evening group showing lower thresholds when compared to the morning group, which is in-line with the idea of sleep-dependent performance gain. No significant difference was observed at 24 hr, $t(23.87) = -0.57$, $p = .572$, $d = -0.20$.

For the that that was not learned, the backward masking luminance LL condition, groups did not show significant difference at Baseline, $t(28) = 0.04$, $p = .969$, $d = 0.01$, or at 0 hr, $t(27.20) = -0.18$, $p = .859$, $d = -0.06$. A large group difference was observed at 12 hr, $t(18.13) = 4.66$, $p < .001$, $d = 1.65$, again with the evening group demonstrating significantly lower thresholds. No significant difference was observed at 24 hr, $t(27.90) = -0.22$, $p = .829$, $d = -0.08$. Similar finding was found for the backward masking orientation UR condition, were there were no significant between-group differences at Baseline, $t(28) = 0.83$, $p = .413$, $d = 0.30$, or at 0 hr, $t(27.35) = 0.06$, $p = .950$, $d = 0.02$. At 12 hr, the evening group again outperformed the morning group, $t(15.56) = 5.73$, $p < .001$, $d = 2.04$, indicating a strong sleep-related advantage. No difference was found at 24 hr, $t(27.45) = -0.03$, $p = .976$, $d = -0.01$. Finally for the backward masking luminance UR condition, no significant differences were found at Baseline, $t(28) = 0.04$, $p = .969$, $d = 0.01$, or at 0 hr, $t(27.95) = -0.21$, $p = .834$, $d = -0.08$. Again at 12 hr, the evening group showed significantly lower thresholds, $t(19.32) = 4.71$, $p < .001$, $d = 1.67$. No differences were observed at 24 hr, $t(26.99) = 0.03$, $p = .975$, $d = 0.01$.

Independent-samples t-tests comparing Morning and Evening at each time point showed no significant difference for all conditions.

2.5.5. Improvement from Baseline to 24 Hours Post-Learning

The backward masking task was used to assessed participants' ability to distinguish between orientation and luminance changes at the LL and UR visual fields, where participants were trained on the backward masking orientation LL. The morning group showed a significant improvement over time based on the decrease in mean scores from baseline to 24 hours post-learning (Table 2.2a). For the morning group, the repeated measures of ANOVA highlighted a significant main effect of time, F (1, 14) = 170.42, $p < .001$, indicating that time explained 92.4% of the variance in performance. Similarly in the evening group, there was also a decrease in mean scores (Table 2.2b) with a significant main effect of time, F (1, 14) = 121.03, $p < .001$. These results indicate a robust improvement in the backward masking orientation (LL) learning over time for both groups.

Learning in the backward masking (orientation LL) task also transferred significantly to related tasks. Both the morning F (1, 14) = 171.96, $p < .001$ and evening group F (1, 14) = 98.91, $p < .001$ showed a significant transfer at the 24-hours re-test to the similar task with luminance difference at LL visual field. Similarly, for backward masking of luminance UR task also showed a significant improvement for both morning, F (1, 14) = 144.05, $p < .001$ and evening F (1, 14) = 121.91, $p < .001$ group. The other untrained task of the backward masking orientation task at the UR visual quadrant also showed significant improvement, with a statistically decreasing mean duration for both the morning (Table 2.2a) and evening (Table 2.2b) group, F (1, 14) = 145.57, $p < .001$ and F (1, 14) = 114.76, $p < .001$, respectively.

However, no significant difference was found on any of the pure discrimination tasks. Repeated measures ANOVA revealed no significant main effects of time for contrast discrimination at LL, F (1, 14) = 0.28, $p < .606$, and UR, F (1, 14) = 1.86, $p < .194$, for the morning group, and similarly for the evening group, F (1, 14) = 2.49, $p < .137$, and F (1, 14) = 1.46, $p < .247$, for the respective tasks. The orientation discrimination task revealed a similar pattern where at the 24 hours post learning it remained unchanged in both the LL F (1, 14) =.69, $p < .422$, or the UR, F (1, 14) = 0.10, $p < .757$, for the morning g, and evening F (1, 14) = 0.16, $p < .700$, F (1, 14) = 0.64, $p < .437$, group respectively. The flicker fusion threshold also showed no significance in performances, with the morning group showing F (1, 14) = 0.16, $p < .698$ for LL, and UR, F (1, 14) = 1.44, $p < .25$ for UR, while the evening group showed F (1, 14) = .016, $p < .901$ for LL and F (1, 14) = 0.317, $p < .582$, for UR.

Table 2.2a

Means, Standard Deviations, and Repeated Analyses of Variance in Backward Masking and Pure Discrimination Task for the Morning Group from Baseline to 24 hours Post-learning

Measures	Baseline		24hrs Post		*F* (1, 14)	η^2
	M	*SD*	*M*	*SD*		
Contrast Discrimination at LL (%)	11.07	4.89	11.93	7.36	.278	.019
Orientation Discrimination at LL (degree)	3.54	1.50	3.14	1.66	.686	.047
Flicker Fusion at LL (ms)	34.10	22.42	36.57	15.67	.156	.011
Backward Masking Luminance at LL (ms)	128.53	31.87	43.20	24.77	171.96	.925
Backward Masking Orientation LL (ms)	138.36	39.15	30.36	15.69	170.42	.924
Contrast Discrimination at UR (%)	12.95	6.69	11.16	4.94	1.86	.118
Orientation Discrimination at UR (degree)	3.23	1.28	3.40	2.36	.100	.007
Flicker Fusion at UR (ms)	38.22	21.27	43.49	19.04	1.442	.093
Backward Masking Luminance at UR (ms)	128.53	31.87	46.22	29.99	144.05	.911
Backward Masking Orientation at UR (ms)	138.36	39.15	33.87	12.66	145.57	.912

Table 2.2b

Means, Standard Deviations, and Repeated Analyses of Variance in Backward Masking and Pure Discrimination Task for the Evening Group from Baseline to 24 hours Post-learning

Measures	Baseline		24hrs Post		*F* (1, 14)	η^2
	M	*SD*	*M*	*SD*		
Contrast Discrimination at LL (%)	9.08	2.42	8.12	2.65	2.49	.151
Orientation Discrimination at LL (degree)	3.75	1.46	3.59	2.54	.155	.011
Flicker Fusion at LL (ms)	36.08	13.95	36.45	143	.016	.001
Backward Masking Luminance at LL (ms)	127.96	46.28	45.11	23.34	98.91	.876
Backward Masking Orientation LL (ms)	126.62	38.21	31.11	10.07	121.03	.896
Contrast Discrimination at UR (%)	8.04	2.90	7.19	2.02	1.46	.094
Orientation Discrimination at UR (degree)	3.34	1.75	3.12	1.76	.639	.044
Flicker Fusion at UR (ms)	38.52	8.75	37.53	12.05	.317	.022
Backward Masking Luminance at UR (ms)	127.96	46.28	45.91	24.65	121.91	.897
Backward Masking Orientation at UR (ms)	126.62	38.21	34.00	10.97	114.76	.891

2.5.6. Improvement from Baseline to 0 Hour Post-Learning

To determine if any online or instantaneous generalisation of learning took place, the threshold mean from Baseline to 0-hour post-learning was compared for both morning (Table 2.3a) and evening (Table 2.3b) groups. Repeated-measures ANOVA revealed that there is a statistically significant main effect of time of the learned task, $F(1, 14) = 200.12$, $p < .001$, indicating that time explained 93.5% of the overall variance in performance. Similarly, the evening group also showed a significant improvement in the backward masking orientation LL learning task, $F(1, 14) = 65.38$, $p < .001$. Indicating that both groups exhibited considerable learning effects in the learning task.

However, no improvement was observed in the untrained backward masking tasks, highlighting a lack of evidence of immediate generalisation and transfer of learning. Both the morning and evening showed no improvement in the backward making task with luminance LL, $F(1, 14) = 0.77$, $p = .394$, luminance UR, $F(1,14) = 2.25$, $p = .155$, or orientation UR, $F(1, 14) = 2.23$, $p = .157$. The evening group also showed no significant transfer to backward masking tasks such as luminance LL, $F(1, 14) = 0.042$, $p = .841$, luminance UR, $F(1, 14) = 0.96$, $p = .343$, or orientation UR, $F(1, 14) = 0.025$, $p = .875$, showing that online learning was specific to the trained task.

For the pure discrimination task, no significant improvement was found from Baseline to immediate re-test (0 hours post-learning). Repeated-measures ANOVA showed no significant main effects of time for contrast discrimination at LL, $F(1, 14) = .718$, $p = .411$, and UR, $F(1, 14) = 0.001$, $p = .977$, for the morning group, as well as for the evening group, $F(1, 14) = .006$, $p = .941$, and $F(1, 14) = 0.325$, $p = .578$, respectively.

Table 2.3a

Means, Standard Deviations, and Repeated Analyses of Variance in Backward Masking and Pure Discrimination Task for the Morning Group from Baseline to immediate retest (0-hr)

Measures	Baseline		0hr Post		*F* (1, 14)	η^2
	M	*SD*	*M*	*SD*		
Contrast Discrimination at LL (%)	11.07	4.89	12.18	7.17	.718	.049
Orientation Discrimination at LL (degree)	3.54	1.50	3.47	1.16	.075	.005
Flicker Fusion at LL (ms)	34.10	22.42	38.92	18.06	.413	.048
Backward Masking Luminance at LL (ms)	128.53	31.87	123.38	47.63	.774	.052
Backward Masking Orientation LL (ms)	138.36	39.15	59.91	25.40	200.12	.935
Contrast Discrimination at UR (%)	12.95	6.69	13.00	6.54	.001	.000
Orientation Discrimination at UR (degree)	3.23	1.28	3.56	1.40	2.40	.146
Flicker Fusion at UR (ms)	38.33	21.27	47.50	23.97	2.67	.160
Backward Masking Luminance at UR (ms)	128.53	31.97	120.53	42.27	2.254	.139
Backward Masking Orientation at UR (ms)	138.36	39.15	127.11	45.37	2.232	.138

Table 2.3b

Means, Standard Deviations, and Repeated Analyses of Variance in Backward Masking and Pure Discrimination Task for the Evening Group from Baseline to immediate retest (0-hr).

Measures	Baseline		24hrs Post		*F* (1, 14)	η^2
	M	*SD*	*M*	*SD*		
Contrast Discrimination at LL (%)	9.07	2.42	9.01	2.55	.006	.000
Orientation Discrimination at LL (degree)	3.75	1.46	3.52	1.78	.66	.045
Flicker Fusion at LL (ms)	36.08	13.95	39.01	16.04	.945	.063
Backward Masking Luminance at LL (ms)	127.96	46.28	126.80	56.66	.042	.003
Backward Masking Orientation LL (ms)	126.62	38.21	71.47	28.82	65.38	.824
Contrast Discrimination at UR (%)	8.04	2.90	8.53	2.54	.325	.023
Orientation Discrimination at UR (degree)	3.34	1.75	3.23	1.40	0.076	.005
Flicker Fusion at UR (ms)	38.52	8.75	41.39	10.35	1.08	.072
Backward Masking Luminance at UR (ms)	127.96	46.28	123.87	44.04	.962	.064
Backward Masking Orientation at UR (ms)	126.62	38.21	126.13	38.86	.025	.002

2.5.7. Improvement from 0-hour to 12 Hours Post-Learning

At 12 hours after the initial learning phase, the evening group showed a significant improvement in the backward masking orientation LL learning task, $F(1, 14) = 33.36$, $p < .001$, and luminance LL, $F(1, 14) = 69.66$, $p < .001$, showing the effect of improvement in learning after an offline sleep period. Similarly, the evening group also showed significant improvements in the luminance UR backward masking task, $F(1, 14) = 164.52$, $p < .001$, and orientation UR, $F(1, 14) = 131.93$, $p < .001$. The overall mean threshold has decreased from 0 hours to 12 hours post-learning retest for both the morning (Table 2.4a) and evening groups (Table 2.4b).

In contrast, the morning group, which did not sleep between 0 hours and 12 hours post-learning, no significant difference were found in learning of the backward masking orientation LL task, $F(1,14) = 0.174$, $p = .683$, or in the relevant task, such as orientation UR, $F(1,14) = 3.52$, $p = .082$. Additionally, the morning group showed no improvement in backward masking luminance LL, $F(1, 14) = 3.19$, $p = .096$, or luminance UR, $F(1, 14) = 0.677$, $p = .424$, suggesting a lack of offline wake learning effect in the absence of sleep.

Again, for all the pure discrimination tasks, no significant improvement was found during the 12-hour retest after initial learning for both the morning (Table 2.4a) and evening (Table 2.4b) groups.

Table 2.4a

Means, Standard Deviations, and Repeated Analyses of Variance in Backward Masking and Pure Discrimination Task for the Morning Group from 0-hr to 12-hrs post learning retest

Measures	0hr Post		12hrs Post		*F* (1, 14)	η^2
	M	*SD*	*M*	*SD*		
Contrast Discrimination at LL (%)	12.18	7.17	10.84	7.36	2.15	.133
Orientation Discrimination at LL (degree)	3.47	1.16	3.17	1.57	.779	.053
Flicker Fusion at LL (ms)	38.92	18.06	36.36	17.79	1.58	.101
Backward Masking Luminance at LL (ms)	123.38	47.63	116.13	54.86	3.19	.185
Backward Masking Orientation LL (ms)	59.91	25.40	59.11	23.31	.174	.012
Contrast Discrimination at UR (%)	13.00	6.54	11.25	6.34	2.03	.127
Orientation Discrimination at UR (degree)	2.56	1.40	3.31	1.56	.488	.034
Flicker Fusion at UR (ms)	47.50	23.97	40.09	15.91	2.37	.145
Backward Masking Luminance at UR (ms)	120.53	42.27	117.60	53.71	.677	.046
Backward Masking Orientation at UR (ms)	127.11	45.37	120.31	54.03	3.52	.021

Table 2.4b

Means, Standard Deviations, and Repeated Analyses of Variance in Backward Masking and Pure Discrimination Task for the Evening Group from 0-hr to 12-hrs post learning retest

Measure	0hr Post		12hrs Post		*F* (1, 14)	η^2
	M	*SD*	*M*	*SD*		
Contrast Discrimination at LL (%)	9.01	2.55	7.78	1.64	2.59	.156
Orientation Discrimination at LL (degree)	3.52	1.78	3.48	1.85	.034	.002
Flicker Fusion at LL (ms)	39.01	16.04	37.10	12.47	.765	.052
Backward Masking Luminance at LL (ms)	126.8	56.66	45.38	21.30	69.66	.833
Backward Masking Orientation LL (ms)	71.47	28.82	35.82	10.32	33.36	.704
Contrast Discrimination at UR (%)	8.53	2.54	7.94	2.66	.493	.034
Orientation Discrimination at UR (degree)	3.23	1.40	3.30	1.62	.037	.003
Flicker Fusion at UR (ms)	41.39	10.35	38.64	10.65	1.69	.108
Backward Masking Luminance at UR (ms)	123.87	44.04	46.18	23.87	164.52	.922
Backward Masking Orientation at UR (ms)	126.13	38.86	38.18	12.76	131.93	.904

2.5.8. Improvement from 12 Hours to 24 Hours post-Learning

To examine whether learning of the backward masking task continued beyond 12 hours post-learning, a repeated-measures ANOVA was conducted to compare performance between the 12-hour and 24-hour retests for both groups. The morning group showed significant improvements in the backward masking orientation LL task, with a significant main effect of time, $F(1, 14) = 61.69$, $p < .001$, highlighting that time accounts for 81.5% of the variance in performance. Similarly, orientation UR, luminance LL and luminance UR showed significant improvement over time, $F(1, 14) = 52.13$, $p < .001$, $F(1, 14) = 51.35$, $p < .001$, and $F(1, 14) = 63.47$, $p < .001$, respectively, suggesting continued consolidation of learning in the morning group.

However, in the evening group, no significant changes were observed in performance from 12 to 24 hours post-learning, indicating that learning had stabilised in the learning task, $F(1, 14) = 1.59$, $p = .228$. Similar non-significant results were observed for backward masking orientation UR, $F(1, 14) = 1.69$, $p = .215$, luminance LL, $F(1, 14) = 0.01$, $p = .922$ and luminance UR, $F(1, 14) = 0.009$, $p = .924$.

For all the pure discrimination tasks, no significant improvement was found during the 12-hour to 24-hour post-learning period. The descriptives provided in Table 2.5a demonstrated the significant decrease in the mean threshold values, further supporting these improvements for the morning group. However, Table 2.5b showed that the mean threshold values remained stable across time points for the evening group, showing the absence of additional improvements.

Table 2.5a

Means, Standard Deviations, and Repeated Analyses of Variance in Backward Masking and Pure Discrimination Task for the Morning Group

Measures	12hr Post		24hrs Post		F (1, 14)	η^2
	M	*SD*	*M*	*SD*		
Contrast Discrimination at LL (%)	10.84	7.36	11.93	7.36	1.06	.070
Orientation Discrimination at LL (degree)	3.17	1.57	3.14	1.66	.01	.001
Flicker Fusion at LL (ms)	36.36	17.80	36.57	15.67	.004	.000
Backward Masking Luminance at LL (ms)	116.13	54.86	43.20	24.77	51.35	.786
Backward Masking Orientation LL (ms)	59.11	23.31	30.36	15.69	61.69	.815
Contrast Discrimination at UR (%)	11.25	6.34	11.16	4.94	.006	.000
Orientation Discrimination at UR (degree)	3.31	1.56	3.40	2.36	.035	.002
Flicker Fusion at UR (ms)	40.09	15.92	43.49	19.04	.603	.041
Backward Masking Luminance at UR (ms)	117.60	53.71	46.22	29.98	63.47	.819
Backward Masking Orientation at UR (ms)	120.31	54.03	33.87	12.66	52.13	.788

Table 2.5b

Means, Standard Deviations, and Repeated Analyses of Variance in Backward Masking and Pure Discrimination Task for the Evening Group

Measure	12hrs Post		24hrs Post		*F* (1, 14)	η^2
	M	*SD*	*M*	*SD*		
Contrast Discrimination at LL (%)	7.78	1.64	8.12	2.65	.290	.020
Orientation Discrimination at LL (degree)	3.48	1.85	3.59	2.54	.084	.006
Flicker Fusion at LL (ms)	37.10	12.47	36.45	10.43	.081	.006
Backward Masking Luminance at LL (ms)	45.38	21.30	45.11	23.34	.01	.001
Backward Masking Orientation LL (ms)	35.82	10.32	33.11	10.07	1.59	.102
Contrast Discrimination at UR (%)	7.94	2.66	7.19	2.12	1.01	.067
Orientation Discrimination at UR (degree)	3.30	1.62	3.12	1.76	.534	.037
Flicker Fusion at UR (ms)	38.64	10.65	37.53	12.04	.417	.029
Backward Masking Luminance at UR (ms)	46.18	23.87	45.91	24.65	.009	.001
Backward Masking Orientation at UR (ms)	38.18	12.76	34.00	10.97	1.69	.108

2.6. Experiment 1: Discussion

The findings from Experiment 1 show a distinct contrast between the effects of learning on the backward masking tasks and pure discrimination tasks. While orientation, contrast discrimination, and flicker fusion tasks were more consistent over time, performance on the backward masking tasks demonstrated notable and long-lasting gains. Mixed-design ANOVAs revealed that Time had a significant impact and that the Group × Time interaction effect was important for all backward masking conditions. However, there were no significant Time or interaction effects for any pure discrimination measure. The backward masking tasks' strong effect sizes highlight the power of timed learning and its consolidation, whereas the other tasks' small effects imply that they might not be as sensitive to time-dependent learning processes. One notable characteristic of the findings from this experiment is the relatively large effect sizes seen across all backward masking tasks, especially in the backward masking with luminance LL and orientation LL, where η^2 values were more than 0.80. These important findings suggest that offline consolidation and sleep had a significant role in perceptual learning. These effects are strong enough to suggest that the learning task induces neuroplasticity, most likely in higher-order processing areas and visual cortical areas, such as V1 (Karni & Sagi, 1993; Stickgold, 2005). On the other hand, the pure discrimination tasks (flicker fusion, orientation discrimination, and contrast discrimination) had much smaller effect sizes. This suggests that they depend on more stable sensory thresholds that are less affected by processes that occur during sleep. This finding is consistent with other studies, which show that sleep-related benefits are higher for tasks involving more complex perceptual integration and attention-dependent mechanisms than for simple discriminating tests (Fenn et al., 2003).

It is important to note that the baseline mean score across tasks showed similarity. This demonstrates experimental design rather than behavioural equivalence: the adaptive staircase methods started from an identical initial threshold for all individuals, which means a baseline value was fixed to a uniform starting point. Consequently, the comparable baseline means do not indicate similar basic perceptual skills; instead, they indicate controlled initial conditions prior to the process of learning.

The analyses between groups show convincing support for how sleep affects performance trajectories. Independent-samples t-tests revealed no significant differences between groups at Baseline or 0 hours, suggesting that both groups commenced from similar performance levels. However, at the 12-hour re-test, there were considerable differences, with the Evening group (sleep period before re-test) consistently performing better than the Morning group (wake period before re-test) in all backward masking conditions. These differences were absent during the 24-hour re-test, after the Morning group encountered their sleep period, suggesting that the two groups eventually aligned. This temporal pattern strongly supports the hypothesis that sleep, rather than simply the passing of time, is what makes offline performance improvements possible. Sleep happening promptly after training (Evening group) resulted in earlier enhancements but sleep postponed until after 12 awake hours (Morning group) yielded similar enhancements solely at the subsequent re-test. This aligns with substantial studies demonstrating that sleep promotes both performance improvement and the transfer of learning to untrained under comparable stimulus situations (Stickgold & Walker, 2013). Furthermore, Group × Time interactions were observed across all backward masking tasks, which were again absent in the pure discrimination tasks. This interaction effect assesses whether the pattern of change over time differs between the groups. Statistically, these interactions show that the learning and performance trajectories were significantly different between the Morning and Evening groups, rather than showing parallel improvement at the same time, mirroring the t-test results.

The within-group analysis also provided support for the distinct effect of the time of day on learning and consolidation. Both groups showed significant improvements on the learned backward masking orientation LL task, however, the trajectory of learning varied between groups. The evening group demonstrated notable improvements in the 12-hour post-learning re-test, indicating that sleep was crucial in enhancing performance. On the other hand, the morning group, which stayed awake from 0 to the 12 hours period, showed no notable gains throughout this period. Yet, following a night of rest, the morning group demonstrated significant enhancements during the 24-hour testing. The results further support the significance of sleep dependency in learning generalisation through observed transfer effects. After a night of sleep, the morning group demonstrated a notable transfer of learning to other untrained backward masking tasks (including orientation UR, luminance LL, and luminance UR). This suggests that sleep has benefits for associated perceptual abilities beyond the training task, possibly due to synaptic reorganisation and the incorporation of learnt patterns into a larger brain network (Stickgold & Walker, 2013). The evening group, on the other hand, had significant transfer effects at the 12-hour test after sleep, but these benefits did not hold up at the 24-hour retest. This indicates that although there was an initial transfer of learning, it was not sustained as long as in the morning group, suggesting that consolidation processes may vary depending on when learning takes place in relation to when the sleep period occurred.

Circadian effects on learning and memory consolidation might be one of the causes of the observed variances between groups. Performance may be impacted by learning sessions that correspond with an individual's peak cognitive times, and the evening groups showed faster improvements, possibly due to circadian synchronisation with their sleep cycle (Blatter & Cajochen, 2007). Learning earlier in the day may allow for higher consolidation effects, especially when followed by nighttime sleep, as indicated by the morning group's improved long-term retention. These findings are in line with other studies on sleep-dependent memory consolidation and provide weight to the idea that planning learning sessions that align with sleep-wake cycles may optimise learning outcomes (Gais et al., 2000).

Careful interpretation of the findings is needed in this experiment, as it relies on self-reported sleep habits and a relatively small sample size. The findings' generalisability is always limited by these characteristics, which also raise questions about the possible impact of unmeasured confounding variables, including differences in circadian type across individuals and sleep quality. In order to provide stronger support for the sleep-dependent hypothesis, future research should build a stronger methodological framework, objective sleep metrics, and a larger sample size. Overall, this experiment provides strong evidence that sleep is essential for PL and its transfer to related tasks. The substantial effect sizes observed in backward masking tasks demonstrate the significance of offline neuronal reorganisation and sleep-related consolidation in complex perceptual learning, which will be further discussed in the main discussion. On the other hand, the lack of noticeable improvements across all pure discrimination tests indicates that specific perceptual abilities do not change over time and are not significantly affected by sleep.

2.7. Experiment 2: Introduction

An investigation into the methods by which learning influences the backward masking (orientation) task is presented in the first experiment discussed in this chapter. Not only did performance in the task increase for the characteristics and locations that were learnt, but it also improved for other areas of the task. The significance of this discovery lies in the fact that it provides evidence that our perception systems are adaptable and able to apply information that was previously learned to other circumstances. Additionally, it raises questions about the way in which the brain localises activities, demonstrating that the consolidation of learning is not restricted to certain tasks. One example is that having a strong command of the backward masking orientation task led to an improvement in performance on the luminance backward masking test, despite the fact that there was no prior experience with the latter. For example, being skilled in the backward masking orientation task also improved performance in the backward masking luminance task, even though there was no practice with it. The presence of this crossover provides evidence that higher-level brain areas may play a role in the process of generalising learning and transferring information between different types of activities. If this were confirmed, it would be a revolutionary step that would completely transform our understanding of how information is processed and disseminated in the brain throughout the learning process.

Experiment 2 takes a deeper look at examining individuals who were trained primarily on the backward masking luminance task, concentrating particularly on their left visual field. This is carried out in light of the insights that were already gained from the first experiment within this chapter. This focus on luminance is based on what is known about how V1 neurones work and how they respond to changes in both direction and illumination stimuli (Wang et al., 2015). The purpose of this investigation is to determine if the benefits that have been reported are based on processing or involve more complicated cognitive functions. Taking into account the fact that visual perception includes different parts of the brain, the improvement in task performance that was seen demonstrates that different regions of the brain operate together rather than acting separately. Although these findings are convincing, further research is needed to understand how the brain's activity is mapped during learning and its generalisation. The value of carrying out such an experiment comes from the fact that it has the ability to shed light on the mechanisms that are responsible for learning and generalisation within the system. Researchers can assess whether increases in performance are due to changes in processing or if they result from enhanced cognitive skills, such as attention, memory, or decision-making, by training participants on the backward masking luminance task and analysing the effects of the task. To establish focused learning methods that can improve abilities, it is essential to make this distinction. Furthermore, having a better understanding of how learning in one area can affect performance in another may have implications for rehabilitation efforts, particularly for visual impairments, and even for the creation of artificial intelligence systems capable of simulating human perceptual learning processes.

2.8. Experiment 2: Materials and Methods

2.8.1. Participants

For the study, a fresh new cohort of 25 naive volunteers who had never been exposed to the task before the learning period were recruited. Five participants were excluded from final data analysis due to withdrawal from the study. The remaining 20 participants were evenly allocated to two groups, the morning group (n = 10, mean age = 19.5, SD = 1.51) and the evening group (n = 10, mean age = 20.6, SD = 1.84). Both groups of participants have completed a self-reported sleep log which confirms that they adhered to the study's requirements identical to Experiment 1.

2.8.2. Set-up, Stimuli/Tasks, Assessment/Timeline

Experimental set-up, task used, and the timeline were identical to Experiment 1, except that this time participants were trained on the lower left visual field of the backward masking luminance task and committed approximately 5 hours across three experimental sessions. Matlab was used to present the visual stimuli on a computer screen, with a screen size of 54.3cm. Participants were placed in a completely dark testing lab that consist of a chinrest, which serves the purpose of keeping their head location at the same location throughout the testing sessions. An eye tracker was also used to ensure that participant is always fixating at the centre location as requested.

There is also a change in the order of the learning and retest for backward masking tasks. In the learning phase (Session 1) participants underwent training on the backward masking Luminance task at the lower-left (LL) visual field. The backward masking learning task consisted of five blocks of 96 trials each (as detailed in the 'Experiment Design' section)

In 0-hour post-learning phase (Session 2), participants completed immediate post-learning re-tests. The 12-hour and 24-hour retests followed the same structure, including both backward masking of Luminance and orientation (LL & UR), For all pure discrimination tasks, it also follows the same paradigm as stated in Experiment 1.

2.9. Experiment 2: Results

Shapiro–Wilk tests was used to check for normality in each group. Most of the variables exhibited no statistically significant deviation from normality ($p > .05$), with a few instances of significance occurring at certain time intervals. Given that the groups were small but equal in size ($n = 10$ per group) and mixed ANOVA and independent samples t-tests are strong enough to handle modest normality violations (Field, 2024), parametric analyses were maintained.

2.9.1. Overall Group × Time Effects

A 2 (Group: Morning, Evening) × 4 (Time: Baseline, 0 h, 12 h, 24 h) mixed-design ANOVA was carried out on all the backward masking tasks. There was a significant main effect of Time, $F(1.40, 25.22) = 105.44$, $p < .001$, indicating a significant decrease in thresholds across sessions. There was also a significant Group × Time interaction, $F(1.40, 25.22) = 5.53$, $p = .018$, indicating different learning trajectories between the Morning and Evening groups.

