

University of Nottingham
UK | CHINA | MALAYSIA

Neural and Cognitive Insights into Categorisation and Interference Resolution in Visual Working Memory

Thesis submitted to the University of Nottingham for the degree of Doctor of Philosophy

June 2026

Uma Ajmeria

20066134

Supervisors: Dr. Nicholas Myers

Dr. Jan Derrfuss

School of Psychology, Faculty of Science

University of Nottingham

Table of Contents

Abstract 7

Acknowledgements 9

Chapter 1: Exploring the Role of Working Memory and its Importance in Cognitive Function 10

Overview of Working Memory 10

Evolution of Working Memory Models 12

The Role of Working Memory in Cognitive Functions 20

Neural Mechanisms Underlying Working Memory 27

Scope of thesis 41

Chapter 2 – The Neural Basis of Generalisation and Conflict Resolution in Categorisation 43

Chapter Summary 43

Introduction 45

Methods 50

Participants 50

Materials 50

Apparatus 53

Design 54

Procedure 55

Behavioural Analysis 57

EEG Preprocessing 59

EEG Analysis 59

Within-task and Cross-task Decodability 60

Results 62

Behavioural Analysis 62

Neural Analysis 70

Discussion 95

Chapter 3 – Exploring Dual Task Interference in Visual Working Memory 102

Chapter Summary 102

General Introduction 102

Chapter 3.1 – Dual-task Interference in Working Memory: Impairments in Temporal Prioritisation Despite Practice 111

Introduction 111

Methods 114

Design 114

Participants 115

Materials 116

Procedure 116

Results 119

No Significant Difference in Accuracy Across Single and Dual-task Conditions 119

Reaction Time Increased as Target Load Increased 121

Practice Did Not Improve Accuracy 125

Reaction Time Reduced Throughout the Experiment 126

Discussion 129

Chapter 3.2 – Exploring Dual Task Interference in Working Memory and ADHD: A Simplified Paradigm Exploring Effects of Cognitive Load on Performance and Relationship to Inattention and Hyperactivity 133

Introduction 133

Methods 137

Design 137

Participants 138

Procedure 139

Results 143

No Dual-Task Cost Observed in Accuracy 143

Dual-Task Cost Observed in Reaction Time 143

Dual-Task Reaction Time Costs Reduced with Practice 144

ADHD Analyses 145

Discussion 151

Chapter 3.3 – The Effect of Cognitive Load and Short-term Practice on Working Memory Prioritisation in ADHD 155

Introduction 155

Methods 156

Participants 157

Materials 157

Design 158

Procedure 160

Results 161

Prioritisation Improves Accuracy and Reduces Load Effect 161

Reaction Time Improves with Practice, but is Sensitive to Load 162

Prioritisation Benefits Accuracy and Eliminates Response Costs 163

ADHD Traits Do Not Affect Accuracy, but Impact Reaction Time Under Load 165

Hyperactivity, but Not Inattention, Reduces Benefit of Prioritisation 167

Discussion 168

Chapter 4 – Does Training Help Distinguish Prioritised Working Memory Representations via Subspace Orthogonalisation? A Preregistration. 173

Chapter Summary 173

Introduction 174

Methods 180

Design 180

Participants 182

Materials 183

Procedure 183

EEG Recording 184

Data Analysis Plan 184

Expected Results 188

Simulations 189

Simulation Results 191

Significance 194

General Conclusion.....195

References.....197

Appendices.....247

Chapter 3.1 – Dual-task Interference in Working Memory: Impairments in Temporal Prioritisation Despite Practice.....247

Chapter 3.2 – Exploring Dual Task Interference in Working Memory and ADHD: A Simplified Paradigm Exploring Effects of Cognitive Load on Performance and Relationship to Inattention and Hyperactivity.....249

Chapter 3.3 – The Effect of Cognitive Load and Short-term Practice on Working Memory Prioritisation in ADHD.....250

Supplemental Figures.....266

Chapter 2 – The Neural Basis of Generalisation and Conflict Resolution in Categorisation 266

Chapter 3.1 – Dual-task Interference in Working Memory: Impairments in Temporal Prioritisation Despite Practice.....290

Abstract

Working memory is typically constrained by limited capacity, yet humans are able to flexibly prioritise relevant information and adapt to varying task demands. This thesis investigated how the brain manages interference under competing representational demands, focusing on whether information is supported by shared neural codes which generalise across contexts, or by independent codes which minimise conflict. Using EEG decoding, behavioural experiments, and a pre-registered EEG protocol, this thesis examines how category representations adapt when tasks shift from independent to overlapping stimulus structures; how cognitive load, response configuration, practice, and ADHD traits influence performance in visual working memory; and whether training or response effector separation could reduce interference between prioritised and unprioritised working memory representations.

In Chapter 2 we explored multivariate decoding of EEG data which indicated that category-selective neural patterns generalised across tasks when stimulus sets were independent, but cross-task generalisation was reduced when overlapping stimuli were introduced (consistent with adaptive changes to representational structure in response to interference). In Chapter 3 we explored how interference between concurrently executed working memory tasks could be resolved through scheduling. The behavioural results indicated that increasing cognitive load from the interfering task impaired performance, which was not reduced by practice. Some ADHD traits correlated with interference-based impairment, suggesting some inefficiency in scheduling multiple tasks. Chapter 4, a pre-registered EEG study, was designed to test whether training could reduce this interference between conflicting prioritised and unprioritised working memory representations could be resolved by neural orthogonalisation, whilst also evaluating whether response effector separation contributes to representational separation.

This thesis supports the view that cognitive limitations reflect working memory capacity constraints, but also interference occurring due to overlapping representations, and that the brain attempts to mitigate these limitations via flexible reformatting, prioritisation, and learning-dependent optimisation of neural correlates.

Acknowledgements

Writing this thesis is one of my proudest achievements, and it would not have been possible without the support of a few special people I hold close to my heart.

Firstly, I need to thank my supervisor, Nick Myers, for his patience, guidance, and 'mini rants' which made this initially unreachable target even possible. Thank you for your endless support regardless of the time of day and always encouraging me when I needed it the most. Thank you to Jan, for your invaluable advice, and to Mimma, for adding laughter when I needed it the most.

Thank you to my **whole** family for their support, especially my parents, grandparents, and brothers who loved me through my sleep-deprived and exhausted moments. Mostly, thank you for encouraging me to do this PhD in the first place. Thank you to my (soon-to-be) in-laws for their unconditional support, but also to my dear friends who held me together when I unknowingly needed them the most. I went through some of the darkest moments these past few years, and I appreciate you all for checking in on me, especially Daneesha, Mica, Holly, and Riya.

I want to dedicate Chapter 2 to a brilliant individual we lost too soon. Thank you, Cal. Your ideas made this chapter possible, and I hope I did it justice.

Finally, Shyam, thank you will never be enough. After 10 years I still can't believe my luck in finding you in Mr. Ridgeway's class (and that our story started with a samosa), but I can't wait to become your wife.

Chapter 1: Exploring the Role of Working Memory and its Importance in Cognitive Function

Overview of Working Memory

Working memory (WM) is a brain system which temporarily holds items in mind whilst maintaining and manipulating information needed for complex cognitive tasks (Baddeley, 1992). This limited-capacity system is essential for many cognitive functions, including logical thinking, decision making, and planning (Wen & Schwieter, 2022). We require and rely heavily on the use of this system for tasks as common as driving and grocery shopping (Broadbent et al., 2023; Luna & Kim, 2009), illustrating the unique flexibility and fundamental function of WM (Buschman, 2021). This task involves not only mental arithmetic to calculate the additional cost of each item, but also maintaining the item cost in mind, and decision-making to determine whether to purchase additional items (Baddeley, 2003). These mundane tasks are only thought of as such due to the remarkable ability of working memory to handle the information required, as well as adapting when needed for more complex and challenging situations (such as tasks involving concurrent storage and processing).