For the unlearned backward masking orientation LL condition, there was a significant main effect of Time, $F(1.60, 28.85) = 63.24$, $p < .001$, indicating a decrease in thresholds across sessions. The Group × Time interaction was also significant, $F(1.60, 28.85) = 15.24$, $p < .001$, again suggesting differential patterns between the groups over time. Similar patterns were observed for the backward masking luminance UR condition, where there was a significant main effect of Time, $F(1.70, 30.55) = 81.86$, $p < .001$, and a significant Group × Time interaction, $F(1.70, 30.55) = 21.27$, $p < .001$. Again, the same pattern was found for the backward masking orientation UR condition. A significant main effect of Time was observed, $F(1.95, 35.15) = 54.48$, $p < .001$, and a significant Group × Time interaction, $F(1.95, 35.15) = 11.47$, $p < .001$.

For all the pure discrimination tasks, mixed ANOVAs revealed no significant Time effects or Group × Time interactions for any measure (Table 2.6), which is in line with what was observed in Experiment 1.

Taken together, these findings indicate that both learned and unlearned backward masking tasks, involving luminance and orientation, showed strong performance improvements over time, as reflected in significant main effects of Time. In addition, all unlearned tasks exhibited significant Group × Time interactions, highlighting that both groups followed different performance trajectories across sessions, similar to the learned condition.

Table 2.6

Results of Mixed ANOVAs Examining the Effects of Time and Time × Group Interactions Across All Variables, with the Backward Masking Luminance LL as the learned task

Dependent Variable	Effect	df_1	df_2	F	p	η^2
Backward Masking Luminance at LL (ms)	Time	1.40	25.22	105.442	<.001	.854
	Time × Group	1.40	25.22	5.532	0.018	.235
Backward Masking Orientation LL (ms)	Time	1.60	28.85	63.239	<.001	.778
	Time × Group	1.60	28.85	15.243	<.001	.459
Backward Masking Luminance at UR (ms)	Time	1.70	30.55	81.856	<.001	.820
	Time × Group	1.70	30.55	21.271	<.001	.542
Backward Masking Orientation at UR (ms)	Time	1.95	35.15	54.476	<.001	.752
	Time × Group	1.95	35.15	11.474	<.001	.389
Contrast Discrimination at LL (%)	Time	2.62	47.15	1.167	.329	.061
	Time × Group	2.62	47.15	.455	.689	.025
Orientation Discrimination at LL (degree)	Time	2.67	48.09	1.468	.237	.075

	Time × Group	2.67	48.09	.484	.673	.026
Flicker Fusion at LL (ms)	Time	2.44	43.96	.374	.731	.020
	Time × Group	2.44	43..96	.435	.689	.024
Contrast Discrimination at UR (%)	Time	2.39	43.01	.087	.942	.005
	Time × Group	2.39	43.01	.202	.854	.011
Orientation Discrimination at UR (degree)	Time	2.17	39.04	.167	.863	.009
	Time × Group	2.17	39.04	.275	.778	.015
Flicker Fusion at UR (ms)	Time	2.63	47.27	.067	.977	.004
	Time × Group	2.63	47.27	.610	.591	.033

Note. df_1 = numerator degrees of freedom (effect), df_2 = denominator degrees of freedom (error). Greenhouse–Geisser corrected values are reported where Mauchly's test indicated violations of sphericity.

2.9.2. Between-Group Comparisons

To look at between-group differences, independent-samples t-tests were conducted to compare the Morning and Evening groups on all backward masking and pure discrimination tasks at Baseline, 0 hr, 12 hr, and 24 hr.

For the trained task (backward masking luminance LL), there were no significant differences between groups at Baseline, $t(18) = 0.14$, $p = .892$, $d = 0.06$, or at 0 hr, $t(14.58) = -1.33$, $p = .205$, $d = -0.57$. A significant difference emerged at 12 hr, $t(16.31) = 2.46$, $p = .026$, $d = 1.05$, with the Evening group showing lower thresholds than the Morning group. By 24 hr, this difference was no longer significant, t (17.67) = −0.82, p = .425, d = −0.35.

For the untrained backward masking orientation LL task, no significant differences were found at Baseline, t (17.49) = 0.01, p = .991, d = 0.01, or at 0 hr, t (16.01) = −0.15, p = .883, d = −0.06. At 12 hr, the Evening group outperformed the Morning group, t (11.01) = 5.26, p < .001, d = 2.25. No significant difference remained at 24 hr, t (14.81) = −1.39, p = .185, d = −0.60. Similarly, for TDT Luminance UR, there were no between-group differences at Baseline, t (17.80) = 0.14, p = .892, d = 0.06, or at 0 hr, t (18) = 0.18, p = .860, d = 0.08. A significant difference emerged at 12 hr, t (13.13) = 5.38, p < .001, d = 2.31, favouring the Evening group. No significant difference was observed at 24 hr, t (17.44) = −0.86, p = .400, d = −0.37. Following the same pattern, the backward masking orientation UR also showed no significant group differences at Baseline, t (17.49) = 0.01, p = .991, d = 0.01, or at 0 hr, t (17.29) = −0.25, p = .804, d = −0.11. At 12 hr, there was a large and significant difference, t (12.18) = 3.97, p = .002, d = 1.70, with the Evening group again outperforming the Morning group. By 24 hr, this difference had disappeared, t (16.23) = −1.22, p = .239, d = −0.52.

There were no significant differences between groups at any time point for any of the pure discrimination conditions. This is in line with the mixed-ANOVA results, which showed that these measures did not have any Time or Group x Time effects. This suggests that sleep is more beneficial for the backward masking tasks that need a lot of time to process than for simple sensory thresholds.

2.9.3. Improvement from Baseline to 24 Hours Post-Learning

In Experiment 2, the performance of individuals on various tasks at baseline to 24 hours after initial learning was examined. Repeated-measures ANOVA showed a significant main effect of time for the learning task, showing a substantial improvement in the backward masking luminance LL task for both the morning and evening groups. The morning group showed a significant improvement, $F(1, 9) = 75.56$, $p < .001$, with the η^2 indicating that time explained 89.4% of the variance in performance and not by random chance (Table 2.7a). Similarly, the evening group also demonstrated a strong learning effect, $F(1, 9) = 58.75$, $p < .001$, with the η^2 indicating that time explained 86.7% of the variance.

In addition to the improvement in the learning task, both groups demonstrated significant improvement in related untrained backward masking tasks. Firstly, the morning group showed a significant transfer of learning to the backward masking tasks, including, luminance UR, $F(1, 9) = 58.50$, $p < .001$, orientation LL, $F(1, 9) = 41.66$, $p < .001$, and orientation UR, $F(1, 9) = 41.16$, $p < .001$. Additionally, the evening group experienced comparable transferred skills, $F(1, 9) = 52.60$, $p < .001$, $F(1, 9) = 39.73$, $p < .001$, and $F(1, 9) = 35.77$, $p < .001$, respectively. The mean score across the tasks for the morning (Table 2.7a) and evening (Table 2.7b) groups suggests an overall decrease in threshold scores, highlighting that learning of the backward masking luminance LL task generalised to other backward masking-based perceptual tasks.

However, no significant difference was found for any of the pure discrimination tasks. Repeated-measures ANOVA showed no significant main effects of time for contrast discrimination at LL, $F(1,9) = 0.266$, $p = .618$, and UR, $F(1, 9) = 0.317$, $p = .585$, in the morning group. Similarly, the evening group showed no significant improvement in these tasks, as indicated by $F(1, 9) = 0.004$, $p = .953$, and $F(1, 9) = 0.001$, $p = .975$, respectively. Likewise, no significant changes were found for orientation discrimination at LL, $F(1, 9) = 0.943$, $p = .357$, and UR, $F(1, 9) =$

0.368, p = .559, for the morning group, or for the evening group, F (1, 9) = 1.56, p = .243, and F (1, 9) = 0.011, p = .917. The flicker fusion task also showed no significant differences in both morning and evening group, F (1, 9) = 1.31, p = .315 (LL), F (1, 9) = 0.317, p = .587 (UR) and F (1,9) = 0.045, p = .837 (LL), F (1, 9) = 0.166, p = .693 (UR), respectively.

Based on these findings, participants' performance on pure discrimination tasks was constant over time. However, they demonstrated strong gains on the learnt backward masking luminance LL task and a notable transfer to related backward masking tasks. This indicates that gains did not transfer to more general visual discriminating skills, but instead were task-specific to temporal learning processes.

Table 2.7a

Means, Standard Deviations, and Repeated Analyses of Variance in Backward Masking and Pure Discrimination Task for the Morning Group from Baseline to 24 hours post-learning

Measures	Baseline		24hrs Post		*F* (1, 9)	η^2
	M	*SD*	*M*	*SD*		
Contrast Discrimination at LL (%)	12.73	5.02	12.16	4.34	.266	.029
Orientation Discrimination at LL (degree)	2.66	1.38	2.37	.85	.943	.357
Flicker Fusion at LL (ms)	38.15	6.57	36.53	6.80	1.31	.112
Backward Masking Luminance at LL (ms)	129.87	43.86	35.20	14.08	75.56	.894

Backward Masking Orientation LL (ms)	126.67	47.75	34.60	10.59	41.66	.822
Contrast Discrimination at UR (%)	11.83	6.69	12.88	6.57	.321	.034
Orientation Discrimination at UR (degree)	2.43	.485	2.58	.796	.368	.039
Flicker Fusion at UR (ms)	37.64	7.42	39.63	11.24	.317	.034
Backward Masking Luminance at UR (ms)	129.87	43.86	38.00	15.04	58.5	.867
Backward Masking Orientation at UR (ms)	126.67	47.75	40.13	14.38	41.16	.821

Table 2.7b

Means, Standard Deviations, and Repeated Analyses of Variance in Backward Masking *and Pure Discrimination Task for the Evening Group*

Measures	Baseline		24hrs Post		F (1, 9)	η^2
	M	*SD*	*M*	*SD*		
Contrast Discrimination at LL (%)	12.87	4.41	12.76	7.42	.004	.000
Orientation Discrimination at LL (degree)	2.31	.69	2.07	.80	1.56	.148
Flicker Fusion at LL (ms)	35.74	7.88	35.14	10.13	.045	.005
Backward Masking Luminance at LL (ms)	127.0	48.80	40.73	16.17	58.75	.867
Backward Masking Orientation LL (ms)	126.40	56.72	43.60	17.50	39.73	.815

Contrast Discrimination at UR (%)	13.13	5.14	13.16	6.58	.001	.000
Orientation Discrimination at UR (degree)	2.12	.467	2.14	.938	.011	.001
Flicker Fusion at UR (ms)	36.11	9.00	34.95	6.91	.166	.018
Backward Masking Luminance at UR (ms)	127.0	48.80	44.40	18.02	52.60	.854
Backward Masking Orientation at UR (ms)	126.40	56.72	49.73	20.27	35.77	.799

2.9.4. Improvement from Baseline to 0 Hour Post-Learning

To examine whether any immediate learning effects occurred after the initial learning session, performance at baseline was compared to the 0-hour re-test for both groups. A significant main effect of time was observed for the training of the backward masking luminance LL task, showing a substantial effect of immediate learning. The morning group showed a significant improvement in the learning task, $F(1, 9) = 51.94$, $p < .001$. Similarly, the evening group also exhibited a strong learning effect, $F(1, 9) = 80.69$, $p < .001$. The larger effect size found in the evening group (Table 2.8b) compared to the morning group (Table 2.8a) suggests a potentially greater immediate consolidation of learning.

Apart from the improvement found for the learning task, no evidence of immediate learning transfer was found. Firstly, the performance of both the morning and evening groups remained stable for the backward masking luminance UR task, $F(1, 9) = 0.02$, $p = .892$, and $F(1, 9) = 0.002$, $p = .964$, respectively. For the backward masking orientation task, similar results were found at LL, $F(1, 9) = 2.33$, $p = .161$

(morning) and F (1, 9) = 1.68, p = .228 (evening). Similarly, for the backward masking orientation UR, F (1, 9) = 0.927, p = .361 (morning) and F (1, 9) = 0.108, p = .750 (evening). The finding suggests that learning was highly task-specific, with no immediate generalisation to different visual quadrants or to other task features.

Additionally, performance in the pure discrimination tasks also remained unchanged, suggesting that the perceptual learning effect was specific to the backward masking rather than to more general tasks. Repeated-measures ANOVA showed no significant main effects of time for Contrast Discrimination at LL, F (1, 9) = 1.11, p = .319, and UR, F (1, 9) = 0.428, p = .530, in the morning group. Similarly, the evening group showed no significant improvement in these tasks, F (1, 9) = 0.087, p = .775, and F (1, 9) = 0.043, p = .841, respectively. For the pure Orientation Discrimination task, no improvement was found at the LL, F (1, 9) = 0.002, p = .968 and UR, F (1, 9) = 0.851, p = .380 for the morning group, or for the evening group, F (1, 9) = 0.976, p = .349 and F (1, 9) = 0.622, p = .451, for the respective tasks. Finally, the Flicker Fusion task was also consistent with the previous two tasks where non-significance in performance were found at the LL, F (1, 9) = 0.878, p = .373 and UR, F (1,9) = 0.962, p = .352 for the morning group, and the same for evening group, F (1, 9) = 0.081, p = .782 and F (1, 9) = 0.845, p = .382. Overall, reinforces the idea that immediate post-learning benefits do not extend to general discrimination abilities.

Overall, both morning and evening groups demonstrated immediate learning for the trained backward masking luminance task at the LL visual quadrant, where the transfer effects were not found to be related to backward masking tasks, as evidenced by the decrease in mean performance for both groups (Table 2.8a and Table 2.8b). However, the evening group showed a larger immediate effect, potentially reflecting differences in time-of-day influences on the consolidation of learning.

Table 2.8a

Means, Standard Deviations, and Repeated Analyses of Variance in Backward Masking and Pure Discrimination Task for the Morning Group from Baseline to 0-hour post-learning

Measures	Baseline		0hr Post		*F* (1, 9)	η^2
	M	*SD*	*M*	*SD*		
Contrast Discrimination at LL (%)	12.73	5.02	13.81	5.79	1.11	.110
Orientation Discrimination at LL (degree)	2.66	1.38	2.65	1.07	.002	.000
Flicker Fusion at LL (ms)	38.15	6.57	36.99	5.92	.878	.089
Backward Masking Luminance at LL (ms)	129.87	43.86	68.13	23.97	51.94	.852
Backward Masking Orientation LL (ms)	126.67	47.75	119.93	38.37	2.33	.206
Contrast Discrimination at UR (%)	11.83	6.69	12.79	5.46	.428	.045
Orientation Discrimination at UR (degree)	2.43	.485	2.56	.635	.851	.086
Flicker Fusion at UR (ms)	37.64	7.42	40.09	8.56	.962	.097
Backward Masking Luminance at UR (ms)	129.87	43.86	130.53	46.00	.020	.002
Backward Masking Orientation at UR (ms)	126.67	47.75	119.33	44.88	.927	.093

Table 2.8b

Means, Standard Deviations, and Repeated Analyses of Variance in Backward Masking and Pure Discrimination Task for the Evening Group from Baseline to 0-hour post-learning

Measures	Baseline		24hrs Post		*F* (1, 9)	η²
	M	*SD*	*M*	*SD*		
Contrast Discrimination at LL (%)	12.87	4.41	12.48	4.62	.087	.010
Orientation Discrimination at LL (degree)	2.31	.686	2.13	.632	.976	.098
Flicker Fusion at LL (ms)	35.74	7.88	35.14	7.39	.081	.009
Backward Masking Luminance at LL (ms)	127.0	48.80	87.93	40.64	80.69	.900
Backward Masking Orientation LL (ms)	126.40	56.72	123.13	55.46	1.68	.157
Contrast Discrimination at UR (%)	13.13	5.14	12.73	5.34	.043	.005
Orientation Discrimination at UR (degree)	2.12	.467	2.01	.654	.622	.065
Flicker Fusion at UR (ms)	36.11	9.00	33.61	10.36	.845	.086
Backward Masking Luminance at UR (ms)	127.0	48.80	126.87	45.89	.002	.000
Backward Masking Orientation at UR (ms)	126.40	56.73	125.0	55.13	.108	.093

2.9.5. Improvement from 0 Hour to 12 Hours Post-Learning

To examine the potential impact of learning within the first 12 hours post-learning, and compared performance between immediate and 12-hour post-learning tests for both the morning and evening groups. For the learned backward masking luminance task at LL, the morning group did not show any improvement, $F(1, 9) = 2.62$, $p = .140$, indicating no substantial change in learning during this offline wake period. On the other hand, the evening group showed a significant decrease in mean threshold, $F(1, 9) = 30.67$, $p < .001$, suggesting a strong offline sleep consolidation effect (Table 2.7a and Table 2.7b).

Similar patterns were found for the untrained backward masking tasks. The morning group did not show improvement in the backward masking luminance UR, $F(1,9) = 1.04$, $p = .334$, backward masking orientation LL $F(1,9) = 0.47$, $p = .510$, or backward masking orientation UR, $F(1,9) = 1.08$, $p = .327$, suggesting that with the absence of sleep offline learning effect were minimal. In contrast, the evening group, which had a sleep period between the sessions, showed a significant improvement in backward masking luminance UR, $F(1,9) = 72.09$, $p < .001$, backward masking orientation LL, $F(1,9) = 32.00$, $p < .001$, and backward masking orientation UR $F(1,9) = 44.66$, $p < .001$, supporting the idea of sleep in improving the generalisation of learning.

For all pure discrimination tasks, no improvement was found for the Contrast Discrimination LL, $F(1, 9) = 3.62$, $p = .090$, and UR, $F(1, 9) = 0.27$, $p = .614$, for the morning group. The evening group also showed the same pattern, $F(1, 9) = 0.993$, $p = .345$ and $F(1, 9) = 0.179$, $p = .682$ for the respective tasks. For the Orientation Discrimination task, no improvement was found at LL, $F(1, 9) = 0.517$, $p = .490$ and UR, $F(1, 9) = 0.017$, $p = .899$, for the morning group, and for the evening group, F (1,

9) = 0.158, p = .709 and F (1, 9) = 0.369, p = .559, respectively. In addition, for the Flicker Fusion task performance also remained stable for the morning group at LL, F (1, 9) = 0.189, p = .674 and UR, F (1, 9) = 0.423, p = .532 and evening group at LL, F (1, 9) = 0.897, p = .368 and UR, F (1, 9) = 0.202, p = .664. The results reinforce the idea that sleep-related benefits are specific to visual perceptual tasks rather than general discrimination abilities.

Table 2.7a

Means, Standard Deviations, and Repeated Analyses of Variance in Backward Masking and Pure Discrimination Task for the Morning Group from 0 hour to 12 hours post-learning

Measures	0hr Post		12hrs Post		*F* (1, 9)	η^2
	M	*SD*	*M*	*SD*		
Contrast Discrimination at LL (%)	13.81	5.79	11.57	4.32	3.62	.287
Orientation Discrimination at LL (degree)	2.65	1.07	2.83	1.12	.517	.054
Flicker Fusion at LL (ms)	36.99	5.92	37.69	7.58	.189	.021
Backward Masking Luminance at LL (ms)	68.13	23.97	66.40	24.42	2.62	.225
Backward Masking Orientation LL (ms)	119.93	38.37	122.20	42.82	.470	.050
Contrast Discrimination at UR (%)	12.79	5.46	12.16	5.34	.273	.029
Orientation Discrimination at UR (degree)	2.56	.635	2.53	.526	.017	.002

Flicker Fusion at UR (ms)	40.09	8.56	38.47	8.32	.423	.045
Backward Masking Luminance at UR (ms)	130.53	46.0	127.13	44.71	1.04	.104
Backward Masking Orientation at UR (ms)	119.33	44.88	113.20	47.73	1.08	.107

Table 2.7b

Means, Standard Deviations, and Repeated Analyses of Variance in Backward Masking and Pure Discrimination Task for the Evening Group from 0 hour to 12 hours post-learning

Measure	0hr Post		12hrs Post		*F* (1, 9)	η^2
	M	*SD*	*M*	*SD*		
Contrast Discrimination at LL (%)	12.48	4.62	11.61	5.09	.993	.099
Orientation Discrimination at LL (degree)	2.13	.632	2.20	.912	.148	.016
Flicker Fusion at LL (ms)	35.14	7.39	33.15	7.08	.897	,091
Backward Masking Luminance at LL (ms)	87.93	40.64	43.07	17.50	30.67	.773
Backward Masking Orientation LL (ms)	123.13	55.46	47.07	14.39	32.0	.781
Contrast Discrimination at UR (%)	12.73	5.34	13.36	4.41	.179	.020
Orientation Discrimination at UR (degree)	2.01	.654	2.14	.620	.369	.039

Flicker Fusion at UR (ms)	33.61	10.36	34.44	7.52	.202	.022
Backward Masking Luminance at UR (ms)	126.87	45.89	42.27	22.04	72.09	.899
Backward Masking Orientation at UR (ms)	125.0	55.13	48.07	20.38	44.66	.832

2.9.6. Improvement from 12 Hour to 24 Hours Post-Learning

At the 24-hour interval, significant transfer of learning to untrained backward masking tasks was found in the morning group but not in the evening group. ANOVA analysis has shown that there was improvement to the task of other backward masking, including, luminance UR task, $F(1, 9) = 48.66$, $p < .001$, orientation LL, $F(1, 9) = 50.90$, $p < .001$, and orientation UR, $F(1, 9) = 33.49$, $p < .001$, and when compared to the 12-hour test. However, the evening group did not show the same effects, with a non-significant change to untrained tasks, $F(1, 9) = 0.347$, $p = .570$, $F(1, 9) = 3.31$, $p = .102$, and $F(1, 9) = 0.226$, $p = .646$, respectively. Furthermore, there was a significant consolidation of learning observed only in the morning group for the backward masking luminance LL task, with a substantial improvement from 12 hours to 24 hours, $F(1, 9) = 59.53$, $p < .001$. However, the evening group did not exhibit the same learning effect, $F(1, 9) = 3.72$, $p = .086$, indicating that there is a lack of continued learning beyond the 12-hour post-learning mark.

As expected and consistent with previous findings from Experiment 1, the pure discrimination tasks did not show any significant changes in either group, suggesting that the observed improvement was highly specific to the backward masking-based PL tasks. Repeated-measures ANOVA found no significant changes in contrast discrimination at LL, $F(1, 9) = 0.298$, $p = .598$, and UR, $F(1, 9) = 0.477$, p

= .507, in the morning group, nor for the evening group, F (1, 9) = 1.08, p = .326 (LL), F (1, 9) = 0.039, p = .847 (UR). Similarly, no significant differences were found in orientation discrimination at LL, F (1, 9) = 3.37, p = .100, and UR, F (1, 9) = 0.051, p = .826, for the morning group, or for the evening group, F (1, 9) = 0.449, p = .520, and F (1, 9) = 0.001, p = .979. Likewise, flicker fusion task performance remained unchanged, with no significant differences observed for the morning, with LL, F (1,9) = 0.588, p = .463 and UR, F (1, 9) = 0.12, p = .73, and the evening group, with LL, F (1, 9) = 0.326, p = .582, and UR, F (1, 9) = 0.076, p = .789.

These findings indicate that while the morning group continued to consolidate learning and exhibited further transfer to untrained tasks, the evening group's improvements plateaued beyond 12 hours. The descriptive statistics (Table 2.8a) highlight the reduction in threshold scores for the morning group compared to the evening group (Table 2.8b), further supporting the presence of sleep-dependent consolidation effects.

Table 2.8a

Means, Standard Deviations, and Repeated Analyses of Variance in Backward Masking and Pure Discrimination Task for the Morning Group

Measures	12hr Post		24hrs Post		*F* (1, 9)	η^2
	M	*SD*	*M*	*SD*		
Contrast Discrimination at LL (%)	11.57	4.32	12.16	4.34	.298	.032
Orientation Discrimination at LL (degree)	2.83	1.12	2.37	.849	3.37	.272

Flicker Fusion at LL (ms)	37.69	7.58	36.53	6.80	.588	.061
Backward Masking Luminance at LL (ms)	66.40	24.42	35.20	14.08	59.53	.869
Backward Masking Orientation LL (ms)	122.20	42.82	34.60	10.59	50.90	.850
Contrast Discrimination at UR (%)	12.16	4.32	12.88	6.57	.477	.050
Orientation Discrimination at UR (degree)	2.53	.53	2.58	.796	.051	.006
Flicker Fusion at UR (ms)	38.47	8.32	39.63	11.24	.120	.013
Backward Masking Luminance at UR (ms)	127.13	44.71	38.0	15.04	48.66	.844
Backward Masking Orientation at UR (ms)	113.20	47.73	40.13	14.38	33.49	.788

Table 2.8b

Means, Standard Deviations, and Repeated Analyses of Variance in Backward Masking and Pure Discrimination Task for the Evening Group

Measure	12hrs Post		24hrs Post		*F* (1, 9)	η^2
	M	*SD*	*M*	*SD*		
Contrast Discrimination at LL (%)	11.61	5.09	12.76	7.42	1.08	.107
Orientation Discrimination at LL (degree)	2.20	.914	2.07	.801	.449	.047
Flicker Fusion at LL (ms)	33.15	7.08	35.14	10.13	.326	.035
Backward Masking Luminance at LL (ms)	43.07	17.50	40.73	16.17	3.72	.292
Backward Masking Orientation LL (ms)	47.07	14.39	43.60	17.50	3.31	.269
Contrast Discrimination at UR (%)	13.36	4.41	13.16	6.58	.039	.004
Orientation Discrimination at UR (degree)	2.13	.620	2.14	.094	.001	.000
Flicker Fusion at UR (ms)	34.44	7.52	34.95	6.91	.076	.008
Backward Masking Luminance at UR (ms)	42.27	22.05	44.40	18.01	.347	.037
Backward Masking Orientation at UR (ms)	48.07	20.38	49.73	20.27	.226	.025

2.10. Experiment 2: Discussion

Experiment 2 examined how sleep affects perceptual learning as well as learning generalisation across task elements and visual field locations. In particular, the experiment examined whether training on the backward masking luminance LL task enhanced performance on untrained backward masking tasks, pure discrimination tasks, and the trained task. Strong learning effects was observed for the learnt task in both groups, which is in line with the findings in Experiment 1. However, no significant generalisation was shown in the evening group after 12 hours post-learning, and generalisation effects were observed solely in the morning group at the 24-hour period. Further supporting the specificity of learning-related enhancements to temporal learning processes rather than general perceptual abilities is the fact that performance on pure discrimination tests was constant across all time points.

The learnt luminance LL task demonstrated considerable improvement for both the morning and evening groups, indicating robust PL effects. The improvement paths, however, varied among groups. By the 12-hour point, the evening group had shown significant improvement, indicating offline consolidation effects related to sleep. In contrast, the morning group, which stayed awake for the first 12 hours, showed no immediate improvement, but a significant gain was found at 24 hours, following a sleep period. These results are consistent with the findings in Experiment 1 and other research in the literature, providing the idea that sleep improves performance on PL tasks and helps in memory consolidation (Fenn & Hambrick, 2012; Stickgold & Walker, 2005).

Furthermore, throughout the 24-hour test, only the morning group demonstrated the transfer of learning to untrained backward masking tasks. Backward masking tasks, including luminance UR, orientation LL, and orientation UR, exhibited notable transfer effects. This finding indicates that there is a delayed consolidation process, potentially requiring an extended sleep period for this effect to occur. The 12-hour retest revealed transfer effects after the evening group's participants had their offline sleep period. However, the 24-hour retest did not sustain the effect. The observed pattern suggests that while sleep can facilitate the transfer of learning, the effects were less long-lasting due to time-of-day limits (Kuriyama et al., 2004).

The between-group comparison results further support this point of view. Both groups began with the same baseline, but differences became clear after the first 12-hour period, when the evening group, who had received the first sleep period, performed better on both the learned and unlearned backward masking tasks compared to the morning group. After the morning group had their own sleep period, the differences had disappeared in 24 hours, and both groups performed at around the same level. This trend strongly shows that sleep is contributing and making a difference in both performance and the transfer of learning, not time or repeated testing. The evening group had shown this performance gain earlier, as they had a sleep period between their first and second learning periods. However, the morning group did not catch up until after they had the sleep period at a later time point. The lack of differences between groups on the pure discrimination conditions further emphasises that these effects are particular to the consolidation of masking-related learning, rather than to overall enhancements in visual sensitivity.

Perceptual learning is not primarily controlled by low-level visual processing, as shown by the reported generalisation of learning to untrained backward masking tasks but not to pure discriminating tasks. Improvements would have been anticipated in tasks with comparable sensory characteristics (e.g., contrast discrimination) if generalisation had been limited to early visual regions. The involvement of higher-order cortical processes in PL was supported by our discovery that generalisation extended to other backward masking tasks with distinct spatial locations and feature attributes. This notion aligns with neurophysiological studies that demonstrate a connection between the prefrontal cortex and parietal areas, as well as the relationship between extractive learning and cross-task generalisation (Jing et al., 2021). Furthermore, learning benefits may be due to task-specific changes in temporal processing rather than a general gain in visual perception, as shown by the fact that perception did not improve on any purely perceptual tasks (Watanabe & Sasaki, 2015). These findings highlight the fact that higher-level cognitive processes, rather than just cognitive process flexibility, are responsible for the generalisation of perceptual learning.

The results of this experiment showed that circadian rhythms play a role in determining the effectiveness of learning processes and memory consolidation. The morning group demonstrates long-term recall and generalisation improvements after sleep through delayed yet sustained memory gains at the 24-hour mark. The evening group displayed significant early improvements at the 12 hours post-learning period with consistent benefits throughout the rest of the retest session. Research confirms that circadian variables influence the encoding and consolidation of procedural learning (Della-Maggiore et al., 2017), supporting the observed trend.