Despite sharing similarities with short-term (STM) and long-term (LTM) memory, working memory is a distinct memory system in itself (Cowan, 2008). The notion of working memory has evolved significantly over time, from initially being labelled as an extension of STM (Nairne & Neath, 2012), to its now more common conception as a dynamic system involving the combination of cognitive processes in the moment of a task to guide behaviour (Simmering, 2016). Short-term memory and working memory reflect different cognitive functions (Aben et al., 2012). Short-term memory is commonly conceptualised as the general retention of information before becoming permanently stored (Fuster, 2001), with rapid

decay (Aben et al., 2012), whereas WM includes both the maintenance and controlled manipulation of information (Baddeley, 1992, 2012).

Early research identified memory as a single system, with the first scientific study exploring memory usually traced back to Hermann Ebbinghaus (1885). Ebbinghaus (1885) memorised syllables tested in a period of 31 days and noticed he had 'a fleeting grasp…of the series in moments of special concentration', but that this didn't mean he could recall the series afterwards. Distinctions between types of memory only emerged later, with researchers like James (1890) proposing 'primary memory' (a small amount of information held in present momentarily) and 'secondary memory' (a vast body of memories stored over a lifetime), (James, 1890; cited in Cowan, 2008). This idea of 'primary memory' developed into STM, but there was still a lack of understanding of which memory system could support more complex cognitive processes which require the manipulation and retrieval of information (Cowan, 2008). The conceptual jump from STM to WM was coined by Miller et al. (1960) who used the term 'working memory' to refer to a type of memory needed when completing tasks such as solving a maths problem without writing it down, or baking a cake and somehow knowing not to repeat the same instructions twice (Miller et al., 1960; cited in Cowan, 2008). Baddeley and Hitch (1974) built on the STM-WM distinction by demonstrating that a single module is not enough to account for all temporary memory and instead proposed a dynamic model which emphasised storage and processing, rather than limits on mental processes being attributed to a single source (Miller, 1956). This model allowed WM to be identified as an active workspace in which information could be held and manipulated (Baddeley & Hitch, 1974). The work from Baddeley and Hitch (1974) redefined WM to be generally viewed as the combination of multiple components working together. Long-term memory (the vast store of knowledge and a record of prior events, Cowan, 2008) research also heavily contributed towards developing the concept and our understanding of

working memory, particularly the idea that LTM reduces WM load by organising information into smaller units (Miller, 1956), which can be seen in Cowan's embedded process model (1988, outlined below). These developments suggest that WM is critical not only for information storage, but also more broadly involved in memory interactions with LTM. More recent theories have shifted from focusing on storage capacity to how WM functions, such as the notion that WM relies on attention control (Engle et al., 1999).

Evolution of Working Memory Models

In this section, I will further explore four significant models which each transformed the direction of WM research in their own way: the multi-store model of memory (Atkinson & Shiffrin, 1968), the multicomponent working memory model (Baddeley & Hitch, 1974), the embedded-processes model (Cowan, 1998), and finally, Engle's view on working memory capacity (Engle, 2002).

The Multi-Store Model of Memory – Atkinson and Shiffrin (1968)

Atkinson and Shiffrin (1968) introduced a key memory model which outlined an information processing theory of human memory, permanently changing our outlook on the distinction between STM and LTM (Wixted, 2023). This model assumes there are three separate memory stores which differ in capacity: the sensory store, the short-term store, and the long-term store. According to this model, each memory store differs in its encoding (conversion of information into code), capacity (the amount of information which can be held in store), and duration (the amount of time the information can be held in the memory store, Shiffrin & Atkinson, 1969). Sensory information is available in the sensory store which has a large capacity but can store information for only a limited duration. If the item is attended, then the information is transferred to the STM store. The STM store (or working memory store) has a duration of (up to) 30s but a smaller capacity of 7+/-2 items which primarily

encodes auditory information. Information is maintained via rehearsal or is lost through displacement or decay within 15-30 seconds. If maintained, information can be transferred to the unlimited capacity of LTM, with the ability to transfer back into STM store when required.

Key evidence in support of multiple memory systems originally derived from neuropsychological studies of patients with impaired abilities following hippocampal damage (Poldrack & Packard, 2002). One of the best-known cases of this is Henry Gustav Molaison, more commonly known as 'HM' (Scoville & Milner, 1957). HM suffered from epilepsy and extreme seizures from childhood, which worsened with age and due to a lack of effective treatments available, greatly impacted his quality of life (Chai et al., 2018). Eventually, he agreed to undergo surgery where an excision of the medial temporal lobe was conducted, affecting the hippocampus and anterior parahippocampal gyrus (core regions thought to be the cause of seizures, Scoville & Milner, 1957). As a result of this procedure, HM successfully experienced fewer seizures, but at the cost of developing severe anterograde and retrograde amnesia. Nonetheless, HM's short-term memory remained intact, although he lacked the ability to form new, long-lasting memories, suggesting that LTM and STM are two separate memory stores (Norris D, 2017).

Further support for the multi-store model theory can be demonstrated with the case of KF, a patient who suffered from impaired STM (Shallice & Warrington, 1970). A motorcycle accident resulted in damage to the left parieto-occipital region of KF's brain, causing an impaired STM but normally functioning LTM (Shallice & Warrington, 1970). In a series of studies on patient KF conducted by Shallice and Warrington (1970), it was found that KF was only able to recall a limited 1-2 items, in comparison to a typical ~7 items. Further experiments also displayed an impairment in remembering information such as numerical digits and letters at a greater speed when prompted auditorily, compared to visually (Shallice

& Warrington, 1970). In terms of KF's STM deficit, this was found to be limited to verbal stimuli, such as letters and words, and did not extend to meaningful sounds, like cats meowing (Shallice & Warrington, 1970). KF's STM impairment appeared specific to only certain situations, suggesting the presence of multiple STM stores and a clear distinction between STM and LTM, further supporting the multi-store model theory (MSM).

Nevertheless, the multi-store model faced some major flaws and was challenged by contradicting evidence. Firstly, the proposal that the maintenance of information in STM would guarantee long-term learning was proven to be incorrect. Instead, it was found that the degree of learning depends on the nature of processing, meaning processing a word using its perceptual appearance or spoken sound is less effective for learning in comparison to encoding the word using meaning or emotional tone (Baddeley, 2010). Secondly, Atkinson and Shiffrin (1968) proposed that when STM is impacted, information should be typically lost at a rapid pace resulting in patients being unable to learn. If this STM store did act as 'working memory', then patients with impaired STM should be severely impacted on a cognitive level with an impaired LTM. Instead, these lesioned patients were found to demonstrate typical long-term learning and live 'normal' lives (Norris D, 2017). Also, the MSM is oversimplified in its argument that STM and LTM each operate as a single system, as research has identified multiple types of LTM (Johnson, 2014). LTM is suggested to be divided into two categories: explicit memories, which are consciously accessible (and further divided into episodic and semantic), and implicit memories, which relates to knowledge observable in performance with no requirement of conscious awareness (Johnson, 2014). Similarly, STM has also been identified as more intricate than laid out in the MSM, with further theories (such as those proposed by Baddeley & Hitch, 1974), suggesting multiple stores and various components.

Despite the criticisms of Atkinson and Shiffrin's (1968) multi-store model, it was foundational in shaping the field by providing a conceptual framework of working memory. Importantly, this prompted Baddeley and Hitch (1974) to develop their own memory model to distinguish their views and present answers for the complex systems within our brain.