Everything considered, the results from this experiment demonstrate strong perceptual learning as well as its generalisation to novel tasks, which is strong evidence for the importance of sleep. Only the morning group had additional delayed generalisation effects that were still noticeable after 24 hours, but neither group performed poorly after the specific training; both morning and evening learners did well on the trained backward masking luminance LL task. Furthermore, the findings suggest that the transfer of learning across task changes stems from the action of higher-order cortical processes rather than from low-level visual processing. Moreover, the amount and persistence of learning increments appear to be circadianly controlled, so that long-term consolidation is achieved more effectively by morning learners. With implications for improving training paradigms in skill acquisition and rehabilitation, these results together advance our knowledge of the interaction among sleep, circadian rhythms, and higher-level cognitive processes in perceptual learning.

2.11. General Discussion

The brain's ability to adjust to experience is reflected in PL, which improves sensory discrimination via repeated practice. Although studies have shown that sleep promotes learning consolidation (Stickgold & Walker, 2005; Yotsumoto et al., 2009), little is known about how sleep affects learning generalisation across unfamiliar tasks, characteristics, or locations. The present research examined whether perceptual learning is task-specific and restricted to learnt stimuli or whether sleep acts as a mechanism for generalisation. The two experiments showed that sleep is essential for learning transfer, allowing the acquired perceptual abilities to transcend their initial context. Experiment 1, which used backward masking tasks to test orientation-based learning, showed small transfer during wakefulness but significant transfer effects after sleep. These results were supported by Experiment 2, which used a backward masking task with luminance-based learning. While offline wakefulness alone resulted in insignificant generalisation, gains were still seen in both trained and untrained tasks after a night of sleep. Generalisation was task dependent. However, sleep improved learning transfer in backward masking-based tasks, but it had no apparent impact on pure discrimination tasks (flicker fusion, orientation discrimination, and contrast discrimination). These results highlight the need to investigate task-specific processes of generalisation, as they imply that sleep-dependent consolidation does not enhance all types of perceptual learning equally.

2.11.1. The Effect of Sleep

One of the main conclusions of this research is that sleep improved with generalisation in PL, especially when it came to tasks that required the detection of structured patterns as opposed to low-level sensory discrimination (Cousins et al., 2021; Drouin et al., 2023b; Qin & Zhang, 2019; Walker & Stickgold, 2004). This is consistent with other studies that found sleep reinforces cortical representations, enabling learnt gains to transcend their training environment (Wamsley, 2022). The results of Experiment 1, which concentrated on orientation-based learning, showed strong transfer effects after sleep but little transfer during wakefulness. This trend was repeated in Experiment 2, which employed training based on luminance. These results support the notion that sleep is essential for reorganising neuronal representations, which increases learning flexibility and cross-context transferability (Durrant et al., 2011; Nieuwenhuis et al., 2013).

Between group comparison showed when the learning trajectory start to differ. In both experiments, the Morning and Evening group showed no differences at baseline or immediately after learning (0 hr), suggesting a similar baseline performance. However, after 12 hours, the Evening group shown an improvement on all the backward masking task compared to the Morning group. This improvement is likely to be the benefits of sleep as at the 12-hour timepoint only the those who were I the evening group encountered episode of sleep. However, at the 24-hour timepoint, when the Morning group had also slept, the difference between the groups were gone. In relation to the pure discrimination tasks, no differences between groups were found on any of the task at any time point. This time-locked difference strongly suggests that sleep, not just simply the passage of time, caused the offline improvements and transfer.

However, while improvement was observed, they did not consistently develop across all retest periods or tasks. In contrast to the weak or insignificant effects in pure discrimination tasks, the findings showed considerably large effect sizes in sleep-dependent learning for backward masking-based tasks ($\eta^2 > 0.80$). Even though the effect sizes observed were big in both experiments, this trend is likely to occur in studies of perceptual learning and is also partly due to how the trials were set up. One factor can be related to the within-subject adaptable behavioural paradigms, which generate highly correlated repeated measures characterised by low error variance, resulting in inflated partial η^2 values (Bakeman, 2005; Olejnik & Algina, 2003). Staircase methods that employ fixed baselines often cause post-training variances to be compressed and floor effects, which make contrasts more apparent (García-Pérez, 1998). Additionally, small samples decrease the stability of η^2, leading to increase of probability of overestimation (Levine & Hullett, 2002). When looking at the size of the effects that were seen, these problems should be taken into account. Future analyses should incorporate confidence intervals and possibly other measures of effect size (such as generalised η^2) to assess the stability of the effects.

Mixed-design ANOVA was used to look at the Time x Group interaction, and independent t-tests were used to look at the group effect. These analyses were chosen because the mixed-design ANOVA can examine whether learning trajectory changes over time for the Morning and Evening groups. However, the independent t-test was used to examine at each time point where the differences emerged, isolating the specific effects of sleep (at 12 hours) and their resolution after both groups had slept (at 24 hours). This two-step method keeps group differences separate from overall main effects and correlates well with repeated measures designs that have more than one retest.

Furthermore, the study in this Chapter revealed that morning learners exhibited improved performance in online learning tasks, which aligns with the hypothesis that the brain must undergo changes and form new connections to learn online effectively. Tononi and Cirelli (2003) proposed that sleep eliminates non-essential synaptic connections, which provides a compelling foundation for understanding why sleep could be essential to learning. According to the theory of homeostasis, reducing the strength of synapses during sleep is an important step in maintaining the brain's ability to change and adapt. This downsizing process may create extra room for learning, which could explain why one tend to have an overall understanding after a good night's sleep. However, further research is necessary to validate this theory and explore how performance improvements carry over to testing sessions on the day of learning. It would also be valuable to investigate how variables like age, gender and sleep quality affect learning and memory consolidation. By conducting these types of studies, more profound insights can be gained into how sleep facilitates learning and optimises our cognitive abilities both when awake and asleep.

The concept that learning generalisation happens during sleep has support from research on sessions conducted 12 hours and 24 hours after learning. Specifically for individuals who learned in the evening and then slept, there was an improvement in performance on tasks during the 12-hour retest. This suggests that sleep plays a role in promoting generalisation. Interestingly, those who learned in the morning and then retested after some sleep did not show the improvement. Furthermore, individuals who learned in the evening showed transfer of learning during the 12-hour retest compared to those who learned in the morning. This indicates that when sleep occurs might have an impact on the extent of generalisation achieved. However, during the 24-hour retest, this pattern was reversed; morning learners who had slept exhibited an increase in task performance.

In general, the findings of this study align with previous research (Fenn et al., 2003; Tandoc et al., 2021; Yotsumoto et al., 2009) that suggests sleep plays a role in promoting the generalisation of learning. However, it is important to note that the study design did not allow for a comparison between learning on sleep and learning independent of sleep since all participants experienced both periods of wakefulness and sleep. To confirm the importance of sleep for generalisation and explore the underlying mechanisms, future studies with a more robust experimental design will be needed.

2.11.2. The Effect of Transfer

Sleep facilitates generalisation in perceptual learning, but this is not a universal phenomenon. According to the findings from Experiments 1 and 2, although some visual tasks showed transfer effects, the absence of improvement in pure discrimination tasks (flicker fusion, contrast, and orientation), indicates that generalisation depends on how learnt representations are reorganised during sleep rather than just memory retention. This distinction offers crucial information about the processes underlying perceptual learning, especially with relation to the kinds of learning that may be transferred and consolidated.

The lack of transfer to tasks involving just pure visual discrimination is in line with other studies showing that intensive, repetitive training is usually necessary to improve performance on these tasks. Basic discrimination tasks seem to rely on low-level sensory processes that do not easily benefit from sleep-dependent consolidation in the same manner as the backward masking tasks, which involve higher-level perceptual and cognitive processing (Fahle & Edelman, 1993; Karni & Sagi, 1993).

There is potential that pure discrimination learning will develop slowly and incrementally, requiring many trials and sessions before any changes and improvement to be seen, which is a gap the experiment in this Chapter, a this were not directly examined. However, as shown by Karni and Sagi's (1993) study, which demonstrated that significant gains in a visual discrimination test needed numerous sessions spaced out over a long period (i.e., several days). Similarly, Fahle and Edelman (1993) found that sustained gains in the vernier acuity tests only occurred after a long and intensive training sessions. According to these results, improvements in visual discrimination are usually dependent on extended and regular exposure to stimuli, whereas the backward masking tasks enable comparatively quick learning and transfer because they activate higher-order visual and attentional processes.

The difference between supressed learning effect in the pure discrimination tasks and quick learning in the backward masking tasks suggests the possibility of underlying brain differences in the processing and consolidation of these tasks. One possible explanation of PL in the backward masking tasks includes the idea of top-down regulation from higher cortical areas such as the prefrontal cortex (PFC) and parietal regions, as well as local plasticity in early visual areas (V1) (Seitz & Watanabe, 2005; Watanabe & Sasaki, 2015). Pure discrimination tasks, on the other hand, could rely more on low-level retinotopic plasticity in V1 (Karni & Sagi, 1991; A. Schoups et al., 2001), which depends on a very narrow population of orientation and contrast sensitive neurons. Therefore, to have any measurable changes, the same neurons need to get-togethers ad repeatedly co-activate while neighbourhood neurons remain inactive (Gilbert et al., 2001; Li et al., 2004). Synaptic performance can only be changed by this highly selective and recurrent recruitment process. As a result, low=-level visual tasks are very sensitive to the parameters of the stimulus and to the location in space. Even small changes can affect the precise neuronal co-firing that is needed for plastic change (Seitz & Watanabe, 2005). These limitations are one possible explanation to the limited learning and generalisation found in the pure discrimination tasks and shows the need for extensive, location-specific learning.

The amount of practical learning capacity in pure discrimination tasks may be fundamentally lower than in the backward masking learning if the lack of transfer to these tasks is to be argued to be a result of chance. Since fundamental sensory discrimination processes are already well optimised by past visual experience, pure discrimination tasks may have less space for improvement than tasks involving complicated feature integration, contextual modulation, or sequential processing (Fine & Jacobs, 2002). Prior studies have attempted to enhance pure discrimination tasks even further, but these efforts sometimes require a lengthy training period (Astle et al., 2010). Therefore, the findings from this chapter are consistent with previous research, indicating that the restricted transferability of pure discrimination tasks reflects basic differences in learning processes. While low-level sensory changes in V1 need extended and highly task-specific training to show any apparent gains, perceptual learning that relies on higher-order integration, feature binding, and attentional control is more transferable and generalisable.

2.12. Strength and Limitations

These tasks are widely utilised in visual learning research and allow for the accurate monitoring of changes in perceptual capacity over time by evaluating learning specificity and generalisation using well-established perceptual learning paradigms, such as the backward masking test. Additionally, the calculation of threshold estimations exposes a significant methodological flaw. Instead of using the complete trial data, overall thresholds are commonly derived from the average inter-stimulus interval (ISI) of the final six reversals. This approach minimises early changes in performance arising from task familiarisation or fatigue effects, therefore providing a more reliable and correct threshold estimate (García-Pérez, 1998; Levitt, 1971).

However, some limitations should be acknowledged. Firstly, the interpretation and analysis of the data assumes that participants are not too tired, and performance remained stable both within and between sessions. If tiredness develops randomly, it might provide a confound as performance reductions could not follow a regular trend across individuals or sessions. The inherent unpredictability complicates the determination of whether the changes in threshold represent actual learning effects or merely temporary reductions in attentional capacity. Integrating objective or subjective markers of consciousness, such as self-reported tiredness or changes in reaction time, could help identify the difference between improvements in learning and short-term changes in performance. Secondly, the possible small sample size and strongly related repeated-measures methodology are effective for identifying within-subject changes. This problem fits with established statistical artefacts in perceptual-learning research and must be considered when assessing the significance of observed effects.

2.13. Conclusion

The field of perceptual learning has both important theoretical applications and considerable practical applications. It offers crucial theoretical insights into the flexibility and plasticity of adult perceptual systems, as well as an in-depth understanding of the constraints that are placed on how information is processed by an individual subject. It also explains how systematic training affects the development of the subject's perceptual state. On a practical level, PL implies a potentially beneficial non-invasive technique for developing perceptual proficiency in healthy individuals. Additionally, it provides a successful training-based intervention approach for treating perceptual deficiencies among individuals with a range of cognitive difficulties.

Our empirical results add to the body of behavioural research that is currently being conducted, particularly regarding the transferability of learned skills and the important role that sleep plays in the process of learning. In the past two decades, a growing number of studies have shown that learning continues in the brain even after initial training is complete. Instead, it continues to learn even when there is no additional practice - a phenomenon known as "offline" learning. Interestingly, this kind of learning seems to be most prominent while asleep. However, the underlying brain processes that support this offline learning during sleep are still unclear and completely undefined despite much investigation.

CHAPTER 3:

The Role of Sleep and Wakefulness in Attentional Learning: Investigating Online and Offline Consolidation

3.1. Abstract

In the field of selective attention, the focus is on the complex interaction of brain functions that enable individuals to filter and evaluate sensory input. This research is crucial for understanding learning mechanisms and the performance of daily tasks. The objective of this study is first to evaluate whether attentional learning can be learned, and secondly, whether the time of learning (online and offline sleep) would have an impact on the effect of learning. Specifically, the study differentiates between top-down, goal-oriented attention and bottom-up, stimulus-driven attention. Two tasks (Attentional Capture and Visual Search) were used to test the different process streams. The purpose of the tasks was to evaluate the effectiveness of attention distribution before and after periods of sleep or wakefulness. Participants were separated into groups that were either morning or evening in order to investigate the temporal structure of learning as well as the potential function that sleep plays in consolidating learned tasks.

Two separate groups of participants were recruited, one for the attentional capture task and one for the visual search task. Both online and offline were tested by allocating the participant to either the morning or evening group. Interestingly, online learning sessions demonstrated improvements in reaction times, indicating significant performance enhancements. However, there was no enhancement observed after sleep, which contradicts prior research that sleep aids the consolidation of perceptual learning tasks. This research indicates that the relationship between sleep and attentional learning is more intricate than previously thought. While perceptual learning seems to depend on sleep, attentional learning does not necessarily follow the same pattern. This disparity could be due to its integration of the learning processes. The study highlights the need for exploration using methodologies to unravel the complexities of sleep's role in learning,

particularly regarding individual differences, task specificity and involvement of different sleep stages.

3.2. Introduction

In many reviews and research in the literature, selective attention represents the cognitive ability necessary for individual to focus on important details while ignoring distractions (Desimone & Duncan, 1995; Treisman, 1960). This allows people to learn and digest information in a way that makes sense to them and to make choices when issues get difficult. From navigating a complex visual world to sustaining concentration in the face of conflicting stimuli, the capacity to flexibly allocate attentional resources is essential for completing goal-directed activities. Imagine being in a café trying to have a conversation with someone next to you. Despite the surrounding environmental factors, our minds possess the ability to focus on the words spoken by our friends or family members effortlessly by filtering out the background noise of other conversations, clattering dishes, and the whining of a coffee machine. This skill of paying attention is not just convenient; it is a cognitive technique that allows us to engage in meaningful interactions even in distracting surroundings. Therefore, selective attention is believed to be critical for understanding many occurrences in learning.

A long-standing topic in the field of psychology is whether learning and experience can improve attentional processes and if offline consolidation mechanisms, such as sleep, can affect such learning (Ahissar & Hochstein, 1997; Jiang & Chun, 2001). This is because attention plays a crucial role in directing cognition. Only a small amount of research has been conducted to investigate how much attentional learning follows similar consolidation trajectories to perceptual learning, which is the improvement of sensory discrimination via repeated exposure (Fahle, 2005; Karni & Sagi, 1991). The process of learning is influenced by selective attention, which has implications for generalisation. When learners focus on the characteristics of a task, they become better at recognising and adapting to similar situations. This ability to selectively attend to components is crucial for developing thinking and applying learned knowledge in various academic and real-world scenarios.

Furthermore, the development of selective attention can be understood by considering it from previous literature contributing to this field. From an evolutionary perspective, having the ability to give preference to salient stimuli—such as threats or food sources—over meaningless background activity would have provided significant survival benefits through the selective allocation of cognitive resources. From an evolutionary viewpoint, the ability to prioritise salient or survival-relevant stimuli explains the power and universality of selective attention as a mechanism (Cosmides & Tooby, 1994; Öhman & Mineka, 2001). However, while this viewpoint offers a compelling framework, it is primarily theoretical and may oversimplify the many processes behind attention in contemporary cognitive environments.

In contrast to early deterministic models of attention, which characterised it as an involuntary bottleneck (Broadbent, 1958), modern ideas stress its dynamic, adaptive character. For example, reviews looking into the biased competition model (Desimone & Duncan, 1995) highlights that selective attention is not a filter but rather an active and dynamic system that shapes our experiences, learning, and relationships. This suggests that stimuli will compete for neural representation, and attention assists in selecting goal-relevant information by biasing this conflict. Still, this model is not without its limitations; criticism has arisen for failing to properly account for how top-down motivation affects attention distribution (Pessoa, 2009).

Converging psychological frameworks demonstrate this interaction. Corbetta and Shulman's (2002) dual-network model distinguishes between goal-directed (dorsal) and stimulus-driven (ventral) systems, while Treisman and Gelade's (1980) Feature-Integration Theory and Wolfe's Guided Search (1994) model elucidate the joint influence of features and goals on cognitive selection. These viewpoints collectively underscore selective attention as an evolutionarily established yet cognitively adaptable system, perpetually influenced by external needs and internal objectives.

Additionally, selective attention is not unchanging; differences in cognitive ability, previous knowledge, and neurodevelopmental characteristics cause significant variances between individuals. Studies have shown, for example, that selective attention performance is substantially predicted by working memory capacity (Engle, 2002) implying that executive functioning is tightly correlated with attentional control. Still up for debate, however, is the causality of this association. Therefore, even if it is helpful to understand selective attention as an adaptable and enhanced cognitive process, this must be balanced by a knowledge of its limitations and variability.

Although, as previously mentioned, selective attention is often characterised as a basic cognitive mechanism allowing individuals to focus relevant inputs while preventing distractions, it is now increasingly viewed as a flexible process moulded by learning and experience. The conventional view once held that sensory salience or inbuilt biological limitations governed attentional selection. More recently, however, studies have shown that with repeated exposure and reinforcement, attention may be taught to develop into more efficient and goal-directed (Chun & Jiang, 1998; Leong et al., 2017; Rehder & Hoffman, 2005). This process is often referred to as 'learnt selective attention', which reflects the ability of individuals to fine-tune attentional resources based on the demand of a task, influence of the environment and the acquired expectation (Kruschke, 2001; Turk-Browne et al.,

2005). In order to allocate cognitive resources efficiently, attention entails either enhancing or suppressing input processing (Reynolds & Chelazzi, 2004). The selectivity ensures that attention is regulated differently to give priority to information that is important to the goal over distractions, rather than being evenly distributed across all stimulus elements (Broadbent, 1958; Desimone & Duncan, 1995; Treisman, 1960). The term "learning" here refers to the experience-dependent alteration of attentional allocation, which implies that attentional biases may be formed by past exposure and used in future circumstances. However, the distribution of attention is very context-sensitive and changes constantly based on the demands of the task and the cognitive control skills of an individual.
Learning could change selective attention, according to empirical studies, and task relevance and stimulus salience have been identified as key determinants of attentional regulation (Chun & Jiang, 1998; Leber et al., 2008). Task salience ensures that attention is automatically drawn to high-contrast or novel stimuli, regardless of their relevance to a task (Forschack et al., 2023), whereas task relevance focuses attention on goal-driven stimuli, thereby improving processing efficiency (Boehler et al., 2011; Fecteau & Munoz, 2006).

One of the most important questions in this area is whether these attentional improvements are merely wake-dependent or whether they are consolidated during offline processes, such as sleep. According to research on perceptual learning, discrimination and efficiency are improved by repeated exposure to sensory stimuli, while retention and generalisation are improved by post-training sleep (Stickgold et al., 2000; Walker & Stickgold, 2004). It is unclear, however, whether attentional learning has a similar consolidation trajectory. It was shown by Sigman et al. (2005) that training in a visual conjunction search task made people respond faster and more accurately. This suggests that practice may help attentional selection. Although performance was only evaluated during training sessions, their results were regarded as evidence of improved neural efficiency in attentional networks. However, it remains unclear whether offline consolidation maintains or strengthens these gains. However, in a visual discrimination test, Schoups et al. (2001) found that attention-related brain plasticity depended on post-training sleep, suggesting that specific components of attentional learning may be sleep-dependent. The degree to which this holds true for top-down compared to bottom-up stimulus-driven attentional regulation has not been well investigated.

Selective attention is a complex concept that encompasses two main processes: processes that operate from the top down and processes that operate from the bottom up. Top-down attention is focused on a goal-oriented decision (Theeuwes, 2010). An individual's cognitive targets, expectations, and intentions serve as their compass (Desimone & Duncan, 1995). Basically, it is a proactive way of choosing what to pay attention to when faced with a particular circumstance. Individuals can intentionally direct their cognitive resources towards certain information using this type of attention, frequently in line with their present goals. Top-down attention is helpful for many kinds of everyday tasks. For example, individuals use top-down attention to focus on the content and understand the meaning of words when reading a book (Egeth & Yantis, 1997). Theoretical frameworks have shed light on the mechanisms of top-down regulation of attention. The Feature-Integration Theory (Treisman & Gelade, 1980) claims that attention integrates different perceptual features, such as colour, shape, and orientation, into cohesive object representations, highlighting its constructive function in perception.

This model shows that when addressing problems, top-down attention ensures that cognitive assets are focused on the task at hand by keeping the individual focused and ignoring irrelevant distractions. Effective use of top-down attention is essential for higher-order cognitive processes, including critical thinking and decision-making.

In contrast, bottom-up attention is uncontrollable and activated by external stimuli regardless of the environment. One possible explanation for this is that it is an unexpected occurrence, such as a loud noise that abruptly grabs our attention. On the other hand, review on works showed that stimuli naturally drive the process of bottom-up attention (Itti & Koch, 2001). Some environmental or sensory factors attract attention regardless of cognitive goals, which is why it happens. This type of attention, which is characterised by its reactive nature, functions as a warning system for information that is perceived in the environment that is uncommon or may be noteworthy (Belopolsky et al., 2010). The research that is conducted on bottom-up attention makes it feasible to get a good understanding of how humans prioritise and interpret sensory input in real-time, which is often necessary when rapid responses are required. To have a complete understanding of how people make decisions, how they deal with challenges, and how they effectively traverse their environment, it is vital to have a dynamic interaction between top-down and bottom-up attention processes.

Overall, attention can be consciously directed toward an item in a goal-directed way (e.g., when you are looking for your bike among other bikes); attention can also be acquired subconsciously by a physically salient stimulus (e.g., a flashing light) that distinguishes itself from the surrounding items in some fundamental feature (e.g., colour and orientation). This is a crucial aspect relating to learning. It was hypothesised that the effective learning occurs when both types of attention work well together. Top-down attention assists us in maintaining focus on our learning objectives, managing distractions, and establishing connections between new information and our existing knowledge. At the same time, bottom-up attention signals us to pay attention to new information that might be important.

Studies on perceptual learning have shown that exposure to certain visual characteristics on a regular basis improves discriminating skills, which in turn improves task performance (Censor et al., 2006; Chen et al., 2016; Fiorentini & Berardi, 1980). These enhancements suggest that PL plays a crucial role in focusing attention on complicated stimuli, potentially enhancing both top-down and bottom-up processing. Su et al. (2014), for example, investigated the effects of training in colour-orientation conjunction tasks on perceptual discrimination. Participants learnt to distinguish a goal stimulus from distractions using elements that changed in colour and orientation. According to the research findings, learning significantly improved accuracy and decreased response time, indicating that perceptual learning improved attentional selection efficiency. Importantly, post-training enhancements were restricted to combinations of learnt features, suggesting that learning effects strengthened attentional selection for the learnt characteristics rather than being generalised across all visual stimuli. The findings highlights that perceptual learning could be a technique for gradually improving selective attention to intricate, task-relevant inputs.

In the same vein, Sigman et al. (2005) investigated the effects of extended learning on brain plasticity and attentional efficiency in a visual conjunction search task. To test top-down attentional control, participants had to locate a specific shape among a field of distractors. Participants' response times gradually decreased across many training sessions, indicating improved cognitive efficiency and attentional selection. Significantly, these enhancements were linked to decreased activity in frontoparietal attentional networks, according to functional imaging data, indicating that repeated practice of the task resulted in a more effective brain processing approach. These results demonstrate that attentional learning reduces the cognitive load necessary to perform visual search tasks by enhancing perceptual sensitivity and optimising brain resource allocation. As a result, it is hypothesised that perceptual learning facilitates the allocation of attention to learnt complex stimuli, due to the idea proposed by Dowd and Mitroff (2013), which suggests that attention is sorted through a selection process driven by bottom-up cues (e.g., when attention is captivated by an item's physical uniqueness) and top-down cues (e.g., when attention is guided toward a task-relevant location). These results are consistent with theoretical models that propose PL improves both top-down and bottom-up processes to enhance attention allocation. Dowd and Mitroff (2013) state that attentional selection processes via a dual-process framework in which top-down signals (such as task-relevant objectives that direct attention) and bottom-up cues (such as salient objects that naturally catch attention) interact to maximise visual processing. Their study demonstrated that working memory signals are crucial for directing both top-down and bottom-up attention, thereby supporting the notion that attentional selection involves a dynamic interplay between goal-directed processes and stimulus salience.

Perceptual learning research has found that practice can increase performance in discriminating (Karni & Sagi, 1991; Li et al., 2004) and detection (Meyer & Petrov, 2011; A. A. Schoups & Orban, 1996). These experiments have shown a significant improvement in a spatially or featurally specific way, implicating the early sensory cortex as the location of plasticity, which has also been shown in electrophysiological experiments. For instance, in the study by Schoups et al (2001), they found that the neuronal correlates are significantly related to behavioural improvement and that training in monkeys induces a specific and efficient neuronal sensitivity in the V1 region. This indicates that the characteristics of stimuli are tuned to individual neurons. Although most research focuses on training on specific regional locations or stimulus feature categories, there has been considerable discussion regarding the causes of more general task improvement. Some research, for instance, has linked learning to higher cortical regions (Law & Gold, 2008). Plasticity effects in later visual cortical regions, including areas such as V4, have been observed because of perceptual learning (T. Yang & Maunsell, 2004). It has also been demonstrated that learning in activities, including visual search, is less specific (Fahle, 2005). In the study carried out by Sireteanu and Rettenbach (1995), they highlighted the non-specificity of perceptual learning effects in visual search tasks and therefore set a new insight that plasticity for acquiring a visual search task is higher than in sensory cortices. One open question is whether learning can improve the effectiveness of the dynamic top-down attention-biasing process itself through practice learning, as opposed to expressing stronger visual discrimination abilities for a specific type of goal or location or improving speed and/or performance on a task in general. This form of non-specific learning is still unclear, and more precisely, the coupling of learning inside a visual search task to investigate the impacts of training top-down attention is open to research. Another intriguing question is to evaluate how the learning effect differs between top-down and bottom-up attentional learning, which remains unclear within the literature.

The field of science has devoted attention to exploring the relationship between sleep and learning. Many studies have shown that sleep has effects on learning activities. Early research by Smith (2001) and subsequent studies by Marshall and Born (2007) and Fattinger et al. (2017) have collectively provided evidence that sleep can significantly enhance memory consolidation and learning across different domains. While the focus has often been on the immediate results, this improvement can be extended over time. For instance, Wagner et al. (2006) found that sleep following the acquisition of learnt information can enhance memory retention for up to four years. While it is commonly assumed that sleep aids are involved in memory consolidation within the visual perceptual learning domain, recent investigations have unveiled a more intricate understanding (Gais et al., 2000; Mednick et al., 2003). Some previous research indicates that sleep may not universally benefit all forms of learning in the way it has not been consistently demonstrated to improve tasks. For example, when it comes to memory tasks that involve remembering information, sleep has shown improvements. However, when it comes to learning tasks related to adapting our perception, the role of sleep might not be as crucial. This suggests that the process of consolidating memories during sleep is influenced by the type of learning and the neural circuits involved.

Furthermore, within the realm of learning itself, there can be variations in how sleep affects task performance. Some complex tasks show an improvement after a night of sleep, while others do not demonstrate any substantial changes. This variation not only sheds light on the relationship between sleep and learning but also raises an important question: Does attention-based visual learning rely on sleep for consolidation, or does it follow a different trajectory? As researchers delve deeper into understanding how sleep impacts various forms of learning, the controversy surrounding this topic persists. However, it requires more experimental studies to ascertain the specific impact of sleep on attention-based learning. By focusing on this chapter of research, it can uncover whether attention-based learning is as dependent on sleep as it is and if it exhibits different characteristics in terms of consolidation. The impact of this research goes beyond the sphere. It has real-world implications for methods, cognitive recovery, and our understanding of development and functioning.

Attention is a network of specialised brain systems that assist in selecting relevant inputs while suppressing irrelevant information, rather than a single cognitive function. To ensure maximum cognitive function, these networks undertake intricate calculations to filter competing distractions, resolve target selection conflicts, and control attentiveness (Lega et al., 2019; Oberauer, 2019). Salient environmental cues may attract attention involuntarily (bottom-up processing) or actively (top-down processing), which is motivated by task objectives and expectations (Itti & Koch, 2001; Theeuwes, 2010). Learning, decision-making, and behavioural results are all impacted by how individuals assign cognitive resources to their environment, and this dual process is crucial in deciding these outcomes.

Empirical evidence supports the significance of attentional control in cognitive information processing, demonstrating that problems with attention are linked to inefficient encoding, increased impulsivity, and accuracy-speed trade-offs (Heitz, 2014; Metin et al., 2013). In settings like air traffic control, clinical diagnostics, or complex visual search tasks, where quick decisions must be made under a lot of cognitive strain, sustained attention is especially crucial. According to research, attentional engagement problems happen when cognitive demands are higher than available attentional resources. This leads to poor task performance, lower accuracy, and slower reaction times (Oberauer, 2019). These results emphasise how important it is to comprehend how training might improve attentional processes and whether these gains are long-lasting.

The effect of sleep on attentional maintenance is one topic of growing scientific interest. It is well acknowledged in a meta-analysis that sleep is crucial for cognitive function, especially executive control and memory consolidation (Lim & Dinges, 2010). Fewer studies have looked at whether post-training sleep-dependent consolidation enhances attentional learning itself, even though a large body of research has studied how sleep deprivation (SD) affects attentional ability. It remains unclear whether attention-based learning follows a similar trajectory or whether gains are only wake-dependent, given that sleep has been shown to enhance perceptual learning (Walker & Stickgold, 2006)

To investigate whether visual attention tasks can be learnt and whether sleep would help with the learning for both top-down and bottom-up processes, two different tasks will be used. Attentional capture tasks provide a classic illustration of bottom-up attention. These tasks include presenting participants with items that, because of their importance, novelty, or sudden presence, naturally and involuntarily grab their attention. Individuals respond to these stimuli—which are well-known attention-getters—without realising it (such as colours, brightness, and shape). Individuals in these activities must react when certain, noticeable stimuli emerge, making them reactive in nature. The idea of a stimulus-driven, external process is reinforced by their limited cognitive control over what attracts their attention (Belopolsky et al., 2010; Yantis & Jonides, 1984). Therefore, the attentional capture task is a good example of a bottom-up process task because the features of the stimuli, like the colour of the presented stimuli, in this instance, usually play a role in capturing our attention. Our motives or internal states do not influence these inherent features of the world around us.

On the other hand, visual search tasks represent top-down attention. Under the direction of predetermined objectives, participants actively search among distractions for a specified target item in these activities. Goal-oriented, voluntary, and regulated procedures are required for these activities. To find the target, individuals concentrate on specific characteristics or qualities using their cognitive resources. Participants have a considerable cognitive responsibility from this active and purposeful search since they must stay focused on their objectives and ignore distractions in order to achieve their objectives (Wolfe et al., 1989). Notably, bottom-up and top-down attention function independently of one another and interact to affect how individual interpret and comprehend the outside environment. However, bottom-up and top-down attention may operate simultaneously, according to previous studies (McMains & Kastner, 2011; Pinto et al., 2013). Both top-down (such as task-related goals) and bottom-up (such as prominent aspects of stimuli) elements affected the attention of participants in a visual display used in the study (Leber et al., 2008; Theeuwes, 1994). According to the results, top-down variables influenced how much attention was assigned, even when bottom-up elements did indeed catch attention.

Examining the relationship between attention mechanisms and sleep is essential for getting an insight into the temporal dynamics of learning. This becomes especially significant when assessing whether sleep contributes to the strengthening of attentional learning or if enhancements arise solely from processes occurring while awake. The research presented in this chapter seeks to ascertain if attentional learning takes distinct routes during offline and online learning scenarios. In this context, offline learning refers to periods when an individual is not actively participating in the task at hand. This can include both offline sleep (e.g., sleep-dependent consolidation) and offline wakefulness (e.g., inactive consolidation in the absence of further exposure to the learning task). Whether sleep enhances attentional learning, as suggested by perceptual learning research, or whether attentional gains occur only as a result of repeated task exposure and reinforcement while awake, is a key topic.

Whether sleep consolidates attentional learning has been the subject of contradictory studies in the past. According to some research, active reinforcement rather than passive consolidation is the primary mechanism behind attentional control, which means that performance gains only happen during training sessions and are not enhanced by post-training sleep (Law & Gold, 2008; Lim & Dinges, 2010). However, other research suggests that sleep has little to no impact on bottom-up, stimulus-driven attention but selectively improves specific attentional processes, especially those related to top-down control mechanisms (Gevers et al., 2015; A. Schoups et al., 2001). These differences bring up a crucial empirical question: Is attentional learning exclusively wake-dependent, or does it also follow the same sleep-dependent consolidation trajectory as perceptual learning?

The current work investigates attentional learning in two different paradigms to answer this question: visual search tasks, which evaluate top-down, goal-directed attention, and attentional capture tasks, which evaluate bottom-up, stimulus-driven attention. This research attempts to ascertain if offline consolidation processes alter attentional performance improvements by varying the training period (morning vs. evening) and post-training interval (sleep vs. awake). Performance gains during post-learning sleep should be higher than during a comparable period of awake if attentional learning is sleep-dependent. On the other hand, enhancements should only occur during training sessions and not after sleep if attentional learning is only wake-dependent.

The present study intends to add to the larger body of literature on attentional learning, executive control, and memory consolidation by methodically examining these processes and advancing theoretical debates on the function of sleep in cognitive plasticity. Gaining further insight into whether offline brain reorganisation affects attentional learning might have important ramifications for educational tactics, cognitive training therapies, and performance optimisation in high-demand settings.

3.3. Materials and Methods

3.3.1. Participants

Thirty healthy volunteers with normal or corrected-to-normal vision were recruited for the attentional capture task. A separate group of thirty participant were recruited for the visual search. All participants were recruited via the university's internal system and were compensated for their time with either 16 course credits or £13. The study received approval from the research ethics committee at Cardiff University (EC.18.02.13.5226G). Participants were instructed to maintain their regular sleep patterns and refrain from consuming alcohol or caffeinated beverages for two weeks prior to the study's commencement and throughout all testing sessions.

3.3.2. Experimental Set-up

Matlab was used in combination with the Psychotoolbox program to create the visual stimuli, which were used in both of the tests (Attentional Capture and Visual Search). Following this, the stimuli were presented on a computer monitor (ASUS VG248QE, viewing distance: 61.5 cm, screen size: 54 × 30 cm). To ensure that there was no interference from daylight or any other brightness, the participants were situated in a completely dark room. During the course of the experiment, a chin rest had been used in order to keep the head in a constant posture and to minimise any movement that would have the potential to influence the results. No eye-tracker was used in this experiment, due to the limited resources available due to the COVID-19 impact.

3.3.3. Visual Stimuli

In the AC task (without the top-down component), the stimuli display included one diamond and 4, 6, or 10 blue circles. In this task, one of the circles could be the distractor, in which case it would be red, rather than blue. Within each shape was the letter "L" or the letter "R". All the presented shapes that were given were different in terms of the distance between them on an imagined circle that had a diameter of three, five, or ten around the fixation dot that was placed on a black the background of the screen (see Figure 1.1 for example).

On the other hand, in the VS task, the display consisted of a rotating set of letters arranged in a circle around a central fixation dot. Among the letters in this circular array, one was a 'T', rotated either the tail of the 'T' pointing left or right, and the other letters were rotated 'Ls' (see Figure 1.2 for example). The stimuli were presented in white letters on a black background.

3.3.4. Experimental Design

The experiment comprises two distinct perceptual tasks designed to assess attentional capture and visual search abilities. The tasks were conducted over four days, with each day containing a specific number of trials based on the parameter setups of each task.

In the AC task, participants were instructed to search for the only diamond in the display and indicate whether there was a letter "L" or letter "R" displayed inside the diamond (by pressing the left or right key on the keyboard). Participants were instructed to react as quickly and accurately as possible. The number of circles varied across trials, and each set size included trials with different distractor conditions. In some trials, one of the circles was the only red item on display, acting as a distractor. In other trials, the distractor will be absent, and all shapes will be displayed in blue colour. The identity of the letter within each shape was randomly determined, with the constraint that there was an equal number of "L" and "R" letters across trials. The trials were randomly intermixed to prevent predictability. The AC task consisted of 144 trials per day, conducted over four days, resulting in a total of 576 trials. The 144 trials per day were structured based on 18 parameter setups, combining 3 eccentricities (3, 5, 10), 3 set sizes (4, 6, 10), and 2 distractor conditions (absent or present). Each parameter setup included 8 trials.

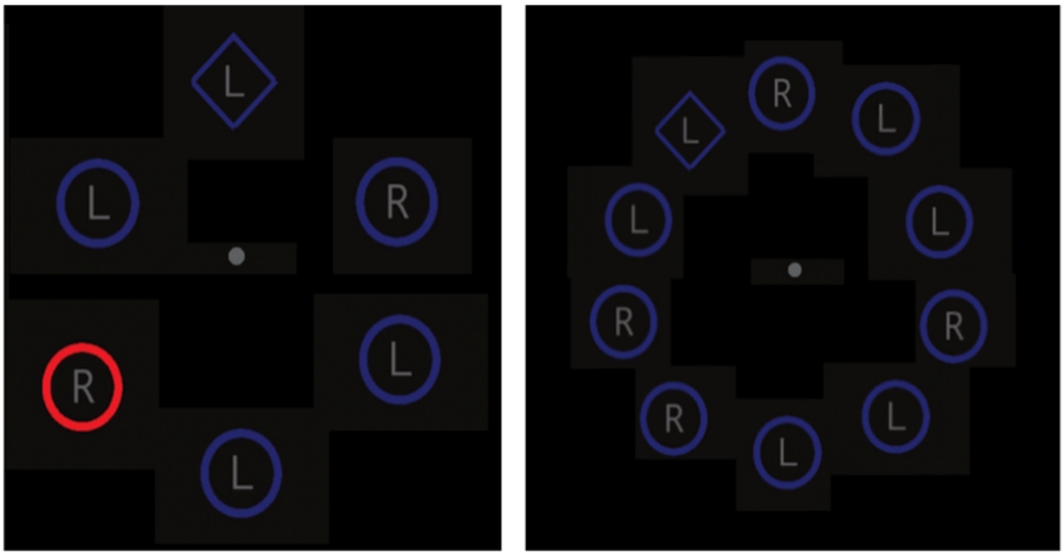

Figure 1.1. Example of the attentional capture task (no top-down component). Participants were instructed to indicate the letter located inside the diamond. The left panel illustrates the distractor is different from the target with a set size 6; the right panel illustrates no distractor is present with a set size of 10.

During the VS task, participants were instructed to keep their eyes fixated on a dot without any movement, which was located at the centre of the screen at the exact location throughout the whole testing session. This strict requirement ensured that each participant was relying on their peripheral vision to locate the target stimulus. On the screen, a circle of letters was displayed, with one letter "T" being rotated. The crucial aspect was that participants had to identify which direction the tail of the 'T' was pointing (either left or right). To respond, participants were given a choice; if they observed the tail of the "T" pointing towards the left, they pressed the 'left' key; conversely, if it pointed towards the right, they pressed the 'right' key. This task aimed not only to measure participants' peripheral vision acuity but also to assess their ability to process and respond to information while maintaining a fixed gaze. Similar to situations in real life, where a individual must remain aware of our surroundings despite focusing on something specific.

Based on the conditions within the VS task, each session consisted of 132 trials per day, conducted over four days, resulting in a total of 528 trials. In each session, it includes 9 parameter setups, combining 3 eccentricities (3, 5, 10) and 3 set sizes (2, 6, 10). The number of trials per parameter setup varied, with 20 trials per setup for set size 10 and 12 trials per setup for set size 2 or 6.

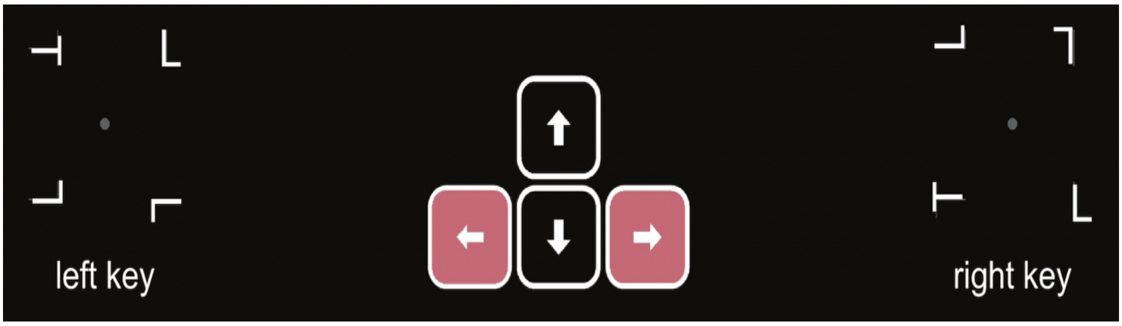

Figure 1.2. An example of the visual search task. Participant were instructed to answer whether the target stimuli ('T') was pointing to the left (left diagram) or pointing to the right (right diagram). Participant were instructed to make the response on the keyboard.

Both tasks were assessed based on how fast participants reacted and how accurate they were in their responses. The AC task looked at how much the distracting element affected participants' ability to focus on the task at hand, whereas the VS task focused on how participants could keep their gaze fixed and accurately respond using their side vision. The study aimed to understand how bottom-up and top-down attention processes interact by analysing reaction times and accuracy levels under different conditions. The goal was to determine if sleep could improve learning in an attentional-based perceptual learning task, similar to the effect found in Chapter 2 with the backward masking task.

3.3.5. Assessment and Experimental Timeline

For both the AC and VS task, participants were randomly allocated to either the morning or evening group. To reduce the potential for confounding effects related to task familiarity, practice effects, and cognitive fatigue, a between-groups design was used. This can also avoid prior experience with one task, which could influence performance on the other, which will make it difficult to differentiate the effects of sleep on learning. Furthermore, learning in one task may unintentionally improve or impair performance in another due to transfer effects, which may result from overlapping cognitive pathways across different attentional tasks. To ensure that the effects were more directly related to sleep and time of day rather than to the inter-task interference, separate participants were allocated to the two tasks.

In the morning group participants completed the first session in the morning and were retested after 12 hours of wake period (no nap in between), followed by a 24-hour retest after a night of sleep, then another retest after 36 hours. In contrast, the evening group participants completed the first session (learning) in the evening and completed their retest after an overnight sleep and their 24-hour retest after another 12 hours of wakefulness, then tested again after another 12 hours (Figure 1.3). By manipulating the time-of-day which the tasks were learned, the experiment design could allow for the examination of whether there is any improvement in the task that was learned and by testing participants after sleep can help identify whether sleep is beneficial to the learned task.

During the first session participants complete four blocks of the AC task which allows us to record a baseline pre-learning measure which can be used to compare to participants' post-learning session. Session 2 was held 12-hours after the first session with the same task and for the same time-length, this will allow for the assessment of the need for sleep for the consolidation of the learning to occur. Session 3 was then carried out another 12 hours after the second session (i.e., 24 hours post-learning). Finally, session 4 was carried out after a further 12 hours of either wake or sleep period. Following this pattern, we can assess at which stage of time spent offline is needed (sleep or wake) for the consolidation of learning to occur.

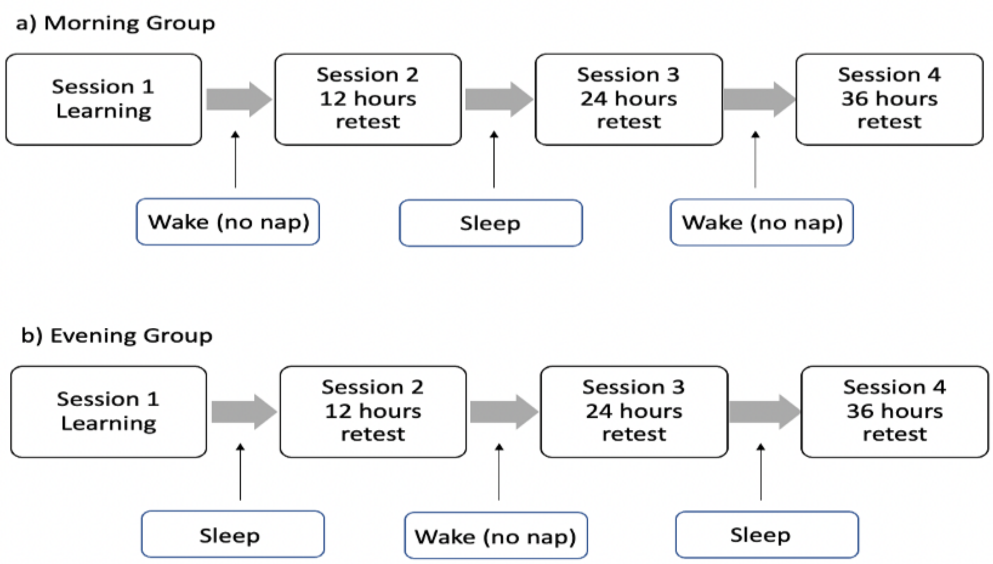

Figure1.3. Participants were randomly assigned to either the morning or the evening group, for both tasks. Diagram a) showing the experimental timeline for morning learning group. Diagram b) showing the experimental timeline for evening group learners.

Participant data were recorded and pre-processed using MATLAB R2021b (MathWorks, Inc., Natick, MA, USA). During pre-processing, trials in which participants failed to respond or provided incorrect responses were excluded from the RT analysis to ensure accurate estimation of perceptual processing speed. The RTs were calculated based on correct trials only, and accuracy was calculated as the proportion of correct responses. Based on the distribution of the data, it was found that the data did not follow a normal distribution. Therefore, a non-parametric t-test (Wilcoxon rank-sum) was used for the analysis. Since the Wilcoxon rank-sum test add together all the individual observations to get the Sum of Ranks, therefore the numbers can look very big. In this study, every participant's trial was considered as a separate observation instead of averaging by individual. This was done to get a more comprehensive look at the subtle changes occurring within a session and to make it easier to identify small effects. Furthermore, multiple t-tests were conducted, and the Benjamini-Hochberg correction was applied to control for the false discovery rate and maintain statistical rigour. This method effectively minimises the risk of Type I errors while preserving sensitivity to detect significant learning effects.

Online learning (within-session improvement) was examined by comparing RTs between the start and end of each testing session for the morning and evening groups. To investigate offline learning, experiment was conducted with comparison between sessions separated by sleep or rest. To analyse between-group differences, time comparisons (between-group) was conducted to assess whether learning trajectories differed between the morning and evening groups.

In addition to analysing parameter-specific data, statistical analyses was also performed on the overall performance regardless of parameter variations, providing a holistic evaluation of learning effects. The study aimed to determine if attentional capture and visual search skills showed enhancement over sessions and whether these improvements varied between the morning and evening groups. RT and accuracy analyses collectively yielded convincing evidence of any learning effects, confirming that both speed and precision were assessed as measures of attentional enhancement.

Following common research practice, the experimental data and analytic scripts are kept safe and private on a cloud server (OneDrive). Access is available only through a private link (Appendix xxxx). Once current study is accepted for publication, the data and code will be made publicly accessible via Open Science Framework. This approach ensures both transparency and data protection prior to formal publication.

3.4. Results

3.4.1. Demographic Data

For the attention capture task, 30 participants were recruited for the study. Following the exclusion of one participant who felt unwell during the session, the morning group included a group of 14 participants, with a mean age of 20.43 and an SD of 0.76. The evening group contained a group of 15 participants with a mean age of 21.33 and an SD of 2.41.

For the visual search task, a separate group of 30 participants was recruited for the study. Three participants were excluded from the final analysis, one from the morning group and two from the evening group, due to no-show for experimental sessions. The morning group consists of 14 participants with a mean age of 19.23 and an SD of 2.13, and the evening group consists of 13 participants with a mean age of 18.38 and an SD of 0.51.

3.4.2. Learning of Attentional Capture Task

3.4.2.1. Online Within-Session Performance

The reaction time (RT) performance was assessed for online learning for the morning and evening groups separately for each parameter, as well as a combined analysis of all parameters. When examining individual parameters, the morning group showed significant reduction in RT for the 10-degree eccentricity, set size 10, distractor absent condition from session 1 start to session 1 end ($Z = 4.153$, $p = .012$). This shows that attentional efficiency significantly improved in the morning group, especially for this specific condition, particularly under conditions with larger eccentricity and set size (detailed in statistical table, Appendix A). On the other hand, the evening did not show any significant improvement in RT across the parameters, as detailed in Appendix B. This implies that the impact of attentional learning may be affected by circadian components, indicating that the morning groups seem to have more significant benefits. Furthermore, as shown in Figure 2, the RT performance for the set of parameters with error bars indicating the standard error mean and the central dot represent the average RT for each parameter for the morning (red) and evening group (blue).

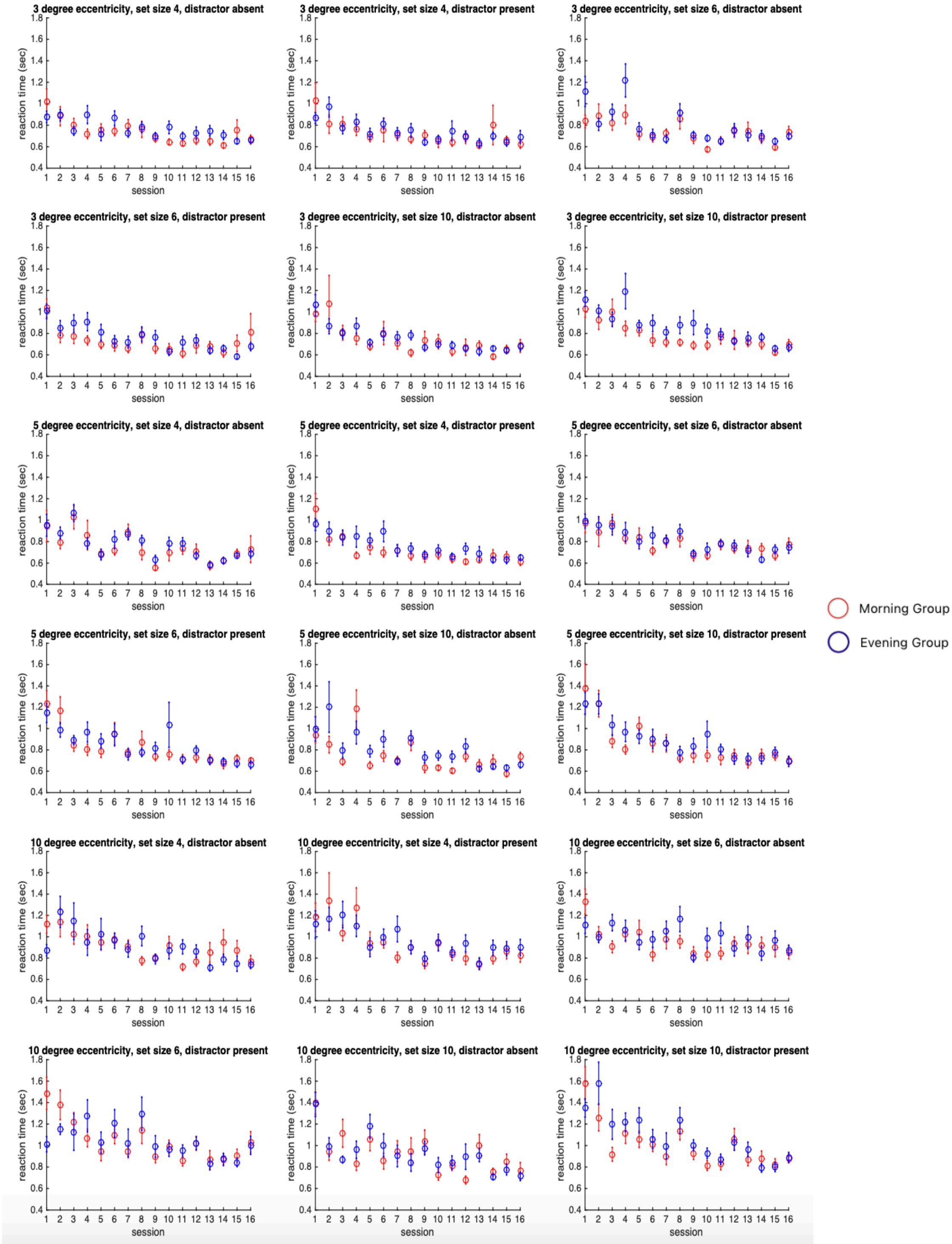

Figure 2. Each figure presents the reaction time (RT) data across different set of parameters plotted separately by eccentricity (3°, 5°, 10°), set size (4, 6, 10), with error bars representing the standard error of the mean and dots indicating the average values for each session. The red dot represents the morning group performance and blue dot represent the evening group.

In addition, analysis was conducted by combining all parameters together (Table 1), significant improvement was found in the morning group between session 1 start and session 1 end ($Z = 6.989$, $p < .001$). However, under this case, the evening group also demonstrated a significant reduction in RT ($Z = 4.224$, $p < .001$), with additional improvement found between session 4 start and session 4 end ($Z = -1.430$, $p < .001$). This suggested that both groups benefited from online training for the AC in general rather than learning only for specific parameters. As shown in Figure 2.1, both groups showed a clear decrease in RT over the sessions.

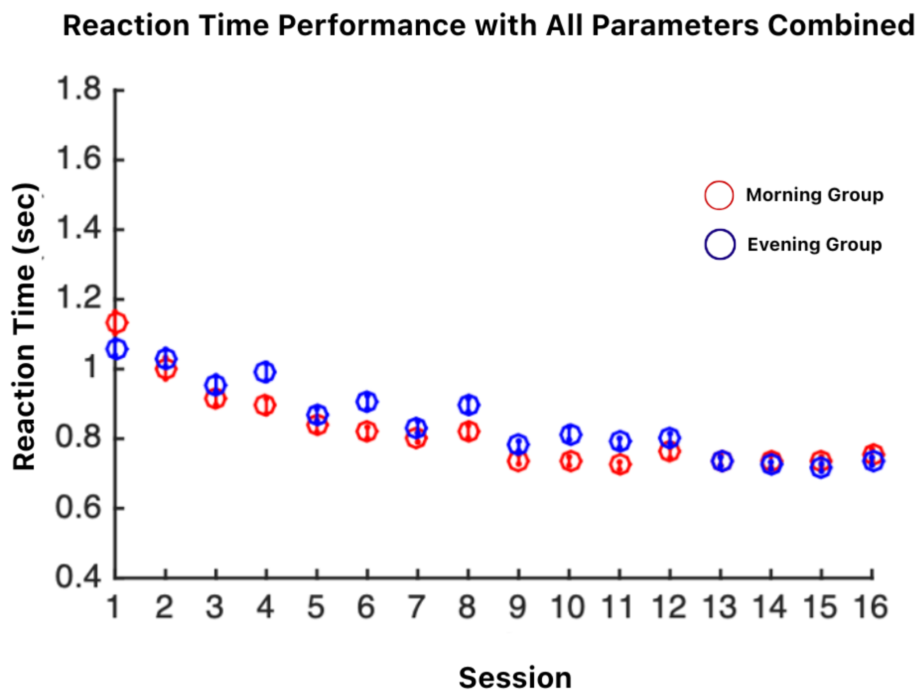

Figure 2.1. The figure represents the reaction time (RT) when all parameters are combined, with error bars representing the standard error of the mean and dots indicating the average values from session 1 to 4 (each session further breakdown into 4 sub-sessions). The red dot represents the morning group performance and blue dot represent the evening group.

Table 1.

All parameters combined: RT performance across online learning session for the morning and evening group

Online Session Comparison (RT)	Morning			Evening		
	Sum of Rank	*Z*	*p (corrected)*	Sum of Rank	*Z*	*p (corrected)*
S1_Start vs S1_End	246478	6.989	<.001***	248358.5	4.224	<.001
S2_Start vs S2_End	226665	1.225	0.286	241995	-1.421	0.256
S3_Start vs S3_End	219556	-0.817	0.464	240338	-1.294	0.277
S4_Start vs S4_End	216951	-1.213	0.286	253605	-1.430	<.001

Note. Significant levels: *<0.05, **<0.01, ***<0.001. The large sum-of-rank values show that the analysis was done on consolidated trial-level data. This means that all of the participants' trials were combined within each condition, so the analysis treated all of the trials as one aggregated sample per session to find within-session learning trends.

When looking at the accuracy scores during each session of online learning, neither the morning (Appendix C) nor the evening group (Appendix D) showed significant improvement across all parameters. Combined parameter analysis also showed that there are no significant changes in accuracy scores between the start and end of all the learning sessions (Table 1.1). However, from the plot displayed in Figure 2.3 and Figure 2.4, and can see that individuals maintained a high accuracy rate throughout the sessions for both the morning (red) and evening (blue) group.

Table 1.1

All parameters combined: Accuracy score across online learning session for the morning and evening group

Online Session Comparison (Accuracy)	Morning			Evening		
	Sum of Rank	*Z*	*p (corrected)*	Sum of Rank	*Z*	*p (corrected)*
S1_Start vs S1_End	252523.5	-0.724	0.664	289741	-0.674	0.667
S2_Start vs S2_End	256788	1.222	0.490	289440	-1.051	0.513
S3_Start vs S3_End	251244	-1.622	0.367	287550	-1.858	0.331
S4_Start vs S4_End	250758	-1.735	0.331	290790	-0.539	0.935

Note. Significant levels: *<0.05, **<0.01, ***<0.001. The large sum-of-rank values show that the analysis was done on consolidated trial-level data. This means that all of the participants' trials were combined within each condition, so the analysis treated all of the trials as one aggregated sample per session to find within-session learning trends.