The Multicomponent Working Memory Model – Baddeley and Hitch (1974)

The multicomponent working memory model by Baddeley and Hitch (1974) is a prominent and well-respected WM model, commonly cited in research as it suggests a modular system (D'Esposito & Postle, 2015). The multicomponent WM model transformed the view of memory from rigid and flat into a complex system full of multiple sophisticated LTM, STM, and WM stores. Working memory was now introduced as a composite system with the ability to manipulate information storage for complex cognitive tasks (Baddeley & Hitch, 1974), compared to the more simplistic view of STM which provides limited storage of information (Chai et al., 2018). The WM model proposed that STM is composed of three stores which are limited in capacity: the central executive, visuo-spatial sketchpad, and articulatory-phonological loop (Baddeley & Hitch, 1974). The central executive system is proposed to act as the processor, responsible for allocating data to the other subsystems and guiding behaviour (Adams et al., 2018). It is thought to be the most important component of the model, despite being the least understood. The central executive handles which information should be attended to, and which areas of WM should receive this information (importantly for this thesis, including conflicting information). The visuospatial sketchpad is thought to be involved in storing and processing visual and spatial information, later retrieved for navigation. This means the visuospatial component is likely to play a vital role in providing information regarding where we are in relation to other objects in our environment (Baddeley, 1997). Also, an important aspect of the sketchpad is its ability to display and manipulate information in LTM, such as the spatial layout of your bedroom. Finally, the

phonological loop handles verbal information and is further subdivided into the phonological store and the articulatory control process. The phonological store is proposed to process speech perception and store spoken words heard for a short duration of a few seconds, whereas the articulatory process is proposed to handle speech production and store verbal information.

Baddeley (2000) further updated the working memory model by adding another component, the episodic buffer (Baddeley, 2000). This store is suggested to act as a temporary storage which modulates and integrates sensory information, communicating with both LTM and WM components (Baddeley, 2000). Baddeley (2000) also suggested that the central executive's use of the episodic buffer provided the ability to create alternative models of the environment, such as preparing to solve old and new problems, plan for future actions, and debate courses of action (Coolidge, 2023). Baddeley (2000) further suggested that planning could be adjusted and executed if initially unsuccessful, hypothesising that the episodic buffer generates new solutions to solve novel problems.

Most notable for this thesis, Hitch and Baddeley (1976) also aimed to see if different parts of our WM system can be used simultaneously. To test this, an experiment involving participants performing two tasks at the same time, also known as 'dual tasking', was conducted. This involved a digit span task where participants repeated a series of numbers, and a verbal reasoning task with true or false answers (Baddeley & Hitch, 1974). As the list length increased in the digit span task, participants required marginally longer time to answer the reasoning question, with no further errors in the verbal reasoning task when the number of digits increased (Baddeley & Hitch, 1974). This suggests different components were required for the different tasks, most likely the verbal reasoning task using the central executive, and the digit span task using the phonological loop (Baddeley & Hitch, 1974). It was found that when having to process multiple tasks simultaneously, interference only arises when the

information is being retained or processed within the same component or store at the same time (Adams et al., 2018).

In summary, the multi-component working memory model redefines WM to be a limited-capacity system which allows for the manipulation of information required for complex tasks but also allows for temporary storage (Baddeley, 2012). It suggests WM to be dynamic, and that there are specialised subsystems devoted to representing specific information which are structurally independent of one another, but also that information storage in memory is distinct from processes underlying stimulus perception (Buchsbaum, 2016). This model introduced the concept of a multicomponent working memory system which provided a useful theoretical structure for researchers to understand the role of memory in our capacity to think (Baddeley, 2010).

The Embedded-Processes Model – Cowan (1999)

Despite the popularity of Baddeley and Hitch's (1974) multi-component working memory model, Cowan (1999) proposed a further model which highlights the role of long-term memory and attention in facilitating WM functioning: the embedded-processes model. Cowan (1999) argued Baddeley and Hitch (1974) WM model simplified perceptual information processing to WM without considering the focus of attention to stimuli. Instead, Cowan (2005) redefines WM as 'cognitive processes which retain information in an unusually accessible state'. In this model, WM consists of four components: central executive, LTM, activated memory (the subset of LTM in a state of temporary activation), and the focus of attention (Cowan, 1999).

Cowan (1999) conceptualised WM storage to emerge from the interaction of activated long-term memory with attention and other central executive functions. Cowan (2008) emphasises WM includes short-term memory and other processing mechanisms which help

to make use of STM. Another core component of this model is the focus of attention which is thought to determine which items are actively processed (Cowan, 2008, 2010). Information is maintained in either an accessible state within the focus of attention or in (activated) LTM and is consciously processed whilst other information is maintained in the background (Cowan, 1996). Also, the focus of attention is proposed to be capacity-limited, holding a maximum of 4± items, whereas active LTM is time-limited, needing to be refreshed with attention or rehearsal otherwise decaying after 10-20 seconds (Cowan N, 2010). Ultimately, the embedded-processes model argues that WM is not a separate system but instead the activated part of long-term memory, and that the 'focus of attention' is a further subset of activated long-term memory (Schweppe & Rummer, 2014). Cowan (1988) also argues that awareness influences encoding, and that more features are encoded when in the focus of attention allowing for richer memory, and for new episodic memories to be recalled later. Interestingly, Cowan (2008) argues the distinction between STM and WM may be an issue of semantics, and rather it is more important to investigate why some tasks are more closely linked to individual ability than others. The embedded processes model offers an integrative view of how memory, attention, and LTM interact during cognitive tasks, providing insight into the processing limits of memory and the importance of attention (Cowan, 1996).

Engle's View on Working Memory Capacity (2002)

Cowan's (1999) framework towards WM is consistent with Engle's view on working memory capacity (2002), suggesting that WMC is different from STM but still related to general fluid intelligence and executive attention. Specifically, Engle (2002) suggests WMC is not about individual differences in the number of items which can be stored, but differences in the ability to control attention to maintain information in an active, retrievable state. This would suggest that WMC is equally important in the retention of a single representation (e.g., the representation of a goal), as determining how many items can be

maintained (Engle, 2002). Ultimately, Engle (2002) suggests WMC is not directly about memory, but instead using attention to maintain or suppress information. Engle (2002) also highlights WMC to be strongly correlated with general fluid intelligence, involving reasoning and problem-solving, and that WM tasks can predict performance on intelligence tests because they measure executive attention (Engle et al., 1999). WMC is also suggested to be a domain-general resource, meaning it can be applied to all tasks requiring attention control (and is not limited to specific types of information, Engle, 2002). This can be demonstrated via the anti-saccade task where individuals with high and low WMC were asked to suppress automatic eye movements (Kane et al., 2001). Individuals with higher WMC exhibited better attention control, even when distracted by conflicting stimuli (Kane et al., 2001). This proposal contradicts the view of Baddeley & Hitch's multicomponent model, as their model emphasises that storage is domain-specific with some degree of domain-specific attentional processes (Baddeley & Hitch, 1974). Engle (2002) also mentions how individuals with high WMC can manage proactive interference better (which occurs when past information disrupts novel information processing) and maintain focus on task-relevant information (Kane & Engle, 2000). Engle's framework proposes that working memory capacity is a reflection of executive attention ability, a vital cognitive resource required for filtering distractions and maintaining task goals. Engle (2002) highlights WM capacity as a domain-general executive action, with attention being the focus of managing interference and maintaining task-relevant information, not storage (Engle, 2002).

Exploring the theories and models above is crucial in understanding the evolution of working memory. These models have each influenced the way we understand the concept of WM by addressing similar matters from different perspectives. Each model successfully conceptualised different mechanisms including, but not limited to, the focus of attention (Cowan, 1999), information manipulation (Baddeley, 2000), capacity limits (Cowan N,

2001), and inhibitory control (Engle, 2002). Numerous other theories of WM further highlight its complexity, with each theory exploring the concept from different perspectives (e.g., time-based resource sharing model (Barrouillet et al., 2004); Daneman and Carpenter's (1980) view of WMC; the three-embedded-components theory (Oberauer, 2002). These models highlight the difficulty in compressing working memory into a single framework but successfully portray its importance as a foundation of cognitive functioning.

The Role of Working Memory in Cognitive Functions

Highlighting the role of WM in cognitive functions, from its interaction with attention to perception and LTM, will further demonstrate the vital role WM plays in our everyday lives. Furthermore, the crucial role of WM in executive functions including planning, inhibitory control, and cognitive flexibility will be discussed. Finally, the impact of cognitive load on WM will be emphasised, and how task complexity affects WMC and performance, to provide a deeper understanding of how WM supports essential cognitive functions.