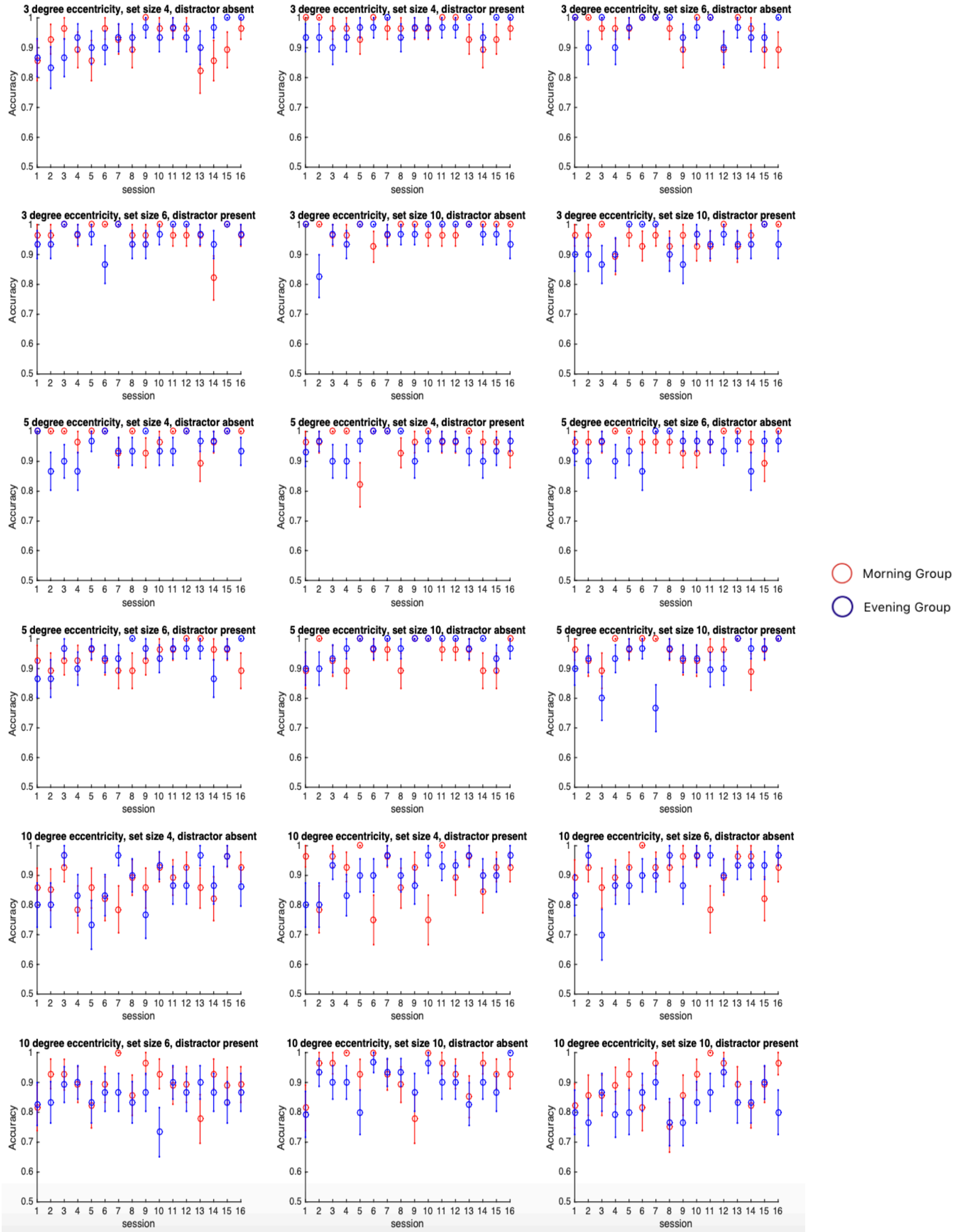

Figure 2.2. Each figure presents the accuracy data across different set of parameters, with error bars representing the standard error of the mean and dots indicating the average values for each session. The red dot represents the morning group performance and blue dot represent the evening group.

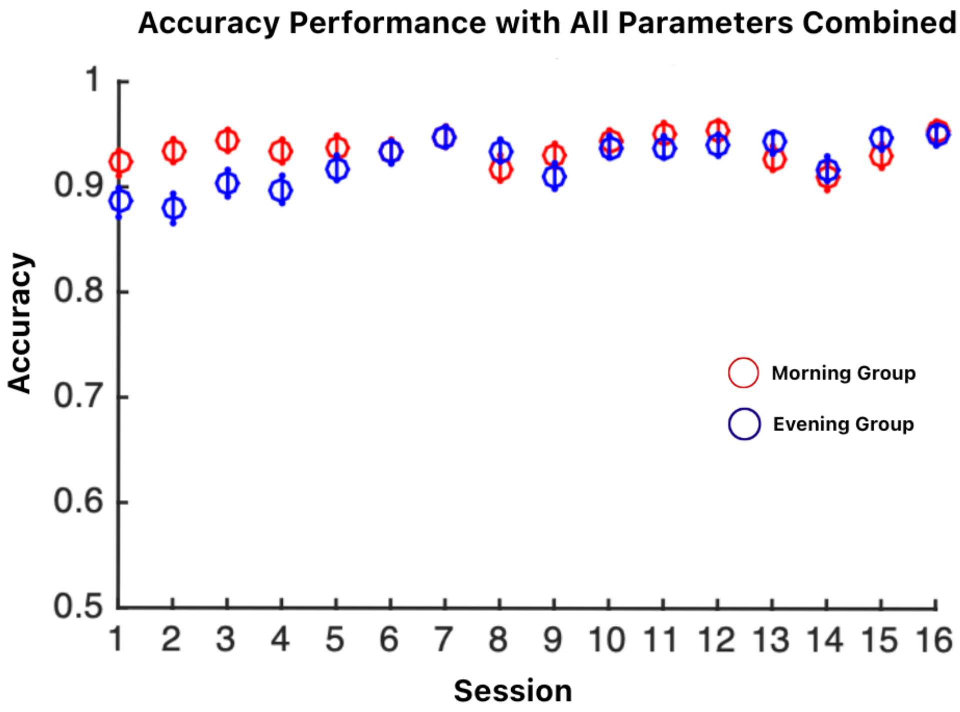

Figure 2.4. The figure represents the accuracy data when all parameters are combined, with error bars representing the standard error of the mean and dots indicating the average values from session 1 to 4 (each session further breakdown into 4 sub-sessions). The red dot represents the morning group performance and blue dot represent the evening group.

These results show that during online sessions, RT changes were more noticeable than accuracy changes.

3.4.2.2. Offline Learning (Offline-Wake and Offline-Sleep)

Offline learning was also examined, and RT comparisons between offline-wake and offline-sleep intervals were assessed. For the morning group, RT performance was not statistically significant for the offline wake condition (S1_End vs S2_Start: $Z = 1.820$, $p = .131$; S3_End vs S4_Start: $Z = 1.811$, $p = .131$). However, a significant improvement was observed after offline sleep when comparing S2_End vs

S3_Start (Z = 3.537, p = .001) (Table 2). This indicates that sleep may play an important role in consolidating attentional learning, particularly for tasks involving complex attentional processing.

Table 2.

All parameters combined: RT performance of offline session comparison for the morning and evening group

Morning Group	Sum of Rank	*Z*	*p (corrected)*	Evening Group	Sum of Rank	*Z*	*p (corrected)*
S1_End vs S2_Start (Offline Wake)	229453	1.820	0.131	S1_End vs S2_Start (Offline Sleep)	256319	4.270	<.001***
S2_End vs S3_Start (Offline Sleep)	230523	3.537	0.001***	S2_End vs S3_Start (Offline Wake)	274093	4.861	<.001***
S3_End vs S4_Start (Offline Wake)	236121	1.811	0.131	S3_End vs S4_Start (Offline Sleep)	279587	4.487	<.001***

Note. Significant levels: *<0.05, **<0.01, ***<0.001. The large sum-of-rank values show that the analysis was done on consolidated trial-level data. This means that all of the participants' trials were combined within each condition, so the analysis treated all of the trials as one aggregated sample per session to find within-session learning trends.

In contrast, the evening group showed significant improvements in RT after both offline wake and offline sleep conditions. Specifically, RT improved significantly after offline sleep (S1_End vs S2_Start: $Z = 4.270$, $p < .001$) and offline wake (S2_End vs S3_Start: $Z = 4.861$, $p < .001$). Further significant improvement was also observed when comparing S3_End vs S4_Start after offline sleep ($Z = 4.487$, $p < .001$) (Table 2). The findings suggest that both offline wake and offline sleep in the evening group contributed to the learning of the AC task, unlike the morning group, where offline sleep seems to be more critical. However, the accuracy performance of offline learning across both groups remains non-significant (Table 2.1) regardless of the offline condition.

Furthermore, when looking at individual parameters, both RT and accuracy scores showed no significant changes for both the morning (Appendix E) and evening (Appendix F) group.

Table 2.1.

All parameters combined accuracy performance of offline session comparison for the morning and evening group

Morning Group	Sum of Rank	*Z*	*p (corrected)*	Evening Group	Sum of Rank	*Z*	*p (corrected)*
S1_End vs S2_Start (Offline Wake)	252992.5	-0.266	0.885	S1_End vs S2_Start (Offline Sleep)	288068	-1.169	0.490
S2_End vs S3_Start (Offline Sleep)	252756	-0.715	0.664	S2_End vs S3_Start (Offline Wake)	295380	1.484	0.429
S3_End vs S4_Start (Offline Wake)	257544	1.743	0.331	S3_End vs S4_Start (Offline Sleep)	291600	-0.130	0.935

Note. Significant levels: *<0.05, **<0.01, ***<0.001. The large sum-of-rank values show that the analysis was done on consolidated trial-level data. This means that all of the participants' trials were combined within each condition, so the analysis treated all of the trials as one aggregated sample per session to find within-session learning trends.

Time comparison (between-group) analysis was also conducted to examine the change in performance between the morning and the evening groups. The results showed that there is improvement in RT at specific timepoints, particularly in mid-study sessions (Table 2.2) during Session 1-2 ($Z = -3.26$, $p = .005$), Session 1-4 ($Z = -3.45$, $p = .003$), Session 2-2 ($Z = -3.95$, $p = .001$), Session 2-4 ($Z = -3.68$, $p = .002$), Session 3-1 ($Z = -2.77$, $p = .016$), Session 3-2 ($Z = -4.55$, $p < .001$), Session 3-3 ($Z = -4.01$, $p = .001$), and Session 3-4 ($Z = -3.15$, $p = .007$), indicating enhanced attentional processing speed over time. On the other hand, accuracy performance did not show the same pattern, with a marginal increase found in Session 1-2 (Z = 3.04, p = .019). These results indicate that although attentional learning enhances RT, accuracy stayed consistent, which shows a trade-off between speed and accuracy.

Table 2.2.

Overall Time comparison between the morning and evening group

	RT			Accuracy		
Session Timepoint	Sum of Rank	*Z*	*p (corrected)*	Sum of Rank	*Z*	*p (corrected)*
Session 1-1	220332	0.204	0.895	268434	2.043	0.119
Session 1-2	209311	-3.262	0.005**	270810	3.037	0.019*
Session 1-3	224082.5	-1.293	0.314	268884	2.471	0.054
Session 1-4	209750.5	-3.449	0.003**	267253.5	2.112	0.111
Session 2-1	225110	-0.986	0.451	266058	1.248	0.415
Session 2-2	212513	-3.945	0.001***	263502	0.077	0.969
Session 2-3	233135	-0.826	0.545	263376	0.019	0.985
Session 2-4	208354	-3.675	0.002	261090	-1.027	0.451
Session 3-1	213660	-2.773	0.016	265986	1.160	0.415

Session 3-2	213972	-4.545	<.001***	264096	0.382	0.803
Session 3-3	219179.5	-4.008	0.001***	265176	0.958	0.451
Session 3-4	223948.5	-3.151	0.007**	265194	0.984	0.451
Session 4-1	227637	-0.276	0.864	261432	-0.923	0.456
Session 4-2	212167	-1.699	0.159	262278	-0.451	0.773
Session 4-3	229588	-0.103	0.948	261198	-1.059	0.451
Session 4-4	236019	-0.563	0.684	263146.5	0.322	0.824

Note. Significant levels: *<0.05, **<0.01, ***<0.001. The large sum-of-rank values show that the analysis was done on consolidated trial-level data. This means that all of the participants' trials were combined within each condition, so the analysis treated all of the trials as one aggregated sample per session to find within-session learning trends.

The results demonstrate that RT performance improves significantly with offline sleep in the morning group, whereas the evening group benefits from both offline wake and sleep conditions. Which may indicate a role of the circadian rhythms in how learning is consolidated in the AC task.

3.4.3. Learning of Visual Search Task

3.4.3.1. Online Within-Session Performance

The visual search task aims to evaluate how well an individual can locate a target among a set of distractors, reflecting the efficiency of selective attention. When examined the data parameter by parameter (eccentricity and set size) separately, no significant improvement in RT was observed for both the morning and evening (Appendix G and Appendix H). This pattern was consistently observed across different eccentricities (3°, 5°, and 10°) and set sizes (2, 6, and 10), as shown in Figure 3.1. In the figure, the morning and evening group is represented in red and blue dots, respectively, and it shows a similar trajectory across each of the sessions across parameters without a significant difference, suggesting that VS learning is limited or has no sleep-dependent improvement.

When combining all parameters, the overall comparison between the start and end of session 1 for both morning and evening groups showed that RT significantly improved (Morning: $Z = 3.834$, $p < .001$; Evening: $Z = 6.553$, $p < .001$). This significant improvement was also observed in the morning group in session 2 ($Z = 4.018$, $p < .001$), suggesting a persistence or maintenance of improvement in performance. This trend is represented in Figure 3.2. The figure demonstrated that both the morning (red) and evening (blue) groups showed a similar decline trajectory in RT across sessions and parameters, which reflects a general practice effect rather than being restricted to certain eccentricities or set sizes.

Table 3.

All parameters combined: RT performance across online learning session for the morning and evening group

Online Session Comparison (RT)	Morning			Evening		
	Sum of Rank	*Z*	*p* *(corrected)*	Sum of Rank	*Z*	*p* *(corrected)*
S1_Start vs S1_End	181795	3.834	<.001***	141041.5	6.553	<.001***
S2_Start vs S2_End	193195	2.573	0.026	151937	4.018	<.001***
S3_Start vs S3_End	195185	0.482	0.630	159200	0.988	0.377
S4_Start vs S4_End	185001	0.743	0.475	148948	-1.340	0.277

Note. Significant levels: *<0.05, **<0.01, ***<0.001. The large sum-of-rank values show that the analysis was done on consolidated trial-level data. This means that all of the participants' trials were combined within each condition, so the analysis treated all of the trials as one aggregated sample per session to find within-session learning trends.

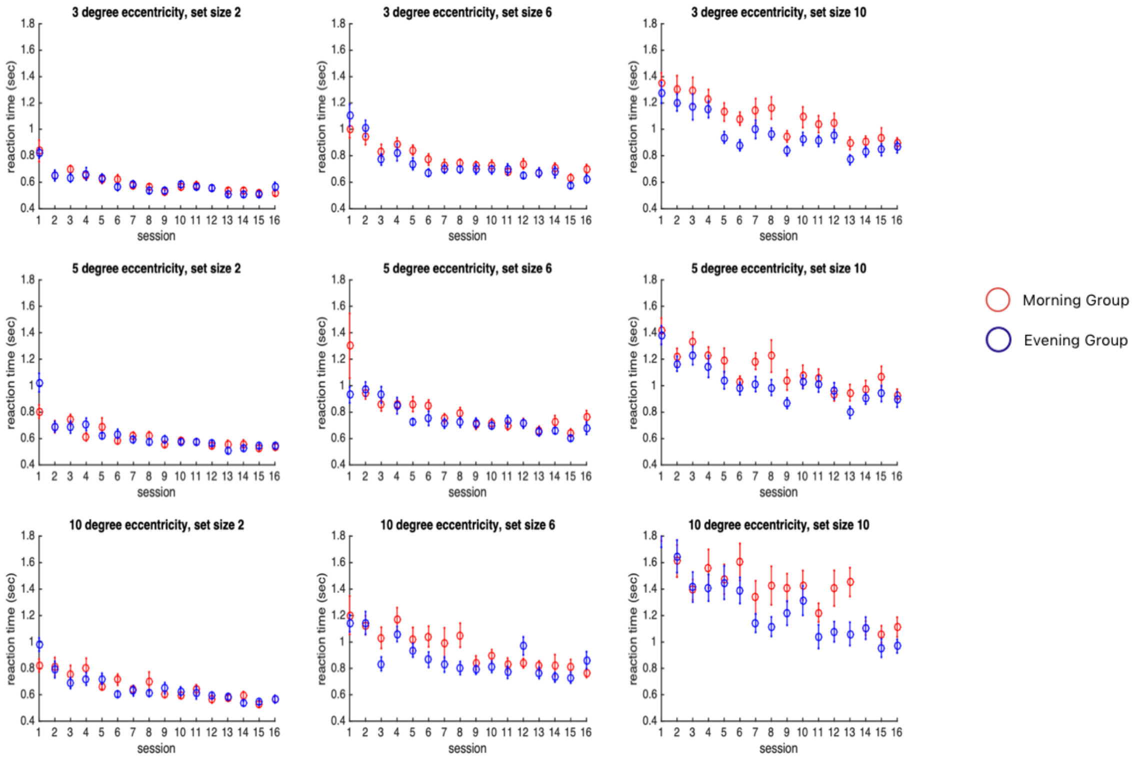

Figure 2.1. *Each figure presents the RT performance across different set of parameters, with error bars representing the standard error of the mean and dots indicating the average values for each session. The red dot represents the morning group performance and blue dot represent the evening group.*

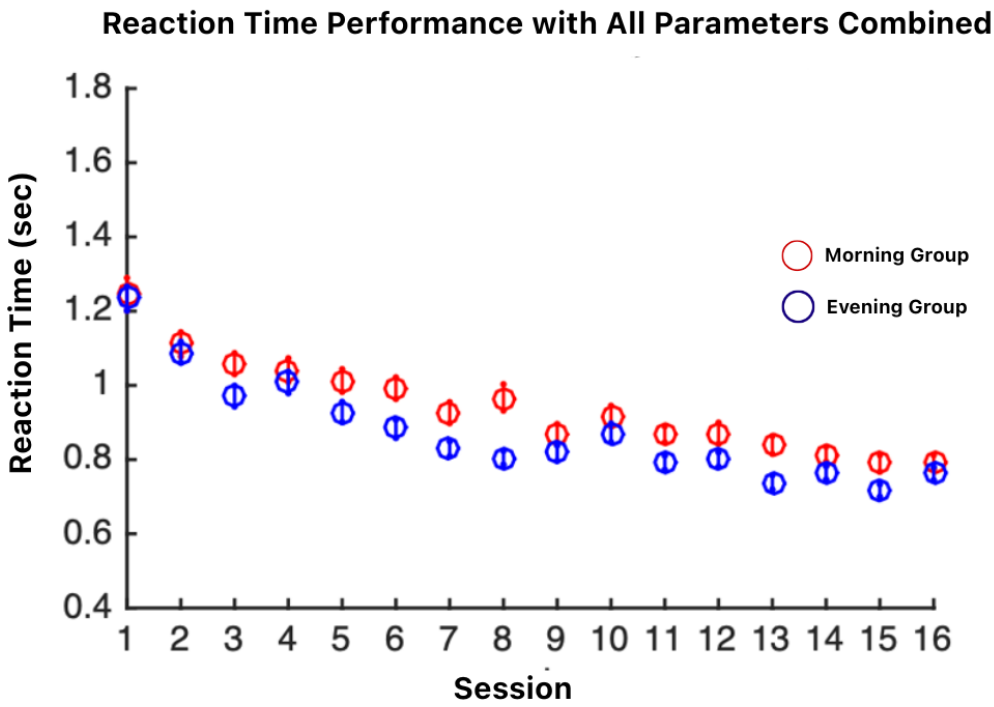

Figure 3.2. The figure represents RT performance when all parameters are combined, with error bars representing the standard error of the mean and dots indicating the average values for each session from session 1 to 4 (each session further breakdown into 4 sub-sessions). The red dot represents the morning group performance and blue dot represent the evening group.

Analysis of accuracy performance on the other hand showed no statistically significant differences between start and end sessions for both morning (Appendix I) and evening (Appendix J) groups when parameters are examined separately (Figure 3.3). This finding was further supported by combining all parameters together to examine accuracy scores between the start and end of each session, which also did not reach statistical significance (Table 3.1; see also Figure 3.4). This consistent pattern shows that accuracy performance remained stable throughout the learning sessions for both groups, which indicates that to a certain degree, participants did not trade speed for accuracy.

Table 3.1.

All parameters combined: Accuracy score across online learning session for the morning and evening group

Online Session Comparison (Accuracy)	Morning			Evening		
	Sum of Rank	*Z*	*p (corrected)*	Sum of Rank	*Z*	*p (corrected)*
S1_Start vs S1_End	216678	1.325	0.490	185757	0.614	0.686
S2_Start vs S2_End	212289	-0.777	0.664	184255.5	0	1.000
S3_Start vs S3_End	215061	0.889	0.616	183612	-0.381	0.820
S4_Start vs S4_End	213906	0.123	0.935	180609	-2.161	0.215

Note. Significant levels: *<0.05, **<0.01, ***<0.001. The large sum-of-rank values show that the analysis was done on consolidated trial-level data. This means that all of the participants' trials were combined within each condition, so the analysis treated all of the trials as one aggregated sample per session to find within-session learning trends.

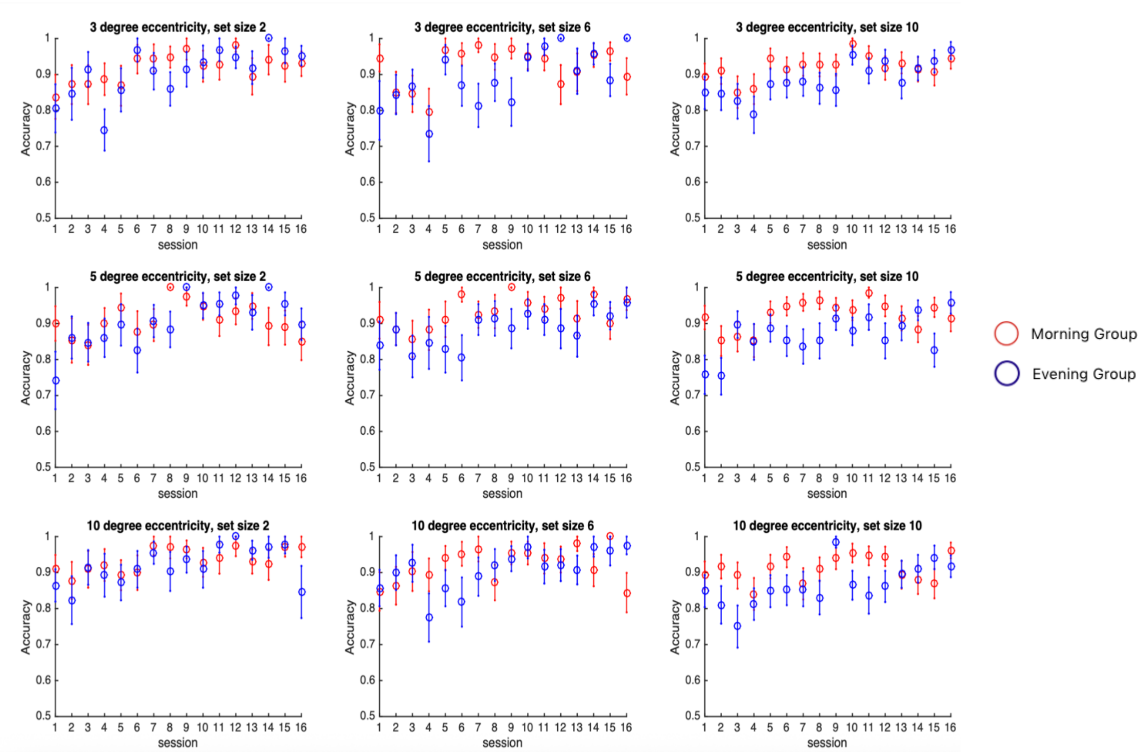

Figure 3.3. Each figure presents the accuracy performance across different set of parameters, with error bars representing the standard error of the mean and dots indicating the average values for each session. The red dot represents the morning group performance and blue dot represent the evening group.

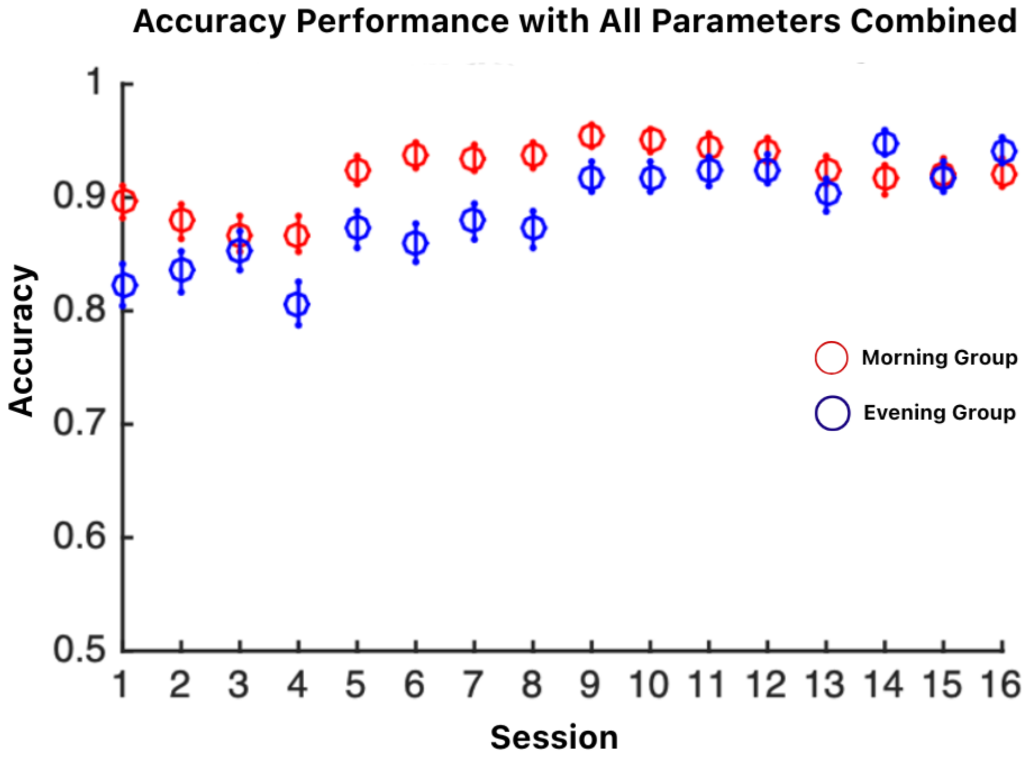

Figure 3.4. The figure represents the accuracy performance when all parameters are combined, with error bars representing the standard error of the mean and dots indicating the average values for each session from session 1 to 4 (each session further breakdown into 4 sub-sessions). The red dot represents the morning group performance and blue dot represent the evening group.

3.4.3.2. Offline Learning (Offline-Wake and Offline-Sleep)

Offline learning was examined for both offline-wake and offline-sleep. The results revealed distinct patterns in RT changes between the two conditions, indicating differences in how sleep and wakefulness impacted attentional performance. The morning group showed no significant difference in RT performance across offline sessions when examined the parameters individually (Appendix K), suggesting neither offline-wake and offline-sleep had an impact on learning. Evening group showed a similar pattern ((Appendix L). Combined parameter analysis also showed that there are no significant changes in accuracy scores between the offline sessions (Table 4.1).

However, when the analysis was run by combining all parameters together (regardless of eccentricity and set size), the evening group showed a notable difference (Table 4). Significant improvement in RT was found between the end of session 3 and the start of session 4 ($Z = 2.788$, $p = .015$), which is a period where the individual would have encountered sleep in the evening group. This suggests that offline sleep significantly improved RT performance after the third session. This result suggests that sleep between evening sessions played a crucial role in enhancing reaction time, likely due to sleep consolidation processes that facilitate quicker attentional responses.

Table 4.

All parameters combined: RT performance of offline session comparison for the morning and evening group

Morning Group	Sum of Rank	*Z*	*p (corrected)*	Evening Group	Sum of Rank	*Z*	*p (corrected)*
S1_End vs S2_Start (Offline Wake)	170646	1.288	0.277	S1_End vs S2_Start (Offline Sleep)	129881	1.846	0.131
S2_End vs S3_Start (Offline Sleep)	196543.5	1.904	0.131	S2_End vs S3_Start (Offline Wake)	141465.5	-0.761	0.475
S3_End vs S4_Start (Offline Wake)	191650	1.080	0.341	S3_End vs S4_Start (Offline Sleep)	164662	2.788	0.015*

Note. Significant levels: *<0.05, **<0.01, ***<0.001. The large sum-of-rank values show that the analysis was done on consolidated trial-level data. This means that all of the participants' trials were combined within each condition, so the analysis treated all of the trials as one aggregated sample per session to find within-session learning trends.

Table 4.1.

All parameters combined accuracy performance of offline session comparison for the morning and evening group

Morning Group	Sum of Rank	Z	*p (corrected)*	Evening Group	Sum of Rank	*Z*	*p (corrected)*
S1_End vs S2_Start (Offline Wake)	207669	-2.801	.130	S1_End vs S2_Start (Offline Sleep)	178249.5	-2.600	.130
S2_End vs S3_Start (Offline Sleep)	211827	-1.162	.490	S2_End vs S3_Start (Offline Wake)	179965.5	-2.227	.215
S3_End vs S4_Start (Offline Wake)	215523	1.051	.513	S3_End vs S4_Start (Offline Sleep)	186400.5	1.215	.490

Note. Significant levels: *<0.05, **<0.01, ***<0.001. The large sum-of-rank values show that the analysis was done on consolidated trial-level data. This means that all of the participants' trials were combined within each condition, so the analysis treated all of the trials as one aggregated sample per session to find within-session learning trends.