Attention

Working memory and attention share a unique relationship in which both are required for us to maintain and manipulate information during cognitive tasks (Oberauer, 2002). There is a consensus that WM and attention are closely linked, but the wide range of theoretical perspectives mean the nature of this relationship remains to be debated (Oberauer, 2019). A key divide lies in recognising the role of attention to either be as a resource or as a mechanism for selecting and prioritising information (Oberauer, 2019). The view of attention as a resource also means a commitment in agreeing this to be responsible for WMC limits, changing the way information is stored and processed (Oberauer, 2019).

To distinguish this link, research has proposed that attentional resources are needed for certain functions: storage and processing information, perceptual attention and memory

maintenance, and the control of attention (Oberauer, 2019). Attention refers to the processing or selection of information at the expense of other information (Fougnie, 2008). Some researchers claim attention control procedure to be complex and reflect the ability of a person to maintain a state of alertness, stay focused for extended periods of time on specific stimuli, and inhibit strong responses (Sperduti et al., 2016). Others claim the focus of attention functions as a gateway to new LTM formation (Cowan et al., 2014). Despite varying theoretical views, there is a general acknowledgement that WM and attention play a crucial role in the function of cognitive mechanisms (Cowan et al., 2014).

As working memory has severely limited capacity, this limit is suggested to reflect the bottleneck of information processing (Luck & Vogel, 2013). Due to the restricted resource of WM, relying on selective attention enables individuals to focus on goal-directed specific aspects of the environment, whilst ignoring others (Ku, 2018). Previous studies have demonstrated individual differences in WMC to be related to the ability to control attention, such as Kane et al. (2001), who found low WMC participants perform poorly when task switching compared to high WMC participants, with slower and less accurate performance. Those with lower WMC have also been found to unsuccessfully filter out distractions during WM maintenance (Vogel et al., 2005). Without the filtering process of selective attention, irrelevant information could overwhelm WM resulting in interference and reduced performance (Engle, 2002). These findings suggest WM is not a passive storage system, but a vital resource in regulating attention (Kane & Engle, 2000). This underscores the perspective that working memory capacity reflects the efficiency of attentional control, required for maintaining task goals, managing interference, and assisting in daily complex cognitive tasks.

Perception and Long-Term Memory

Working memory (WM) serves as a crucial bridge between perception and long-term memory (LTM), acting as a temporary storage of sensory input whilst integrating previously

stored knowledge needed to support information processing and interpretating. When encountering new information, working memory selectively retrieves this from perception or long-term memory in a controlled process to ensure only useful information is entered, guiding behaviour (Baddeley, 2000; Oberauer, 2009). As this is selective, it helps determine whether this information entering WM originates from prior memory, or perceptual input. Evidence from studies support selective integration, such as Oberauer et al. (2017), who demonstrated that long-term memory retrieval facilitates WM performance but only when the information held in store is poor. Oberauer et al. (2017) found that performance improved for participants when previously learned associations reappeared, suggesting LTM enhances WM rather than interfering. This suggests that working memory is actively processing and integrating new sensory information with prior knowledge from LTM to enable efficient decision-making. Working memory is thought as a short-term storage with capacity limitations, whereas long-term memory is understood to be more durable with a larger capacity, referring to the recalling of information after a delayed interval (Aben et al., 2012). Due to this, working memory plays a key role in the link between perception and stored experience, allowing for more efficient decision-making.

Executive functions

Whilst working memory is crucial in integrating perceptual input and long-term memory, its functionality is determined by cognitive mechanisms known as executive functions. Executive functions are essential higher order processes which form the foundation for complex abilities including reasoning, problem-solving, and planning (Collins & Koechlin, 2012). These critical functions are needed for cognitive, social, and psychological development but also for general mental and physical health across the lifespan as it is central to being able to hold information in mind (Baddeley & Hitch, 1974). This allows individuals to maintain and manipulate verbal and visuospatial information, needed for making sense of

language in general (Baddeley & Hitch, 1974). Working memory's limited capacity means it must be used efficiently for executive functions to be effective. For example, Duncan et al. (2008) tested participants in a task involving letters and numbers in which participants were able to recall instructions, but those with poorer executive functions failed to shift their attention when instructed to change the task demands. This suggests they could not clear the irrelevant task from their 'mental workspace', resulting in clutter which reduced their WM capacity, further solidifying the idea that WM is needed to work effectively to allow for successful executive functioning (Diamond, 2013). Executive subfunctions are also thought to demonstrate how WM is a system allowing for dynamic behaviour, by updating (monitoring and revising representations held in WM), shifting (switching attention between tasks), and inhibition (withholding responses to environmental stimuli; Miyake et al., 2000). These executive functions regulate information maintenance and manipulation within working memory, allowing individuals to manage cognitive resources, an important aspect under situations such as high/demanding cognitive load.

Working Memory Capacity

Cognitive load refers to the mental effort required to maintain and process information in working memory, playing an important role in task performance (Barrouillet et al., 2004; Sisakhti et al., 2021). This is thought to reflect working memory capacity, the limited amount of mental content which can be held in the mind, and understanding this is crucial in explaining why human cognition is limited and why individual differences occur (Oberauer et al., 2016). Cognitive load theory has been thoroughly researched and influences how we understanding learning as it highlights the role of WM capacity in retrieving task-relevant information and handling cognitively demanding situations such as multitasking.

Research has attempted to assess cognitive load within WM, with Barrouillet et al. (2004) investigating measuring the extent to which WM was disrupted due to a secondary task. As

the difficulty of the secondary task increased, less time was available for maintaining information within WM, resulting in a faster decline in forgetting and impaired performance (Barrouillet et al., 2004). Similarly, Cotton et al. (2024) suggests that as the difficulty of the secondary task increases, performance on the primary task declines due to less opportunities available for working memory maintenance. Higher cognitive load conditions (such as tasks with high intrinsic and extraneous load), impair working memory by reducing its capacity and ability to process multiple pieces of information at once (Cotton et al., 2024). This strain can impact executive functions, such as shifting and inhibition, resulting in attention becoming stimulus-driven, rather than goal-directed (Broadbent et al., 2023). For example, individuals may struggle to inhibit attention to irrelevant but prominent distractions, leading to reduced efficiency in attention allocation and a decrease in task performance (Eysenck & Calvo, 1992; Eysenck et al., 2007).

Individual differences in WM capacity greatly influence the ability to manage cognitive load. Individuals with high working memory capacity are thought to have a greater ability in maintaining cognitive control and staying task focused (Engle, 2002), suggesting they show fewer deficits when performing a primary task alongside a demanding secondary task (Szameitat et al., 2002). These have real life implications, particularly in common tasks such as driving which is inherently complex and attentionally demanding (Broadbent et al., 2023). This is important as research has shown that secondary tasks, such as mobile phone use or engaging in conversation whilst driving, can divert attention away from hazards and strain WM (Ellmers et al., 2016). Studies have also shown that if cognitive load is increased during driving, horizonal visual scanning and mirror use are reduced, suggesting a change in strategy to try and conserve attentional resources in WM for the primary task at hand (Ellmers et al., 2016; Recarte and Nunes, 2003). Wood et al. (2016) explored the relationship between WM capacity and hazard perception performance when dual-tasking and found lower WM

capacity individuals performed significantly poorer in dual-task conditions compared to those with higher WM capacity, with poor hazard perception and high inattention reported. Interestingly, training working memory capacity has been found to be successful in the context of improving driving in older adults (Cuenen et al., 2016), providing a promising outlook for maintaining safety and cognitive ability of individuals. It is important to note that the term 'cognitive load' in the context of these studies refers to the mental effort and attentional resources demanded by the tasks at hand, and despite this term being commonly used in research to describe the cognitive burden experienced, this is not directly quantifiable and so must be interpreted with caution in relation to empirical studies. Nevertheless, these findings emphasise the importance of working memory in meaningful real-life situations but also show the plasticity of the neural mechanisms involved in WM. Particularly, evidence of working memory training successfully improving working memory capacity suggests these neural systems are flexible in their approach and dynamic to the task at hand. Understanding how cognitive load impacts task performance and the role of working memory offers insight into the brain's ability to manage differing cognitive demands.