Time comparison (between-group) was further carried out by breaking down each session into 4 timepoint to examine the change in performance between the morning and the evening groups in deeper depth. Several significant differences across sessions were found. In particular, RT showed significant differences at specific session time points, indicating variability in performance depending on the time of day. For instance, the morning group demonstrated a significant improvement in RT during Session 1-3 compared to the evening group (Z = 3.008, p

= .008), and from Session 2-2 (Z = 3.669, p = .002). Also, there was a significant difference in RT between the groups at Session 2-4 (Z = 3.104, p = .007) and Session 3-3 (Z = 2.470, p = .033), as well as at Session 4-1 (Z = 2.652, p = .021) (Table 4.2). The results indicates that faster RT processing at these specific timepoint. Furthermore, the accuracy performance also exhibited similar findings. Session 1-1 showed significantly higher accuracy in the morning compared to the evening group (Z = 3.155, p = .017). Furthermore, Session 2-2 (Z = 3.832, p = .004), Session 2-3 (Z = 2.902, p = .024), and Session 2-4 (Z = 3.338, p = .014) also showed significant accuracy differences. These results highlight that while both RT and accuracy are affected by the time of day, accuracy improvements appear more pronounced in the morning, particularly during the second learning session.

Table 4.2.

Overall Time comparison between the morning and evening group for RT and accuracy

	RT			Accuracy		
Session Timepoint	Sum of Rank	*Z*	*p (corrected)*	Sum of Rank	*Z*	*p (corrected)*
Session 1-1	152571.5	-2.094	.073	213312	3.155	.017*
Session 1-2	153649	-0.541	.684	210441	1.888	.135
Session 1-3	163204.5	3.008	.008*	207520.5	0.638	.644
Session 1-4	152899	0.994	.451	212140.5	2.488	.054
Session 2-1	177344	1.872	.115	211249.5	2.594	.051

Session 2-2	185848	3.669	.002*	213691.5	3.832	.004*
Session 2-3	182355	2.230	.059	211629	2.902	.024*
Session 2-4	185181	3.104	.007*	212536.5	3.338	.014*
Session 3-1	186170.5	0.527	0.684	209632.5	2.219	.094
Session 3-2	183184.5	0.035	0.972	209203.5	1.921	.135
Session 3-3	190794.5	2.470	.033*	208312.5	1.378	.359
Session 3-4	184737.5	1.028	.451	207652.5	0.968	.451
Session 4-1	182889	2.652	.021*	208246.5	1.175	.415
Session 4-2	180804.5	1.462	.242	202768.5	-1.955	.135
Session 4-3	182010	2.106	.073	206415	0.201	.896
Session 4-4	179141	0.619	.684	204105	-1.159	.415

Note. Significant levels: *<0.05, **<0.01, ***<0.001. The large sum-of-rank values show that the analysis was done on consolidated trial-level data. This means that all of the participants' trials were combined within each condition, so the analysis treated all of the trials as one aggregated sample per session to find within-session learning trends.

3.5. Discussion

The current chapter focuses on first examining whether attentional-related perceptual learning tasks can be learnt and if the role of sleep plays a role in this process, with a focus on the differences between morning and evening groups across attentional capture (AC) and visual search (VS) tasks. The findings showed that the effect of sleep on learning is not uniform and is shaped by the type of task and the time of day, hence questioning previously held assumptions about sleep's universal function in improving cognitive performance (Stickgold & Walker, 2005). The lack of performance enhancement due to sleep may result from the significant cognitive demands placed on attention during the learning process. Tasks that demand attention require a dynamic allocation of cognitive resources, which includes working memory and executive control functions. This contrasts with fundamental perceptual learning tasks, such as the backward masking task discussed in Chapter 2, which mainly depend on sensory processing and have demonstrated beneficial effects from sleep (Karni & Sagi, 1991; Li et al., 2004). The consolidation mechanisms that support PL may not apply to attentional learning in the same way due to the prefrontal cortex's role in top-down attentional regulation and its varying activation across sleep phases (Desimone & Duncan, 1995; Miller & Cohen, 2001). While sleep is linked to the improvement of neural connections and the decrease of memory interference, it does not consistently promote learning that requires higher-level executive functioning. Learning of this kind may depend more heavily on regular practice and reinforcement instead of solely on the passive consolidation that takes place while sleeping (Stickgold & Walker, 2005).

The lack of significant learning effects in this chapter, especially when compared to the pronounced impacts identified in Chapter 2, requires further review. One potential explanation is because attentional learning activates higher-order control systems that are less vulnerable to short-term sleep-dependent consolidation (Barham et al., 2021; Quentin et al., 2021), whereas the perceptual learning task in Chapter 2 depended on other sensory and retinotopic mechanisms that are more effectively stabilised during sleep (Tamaki & Sasaki, 2022). Another possibility is that differences in the design of the task (e.g., trial structure and duration) and statistical power may have restricted the sensitivity to identify minor increases; therefore, further experimentation should include power analysis to examine the power it will require to see an even more reliable effect. However, these differing results show that not all types of learning are equally susceptible to sleep-related advantages, and that the lack of effects here does not mean that strong effects are absent elsewhere (Borragán et al., 2015; Paller et al., 2021).

The sleep protocol used in this chapter allows the exploration of the differences in morning and evening learners by conducting the first learning session at various times of the day. In particular, the morning group completed the first learning session in the morning and then had a time of offline wakefulness before offline sleep. At the same time, the evening group started their learning in the evening and encountered a sleep period directly afterwards. The design of the study allowed for the investigation on how attentional consolidation was affected by the time of sleep in relation to the learning session due to this approach.

The findings suggest that sleep and circadian cycles both affect attentional learning, but the exact nature of this association differs depending on the task. Early in the day, cognitive attention and task engagement may naturally occur, as seen by the morning group's typically faster gains after first task exposure (Hasher & Zacks, 1988). The evening group, on the other hand, showed more steady gains after both waking and sleep periods, indicating that repeated learning and sleep consolidation may be beneficial for evening learners. This result is consistent with other studies, which show that sleep's ability to consolidate learning may differ depending on an individual's chronotype and the time of day (Rasch & Born, 2013).

Nonetheless, it is important to note that these effects were minor in magnitude and did not reach the significant effect sizes observed in Chapter 2. The very large η^2 values reported in the previous chapter could be due to task-specific sensitivity and within-subject dependence that raise variance estimates; by contrast, the more variable and complicated attentional paradigms here naturally create weaker and more diverse effects. This difference demonstrates how important it is to be cautious when interpreting effect sizes across tasks and encourages the use of more robust mixed-effects models in future research to better account for differences between individuals.

A key observation is that the characteristics of the task influence the impact of sleep on attentional learning. The VS task, characterised by selective attention and strategic processing, showed greater enhancement from sleep consolidation. However, the AC task, dependent on rapid attentional changes, did not demonstrate a similar trend. This reinforces the concept that sleep primarily consolidates complicated cognitive processes rather than straightforward or stimulus-driven tasks (Fahle, 2005; Schoups et al., 2001). This assumption has been supported in the literature, which suggests that the influence of sleep on learning is modulated by task complexity. Sleep is more likely to help with emotionally charged activities and complicated sequence learning (Wagner et al., 2006; Rasch & Born, 2013). Given their fundamental stimulus-response nature, the AC tasks used in this chapter could not have activated the brain systems necessary for sleep-dependent consolidation. Attentional learning requires a balance between top-down cognitive control and bottom-up sensory input, in contrast to PL, which benefits from sleep because it helps to improve sensory discrimination (Gais & Born, 2004). Instead of quick overnight consolidation, attentional learning could need longer-term reorganisation of cognitive networks. The consolidation of attentional learning may rely on several processes that are not primarily driven by sleep, as it is more dispersed throughout various brain regions, such as the prefrontal and parietal networks. Maintaining a balance between top-down signals influenced by cognitive strategies, expectations, and knowledge, and bottom-up signals driven by sensory input is crucial for this process. For example, the prefrontal cortex, a region known for the involvement in functions and regulating other brain areas, which plays a more prominent role in the top-down aspect (Miller & Cohen, 2001). Given that these cognitive connections are complicated, the nature of sleep may not exert the same influence on perceptual learning as it does on attentional learning. The consolidation mechanisms that occur during sleep may selectively enhance the types of fundamental sensory discriminations involved in perceptual learning as opposed to the more intricate, strategy-dependent processes involved in attentional learning (Gais & Born, 2004).

Another factor to consider would be the idea of emotional salience to sleep-dependent memory consolidation. As stated by Wagner et al. (2006), sleep is the preferred time for consolidating emotionally important knowledge. Nonetheless, the lack of a benefit related to sleep could be attributed to the exclusion of emotionally significant stimuli in the tasks employed in this study. Future research should also consider whether distinct consolidation patterns are present in attentional learning tasks with emotionally charged content. The results highlight the importance of distinguishing between gains associated with practice and those related to learning that occurs during sleep.

Furthermore, enhancements in RT relative to accuracy suggest that attentional learning primarily enhances processing speed rather than accuracy. This is in line with ideas that there is a trade-off between speed and accuracy in tasks that require quick changes in attention (Desimone & Duncan, 1995). The speed-accuracy trade-off suggests that when individuals develop skill in a task, they often prioritise speed over accuracy (Liu & Watanabe, 2012). In the attentional tasks, this phenomenon may arise because faster responses often include unconsciousness or focused efficiency. However, accuracy tends to be more consistent due to the task's inherent perceptual or cognitive requirements. The similarity of accuracy across sessions suggests that while individuals improve in processing speed, the fundamental processes driving correct attentional allocation remain strong and less prone to changing with learning. This result is important as it implies that attentional learning optimises the efficiency of current processes, rather than implying qualitative changes in how attention is distributed or maintained. As mentioned by Metin et al. (2013), this trend may indicate the efficiency-oriented characteristic of attentional learning, whereby repetition and training primarily reduce processing delay rather than error rates.

The current study was primarily based on non-parametric statistics. This is why the sum-of-ranks figures are so high, as they show the overall ranking of all the observations, not just the raw data values. This should not be considered as inflated effects, but rather as a result of the analytical methodology. Future analyses might use mixed-effects or Bayesian models to evaluate participant-level variance with greater precision.

The research underscores the need of controlling for individual differences when assessing the impact of sleep on learning. The morning learners appeared to benefit from early cognitive activation, resulting in quicker advancement during first sessions, but evening learners demonstrated incremental advancements, indicating that the evening training coupled with sleep may enhance the consolidation of complex attentional processes. These distinctions emphasise the significance of chronotype in determining the interaction between sleep and practice in relation to attentional performance (Smith, 2001).

3.6. Future Directions

To gain an understanding of how sleep impacts learning and attention, future research should adopt a more dynamic approach. One way to investigate the relationship between the effect of cognitive load and how sleep influences learning is by designing a range of tasks with varying levels of complexity. This gradient of task difficulty will enable researchers to pinpoint the threshold at which sleep begins to affect learning consolidation. Additionally, it will help determine which types of learning rely on sleep and which ones do not. Furthermore, conducting long-term studies that span over weeks or months would be valuable in assessing the effectiveness and development of sleep-related learning benefits. These studies would examine the advantages and look into the integration and retention of acquired knowledge and skills over time.

The intricate nature of sleep provides opportunities for exploration with the advancements in polysomnographic devices. By establishing connections between stages of sleep like rapid eye movement (REM) and slow wave sleep (SWS), researchers can enhance their understanding of the underlying processes involved in learning. Exploring intervals and their potential impact on memory consolidation and effective learning could also contribute to this line of investigation. Researchers can gain insights into the impact of experiences between periods of sleep by studying sleep intervals. These wakeful periods provide an opportunity to investigate how learning and exposure to information during these intervals may influence reconsolidation processes during sleep. For instance, does engaging in new learning or being exposed to relevant information during wakeful periods prompt reconsolidation mechanisms during the subsequent sleep (such as during REM or SWS sleep)?

Finally, combining measurements from electroencephalograms (EEG) with neuroimaging methods like structural and functional magnetic resonance imaging (sMRI and fMRI) may improve the application of neurobiological evaluations prior to, throughout, and following sleep. This progress may allow us to identify the circuits involved in the consolidation process and to map alterations in the brain. By combining these measurements with treatments like medication or adjustments to sleep patterns, it could potentially help to establish a clear connection between sleep, learning, and brain function. Additionally, these techniques might shed light on why specific tasks are dependent on sleep (Texture Discrimination Task) while others are not (e.g., visual search task) by identifying the changes in structure or the connectivity change during learning. The scientific community could potentially delve into the relationship between sleep and learning by employing these comprehensive and detailed research methodologies. This exploration may lead to targeted therapies that enhance learning abilities and cognitive performance across populations.

3.7. Conclusion

Research into attention and sleep-dependent learning has revealed a complex relationship, indicating that the interplay between attention mechanisms and sleep is multifaceted. Research into attention and sleep-dependent learning has revealed a complex relationship, indicating that the interplay between attention mechanisms and sleep is multifaceted. While online learning has shown improvements in both top-down and bottom-up attention processes, the anticipated benefits of learning through sleep did not manifest significantly. This evidence suggests that the impact of sleep on learning is multifaceted and dependent on factors, including the type of learning and specific task characteristics. The study found that, in contrast to other forms of perceptual learning, such as the backward masking task discussed in Chapter 2, which can be directly impacted by sleep via mechanisms like the enhancement and decrease of neural noise, attentional learning encompasses a broader array of cognitive processes that might not uniformly derive advantages from sleep. This divergence emphasises the need for a nuanced approach when studying how sleep affects different types of learning. The complexity of attention processes, which integrate input from the environment with control from within, necessitates further exploratory research to understand how sleep interacts with these dual streams of information processing.

In summary, it is important to recognise that the relationship between sleep and learning is intricate and cannot be universally applied to all types of learning (at least in the perceptual learning field). The field is currently making discoveries that could potentially enhance the understanding of processes and optimise learning outcomes. Therefore, exploring this essential relationship between sleep's enigma and the extraordinary capacity of the mind to learn and remember remains an exciting journey for researchers.

Chapter 4:

General Discussion

4.1. Overview

This thesis delves into the concept of learning. It suggests that learning is a complex process, influenced by changes in brain structure over an individual's lifetime. According to this principle, learning is an evolving and dynamic process affected by both internal and external factors. The previous belief that cognitive performance inevitably declines with age has been replaced by research indicating that learning can actually lead to changes in the brain, allowing for the preservation or even improvement of cognitive abilities throughout adulthood (Li et al., 2008; Salthouse, 2019). A fundamental concept that lies in this thesis is the notion of brain plasticity, which highlights the capacity of the brain to modify its structure and function in response to new experiences (Park & Bischof, 2013).

Sleep is an additional process that is closely related to plasticity, which plays a role in the consolidation of newly learned information and skills (Stickgold & Walker, 2013). Therefore, the research in this thesis focuses specifically on the interconnected relationships that exist between learning, sleep, brain plasticity, and cognitive functioning, addressing a critical gap in understanding how and when learned skills become generalisable rather than remaining task specific. To address this, there is a need to explore the different types of perceptual learning tasks to see whether all different forms of perceptual tasks can be learned, and sleep plays a crucial role in this process (Chapters 2 and 3).

These questions and gaps in the literature inspired the research conducted throughout this thesis. It comprises two empirical chapters, each designed to assess a unique but complementary component of the link between sleep and learning.

The primary focus of Chapter 2 is on the generalisability of perceptual learning by employing a well-established learning paradigm of the backward masking task to examine the role of generalisability within perceptual domains, building on existing paradigms emphasising the particularity of perceptual learning (Watanabe & Sasaki, 2015; Zhang et al., 2008), this chapter presented sleep as a variable to investigate whether learnt perceptual abilities can transfer to untrained characteristics or other visual locations. The results showed that although perceptual learning changes were first task-specific, but after sleep there was a modest generalisation to untrained stimuli. This is consistent with the system consolidation model (Diekelmann & Born 2010; Stickgold & Walker 2013) and the hypothesis that sleep helps to integrate new abilities into more general cognitive networks (Maquet et al., 2000).

In Chapter 3, the focus shifts to attentional learning (another form of perceptual learning) to examine whether, firstly, attention-related perceptual tasks can be learned and, secondly, whether sleep differently impacts the development of the attentional task compared to the findings found in Chapter 2. The results showed that although learning had significantly decreased in RT, accuracy was constant across measures within sessions. However, the benefits associated with sleep were limited and task-specific, suggesting that attentional learning may be less dependent on the need for sleep and rely more on active engagement during wakefulness.

These two empirical chapters together indicate that learning mechanisms are not the same in all domains; instead, they rely on working conditions. Empirically, this thesis advances the field by demonstrating that sleep facilitates the generalisation of perceptual learning (Chapter 2), while attentional learning appears to rely more on active engagement during wakefulness (Chapter 3), challenging the assumption of uniform sleep-dependent consolidation. Theoretically, this dissociation leads models of cognitive plasticity by implying that different types of learning activate separate neural systems: perceptual learning matching more closely with early sensory consolidation processes, and attentional and motor learning depending on more extensive executive and procedural systems.

The reminder of this chapter will begin by summarising the findings arising from each of the experiments of this thesis and discuss their limitations. Then, will integrate the results of these experiments with previous literature, looking at learning in general. What can the current experiments in the thesis and previous research tell us about the mechanisms underlying learning and the contribution of sleep in relation to the generalisability of skills. Finally, the discussion will highlight theoretical and practical implications and propose future directions for research.

4.2. Empirical Experiments

4.2.1. Summary of Findings

In Chapter 2, the complex relationship between sleep and the generalisation of learning was explored. This topic is essential to understanding cognitive neuroscience. The main idea behind this research is that sleep not only helps us to recover but also plays a role in our brain's ability to apply what was learned to different situations. The experiment used the backward masking task to assess learning and examine how sleep affects performance improvement in visual tasks. After conducting tests, the research provides evidence that the timing of learning sessions – whether in the morning or evening – has a significant impact on how well one can retain and utilise skills. Specifically compared to those who learned in the evening, individuals who learned in the morning demonstrated improvements in applying their skills after getting some sleep. This finding supports the research premise that sleep following a learning session strengthens the connections related to that task, allowing us to apply what was learned beyond its initial context (Brawn et al., 2008; Deliens et al., 2014; Tamaki et al., 2020).

The findings challenge the held belief that perceptual learning only applies to specific locations or features (Fahle, 1994; Shiu & Pashler, 1992). Instead, the results from Chapter 2 demonstrate that learning can be transferred to untrained tasks and untrained sensory modalities. This suggests that higher level brain functions play a role, in generalising learning beyond stimuli and characteristics, implying a top-down contribution from higher-order cortical regio, such as the prefrontal cortex (PFC) (Kok et al., 2012). The importance of the PFC is especially emphasised, pointing to a top-down impact on the learning processes and bolstering the theory that higher cortical areas enable cognitive control mechanisms that are essential to the observed generalisation. This study not only supports the importance of sleep in learning processes, but it also raises the possibility that the interaction between alertness and sleep may be essential for maximising cognitive capacities. It requires further study to be done in order to fully understand the neuroplasticity processes that are at work during various states of consciousness and to clarify how these mechanisms contribute to our apparently infinite potential for adaptation and learning. All things considered, the chapter integrates a wide range of intricate data into a convincing story that emphasises sleep as a potent facilitator of learning generalisation, with broad ramifications for theoretical frameworks as well as real-world uses in cognitive improvement and rehabilitation.

Chapter 3 aimed to investigate whether selective attention, especially those involving top-down and bottom-up mechanisms, can be improved through repeated learning and whether the role of sleep contributes to this type of learning. While the tasks in Chapter 3 showed a reliable within-session improvement in RT, however, the hypothesis that sleep will help enhance learning was not supported by the findings in this Chapter. These results showed an opposite trend to the sleep-dependant consolidation effect found in Chapter 2 and contradicted previous studies in the literature (Karni & Sagi, 1991; Stickgold & Walker, 2005). The lack of sleep-dependent benefits in attentional tasks is conceptually important and implies an essential distinction between the consolidation paths of perceptual and attentional learning.

The lack of significant effects in Chapter 3, compared to the significant learning and transfer observed in Chapter 2, can be explained by both task-specific and theoretical differences. While both chapters used paradigms that share commonality, the backward masking task in Chapter 2 primarily engaged low-level perceptual learning, dependent on visual plasticity and error minimisation in early sensory cortices (Bao et al., 2010; Op de Beeck et al., 2007). These representations are particularly vulnerable to sleep-dependent consolidation, because reactivation during sleep strengthens and integrates specific feature traces (Diekelmann & Born, 2010; Karni & Sagi, 1991). On the other hand, the AC and VS paradigms in Chapter 3 rely more on the higher-order executive functions, specifically goal-directed and context-sensitive control facilitated by fronto-parietal networks (Miller & Cohen, 2001; Vossel et al., 2014). These types of learning depend on continuous adaptation and selective attention, rather than fixed associative mappings. This means that short-term replaying offline is less likely to be beneficial for these tasks. From a psychological viewpoint, this dissociation corresponds to the differentiation between the Rescorla–Wagner model (Recorla & Wagner, 1972), where prediction error facilitates gradual improvement, in accordance with Chapter 2, and the Mackintosh model (Mackintosh, 1975), which suggests that learning is dependent upon the dynamic distribution of attention according to cue relevance, aligning more closely with Chapter 3.

Furthermore, methodological concerns may have contributed to the absence of measurable effects, including the relatively short training duration, lack of direct feedback, and the potential for ceiling effects in accuracy. Nonetheless, these absences are theoretically informative, suggesting that sleep-related consolidation is not a universal process but a domain-specific mechanism dependent on the representational level and brain circuitry involved in the task.

Previous studies have suggested that sleep helps to strengthen the brain connections involved in learning new abilities or knowledge. This is because perceptual learning has been shown to be highly connected with slow wave sleep (SWS) as it is responsible for consolidating very fine sensory representations in early visual regions (Karni & Sagi, 1991; Walker & Stickgold, 2006; Tamaki et al., 2020). These results in the literature provided a foundation for the widely accepted notion that sleep improves learning by stabilising and integrating newly acquired knowledge into long-term memory. However, the findings in Chapter 3 demonstrated that the assumption on sleep may not extend to all types of learning. Selective attention acquisition is more cognitive in character, particularly when it involves higher-order processes such as goal-directed (top-down attention); therefore, it may not benefit from sleep in the same manner as the backward masking task used in Chapter 2. Nonetheless, attentional learning activates separated frontoparietal control networks (Miller & Cohen, 2001; Vossel et al., 2014) and could consolidate through continuous wakeful engagement rather than offline reactivation. This is in-line with the developing framework that the contribution of sleep in learning is domain-specific and depends on the nature of the task, the neural system involved and the complexity of the learning content (Diekelmann & Born, 2010; Klinzing et al., 2019). These tasks are naturally more dispersed and general, which means that they may not depend on the same offline consolidation mechanisms as the backward masking task, or they might need longer or more focused consolidation windows than those seen in this current experimental setup. Certainly, the absence of sleep-related enhancement could imply that attentional improvement relies more on repeated active engagement and reinforcement during wakefulness than on passive reactivation during sleep.

Furthermore, the results showed that RT consistently improved over sessions, but accuracy did not improve in the same manner. This is often referred to as the speed-accuracy trade-off, which implies that attentional learning may maximise processing efficiency instead of perceptual fidelity (Liu & Watanabe, 2012). Previous research has recorded such a trade-off, which indicates a movement towards automatised, efficient response techniques (Desimone & Duncan, 1995; Liu & Watanabe, 2012). This can be beneficial in situations that demand quick reactions; the result highlights the shortcomings of the present duties in addressing more profound, structural changes in attention control. Future research might use more flexible task designs or provide error-driven feedback to see if training could also hone attentional accuracy.

The theoretical implication of this dissociation is that the term "perceptual learning" could be overly broad to accurately characterise the range of cognitive processes engaged in tasks like backward masking, AC, and VS. Although all of these tasks to some degree involve shared characteristics, they are different in qualitatively diverse ways which rely on different brain systems. AC and VS tasks rely more on higher-order attentional processing, such as stimulus-driven or goal-directed selection. Despite the fact that AC and VS tasks may seem comparable on the surface with PL paradigms, they should not be grouped under the same theoretical category. Treating all of these as instances of "PL" operates the danger of missing important differences in the kinds of representations they interact with and how their representations are combined. From this perspective, learning is more functionally differentiated; therefore, the nature and needs of the task determine the role sleep plays, and maybe the structure of learning itself.

4.2.2. Limitations of the Experiments

Numerous methodological constraints that need to be carefully considered have been brought to light by the research provided in the various chapters. One of the first limitations identified was the use of self-reported data on sleeping habits in Chapter 2. Although individuals may not always remember details well or may not precisely record their sleep habits, such a method is susceptible to prejudice and mistakes. A distorted perception of the connection between sleep and learning may result from this. Secondly, the backward masking was the main learning task for Chapter 2, which raises the question of how broadly applicable the results are. There is also uncertainty about whether the same findings would apply to other learning activities, especially ones that are more complicated or non-visual in nature. The fact that all activities fall under the perceptual learning domain in Chapter 2 and Chapter 3, which restricts the range of inferences that can be made, even though the learning tasks (backward masking, visual search and attentional capture) used in these chapters are comparable tasks. Future research should aim to incorporate multisensory or cross-domain paradigms to discover if sleep-related consolidation serves as a universal or modality-specific phenomenon.

The staircase method was used, which rapidly changed task complexity to keep performance at 70.7% accuracy, to account for variability and maintain consistency. This adaptive quality allows individuals to perform at an ideal level where learning-related increases in sensitivity could be significantly observed, hence avoiding ceiling or floor effects. However, a possible concern with using this method to calculate discrimination threshold is that distinct reversals based on the calculation may introduce variability due to noise or individuals’ approach in completing the task. Future research may consider combining the staircase method with other threshold estimation approaches, such as psychometric function fitting, Bayesian adaptive techniques like QUEST (Watson & Pelli, 1983) or signal detection analysis. These techniques may improve measurement accuracy and confirm that the reported effects of learning are not confounded by response bias or random variation.

Across both chapters, the sample sizes between groups may limit the statistical power to identify modest group differences. While the effect outcomes were aligned with theoretical assumptions, using bigger populations or hierarchical mixed-effects models might enhance sensitivity and generalisability.

Additionally, in consideration of learning session arrangement, the study makes an effort to distinguish between morning and evening sessions, but it is unable to fully explore the range of potential learning periods during the day. Furthermore, individual circadian preferences are not taken into consideration in this study, despite the possibility that they may have a big impact on cognitive function. All participants experience both alertness and sleep across the testing days, consequently the study does not adequately examine the claim that sleep directly affects learning because there is neither a crossover design nor a control group.

Finally, all learning tasks relied on behavioural metrics. Although these serve as strong indicators of performance change, they provide limited understanding and interpretation of the underlying brain mechanisms. Further studies integrating behavioural data with neuroimaging techniques (such as EEG or fMRI) could clarify the relationship between sleep-related consolidation and specific brain networks.

Taken together, although the present methodology effectively identified a sleep-related benefit in perceptual generalisation (Chapter 2) and its lack in attentional learning (Chapter 3), various enhancements, such as objective sleep metrics, increased statistical power, chronotype control, and multimodal imaging, will be essential for comprehensively defining the parameters of sleep-dependent learning.

4.3. The Impact of Sleep in Learning

In-depth understanding of the cognitive psychology of learning is provided by the thesis's investigation into the connection between sleep-related learning conducted to look at online (wake) and offline (sleep) learning in Chapters 2 and Chapter 3. Chapter 2 continues the idea put out by Stickgold (2005) and Diekelmann & Born (2010), which is that sleep can help learning become more consolidated and generalised, especially if the learning task are scheduled in accordance with circadian cycles. The between-group analyses in Chapter 2 showed that individuals who trained in the evening and slept before the retest did significantly better and were able to transfer what they learnt to new locations compared to those who trained in the morning and stayed awake for the first 12 hours after learning. This finding supports the notion that sleep contributes to the stabilisation of complex perceptual traces and their integration into advanced cognitive networks (Maquet et al., 2000; Tamaki et al., 2016). It also shows that the individual's physical condition at the time of encoding affects consolidation. For example, training followed by sleep at an appropriate time of day leads to better strengthening of neural representations (Walker & Stickgold, 2004). In theory, these findings enhance current models of sleep-dependent learning in the field. Instead of illustrating consolidation merely as a neurobiological replay mechanism, the results support a multi-level approach that connects neural reactivation with cognitive resource theories (Craik & Tulving, 1975; Robertson, 2012). Consequently, effective consolidation requires the reactivation of task-specific sensory circuits and the restoration of contextual or attentional connections that structure memory at a psychological level. This combination of perceptual and cognitive points of view makes the link between neuroplasticity and applied learning theory stronger.

The present chapter broadens the comprehension of sleep's function in learning by demonstrating that sleep is crucial for reinforcing previously acquired knowledge, and that the scheduling of the learning session may greatly impact the efficiency of this process (Ahmadi et al., 2018; Al-Sharman & Siengsukon, 2013). Sleep has the ability to improve cognitive flexibility and the transfer of acquired abilities to new situations, as evidenced by the results showing morning learners improved on untrained activities following a 24-hour interval. According to Walker and Stickgold (2004), these benefits imply that sleep after morning sessions may be especially beneficial for memory consolidation and processing. This result offers behavioural evidence that offline consolidation facilitates the integration of localised visual representations into more extensive perceptual networks. Theoretically, these findings align with prediction-error-based learning models (Rescorla & Wagner, 1972), suggesting that sleep may function to reduce remaining error signals by reactivating relevant neural networks. The findings from Chapter 2 also make one think about the mechanisms underlying this consolidation. In the event that sleep is strengthening the brain connections made during learning, the improvements seen in the morning group may indicate that learning is best aligned with normal biological cycles, which may result in more effective encoding and consolidation during sleep.

On the other hand, Chapter 3 presents an alternative analysis to these data, demonstrating that although participating in online learning sessions improves attentional performance, there were no significant differences across the sleep-wake groups. This means that attentional learning can be maintained by active practice when awake without needing further sleep to improve. When interpreted via the Mackintosh model of selective attention, the result shows that practice leads to better attention by changing the weight of predictive cues over time. This happens through conscious awareness rather than unconscious consolidation.

However, at the neurobiological level, this division suggests that the role of sleep plays in learning is task-specific and low-level perceptual tasks that require accurate sensory encoding are enhanced by sleep, while higher-order attentional processes are predominantly influenced by online engagement and feedback-driven adaptation (Miller & Cohen, 2001; Vossel et al., 2014). Which support previous studies that highlight non-sleep dependency on learning. For example, in the study by Atienza (2002), the finding from this study provide support to the fact that both rapid and slow brain alterations underlie the development of enhanced perception. This alteration could occur hours, suggesting the fact that sleep is not necessary for this enhancement. This raises doubt on sleep's more general benefits for learning and raises the possibility that a mechanism of selective consolidation is in operation. Sleep may preferentially consolidate some forms of learning over others, as shown by the absence of discernible sleep-related increases in attentional tasks. These findings challenge the held belief that sleep aids in learning consolidation. Instead, they indicate that the optimal amount of sleep, for enhancing learning consolidation may vary depending on the type of task such as in different perceptual tasks (Gais & Born, 2004; Stickgold, 2005).

These findings indicate that the impact of sleep on learning is dependent on the interaction of task type, visualisation level, and time in relation to the circadian cycle. This thesis presents a task-specific and context-specific model of sleep-dependent consolidation, addressing contradictions in the research by contextualising sleep's effects within particular learning hierarchies. Furthermore, this argument has implications for theories in the field of cognitive science and educational approaches. It suggests that aligning learning sessions with an individual's rhythm and tailoring them to match the learning task could impact the effectiveness of learning outcomes. This study underscores the necessity for exploration, into how sleep contributes to learning consolidation while also calling for a re-assessment of teaching methods to incorporate these findings. Additionally, it also advocates for individualised learning schedules.

4.4. Future Direction

During the discussion of findings, I have made note of some future directions for research. Firstly, an important area to explore further is the development of neuroimaging methods. These methods aim to investigate the functional changes that occur in the brain as a result of learning. By utilizing techniques such as functional magnetic resonance imaging (fMRI) and Diffusion Tensor Imaging (DTI) researchers can delve into the relationships between regions of the brain during the learning process and gain insights into how sleep contributes to neuroplasticity. For instance, fMRI allows us to detect changes in blood flow within the brain, which serves as an indicator of certain activity. This approach provides us with a map of brain activity highlighting which areas are active during tasks or in response to particular stimuli. This information is highly valuable in studying learning and memory activities as it allows us to understand how different tasks may involve distinct neural pathways that evolve over time. In contrast DTI enables researchers to track how water molecules diffuse throughout the brain along white matter pathways. This understanding is crucial for unravelling the interconnectedness of different regions within the human brain.

Overall, these advancements in neuroimaging methods hold promise, for investigating how learning influences the structure and function of our brains. DTI has the capability to capture images of the fibre channels that help brain cells communicate by tracking the movement of water molecules along axons. This imaging method can reveal changes, in the brains matter, such as reorganization or increased density, which are associated with learning. Combining fMRI and DTI provides an understanding of how the brain transforms during the learning process. FMRI shows which areas of the brain become active and how this activity changes throughout learning and after sleep. DTI complements this by illustrating how learning experiences reshape the brains connections and how these changes may contribute to consolidating acquired knowledge and skills. By examining these strategies after learning activities or before and after sleep, insights can be gained regarding to how the brain adapts to information and how sleep can strengthen these neural connections. This knowledge is important for developing therapies that enhance learning capabilities and term cognitive health plans. Additionally, it is important to investigate the basis for differences, in learning abilities. Further exploration into the diversity of brain structure and function along with its connection to learning styles can pave the way for tailored teaching strategies and interventions to enhance cognition. This could potentially revolutionize learning methods by considering the learners psychological needs.

To delve into the applicability of learning principles across inputs and cognitive functions it is crucial to diversify the range of learning tasks in addition to advancements in neuroimaging techniques. Comparative studies that encompass tasks can evaluate how patterns of learning generalise from one domain or sensory modality to another. These research findings might shed light on whether learning's primarily integrative and cross domain or if it tends to be more modular or domain specific. For example, do auditory abilities required for language acquisition correlate with the visual and sensory skills necessary for mastering a musical instrument? Furthermore, this line of inquiry should consider the underlying mechanisms like executive function, working memory and attention that support activities. By comparing activities utilizing different modalities but requiring similar cognitive processes researchers can start mapping out commonalities as well, as distinct neural substrates associated with these processes. By providing the insights on how to promote transferable learning in real life situations, this approach has the potential to reform learning methods and cognitive therapy. It enables an understanding of the underlying mechanisms of learning and cognition.

In addition, future studies should also consider controlling for variables that may impact performance outcomes. Learning goes beyond processes; it is closely connected to motivation and emotional states for example. These aspects significantly influence engagement in learning tasks the effectiveness of learning strategies and overall success in acquiring skills or knowledge. A holistic approach that examines the interplay between emotional aspects of the mind can lead to a more comprehensive understanding of the learning process. Furthermore, considering the impact of moods on neuroplasticity—the brains ability to form neural pathways and connections—provides strong support for investigating these factors further (McEwen, 2000). Motivation and emotional well-being might play a role, in either facilitating or hindering the learning processes. For example, stress is known to inhibit neuroplasticity while positive emotional experiences and a motivated mindset greatly enhance it (Ashby et al., 1999). By comprehending these interconnections, can potentially unlock the gateway to treatments aimed at enhancing the brain's ability to adapt and learn.

4.5. Conclusion

The summary provides an overview of the nature of learning, which is closely intertwined with neuroplasticity, sleep and cognitive performance. It portrays learning as a multidimensional process. The findings emphasised the significance of the role of sleep play in enhancing generalisation of learning, suggesting that the consolidation of information and abilities occurs actively during sleep than passively for specific tasks. The idea of brain plasticity, which highlights the brain's ability to adapt its structure and function in response to experiences or external pressures is fundamental to this theory. It becomes evident that sleep plays a role in brain development and learning processes by not restoring but also strengthening cognitive skills.

Chapter 2 of the thesis explores learning generalisation challenging the notion that perceptual learning is limited to certain activities or stimuli. It demonstrates how the acquired abilities can be transferred to different situations such as different task features and location, suggesting the involvement of higher order brain functions. Additionally, the thesis delves into the dynamics of learning by providing insights into combining online and offline learning phases to facilitate information acquisition and skill development. The complex relationship, between learning and sleep is also addressed in this thesis. The impact of sleep on attention focused tasks seems to differ from its effect on perceptual learning and skill generalisation, as seen in Chapter 2. This suggests that the importance of sleep for consolidating learning may depend on the demands of a task and the level of complexity. Additionally, when considering differences in learning, it becomes evident that learning abilities can be both a general characteristic and specific to particular domains. Therefore, personalised approaches to learning and training are necessary to accommodate variations in individual learning styles and rates of progress.

Chapter 3 look more closely at the link between sleep and learning. It showed that attentional learning takes a different path compared to perceptual learning in Chapter 2. The two studies together show that sleep helps with learning in a specific way and for specific tasks. It helps with certain sensory perceptual plasticity more than higher-order attentional adaptability.

Overall, this thesis provides conceptual and empirical methods to better capture the richness and complexity of human cognitive plasticity, as well as increases the field's knowledge of how learning functions within and across domains. Learning methods, skill development, and rehabilitation programs all benefit greatly from these insights as they help to customise treatments to individual learning profiles and help to know when sleep or repeated practice is most advantageous, hence greatly improving outcomes.

4.5.1. Data and Code Availability

Following common research practice, the experimental data and analytic scripts are kept safe and private on a cloud server (SharePoint). Access is available only through a private link (Appendix M). Once current study is accepted for publication, the data and code will be made publicly accessible via Open Science Framework. This approach ensures both transparency and data protection prior to formal publication.

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Appendices

Appendix A

RT of Online learning session comparison in the morning group

Parameter	Session Comparison	Sum of Rank	*Z*	*p* *(corrected)*
3 degree eccentricity, set size 4, distractor absent	S1_Start vs S1_End	679	1.570	.396
	S2_Start vs S2_End	596	-0.070	.983
	S3_Start vs S3_End	804	0.328	.882
	S4_Start vs S4_End	583	-0.058	.987
3 degree eccentricity, set size 4, distractor present	S1_Start vs S1_End	889	1.759	.337
	S2_Start vs S2_End	705	0.044	.993
	S3_Start vs S3_End	829	1.221	.532
	S4_Start vs S4_End	701	-0.009	1
3 degree eccentricity, set size 6, distractor absent	S1_Start vs S1_End	761	-0.379	.862
	S2_Start vs S2_End	661	-1.401	.484
	S3_Start vs S3_End	585	-1.009	.620
	S4_Start vs S4_End	719	-0.650	.767

3 degree eccentricity, set size 6, distractor present	S1_Start vs S1_End	936	3.339	.050
	S2_Start vs S2_End	777	-0.109	.973
	S3_Start vs S3_End	736	-0.104	.973
	S4_Start vs S4_End	781	0.657	.767
3 degree eccentricity, set size 10, distractor absent	S1_Start vs S1_End	933	2.500	.142
	S2_Start vs S2_End	893	1.549	.402
	S3_Start vs S3_End	824	0.665	.767
	S4_Start vs S4_End	846	0.778	.727
3 degree eccentricity, set size 10, distractor present	S1_Start vs S1_End	818	1.868	.303
	S2_Start vs S2_End	822	1.646	.373
	S3_Start vs S3_End	793	0.615	.778
	S4_Start vs S4_End	701	0.454	.841
5 degree eccentricity, set size 4, distractor absent	S1_Start vs S1_End	832	0.800	.725
	S2_Start vs S2_End	816	0.287	.895
	S3_Start vs S3_End	588	-2.190	.203
	S4_Start vs S4_End	576	-1.755	.337
	S1_Start vs S1_End	896	2.349	.184

5 degree eccentricity, set size 4, distractor present	S2_Start vs S2_End	605	0.591	.785
	S3_Start vs S3_End	717	-0.432	.841
	S4_Start vs S4_End	806	0.615	.778
5 degree eccentricity, set size 6, distractor absent	S1_Start vs S1_End	803	0.783	.727
	S2_Start vs S2_End	815	0.513	.824
	S3_Start vs S3_End	588	-2.190	.203
	S4_Start vs S4_End	699	-1.614	.375
5 degree eccentricity, set size 6, distractor present	S1_Start vs S1_End	832	2.608	.115
	S2_Start vs S2_End	723	0.128	.968
	S3_Start vs S3_End	749	0.580	.793
	S4_Start vs S4_End	702	-0.953	.647
5 degree eccentricity, set size 10, distractor absent	S1_Start vs S1_End	615	-0.427	.115
	S2_Start vs S2_End	629	-2.254	.968
	S3_Start vs S3_End	621	-2.736	.793
	S4_Start vs S4_End	629	-2.130	.647
5 degree eccentricity, set size 10, distractor present	S1_Start vs S1_End	945	3.174	.054
	S2_Start vs S2_End	925	3.149	.054

	S3_Start vs S3_End	686	-0.276	.902
	S4_Start vs S4_End	734	-1.041	.606
10 degree eccentricity, set size 4, distractor absent	S1_Start vs S1_End	630	1.440	.464
	S2_Start vs S2_End	697	1.930	.285
	S3_Start vs S3_End	673	1.175	.547
	S4_Start vs S4_End	662	0.961	.646
10 degree eccentricity, set size 4, distractor present	S1_Start vs S1_End	726	-0.044	.993
	S2_Start vs S2_End	728	-0.248	.912
	S3_Start vs S3_End	654	-0.405	.847
	S4_Start vs S4_End	654	-1.326	.507
10 degree eccentricity, set size 6, distractor absent	S1_Start vs S1_End	716	1.513	.421
	S2_Start vs S2_End	695	0.101	.973
	S3_Start vs S3_End	655	-1.099	.580
	S4_Start vs S4_End	743	0.240	.914
10 degree eccentricity, set size 6, distractor present	S1_Start vs S1_End	622	1.993	.261
	S2_Start vs S2_End	477	-1.585	.391
	S3_Start vs S3_End	589	-1.630	.375

	S4_Start vs S4_End	422	-1.566	.396
10 degree eccentricity, set size 10, distractor absent	S1_Start vs S1_End	774	4.153	.012*
	S2_Start vs S2_End	727	1.727	.352
	S3_Start vs S3_End	659	3.306	.050
	S4_Start vs S4_End	720	2.895	.078
10 degree eccentricity, set size 10, distractor present	S1_Start vs S1_End	666	2.415	.170
	S2_Start vs S2_End	586	-0.802	.725
	S3_Start vs S3_End	589	-0.651	.767
	S4_Start vs S4_End	623	-0.499	.824

Significant level: *<0.05, **<0.01,***<0.001

Appendix B

RT of Online learning session comparison in the evening group

Parameter	Session Comparison	Sum of Rank	*Z*	*p* *(corrected)*
3 degree eccentricity, set size 4, distractor absent	S1_Start vs S1_End	744	0.493	.825
	S2_Start vs S2_End	684	-1.204	.540
	S3_Start vs S3_End	872	0.487	.825
	S4_Start vs S4_End	815	0.503	.824
3 degree eccentricity, set size 4, distractor present	S1_Start vs S1_End	877	1.286	.511
	S2_Start vs S2_End	834	-0.104	.973
	S3_Start vs S3_End	856	0.000	1.000
	S4_Start vs S4_End	874	-0.599	.782
3 degree eccentricity, set size 6, distractor absent	S1_Start vs S1_End	854	-0.248	.912
	S2_Start vs S2_End	760	-1.660	.370
	S3_Start vs S3_End	765	-0.311	.890
	S4_Start vs S4_End	815	-0.826	.714
	S1_Start vs S1_End	894	1.301	.507

3 degree eccentricity, set size 6, distractor present	S2_Start vs S2_End	842	0.008	1.000
	S3_Start vs S3_End	823	-0.039	.995
	S4_Start vs S4_End	806	-0.762	.734
3 degree eccentricity, set size 10, distractor absent	S1_Start vs S1_End	989	1.611	.375
	S2_Start vs S2_End	818	-1.236	.532
	S3_Start vs S3_End	859	-0.159	.957
	S4_Start vs S4_End	823	-0.957	.646
3 degree eccentricity, set size 10, distractor present	S1_Start vs S1_End	814	1.228	.532
	S2_Start vs S2_End	929	0.935	.655
	S3_Start vs S3_End	802	1.239	.532
	S4_Start vs S4_End	871	1.188	.541
5 degree eccentricity, set size 4, distractor absent	S1_Start vs S1_End	909	0.879	.685
	S2_Start vs S2_End	676	-2.626	.115
	S3_Start vs S3_End	810	-1.545	.402
	S4_Start vs S4_End	734	-1.700	.355
5 degree eccentricity, set size 4, distractor present	S1_Start vs S1_End	874	2.266	.193
	S2_Start vs S2_End	892	0.326	.882

	S3_Start vs S3_End	747	-0.361	.868
	S4_Start vs S4_End	731	-1.285	.511
5 degree eccentricity, set size 6, distractor absent	S1_Start vs S1_End	877	1.557	.399
	S2_Start vs S2_End	720	-1.642	.373
	S3_Start vs S3_End	753	-1.397	.484
	S4_Start vs S4_End	785	-1.089	.580
5 degree eccentricity, set size 6, distractor present	S1_Start vs S1_End	781	1.397	.484
	S2_Start vs S2_End	919	0.735	.743
	S3_Start vs S3_End	853	-0.031	.996
	S4_Start vs S4_End	938	1.023	.615
5 degree eccentricity, set size 10, distractor absent	S1_Start vs S1_End	801	0.508	.824
	S2_Start vs S2_End	819	-1.221	.532
	S3_Start vs S3_End	832	-1.220	.532
	S4_Start vs S4_End	784	-1.104	.580
5 degree eccentricity, set size 10, distractor present	S1_Start vs S1_End	910	2.584	.119
	S2_Start vs S2_End	1000	2.239	.194
	S3_Start vs S3_End	862	1.305	.507

	S4_Start vs S4_End	937	0.318	.887
10 degree eccentricity, set size 4, distractor absent	S1_Start vs S1_End	626	0.510	.824
	S2_Start vs S2_End	512	-0.754	.734
	S3_Start vs S3_End	542	-0.651	.767
	S4_Start vs S4_End	778	-0.330	.882
10 degree eccentricity, set size 4, distractor present	S1_Start vs S1_End	568	-0.630	.775
	S2_Start vs S2_End	691	-0.882	.685
	S3_Start vs S3_End	595	-2.069	.243
	S4_Start vs S4_End	730	-1.944	.282
10 degree eccentricity, set size 6, distractor absent	S1_Start vs S1_End	704	1.008	.620
	S2_Start vs S2_End	648	-1.340	.507
	S3_Start vs S3_End	701	-0.009	1.000
	S4_Start vs S4_End	782	-0.471	.831
10 degree eccentricity, set size 6, distractor present	S1_Start vs S1_End	567	-1.066	.586
	S2_Start vs S2_End	571	-1.281	.512
	S3_Start vs S3_End	600	-1.620	.375
	S4_Start vs S4_End	634	-1.681	.362

10 degree eccentricity, set size 10, distractor absent	S1_Start vs S1_End	755	3.270	.050
	S2_Start vs S2_End	786	2.744	.098
	S3_Start vs S3_End	853	2.678	.112
	S4_Start vs S4_End	793	2.307	.189
10 degree eccentricity, set size 10, distractor present	S1_Start vs S1_End	624	1.011	.620
	S2_Start vs S2_End	581	0.096	.973
	S3_Start vs S3_End	616	0.331	.882
	S4_Start vs S4_End	660	0.690	.765

Significant level: *<0.05, **<0.01,***<0.001

Appendix C

Accuracy of Online learning session comparison in the morning group

Parameter	Session Comparison	Sum of Rank	*Z*	*p* *(corrected)*
3 degree eccentricity, set size 4, distractor absent	S1_Start vs S1_End	784	-0.386	.892
	S2_Start vs S2_End	784	-0.386	.892
	S3_Start vs S3_End	812	0.964	.748
	S4_Start vs S4_End	742	-1.697	.748
3 degree eccentricity, set size 4, distractor present	S1_Start vs S1_End	812	0.964	.748
	S2_Start vs S2_End	784	-0.567	.851
	S3_Start vs S3_End	784	-0.964	.748
	S4_Start vs S4_End	784	-0.567	.851
3 degree eccentricity, set size 6, distractor absent	S1_Start vs S1_End	812	0.964	.748
	S2_Start vs S2_End	798	0	1.000
	S3_Start vs S3_End	798	0.000	1.000
	S4_Start vs S4_End	840	1.743	.748
3 degree eccentricity, set size 6, distractor present	S1_Start vs S1_End	798	0	1.000
	S2_Start vs S2_End	812	0.964	.748

	S3_Start vs S3_End	798	0	1.000
	S4_Start vs S4_End	798	0	1.000
3 degree eccentricity, set size 10, distractor absent	S1_Start vs S1_End	812	0.964	.748
	S2_Start vs S2_End	798	N/A	N/A
	S3_Start vs S3_End	812	0.964	.748
	S4_Start vs S4_End	798	N/A	N/A
3 degree eccentricity, set size 10, distractor present	S1_Start vs S1_End	826	1.010	.748
	S2_Start vs S2_End	812	0.567	.851
	S3_Start vs S3_End	784	-0.964	.748
	S4_Start vs S4_End	728	-1.428	.748
5 degree eccentricity, set size 4, distractor absent	S1_Start vs S1_End	812	0.964	.748
	S2_Start vs S2_End	798	N/A	N/A
	S3_Start vs S3_End	770	-1.402	.748
	S4_Start vs S4_End	756	-1.743	.748
5 degree eccentricity, set size 4, distractor present	S1_Start vs S1_End	784	-0.964	.748
	S2_Start vs S2_End	756	-1.187	.748
	S3_Start vs S3_End	798	0.000	1.000

	S4_Start vs S4_End	826	1.402	.748
5 degree eccentricity, set size 6, distractor absent	S1_Start vs S1_End	784	-0.964	.748
	S2_Start vs S2_End	812	0.964	.748
	S3_Start vs S3_End	770	-1.402	.748
	S4_Start vs S4_End	798	N/A	N/A
5 degree eccentricity, set size 6, distractor present	S1_Start vs S1_End	798	0.000	1.000
	S2_Start vs S2_End	826	1.010	.748
	S3_Start vs S3_End	770	-1.402	.748
	S4_Start vs S4_End	840	1.743	.748
5 degree eccentricity, set size 10, distractor absent	S1_Start vs S1_End	798	0.000	1.000
	S2_Start vs S2_End	840	1.743	.748
	S3_Start vs S3_End	812	0.964	.748
	S4_Start vs S4_End	784	-0.964	.748
5 degree eccentricity, set size 10, distractor present	S1_Start vs S1_End	784	-0.964	.748
	S2_Start vs S2_End	798	0.000	1.000
	S3_Start vs S3_End	784	-0.567	.851
	S4_Start vs S4_End	798	N/A	N/A

10 degree eccentricity, set size 4, distractor absent	S1_Start vs S1_End	826	0.679	.851
	S2_Start vs S2_End	784	-0.386	.892
	S3_Start vs S3_End	770	-0.841	.807
	S4_Start vs S4_End	770	-0.841	.807
10 degree eccentricity, set size 4, distractor present	S1_Start vs S1_End	812	0.567	.851
	S2_Start vs S2_End	854	2.039	.748
	S3_Start vs S3_End	812	0.448	.892
	S4_Start vs S4_End	812	0.567	.851
10 degree eccentricity, set size 6, distractor absent	S1_Start vs S1_End	798	0.000	1.000
	S2_Start vs S2_End	798	0.000	1.000
	S3_Start vs S3_End	826	1.010	.748
	S4_Start vs S4_End	812	0.567	.851
10 degree eccentricity, set size 6, distractor present	S1_Start vs S1_End	726.5	-0.799	.829
	S2_Start vs S2_End	784	-0.348	.909
	S3_Start vs S3_End	782.5	0.973	.748
	S4_Start vs S4_End	712.5	-1.130	.748
	S1_Start vs S1_End	686	-2.350	.748

10 degree eccentricity, set size 10, distractor absent	S2_Start vs S2_End	768.5	0.406	.892
	S3_Start vs S3_End	699	-1.557	.748
	S4_Start vs S4_End	727	-0.888	.797
10 degree eccentricity, set size 10, distractor present	S1_Start vs S1_End	758.5	-2.350	.851
	S2_Start vs S2_End	868	0.406	.748
	S3_Start vs S3_End	756	-1.557	.748
	S4_Start vs S4_End	757.5	-0.888	.748

Note. "N/A" indicates that no statistical difference was calculated because the accuracy remained at 100% throughout the compared sessions.

Significant level: *<0.05, **<0.01,***<0.001

Appendix D

Accuracy of Online learning session comparison in the evening group

Parameter	Session Comparison	Sum of Rank	*Z*	*p* *(corrected)*
3 degree eccentricity, set size 4, distractor absent	S1_Start vs S1_End	885	-0.839	.807
	S2_Start vs S2_End	900	-0.448	.892
	S3_Start vs S3_End	930	0.568	.851
	S4_Start vs S4_End	870	-1.743	.748
3 degree eccentricity, set size 4, distractor present	S1_Start vs S1_End	915	0	1.000
	S2_Start vs S2_End	930	0.568	.851
	S3_Start vs S3_End	915	0	1.000
	S4_Start vs S4_End	915	N/A	N/A
3 degree eccentricity, set size 6, distractor absent	S1_Start vs S1_End	960	1.743	.748
	S2_Start vs S2_End	900	-0.967	.748
	S3_Start vs S3_End	930	0.448	.892
	S4_Start vs S4_End	900	-0.967	.748
	S1_Start vs S1_End	900	-0.568	.851

3 degree eccentricity, set size 6, distractor present	S2_Start vs S2_End	930	0.568	.851
	S3_Start vs S3_End	885	-1.403	.748
	S4_Start vs S4_End	915	0	1.000
3 degree eccentricity, set size 10, distractor absent	S1_Start vs S1_End	945	1.403	.748
	S2_Start vs S2_End	930	0.967	.748
	S3_Start vs S3_End	900	-0.967	.748
	S4_Start vs S4_End	945	1.403	.748
3 degree eccentricity, set size 10, distractor present	S1_Start vs S1_End	915	0	1.000
	S2_Start vs S2_End	960	1.743	.748
	S3_Start vs S3_End	870	-1.374	.748
	S4_Start vs S4_End	915	0	1.000
5 degree eccentricity, set size 4, distractor absent	S1_Start vs S1_End	975	2.036	.748
	S2_Start vs S2_End	930	0.568	.851
	S3_Start vs S3_End	915	N/A	N/A
	S4_Start vs S4_End	930	0.568	.851
5 degree eccentricity, set size 4, distractor present	S1_Start vs S1_End	975	0.409	.892
	S2_Start vs S2_End	930	-0.967	.748

	S3_Start vs S3_End	915	-1.009	.748
	S4_Start vs S4_End	930	-0.568	.851
5 degree eccentricity, set size 6, distractor absent	S1_Start vs S1_End	930	0.448	.892
	S2_Start vs S2_End	885	-1.403	.748
	S3_Start vs S3_End	930	0.568	.851
	S4_Start vs S4_End	915	0.000	1.000
5 degree eccentricity, set size 6, distractor present	S1_Start vs S1_End	900	-0.385	.892
	S2_Start vs S2_End	900	-0.967	.748
	S3_Start vs S3_End	915	0	1.000
	S4_Start vs S4_End	900	-0.967	.748
5 degree eccentricity, set size 10, distractor absent	S1_Start vs S1_End	885	-1.009	.748
	S2_Start vs S2_End	930	0.967	.748
	S3_Start vs S3_End	915	N/A	N/A
	S4_Start vs S4_End	915	0	1.000
5 degree eccentricity, set size 10, distractor present	S1_Start vs S1_End	900	-0.448	.892
	S2_Start vs S2_End	915	0	1.000
	S3_Start vs S3_End	930	0.448	.892

	S4_Start vs S4_End	915	N/A	N/A
10 degree eccentricity, set size 4, distractor absent	S1_Start vs S1_End	900	-0.320	.916
	S2_Start vs S2_End	840	-1.643	.748
	S3_Start vs S3_End	870	-0.982	.748
	S4_Start vs S4_End	945.5	1.414	.748
10 degree eccentricity, set size 4, distractor present	S1_Start vs S1_End	900	-0.320	.916
	S2_Start vs S2_End	915	0	1.000
	S3_Start vs S3_End	885	-0.839	.807
	S4_Start vs S4_End	915	0.000	1.000
10 degree eccentricity, set size 6, distractor absent	S1_Start vs S1_End	900	-0.347	.909
	S2_Start vs S2_End	870	-1.374	.748
	S3_Start vs S3_End	900	-0.385	.892
	S4_Start vs S4_End	900	-0.568	.851
10 degree eccentricity, set size 6, distractor present	S1_Start vs S1_End	838.5	-0.793	.829
	S2_Start vs S2_End	915	0	1.000
	S3_Start vs S3_End	915	0	1.000
	S4_Start vs S4_End	930	0.385	.892

10 degree eccentricity, set size 10, distractor absent	S1_Start vs S1_End	823.5	-1.120	.748
	S2_Start vs S2_End	855	-1.494	.748
	S3_Start vs S3_End	900	-0.385	.892
	S4_Start vs S4_End	795	-2.341	.748
10 degree eccentricity, set size 10, distractor present	S1_Start vs S1_End	903	0.054	1.000
	S2_Start vs S2_End	930	0.300	.921
	S3_Start vs S3_End	840	-1.781	.748
	S4_Start vs S4_End	930	0.320	.916

Note. "N/A" indicates that no statistical difference was calculated because the accuracy remained at 100% throughout the compared sessions.