Functional neuroimaging studies have explored how cognitive load modulates working memory performance by increasing the number of items to encode, retrieve, or maintain, as well as changing task demands and therefore difficulty (Sisakhti et al., 2021). Performance deficits and increased neural activation across working memory brain regions have been found when task load increases (Cairo et al., 2004; Todd & Marois, 2004; Vogel & Machizawa, 2004; Vogel et al., 2005; Xu & Chun, 2006). This clearly demonstrates the limits of working memory capacity, with 3 main theories explaining this load limit: firstly, memory representations decay over time, secondly, working memory is a limited resource which is shared across remembered items during both storage and manipulation, and thirdly,

performance is limited by interference between representations which do not decay over time and instead compete for resources, and so disrupt one another (Cowan, 2005).

Cowan N (2001) proposed an influential theory stating adults can hold a limit of 3-5 items in working memory, replacing Miller's (1956) 'famous number 7, ± 2'. Chunking research, such as from Gilchrist et al. (2008) and Cowan N (2001), suggest the size of the chunk and how distinct the remembered item are also influences load. To fully understand this, we also need to distinguish between the processing and storage functions of working memory (Cowan N, 2010). Saults and Cowan (2007) found participants could store a maximum of four items regardless of whether the stimuli were visual or auditory. When attention was split between both the visual array and auditory digits, performance remained the same, unless the addition of a mask introduced greater processing requirements to protect the encoded visual information from interference (Saults and Cowan, 2007). This suggests working memory capacity is stable, but that it is influenced by task demands.

The purpose of capacity limits remains unclear. Cowan N (2010) suggests that biological constraints could be the reason, as maintaining multiple neural representations is metabolically expensive and mentally taxing (Cowan N, 2010). If neurons must fire every 100ms to maintain an item in working memory, then trying to sequentially maintain multiple items may result in delayed reactivation or temporal overlap between different items' representations, resulting in interference (Cowan N, 2010). Cowan N (2010) suggests that if neural patterns for multiple items are active, then interference arises or separate neural populations become assigned to each item, resulting in an inadequate number of neurons to keep these items active simultaneously. Simulation data suggests that holding 3.5 items leads to maximum efficiency and distinctiveness, suggesting that low working memory capacity allows for more reliability in binding reactivated concepts from LTM into a single WM representation without distraction (Cowan N, 2010).

Much of the classic work cited above (Baddeley & Hitch, 1974; Cowan N, 2001) focused on estimating capacity primarily using verbal or phonological tasks. It is not guaranteed that the same capacity limit exists for other sensory modalities. Since visual WM is particularly relevant for this thesis, and since it has been suggested that visual WM capacity is strongly related to overall cognitive ability (Luck & Vogel, 2013), it is important to establish whether it too carries the same limit. Early research suggested that change blindness and the change detection paradigm accurately estimated the limits of visual working memory capacity, allowing for its quantification (Simons & Levin, 1997). Subsequent studies have consistently found that the limit for visual working memory capacity is approximately 3 to 4 items (Luck & Vogel, 1997; Xu et al., 2018).

Neural Mechanisms Underlying Working Memory

There is clear evidence, as discussed throughout this thesis, to suggest that variability in working memory can exist both across individuals and overall functioning. This variability highlights the complexity of working memory and further supports the difficulty in finding a single model or theory to fully capture working memory. The above sections of this thesis delved into behavioural research measures and how they can provide valuable insight into aspects of working memory. However, another perspective which could resolve ambiguities found in behavioural research and further our understanding of WM is the use of brain imaging or other neural recording and interference methods. Neural investigations provide a more comprehensive understanding of working memory by complementing behavioural research but also offer independent perspectives of mechanisms supporting working memory which may confirm or contradict behavioural results. Using both the behavioural and neural evidence will contribute to a more complete understanding of working memory.

Brain Regions Involved in Working Memory

The lateral prefrontal cortex (PFC) has consistently been associated to working memory functioning as it supports executive processes including planning, decision-making, updating, and maintenance (Kim et al., 2015). PFC neurons have been found to show sustained activity during delay periods suggesting working memory maintenance in both single-cell recordings of monkeys (Funahashi et al., 1989; Fuster & Alexander, 1971), and human neuroimaging studies (Courtney et al., 1997; D'Esposito et al., 2000; Sakai et al., 2002; Smith & Jonides, 1997). Funahashi (2006) reviewed studies examining task-related single-neuron activity in the PFC of monkeys performing (primarily oculomotor) working memory tasks and found that sustained delay-period activity of PFC populations reflected the maintained memory stimulus. Classic work further debated the precise location of maintenance in PFC. Some studies proposed a process-based organisation (Petrides, 1996), with specific PFC subregions allocated to the maintenance or manipulation of information. Others proposed content-orientated regional dissociations (Goldman-Rakic, 1987), where different PFC subregions stored different types of information (such as objects or spatial locations)

Lesion studies confirm the necessity of the prefrontal cortex for WM, but challenge the theory that PFC is predominantly for WM storage. For example, damage to the lateral PFC was found to impair performance in delayed-response tasks, but deficits were particularly large in tasks with high distraction or increased task difficulty (D'Esposito & Postle, 1999), suggesting that PFC lesions impair attentional control functions more than mere storage. Pasternak et al. (2015) also found monkeys with lesions of lateral PFC had moderate deficits in their ability to remember the direction of motion in a random dot stimuli task. As this deficit was not dependent on the perceptual fidelity (motion coherence) of the remembered stimulus, the researchers suggested the PFC was not involved in coding for

motion stimuli per se and that the lesions instead impacted the monkeys' ability to attend to remembered stimuli. Voytek and Knight (2010) also explored PFC cortex lesions using EEG recordings of human participants performing a lateralised visual working memory task. Both behavioural and neural deficits were specific to the visual field contralateral to the lesion, suggesting PFC to be required in specific spatial or attentional modulations of visual working memory. These lesion studies demonstrate the importance of the PFC in maintaining attention to goal-relevant information, particularly in task situations where interference occurs.

Recent work has presented a more nuanced view of the role of PFC in WM maintenance. For example, Rigotti et al. (2013) found frontal neurons to display high dimensionality and so encode for combinations of item-related and task-related information, which is consistent with the PFC's involvement in goal-directed behaviour (Miller & Cohen, 2001). Consistent with this forward-looking view of PFC, previous work had already shown that PFC encodes the expected stimulus at the end of a memory delay (Rainer et al., 1999). Since in many WM tasks the probe presented at the end of the memory delay frequently matches the remembered stimulus, previous studies may have conflated this anticipatory function with memory maintenance. This supports the idea that the PFC goes beyond mere sensory storage by manipulating information within working memory, as the ability for these neurons to simultaneously represent item and task-specific information requires it to be a complex and flexible system. Overall, these results propose the PFC to play a crucial role in working memory by focusing attention on and then extracting task- or goal-relevant sensory information (Postle, 2005).

Looking beyond (lateral) PFC, many other brain regions contribute to working memory. The superior parietal cortex is also associated with working memory and may implement top-down attentional control (Collette et al., 2006). Alternatively, the posterior parietal cortex is regarded as a workspace used for maintenance of sensory and perceptual information in working memory (Andersen & Cui, 2009; Owen et al., 2005; Todd & Marois, 2004; Xu & Chun, 2006). EEG imaging research also suggests that parietal cortex activity is directly correlated with WM capacity, as an increase in activity was found with an increase in the number of items held in WM, which levelled off once capacity was reached (Vogel & Machizawa, 2004). More recent work has shown that WM contents can be decoded from activity patterns in parietal cortex (Christophel et al., 2012; Ester et al., 2015; Xu, 2017; Xu, 2024). Lesion studies have again been instrumental in demonstrating the relationship between the parietal cortex and working memory, and right parietal lesion patients were found to exhibit spatial WM deficits (Koenigs et al., 2009; Nee et al., 2013), whereas lateral temporal and temporoparietal lesions were found to impact verbal WM (Binder et al., 2009; Owen et al., 1996). Christophel et al. (2017) suggests representations to be distributed across cortices, with early sensory regions encoding sensory representations, and prefrontal regions involved in abstract representations. Alternatively, the PFC and other regions may share information using coupling of ongoing oscillatory activity (Engel et al., 2001). Human EEG and other imaging techniques have found increased oscillatory activity during working memory in frontal and posterior areas (Roux & Uhlhaas, 2014), with Salazar et al. (2012) finding increased mutual information in item identify and location between PFC and posterior parietal cortex spoke and LFP recordings. This provides evidence to suggest the sensory cortex is storing the information and the PFC uses oscillatory synchronisation to access this information.

The role of other brain areas active during working memory highlights their involvement in either the performance or maintenance of working memory, with suggestions that these surrounding regions interact with the PFC to share information using coupling of oscillatory activity (Liebe et al., 2012; Salazar et al., 2012), or a more direct synaptic connection (Petrides & Pandya, 1984). The purpose of these other brain regions supporting the PFC is suggested to be to actively focus on relevant information, rather than the actual storage of the information (Lara & Wallis, 2015). Ultimately, this distributed network involved in working memory suggests that individual brain regions contribute to working memory (Christophel et al., 2017). This 'coordinated recruitment' (Postle, 2005) of brain regions allows for sensory, representation, and action-related functions.

Although traditional models emphasised higher-order regions focus on prefrontal and parietal cortex as primary substrates of WM maintenance, it is alternatively proposed that the same sensory regions involved in perception also contribute to the short-term retention of visual information. Previous neuroimaging studies including Harrison and Tong (2009) have demonstrated that the orientation of a grating in visual working memory can be decoded from activity patterns in early visual cortex. Serences et al. (2009) also demonstrated that remembered stimulus features can be reconstructed from activity in organised visual areas, suggesting mnemonic representations preserve the same spatial and feature-based organisation as perceptual responses. Further work has demonstrated sensory representations to be dynamic depending on task demands. Derrfuss et al. (2017) found that the brain is able to enhance the distinctiveness of relevant representations when avoiding distractors, suggesting sensory codes can be reconfigured to support goal-directed memory maintenance. Rademaker et al. (2019) also found sensory and mnemonic information to coexist within the visual cortex, with patterns reflecting both current stimuli and remembered items. However, Adam et al. (2025) highlights that there may be variability in decodability across these

studies, as well as that these signals may reflect top-down feedback instead of storage, and that some WM tasks show stronger involvement of parietal and frontal regions. If visual WM representations are partly maintained in sensory cortex, then interference between items may arise when multiple stimuli compete for overlapping coding resources. Nevertheless, mechanisms such as prioritisation or training might reduce interference by separating representations into distinct neural subspaces.

FMRI studies have also revealed the presence of persistent neural activity in brain regions during delays (Wager & Smith, 2003). Early studies focused on the PFC due to previous findings of lesions causing deficits in delayed response tasks (Jacobsen et al., 1936), and further studies showed that PFC successfully encoded memorised positions during the delay (Rainer et al., 1998). Contradicting evidence for the role of PFC in storing working memory was found in human neuroimaging research where PFC activity during delay failed to encode information specific to stimulus held in WM (Curtis & D'Esposito, 2003). They suggest the role of PFC to be involved in aiding posterior regions which actually store the representations. Alterior roles for the PFC in working memory of monkeys other than maintenance have been proposed by Lebedev et al. (2004) who found multiple populations of neurons in the PFC, both encoding for different things (one for spatial location, other for attended location). Lesion studies impacting the PFC have also provided evidence to show no deficits in verbal and memory span tests, or delayed recognition in humans (D'Esposito & Postle, 1999), and monkeys (Rushworth et al., 1997), suggesting it may not directly be involved in the storage.

Working memory's capacity limited system is shown to be highly influenced by interference, with some research suggesting cognitive load may increase this interference within shared networks. Buschman (2021) suggests WM capacity limitations arise when competing representations converge onto overlapping networks, which does allow for WM to

become flexible, but also limits the capacity. Understanding this trade-off would provide a great explanation as to why the brain has evolved to have these constraints, particularly given working memory's importance to cognition.

Interference in Working Memory and Conflict Resolution

A major challenge for working memory is its susceptibility to interference, limiting both capacity and its ability to effectively maintain information. Buschman (2021) proposes working memory interference to arise from two mechanisms: representational overlap and competitive interference. These impact the number of items which can be simultaneously stored and processed within working memory and its neural subspace.

Representational interference occurs when two or more items have overlapping neural representations in working memory. Each item held in working memory is represented across a population of neurons in its own encoding subspace (unique axis within the high-activity brain regions where the neural population resides, Panichello & Buschman, 2021; Rigotti et al., 2013; Wolff et al., 2020; Xie et al., 2022). If the encoding axes of different items are orthogonal, the neural population can represent these items at the same time without interference (Buschman, 2021). However, when the representations are correlated with one another, or non-orthogonal, their axes align with one another causing interference. This interference means that changes to the neural population activity for one item unintentionally change the representation of the other item. Interference is likely to be a prevalent feature of our brain and is observed in perception (when attention resolves competition between simultaneously active stimuli, e.g., Desimone & Duncan, 1995), as well as reinforcement learning (where the brain needs to learn which action/stimulus was responsible for a reward despite overlapping neural representations, e.g., Noonan et al., 2010). These overlapping representations may result in 'catastrophic forgetting', where the correlations in representations cause learning signals to degrade the representation of one item due to the

synaptic changes of another (Gurnani & Cayco Gajic, 2023). This problem can also be present when the brain is categorising stimuli, as if these representations become too specific, then the newly learned categories could interfere with previous learned categories. This may provide evidence as to why shared representations are beneficial, allowing for information to be generalised and effectively reducing interference (Flesch et al., 2018).

Competitive interference occurs when multiple items are represented within a shared neural population, even if their specific representations don't physically overlap in the same activity subspace (Buschman, 2021). This type of interference is prominent in visual working memory, where adding more objects in a visual scene increases interference between the objects' representations (Buschman et al., 2011). At a single-neuron level, responses to a stimulus become reduced when presented alongside other stimuli (Reynolds et al., 1999). From a computational view, Bays (2015) argues that items held in working memory can be protected against 'degradation', but only at a cost to other stimuli held in an unprioritised state. This suggests that a limited quantity of neural signals are allocated between memorised stimuli and when the signal decreases, the representations become impacted by noise, resulting in the degradation of working memory performance. Swan and Wyble (2014) also proposed a binding-pool model suggesting items in working memory draw information from a shared pool of neurons, and when multiple items are stored simultaneously, this results in competition for this shared resource leading to a reduction in clarity of representation. In humans, this pattern has also emerged as Sprague et al. (2014) found when increasing the number of items held within working memory in occipital, posterior and anterior parietal and frontal cortices, the decodability of each item decreased, suggesting a reduction in the clarity of the representation, possibly due to interference and competition between the items. Oberauer and Lin (2017) also suggest an interference model in which items encoded in a

continuous similarity space compete for memory bindings, resulting in errors and confusion when increasing the number of items stored.

Both representational and competitive interference demonstrate apparent working memory storage capacity limits may arise in part from how its neural representations interact within shared networks. These findings also support working memory to be a dynamic, population-based system in which interference can arise due to overlapping or competing neural activity patterns. Yu and Postle (2021) used fMRI to investigate the neural representation of stimuli during visual working memory maintenance, and by using cross-decoding techniques, found that the neural representations of unprioritised items were encoded in distinct neural spaces compared to prioritised items, even when the physical representations did not overlap. Van Loon et al. (2018) also used fMRI data to determine the similarities of memory representations and found that the brain distinguishes between current memories and prospective memories within the same neural populations in ventral visual cortex, but using opposite representational patterns. Wolff and Akyürek (2025) successfully used multivariate pattern analysis of EEG data to investigate how the brain encodes and distinguishes between priority and context within visual working memory. They found that the brain uses distinct neural representations for items based on their context, as well as the priority of the item to the task. These studies highlight how the brain employs different representations depending on task relevance and emphasises flexible prioritisation, consistent with widespread use of high-dimensional coding schemes.