Significant level: *<0.05, **<0.01,***<0.001

Appendix E

RT and Accuracy of offline learning session comparison in the morning group

		RT			*Accuracy*		
Parameter	Session Comparison	Sum of Rank	*Z*	*p* *(corrected)*	Sum of Rank	*Z*	*p* *(corrected)*
3 degree eccentricity, set size 4, distractor absent	S1_End vs S2_Start (Offline Wake)	608	-0.330	.882	812	0.386	.892
	S2_End vs S3_Start (Offline Sleep)	714	0.686	.765	756	-1.743	.748
	S3_End vs S4_Start (Offline Wake)	694	0.097	.973	854	1.697	.748
3 degree eccentricity, set size 4, distractor present	S1_End vs S2_Start (Offline Wake)	784	0.970	.644	812	0.567	.851
	S2_End vs S3_Start (Offline Sleep)	712	-0.519	.824	798	0.000	1.000

	S3_End vs S4_Start (Offline Wake)	797	0.459	.840	826	1.402	.748
3 degree eccentricity, set size 6, distractor absent	S1_End vs S2_Start (Offline Wake)	882	2.405	.170	798	0.000	1.000
	S2_End vs S3_Start (Offline Sleep)	822	1.941	.282	826	1.010	.748
	S3_End vs S4_Start (Offline Wake)	699	0.419	.843	756	-1.743	.748
3 degree eccentricity, set size 6, distractor present	S1_End vs S2_Start (Offline Wake)	792	0.598	.782	784	-0.964	.748
	S2_End vs S3_Start (Offline Sleep)	809	1.142	.570	798	0.000	1.000
	S3_End vs S4_Start (Offline Wake)	729	-0.225	.918	798	0.000	1.000
3 degree eccentricity, set size 10, distractor absent	S1_End vs S2_Start (Offline Wake)	782	0.429	.841	784	-0.964	.748

	S2_End vs S3_Start (Offline Sleep)	755	-0.696	.765	798	N/A	N/A
	S3_End vs S4_Start (Offline Wake)	683	-1.221	.532	784	-0.964	.748
3 degree eccentricity, set size 10, distractor present	S1_End vs S2_Start (Offline Wake)	667	0.073	.983	770	-1.010	.748
	S2_End vs S3_Start (Offline Sleep)	737	0.614	.778	784	-0.567	.851
	S3_End vs S4_Start (Offline Wake)	713	-0.757	.734	812	1.428	.748
5 degree eccentricity, set size 4, distractor absent	S1_End vs S2_Start (Offline Wake)	810	0.901	.684	784	-0.964	.748
	S2_End vs S3_Start (Offline Sleep)	875	1.809	.320	826	1.402	.748
	S3_End vs S4_Start (Offline Wake)	881	2.218	.201	840	1.743	.748

5 degree eccentricity, set size 4, distractor present	S1_End vs S2_Start (Offline Wake)	728	0.000	1.000	868	2.306	.748
	S2_End vs S3_Start (Offline Sleep)	757	0.970	.644	784	-0.567	.851
	S3_End vs S4_Start (Offline Wake)	738	-0.295	.891	784	-0.964	.748
5 degree eccentricity, set size 6, distractor absent	S1_End vs S2_Start (Offline Wake)	826	0.451	.841	798	N/A	N/A
	S2_End vs S3_Start (Offline Sleep)	850	2.144	.209	812	0.567	.851
	S3_End vs S4_Start (Offline Wake)	887	1.450	.463	798	N/A	N/A
5 degree eccentricity, set size 6, distractor present	S1_End vs S2_Start (Offline Wake)	725	0.400	.848	784	-0.567	.851
	S2_End vs S3_Start (Offline Sleep)	648	-0.028	.996	784	-0.448	.892

	S3_End vs S4_Start (Offline Wake)	825	0.434	.841	798	N/A	N/A
5 degree eccentricity, set size 10, distractor absent	S1_End vs S2_Start (Offline Wake)	869	3.448	.050	756	-1.743	.748
	S2_End vs S3_Start (Offline Sleep)	848	3.074	.054	756	-1.743	.748
	S3_End vs S4_Start (Offline Wake)	874	2.266	.193	798	0.000	1.000
5 degree eccentricity, set size 10, distractor present	S1_End vs S2_Start (Offline Wake)	667	-1.961	.277	812	0.964	.748
	S2_End vs S3_Start (Offline Sleep)	749	0.347	.877	812	0.567	.851
	S3_End vs S4_Start (Offline Wake)	834	1.305	.507	784	-0.964	.748
10 degree eccentricity, set size 4, distractor absent	S1_End vs S2_Start (Offline Wake)	507	-0.209	.928	770	-0.679	.851

	S2_End vs S3_Start (Offline Sleep)	570	-1.090	.580	812	0.386	.892
	S3_End vs S4_Start (Offline Wake)	640	-0.437	.841	826	0.841	.807
10 degree eccentricity, set size 4, distractor present	S1_End vs S2_Start (Offline Wake)	793	1.342	.507	770	-1.402	.748
	S2_End vs S3_Start (Offline Sleep)	724	2.165	.209	770	-0.841	.807
	S3_End vs S4_Start (Offline Wake)	708	0.824	.714	770	-1.010	.748
10 degree eccentricity, set size 6, distractor absent	S1_End vs S2_Start (Offline Wake)	680	0.556	.804	784	-0.448	.892
	S2_End vs S3_Start (Offline Sleep)	810	1.913	.285	784	-0.567	.851
	S3_End vs S4_Start (Offline Wake)	704	0.751	.734	770	-1.010	.748

10 degree eccentricity, set size 6, distractor present	S1_End vs S2_Start (Offline Wake)	680	1.383	.489	826	0.743	.851
	S2_End vs S3_Start (Offline Sleep)	700	1.699	.355	744	-1.335	.748
	S3_End vs S4_Start (Offline Wake)	695	2.360	.184	827.5	1.130	.748
10 degree eccentricity, set size 10, distractor absent	S1_End vs S2_Start (Offline Wake)	642	-2.022	.251	812	1.428	.748
	S2_End vs S3_Start (Offline Sleep)	532	-1.213	.535	827.5	1.130	.748
	S3_End vs S4_Start (Offline Wake)	501	-2.975	.065	813	0.888	.797
10 degree eccentricity, set size 10, distractor present	S1_End vs S2_Start (Offline Wake)	622	0.184	.946	741	-0.490	.892
	S2_End vs S3_Start (Offline Sleep)	566	1.877	.301	756	-0.988	.748

S3_End vs S4_Start (Offline Wake)	791	1.374	.493	826	1.010	.748

Note. "N/A" indicates that no statistical difference was calculated because the accuracy remained at 100% throughout the compared sessions.

Significant level: *<0.05, **<0.01,***<0.001

Appendix F

RT and Accuracy of offline learning session comparison in the evening group

Parameter	Session Comparison	*RT* Sum of Rank	*RT* *Z*	*RT* *p (corrected)*	*Accuracy* Sum of Rank	*Accuracy* *Z*	*Accuracy* *p (corrected)*
3 degree eccentricity, set size 4, distractor absent	S1_End vs S2_Start (Offline Sleep)	884	1.675	.362	930	0.448	.892
	S2_End vs S3_Start (Offline Wake)	867	0.870	.685	900	-0.568	.851
	S3_End vs S4_Start (Offline Sleep)	762	-0.362	.868	930	0.448	.892
3 degree eccentricity, set size 4, distractor present	S1_End vs S2_Start (Offline Sleep)	872	0.950	.647	900	-0.568	.851
	S2_End vs S3_Start (Offline Wake)	896	1.333	.507	900	-0.568	.851

	S3_End vs S4_Start (Offline Sleep)	925	0.826	.714	900	-0.967	.748
3 degree eccentricity, set size 6, distractor absent	S1_End vs S2_Start (Offline Sleep)	959	3.099	.054	885	-1.009	.748
	S2_End vs S3_Start (Offline Wake)	1017	2.046	.251	945	1.403	.748
	S3_End vs S4_Start (Offline Sleep)	818	0.787	.727	885	-1.009	.748
3 degree eccentricity, set size 6, distractor present	S1_End vs S2_Start (Offline Sleep)	949	1.446	.463	915	0.000	1.000
	S2_End vs S3_Start (Offline Wake)	817	0.303	.891	915	0.000	1.000
	S3_End vs S4_Start (Offline Sleep)	982	1.236	.532	930	0.967	.748
3 degree eccentricity, set	S1_End vs S2_Start (Offline Sleep)	943	1.813	.320	885	-1.403	.748

size 10, distractor absent	S2_End vs S3_Start (Offline Wake)	1000	2.239	.194	915	0.000	1.000
	S3_End vs S4_Start (Offline Sleep)	979	0.939	.654	915	N/A	N/A
3 degree eccentricity, set size 10, distractor present	S1_End vs S2_Start (Offline Sleep)	814	0.487	.825	870	-1.743	.748
	S2_End vs S3_Start (Offline Wake)	714	-0.258	.912	930	0.385	.892
	S3_End vs S4_Start (Offline Sleep)	881	0.631	.775	930	0.568	.851
5 degree eccentricity, set size 4, distractor absent	S1_End vs S2_Start (Offline Sleep)	828	1.677	.362	870	-1.374	.748
	S2_End vs S3_Start (Offline Wake)	1056	3.571	.045*	885	-1.403	.748
	S3_End vs S4_Start (Offline Sleep)	1034	2.024	.251	930	0.967	.748

5 degree eccentricity, set size 4, distractor present	S1_End vs S2_Start (Offline Sleep)	760	-0.148	.961	885	-1.009	.748
	S2_End vs S3_Start (Offline Wake)	953	1.319	.507	960	1.743	.748
	S3_End vs S4_Start (Offline Sleep)	918	1.221	.532	930	0.568	.851
5 degree eccentricity, set size 6, distractor absent	S1_End vs S2_Start (Offline Sleep)	830	1.237	.532	900	-0.448	.892
	S2_End vs S3_Start (Offline Wake)	1086	2.813	.093	930	0.967	.748
	S3_End vs S4_Start (Offline Sleep)	906	1.492	.431	900	-0.568	.851
5 degree eccentricity, set size 6, distractor present	S1_End vs S2_Start (Offline Sleep)	817	0.771	.731	900	-1.009	.748
	S2_End vs S3_Start (Offline Wake)	884	-0.235	.916	930	0.967	.748

	S3_End vs S4_Start (Offline Sleep)	962	1.648	.373	900	0.000	1.000
5 degree eccentricity, set size 10, distractor absent	S1_End vs S2_Start (Offline Sleep)	944	1.114	.580	900	-0.967	.748
	S2_End vs S3_Start (Offline Wake)	1014	2.176	.207	900	-0.967	.748
	S3_End vs S4_Start (Offline Sleep)	1075	2.646	.115	930	0.967	.748
5 degree eccentricity, set size 10, distractor present	S1_End vs S2_Start (Offline Sleep)	840	0.439	.841	900	-0.568	.851
	S2_End vs S3_Start (Offline Wake)	817	-0.375	.863	930	0.568	.851
	S3_End vs S4_Start (Offline Sleep)	806	0.360	.868	870	-1.743	.748
10 degree eccentricity, set	S1_End vs S2_Start (Offline Sleep)	568	-0.672	.765	960	0.922	.782

size 4, distractor absent	S2_End vs S3_Start (Offline Wake)	777	1.713	.352	975	1.363	.748
	S3_End vs S4_Start (Offline Sleep)	842	1.913	.285	870	-1.374	.748
10 degree eccentricity, set size 4, distractor present	S1_End vs S2_Start (Offline Sleep)	757	1.722	.352	885	-0.741	.851
	S2_End vs S3_Start (Offline Wake)	833	1.841	.308	930	0.385	.892
	S3_End vs S4_Start (Offline Sleep)	970	2.514	.141	900	-0.568	.851
10 degree eccentricity, set size 6, distractor absent	S1_End vs S2_Start (Offline Sleep)	742	0.961	.646	915	0.000	1.000
	S2_End vs S3_Start (Offline Wake)	977	2.773	.095	960	1.374	.748
	S3_End vs S4_Start (Offline Sleep)	726	-0.497	.824	900	-0.448	.892

10 degree eccentricity, set size 6, distractor present	S1_End vs S2_Start (Offline Sleep)	802	1.575	.396	945	0.741	.851
	S2_End vs S3_Start (Offline Wake)	745	1.781	.330	900	-0.347	.909
	S3_End vs S4_Start (Offline Sleep)	840	2.446	.160	900	-0.385	.892
10 degree eccentricity, set size 10, distractor absent	S1_End vs S2_Start (Offline Sleep)	616	-1.613	.375	960	1.064	.748
	S2_End vs S3_Start (Offline Wake)	634	-2.346	.184	945	0.839	.807
	S3_End vs S4_Start (Offline Sleep)	632	-1.312	.507	931.5	0.793	.829
10 degree eccentricity, set size 10, distractor present	S1_End vs S2_Start (Offline Sleep)	579	0.564	.802	867	-0.054	1.000
	S2_End vs S3_Start (Offline Wake)	572	0.681	0.765	915	0.000	1.000

S3_End vs S4_Start (Offline Sleep)	806	0.882	.685	960	1.183	.748

Note. "N/A" indicates that no statistical difference was calculated because the accuracy remained at 100% throughout the compared sessions.

Significant level: *<0.05, **<0.01,***<0.001

Appendix G

RT of Online learning session comparison in the morning group

Parameter	Session Comparison	Sum of Rank	Z	p (corrected)
3 degree eccentricity, set size 2	S1_Start vs S1_End	1452	2.318	.189
	S2_Start vs S2_End	1607	1.189	.541
	S3_Start vs S3_End	1385	-0.444	.841
	S4_Start vs S4_End	1574	0.674	.765
3 degree eccentricity, set size 6	S1_Start vs S1_End	1253	1.028	.615
	S2_Start vs S2_End	1143	2.209	.201
	S3_Start vs S3_End	1212	-0.150	.961
	S4_Start vs S4_End	898	-0.407	.847
3 degree eccentricity, set size 10	S1_Start vs S1_End	4721	1.418	.477
	S2_Start vs S2_End	4550	-0.173	.948
	S3_Start vs S3_End	5197	-0.674	.765
	S4_Start vs S4_End	4584	-0.618	.778

5 degree eccentricity, set size 2	S1_Start vs S1_End	1830	3.360	.050
	S2_Start vs S2_End	1569	0.791	.727
	S3_Start vs S3_End	1713	0.873	.685
	S4_Start vs S4_End	1490	0.474	.831
5 degree eccentricity, set size 6	S1_Start vs S1_End	1008	1.368	.495
	S2_Start vs S2_End	996	0.994	.630
	S3_Start vs S3_End	1132	-0.295	.891
	S4_Start vs S4_End	944	-1.093	.580
5 degree eccentricity, set size 10	S1_Start vs S1_End	4075	0.800	.725
	S2_Start vs S2_End	4200	-0.079	.981
	S3_Start vs S3_End	4203	0.246	.912
	S4_Start vs S4_End	3775	-0.176	.948
10 degree eccentricity, set size 2	S1_Start vs S1_End	2342	1.081	.581
	S2_Start vs S2_End	2222	1.393	.484
	S3_Start vs S3_End	2644	1.536	.406
	S4_Start vs S4_End	2404	0.004	1.000

10 degree eccentricity, set size 6	S1_Start vs S1_End	1545	-0.506	.824
	S2_Start vs S2_End	2044	-0.393	.852
	S3_Start vs S3_End	1739	-0.756	.734
	S4_Start vs S4_End	2261	0.894	.684
10 degree eccentricity, set size 10	S1_Start vs S1_End	3689	1.632	.375
	S2_Start vs S2_End	4847	1.417	.477
	S3_Start vs S3_End	4287	0.897	.684
	S4_Start vs S4_End	4603	2.779	.095

Significant level: *<0.05, **<0.01,***<0.001

Appendix H

RT of Online learning session comparison in the evening group

Parameter	Session Comparison	Sum of Rank	Z	p (corrected)
3 degree eccentricity, set size 2	S1_Start vs S1_End	1427	3.985	.013
	S2_Start vs S2_End	1428	2.298	.189
	S3_Start vs S3_End	1298	-0.835	.713
	S4_Start vs S4_End	1577	-0.295	.891
3 degree eccentricity, set size 6	S1_Start vs S1_End	575	2.615	.115
	S2_Start vs S2_End	1119	0.178	.948
	S3_Start vs S3_End	1038	0.703	.765
	S4_Start vs S4_End	582	0.564	.802
3 degree eccentricity, set size 10	S1_Start vs S1_End	3196	0.882	.685
	S2_Start vs S2_End	3008	-0.422	.843
	S3_Start vs S3_End	2790	-1.914	.285
	S4_Start vs S4_End	2902	-1.800	.320

5 degree eccentricity, set size 2	S1_Start vs S1_End	915	3.238	.050
	S2_Start vs S2_End	980	1.839	.308
	S3_Start vs S3_End	1105	0.708	.764
	S4_Start vs S4_End	881	-1.072	.586
5 degree eccentricity, set size 6	S1_Start vs S1_End	695	1.190	.541
	S2_Start vs S2_End	960	0.874	.685
	S3_Start vs S3_End	968	-0.113	.973
	S4_Start vs S4_End	887	-0.145	.961
5 degree eccentricity, set size 10	S1_Start vs S1_End	2755	2.642	.115
	S2_Start vs S2_End	3507	0.255	.912
	S3_Start vs S3_End	3476	-0.979	.642
	S4_Start vs S4_End	2789	-1.506	.423
10 degree eccentricity, set size 2	S1_Start vs S1_End	2245	3.107	.054
	S2_Start vs S2_End	1542	1.301	.507
	S3_Start vs S3_End	1722	0.533	.820
	S4_Start vs S4_End	1941	0.643	.771

10 degree eccentricity, set size 6	S1_Start vs S1_End	1625	0.787	.727
	S2_Start vs S2_End	1806	1.714	.352
	S3_Start vs S3_End	1672	-2.035	.251
	S4_Start vs S4_End	2043	-1.332	.507
10 degree eccentricity, set size 10	S1_Start vs S1_End	4003	3.049	.054
	S2_Start vs S2_End	3420	1.863	.303
	S3_Start vs S3_End	4184	1.136	.573
	S4_Start vs S4_End	4170	0.000	1.000

Significant level: *<0.05, **<0.01, ***<0.001

Appendix I

Accuracy of Online learning session comparison in the morning group

Parameter	Session Comparison	Sum of Rank	Z	p (corrected)
3 degree eccentricity, set size 2	S1_Start vs S1_End	1635.5	-0.662	.851
	S2_Start vs S2_End	1755	-1.369	.748
	S3_Start vs S3_End	1503	-0.315	.916
	S4_Start vs S4_End	1786	-0.592	.851
3 degree eccentricity, set size 6	S1_Start vs S1_End	1533.5	1.926	.748
	S2_Start vs S2_End	1060.5	0.343	.909
	S3_Start vs S3_End	1438.5	1.580	.748
	S4_Start vs S4_End	1143	0.147	1.000
3 degree eccentricity, set size 10	S1_Start vs S1_End	5720	0.652	.851
	S2_Start vs S2_End	5229.5	0.448	.892
	S3_Start vs S3_End	6301.5	0.183	.997
	S4_Start vs S4_End	5372.5	-0.274	.941

5 degree eccentricity, set size 2	S1_Start vs S1_End	1820	0.000	1.000
	S2_Start vs S2_End	1550	-1.693	.748
	S3_Start vs S3_End	1777	0.866	.807
	S4_Start vs S4_End	1786	1.456	.748
5 degree eccentricity, set size 6	S1_Start vs S1_End	1137	0.343	.909
	S2_Start vs S2_End	1094	-0.304	.921
	S3_Start vs S3_End	1190	0.971	.748
	S4_Start vs S4_End	1159.5	-0.918	.782
5 degree eccentricity, set size 10	S1_Start vs S1_End	4965	1.158	.748
	S2_Start vs S2_End	4712	-0.828	.815
	S3_Start vs S3_End	4639	-0.132	1.000
	S4_Start vs S4_End	4548	-0.015	1.000
10 degree eccentricity, set size 2	S1_Start vs S1_End	2649	-0.167	1.000
	S2_Start vs S2_End	2449	-1.284	.748
	S3_Start vs S3_End	2623	-0.218	.972
	S4_Start vs S4_End	2685	-0.822	.818

10 degree eccentricity, set size 6	S1_Start vs S1_End	2112.5	-0.648	.851
	S2_Start vs S2_End	2529.5	1.135	.748
	S3_Start vs S3_End	2043	0.372	.900
	S4_Start vs S4_End	2552.5	2.355	.748
10 degree eccentricity, set size 10	S1_Start vs S1_End	4503.5	0.871	.807
	S2_Start vs S2_End	5421	0.159	1.000
	S3_Start vs S3_End	4606	-0.141	1.000
	S4_Start vs S4_End	4611	-1.580	.748

Significant level: *<0.05, **<0.01,***<0.001

Appendix J

Accuracy of Online learning session comparison in the evening group

Parameter	Session Comparison	Sum of Rank	Z	p (corrected)
3 degree eccentricity, set size 2	S1_Start vs S1_End	1791.5	0.661	.851
	S2_Start vs S2_End	1625	-0.027	1.000
	S3_Start vs S3_End	1594.5	-0.611	.851
	S4_Start vs S4_End	1829.5	-0.668	.851
3 degree eccentricity, set size 6	S1_Start vs S1_End	777.5	0.562	.853
	S2_Start vs S2_End	1336	0.919	.782
	S3_Start vs S3_End	1169	-2.774	.748
	S4_Start vs S4_End	593	-1.748	.748
3 degree eccentricity, set size 10	S1_Start vs S1_End	4521	0.896	.797
	S2_Start vs S2_End	4087	0.186	.997
	S3_Start vs S3_End	3897	-1.512	.748
	S4_Start vs S4_End	3824	-1.861	.748
	S1_Start vs S1_End	1083.5	-1.268	.748

5 degree eccentricity, set size 2	S2_Start vs S2_End	1066.5	0.158	1.000
	S3_Start vs S3_End	1073	0.793	.829
	S4_Start vs S4_End	1169	0.480	.892
5 degree eccentricity, set size 6	S1_Start vs S1_End	896	-0.063	1.000
	S2_Start vs S2_End	1190	-1.053	.748
	S3_Start vs S3_End	1242.5	0.000	1.000
	S4_Start vs S4_End	1105.5	-1.173	.748
5 degree eccentricity, set size 10	S1_Start vs S1_End	3800	-1.227	.748
	S2_Start vs S2_End	4541	0.581	.851
	S3_Start vs S3_End	4595	1.109	.748
	S4_Start vs S4_End	3573	-1.240	.748
10 degree eccentricity, set size 2	S1_Start vs S1_End	2572.5	-0.363	.906
	S2_Start vs S2_End	1834	-0.406	.892
	S3_Start vs S3_End	1810	-1.410	.748
	S4_Start vs S4_End	2200	1.808	.748
	S1_Start vs S1_End	2285.5	0.992	.748

10 degree eccentricity, set size 6	S2_Start vs S2_End	2096.5	-0.914	.782
	S3_Start vs S3_End	2172.5	0.312	.916
	S4_Start vs S4_End	2516.5	-1.338	.748
10 degree eccentricity, set size 10	S1_Start vs S1_End	4946	0.569	.851
	S2_Start vs S2_End	4394	0.272	.941
	S3_Start vs S3_End	4620.5	2.642	.748
	S4_Start vs S4_End	5062.5	-0.463	.892

Significant level: *<0.05, **<0.01,***<0.001

Appendix K

RT and Accuracy of offline learning session comparison in the morning group

		RT			Accuracy		
Parameter	Session Comparison	Sum of Rank	Z	p (corrected)	Sum of Rank	Z	p (corrected)
3 degree eccentricity, set size 2	S1_End vs S2_Start (Offline Wake)	1975	0.694	.765	2456.5	0.257	.946
	S2_End vs S3_Start (Offline Sleep)	2528	0.690	.765	2675	-0.492	.892
	S3_End vs S4_Start (Offline Wake)	2425	0.805	.725	2600	1.787	.748
3 degree eccentricity, set size 6	S1_End vs S2_Start (Offline Wake)	976	0.444	.841	1264.5	-2.075	.748
	S2_End vs S3_Start (Offline Sleep)	1447	1.082	.581	1465.5	-0.500	.892

	S3_End vs S4_Start (Offline Wake)	1168	1.096	.580	1382.5	-0.443	.892
3 degree eccentricity, set size 10	S1_End vs S2_Start (Offline Wake)	4232	1.101	.580	4924.5	-1.733	.748
	S2_End vs S3_Start (Offline Sleep)	4856	2.039	.251	5101.5	0.008	1.000
	S3_End vs S4_Start (Offline Wake)	5014	1.846	.308	5362.5	-0.332	.916
5 degree eccentricity, set size 2	S1_End vs S2_Start (Offline Wake)	1738	-0.609	.780	2135	-0.730	.851
	S2_End vs S3_Start (Offline Sleep)	2561	1.351	.506	2444	1.118	.748
	S3_End vs S4_Start (Offline Wake)	1738	-0.029	.996	1965.5	-0.260	.946
5 degree eccentricity, set size 6	S1_End vs S2_Start (Offline Wake)	951	0.296	.891	1156	-0.384	.892

	S2_End vs S3_Start (Offline Sleep)	966	1.181	.544	941	-1.495	.748
	S3_End vs S4_Start (Offline Wake)	1173	1.096	.580	1223.5	0.978	.748
5 degree eccentricity, set size 10	S1_End vs S2_Start (Offline Wake)	3481	1.771	.332	3941.5	-1.480	.748
	S2_End vs S3_Start (Offline Sleep)	3639	1.317	.507	3719.5	0.557	.855
	S3_End vs S4_Start (Offline Wake)	3518	0.681	.765	3907	0.766	.850
10 degree eccentricity, set size 2	S1_End vs S2_Start (Offline Wake)	1593	0.781	.727	1835	0.446	.892
	S2_End vs S3_Start (Offline Sleep)	1488	0.853	.698	1490	0.122	1.000
	S3_End vs S4_Start (Offline Wake)	1565	-0.597	.782	1821	0.878	.804

10 degree eccentricity, set size 6	S1_End vs S2_Start (Offline Wake)	2152	2.149	.209	1835	-0.818	.818
	S2_End vs S3_Start (Offline Sleep)	1929	1.881	.301	1490	-1.368	.748
	S3_End vs S4_Start (Offline Wake)	2153	0.650	.767	1821	-1.069	.748
10 degree eccentricity, set size 10	S1_End vs S2_Start (Offline Wake)	3725	0.498	.824	4710	-1.378	.748
	S2_End vs S3_Start (Offline Sleep)	4494	-0.732	.744	5467	-0.671	.851
	S3_End vs S4_Start (Offline Wake)	4220	-1.099	.580	5233.5	1.110	.748

Significant level: *<0.05, **<0.01,***<0.001

Appendix L

RT and Accuracy of offline learning session comparison in the evening group

		RT			Accuracy		
Parameter	Session Comparison	Sum of Rank	Z	p (corrected)	Sum of Rank	Z	p (corrected)
3 degree eccentricity, set size 2	S1_End vs S2_Start (Offline Wake)	1642	-0.083	.981	2687.5	-1.263	.748
	S2_End vs S3_Start (Offline Sleep)	2052	0.411	.847	2596	-0.773	.847
	S3_End vs S4_Start (Offline Wake)	2540	1.170	.548	2737.5	0.539	.869
3 degree eccentricity, set size 6	S1_End vs S2_Start (Offline Wake)	772	0.748	.734	1054	-2.279	.748
	S2_End vs S3_Start (Offline Sleep)	1180	0.129	.968	1596	0.651	.851

	S3_End vs S4_Start (Offline Wake)	1256	-0.223	.918	1353	1.923	.748
3 degree eccentricity, set size 10	S1_End vs S2_Start (Offline Wake)	3178	2.303	.189	4113	-1.277	.748
	S2_End vs S3_Start (Offline Sleep)	3443	2.000	.261	4201.5	0.067	1.000
	S3_End vs S4_Start (Offline Wake)	4161	3.064	.054	4357	1.231	.748
5 degree eccentricity, set size 2	S1_End vs S2_Start (Offline Wake)	1230	0.635	.775	1547	-0.441	.892
	S2_End vs S3_Start (Offline Sleep)	1251	-0.513	.824	1497	-1.877	.748
	S3_End vs S4_Start (Offline Wake)	1656	2.281	.193	1598	0.929	.782
5 degree eccentricity, set size 6	S1_End vs S2_Start (Offline Wake)	632	1.132	.573	814	0.171	1.000

	S2_End vs S3_Start (Offline Sleep)	1029	0.062	.987	1260	0.384	.892
	S3_End vs S4_Start (Offline Wake)	1079	1.189	.541	1291	0.256	.946
5 degree eccentricity, set size 10	S1_End vs S2_Start (Offline Wake)	2624	1.066	.586	3240.5	-0.622	.851
	S2_End vs S3_Start (Offline Sleep)	2792	1.290	.511	3280	-1.109	.748
	S3_End vs S4_Start (Offline Wake)	2745	2.157	.209	3169	-0.655	.851
10 degree eccentricity, set size 2	S1_End vs S2_Start (Offline Wake)	855	0.225	.918	1077.5	0.253	.946
	S2_End vs S3_Start (Offline Sleep)	1064	0.479	.829	1200.5	-0.520	.885
	S3_End vs S4_Start (Offline Wake)	1313	0.249	.912	1348.5	1.071	.748

10 degree eccentricity, set size 6	S1_End vs S2_Start (Offline Wake)	1309	1.802	.320	1719.5	-0.992	.748
	S2_End vs S3_Start (Offline Sleep)	1422	-0.119	.972	1655.5	-0.312	.916
	S3_End vs S4_Start (Offline Wake)	1806	2.885	.078	1781	0.219	.972
10 degree eccentricity, set size 10	S1_End vs S2_Start (Offline Wake)	3940	-0.127	.968	5785	-0.569	.851
	S2_End vs S3_Start (Offline Sleep)	3139	-0.536	.819	3959.5	-3.040	.748
	S3_End vs S4_Start (Offline Wake)	3377	0.555	.804	4248.5	-0.592	.851

Significant level: *<0.05, **<0.01,***<0.001

Appendix M: Link to Experimental Scripts and Data

https://cf.sharepoint.com/:f:/r/teams/ProjectHCP/Shared%20Documents/ZhishanLiu?csf=1&web=1&e=ayEBFF