The dynamic transformation of memory representations is also thought to reduce interference from overlapping representations. Stokes et al. (2013) and Buschman (2021) suggest that if working memory items and sensory inputs are both stored in sensory brain regions they face representational interference, meaning new sensory input is likely to disrupt existing WM representations. The transformation of memories into independent, orthogonal

memory representations allow for the avoidance of interference (Stokes et al., 2013). Stokes et al. (2013) found that prefrontal cortex visual WM representations change over time into separate, orthogonal subspaces. Libby and Buschman (2021) demonstrated that dynamic representations in primary auditory cortex alleviates interference between a previously presented and a current stimulus by limiting the number of neurons involved in their combined representation. In sum, when multiple items are held within working memory, normalisation occurs where items compete for representation, but if the number of neurons representing each item is reduced, then they can share the representational space without degrading, allowing for a reduction in interference.

Addressing these working memory limitations provides some basis as to how we can resolve interference in WM. For example, increasing the orthogonality of the neural representational axes for different items, or equivalently training a network to decorrelate representations so they no longer overlap, could help improve WM performance by specifically targeting one source of capacity limits – representational interference. Further chapters in this thesis will explore whether resolving interference is possible and vital in understanding working memory capacity, particularly when multi-tasking and categorising stimuli.

Dual-Task Interference and Working Memory – Item-specific Interference.

As working memory is highly susceptible to interference, when high cognitive demands are made, the likelihood of interference increases, particularly in dual-task paradigms (Wei & Zhou, 2020). Dual-task interference (DTI) occurs when two tasks draw from the same cognitive resource, resulting in conflicting streams of information attempting to be simultaneously processed (Heninger et al., 2006). This results in reduced accuracy and an increased response time compared to single-task performance (Pashler, 1994).

Neurophysiological studies have also found evidence of dual-task interference (Pratt et al., 2011; Qi et al., 2014). For example, Watanabe and Funahashi (2014) recorded monkey neural activity during a dual-task consisting of spatial WM and covert attention task. Compared to performing either task alone, performance in the dual task condition was impaired. This interference may be the result of neural populations overlapping and therefore being unable to efficiently represent both tasks. The authors suggested that this interference can be seen at a neural level: in the dual-task condition, neural populations engaged in the memory task were also found to be active during the attention task, suggesting the two task components were represented by overlapping populations, suggesting representational interference as the source of the behavioural impairment. The authors concluded that the focal point of dual-task interference is the competitive, overloaded recruitment of overlapping neural populations by two simultaneous tasks. These results support the idea that competitive interactions between task processing within an overlapping neural population explain the presence and effect of dual-task interference.

Research has investigated mechanisms attempting to resolve this conflict, or at least whether it can be reduced. At the behavioural level, practice is thought to reduce dual-task interference over time. Studies have found evidence to suggest practice is able to shorten the 'central bottleneck', in which the theory suggests interference occurs due to some cognitive processes occurring sequentially, meaning a delay in processing and multiple tasks competing for shared resources (Pashler, 1994). Schumacher et al. (2001) also suggests practice to lead to the automatisation of tasks, allowing the central bottleneck to be bypassed, which was found when individuals performed a visual and auditory dual task, in which the cost was initially high, but eliminated after extended practice, suggesting a method of optimising this process. How neural representations change in response to practice and how this resolves or

reduces dual-task interference is still poorly understood (see Garner & Dux, 2015; Garner & Dux, 2023).

As interference is a central contributor to working memory capacity limits, one possibility is that through practice the brain reduces dual-task costs by developing representational strategies to resolve item-specific working memory interference (Buschman, 2021). One method of doing so is increasing the sparsity of neural representations, in which fewer neurons are engaged in the representation of the item, reducing the opportunity for neural representations to overlap (Buschman, 2021). This has been shown in visual perception, where repeated exposure to an object results in neurons becoming more specialised or highly responsive, as well as reducing their response (Olshausen & Field, 1996).

Neural generalisation vs specialisation – Task-specific Interference

An alternative form of interference between neural representations within working memory is related to competing tasks, rather than items. Although both attempt to avoid neurons competing with one another, the origin of between-task interference is different. A major question in cognitive neuroscience is how the brain is able to flexibly represent information and items despite changing task demands. Our brains have the ability to represent high-dimensional sensory information at an abstract, low-dimensional level, allowing us to group sensory inputs into categories, which then allows us to recognise items around us as familiar objects or situations, even if the particular sensory input is novel (Seger & Miller, 2010). This highlights how categorisation is a fundamental cognitive process which allows the brain to make sense of the environment (Gluck et al., 2008). However, categorisation presents a challenge because it is not clear which elements of a given sensory input are incidental to our current goals (and therefore should be abstracted away) and which are task-relevant (and therefore should be represented). Understanding categorisation therefore

requires understanding how neural populations determine whether to represent information as relevant context (Seger & Miller, 2010). The lateral prefrontal cortex is thought to be heavily involved in category representation, as demonstrated by Freedman et al. (2001) who identified neural correlates of visual categories in this region in non-human primates performing a delayed match-to-category task. Category-selective neurons were able to distinguish stimuli based on abstract category membership, with 1/3 of prefrontal cortex neurons involved in categorisation. This paradigm allowed for visually selective neurons which respond to physical similarity to be dissociated from those which categorise the stimuli on an abstract level, showing the prefrontal cortex's flexibility in encoding arbitrary abstractions based on the current task. This leads to a debate in understanding the way neural populations are involved in encoding.

Identifying the way in which neural populations encode information and group within themselves would allow us to uncover this further, particularly whether they choose to generalise, or specialise. Neural generalisation is the term used when the same population of neurons encode multiple, distinct types of information. This is thought to be neurally efficient as it allows for the flexible, dynamic representation of tasks without requiring specific populations for each stimulus (Cromer et al., 2010). It may also facilitate task learning as representations learned in one task can be generalised to another (Musslick et al., 2017). This generalist theory suggests prefrontal cortex neurons are highly adaptable and that individual neurons multitask, and switch between category distinctions when required (Cromer et al., 2010). Alternatively, under certain circumstances prefrontal cortex neurons may specialise, i.e., encode information only in one particular context, while information in other context is encoded in distinct, non-overlapping neural populations or activity subspaces (Rigotti et al., 2013). Despite research finding evidence for both generalisation and specialisation of neurons, the majority of the literature on category learning in non-human primates has

focused on learning a single categorisation problem (e.g., Freedman et al., 2001), in which we cannot test whether information is represented in a generalised or specialised code. Our understanding of how human neural populations represent abstract categories is even more limited (Flesch et al., 2022; Menghi et al., 2025).

Neural populations are proposed to become specialised or generalised depending on the overlap between tasks (Roy et al., 2010). However, there is limited research exploring whether changing task demands (i.e., overlap between two tasks suddenly increases) also affects the neural representation of the task. It is possible that the representational format changes to reduce task-related interference, meaning neural populations may become specialised to avoid this interference. Alternatively, when task interference is low, generalisation may be more beneficial. Few studies have explored whether changing task demands can trigger a change in the neuronal population.

This thesis aims to explore the difference between neural generalisation and specialisation during working memory, particularly in the contexts of dual-tasking and categorising. In particular, we will investigate whether interference results in a change in the type of neural representation, and whether the behavioural costs of dual-task interference can be addressed by practice and how this may relate to reductions in neural interference.

Unresolved Questions within Working Memory Research

Working memory research has many confounding theories which have respectively examined its role in cognitive processes and supporting evidence to highlight its place in attention, perception, and cognition. Despite the overwhelming number of theories, there is still a significant gap in our understanding of the neural mechanisms involved in specific processes which support working memory under varying cognitive loads. This is particularly relevant when trying to understand interference resolution. Interference can arise in working

memory as a result of competing tasks or competing items, and although both attempt to avoid competition between neurons, the purpose of the resolution differs. For example, with categorisation, the two populations of interfering neurons can be divided into separate neural populations, but this would result in less efficiency as without generalisation, learning may be stunted. For dual tasking, this could be resolved using separate subspaces to encode multiple representations without them interfering with one another. Addressing and highlighting these different interference types will provide new insight into how the brain manages complex information processing and whether solutions exist to eliminate this deficit. EEG recordings will allow us to uncover the neural patterns involved in the process of categorisation, and whether increasing working memory demands impact the neural patterns involved as a result of task-specific interference. Also, exploring the impact of item-specific interference on working memory, where overlapping items compete for representation, and whether short-term practice can mitigate this effect. This thesis aims to provide a deeper understanding of whether resolving interference is possible, particularly in the contexts which demand cognitive resources.

Scope of thesis

This thesis examines the behavioural and neural mechanisms involved in visual working memory when undergoing common processes including categorising and dual tasking, what this might reveal about item- and task-based interference, and whether we can reduce said interference. Chapter 2 examines the neural mechanisms of generalisation vs specialisation in categorisation in the absence or presence of between-task interference conditions of task, and how changing neural representations may resolve this interference. The next section explores another form of interference present when dual-tasking. Chapter 3 investigates the effect of short-term practice on dual-task interference in a visual working memory task, where we describe two studies which were conducted to address whether we

can resolve this behavioural cost through practice. Chapter 4 aims to bridge both of the previous chapters by examining how overlapping the neural representations during dual-tasking could provide insight into interference and interference reduction. Finally, Chapter 5 will provide a general discussion of the thesis in a broader context to highlight the interference present in working memory systems and how this influences behaviour.

Chapter 2 – The Neural Basis of Generalisation and Conflict Resolution in Categorisation

Chapter Summary

Theories of categorisation suggest that category-selective neurons may multitask (generalise to multiple categories), increasing capacity and possibly accelerating category learning via transfer from analogous categories. However, if multiple categorisation tasks conflict (for example, because incommensurate category rules are applied to the same stimuli), multi-tasking neurons would not be able to allow sufficient performance, forcing the neurons to become specialised to a specific category, ultimately helping to prevent interference between the neural populations. A third alternative is the presence of both multi-tasking and specialised neurons, which switch depending on the task demands. While studies in non-human primates and neural network models have tentatively identified conditions for multitasking and for specialisation, the distinction between these population coding schemes has not yet been established in humans. Here we tested this hypothesis using a new visual working memory-dependent categorisation experiment using multiple categorisation rules. Importantly, separate task sessions encouraged either multitasking or specialisation by presenting either overlapping (i.e., conflicting) or independent stimuli as participants' brain activity was recorded with EEG. We expected to find corresponding task-generalisable (i.e., multitasking) vs task-unique (specialised) neural category representations. The current chapter provides data which challenges these theories yet also agrees that neural correlates are dynamic in their approach to dealing with complex categorising of competing stimuli. When stimulus sets for the two categorisation tasks were independent, category-selective neural patterns generalised, consistent with the multitasking account. When new stimuli were introduced which were shared across tasks, category-selective patterns were task-unique, consistent with the specialisation account. Interestingly, and contradicting our hypothesis,

after the introduction of these new stimuli, category-selective patterns for previously learned stimuli still generalised, indicating that adding new stimuli to an existing category warps the category representation to accommodate generalisation for some stimuli while orthogonalising those with potential interference.

Introduction

Categorising stimuli is a fundamental cognitive process used in our everyday lives to group items by their commonalities whilst ignoring their differences (Roy et al., 2010). Perceptual categorisation involves grouping distinguishable stimuli by their qualitative appearance and depends on the extraction of combinations of features which define a category (Arterberry & Bornstein, 2002; Freedman et al., 2001). Brain regions required for perceptual categorisation include the temporal (DeGutis & D'Esposito, 2007), parietal (Freedman & Assad, 2006), and frontal cortices (Diester & Nieder, 2007; Freedman et al., 2001), as well as the striatum (Seger & Miller, 2010). The hallmark of perceptual categorisation is the presence of a sharp category boundary, allowing for stimuli belonging in different categories which appear similar (i.e., pool ball and apple) to be categorised differently, whereas distinct stimuli within the same category (apple and orange) are treated alike (Freedman et al., 2001).

In a landmark study, Freedman et al. (2001) used 3D morphs of cats and dogs (continuous variation in shape but precise category boundary) which were presented to two monkeys in a delayed match-to-category (DMC) task. The tasks involved reporting whether the sample and test stimuli belong to the same (match) or different (mismatch) categories. Many lateral prefrontal cortex (LPFC) neurons had similar firing rates for all stimuli within a category, but a step change in activity occurred when the category boundary was crossed, meaning the cells encoded for category membership (rather than just the physical features of the stimuli). Cromer et al. (2010) demonstrated this again testing two monkeys in a DMC task of cat and dog morph stimuli but also introducing additional stimuli of car morphs. Crucially, they found that many LPFC neurons were sensitive to both categories, showing multitasking of neurons as the representations across tasks were shared. Further studies have suggested the presence of multitasking shared representations across categories in parietal

cortex (Fitzgerald et al., 2011; Freedman & Assad, 2006). Neural network modeling studies have suggested that these multitasking representations allow for rapid learning and better generalisation, improving the efficiency of task learning (Musslick & Cohen, 2021).

There are both situational advantages and disadvantages for the use of multitasking neural representations. For example, computational modelling studies have suggested that neural systems are likely to learn shared representations if the categories are statistically related (Musslick & Cohen, 2021). If the features defining the categories overlap, particularly in terms of task-relevant stimulus features, then shared representations are more likely to develop. This is thought to occur as it allows the neural networks to learn rapidly and generalise better by taking statistical regularities in the environment into account (e.g., in related tasks, similar stimuli are linked to the same response). While shared representations can accelerate learning of a second task, this comes at the expense of not being able to execute the two learned tasks in parallel. In contrast, independent representations are more likely to develop in situations where task demands are high (such as needing to execute both tasks simultaneously) or when category schemes are in direct competition (Roy et al., 2010).

When faced with direct competition between category schemes, neurons encode categories independently rather than generalising. Independent neural activity here refers to neurons showing category selectivity only for a single categorisation scheme (whereas multitasking neurons show selectivity for multiple category schemes). When investigating the LPFC of monkeys switching between categorising the same image set along two different category schemes with orthogonal category boundaries, independent sets of neurons were found to reflect the category distinctions (Roy et al., 2010). This is supported further by Lee et al. (2022), who recorded neural activity in the parietal cortex of mice trained to perform two visual detection tasks on the same stimuli but with orthogonal rules and found category selectivity of individual neurons for one task but not the other. This independent activity may

occur due to the presence of conflicting stimulus-response associations between the two tasks, meaning an attempt is made to reduce the interference between categories to prevent miscategorisation (Roy et al., 2010) or incorrect responses (Lee et al., 2022).

An alternative proposal which integrates both viewpoints above has been proposed by Chaisangmongkon et al. (2017), who present evidence for the use of independent or multitasking shared representations depending on the task demands. Artificial recurrent neural networks were trained to perform two DMC tasks with two categorisation rules applied either to two independent stimulus sets or to a single stimulus set (where the category boundaries of the two tasks were orthogonal). The networks exhibited multitasking category-selective representations when trained on independent stimuli for the two categorical schemes but developed four specialised category representations (one for each category, separately for each task) when trained on a single stimulus set across both tasks. Different paradigms may therefore elicit different representations (Chaisangmongkon et al., 2017).

These studies have focused on either animal research or neural network models. Human research exploring neural populations during multi-task categorisation has not yet been clearly established. More generally, work exploring categorisation in humans has focused on identifying the neural correlates of categorisation, often using functional magnetic resonance imaging (fMRI). For example, Li et al. (2017) showed that re-entrant processing in the posterior parietal cortex (PPC) and visual cortex enables flexible abstraction of category information. Jiang et al. (2007) found that categorisation training resulted in adaptations in the lateral occipital cortex compatible with sharpening of representation coding for category-relevant visual stimulus features, as well as LPFC showing sensitivity post-training to explicit changes in category membership.

There are fewer studies explicitly examining category representation across multiple tasks in humans. However, many studies have examined the closely related phenomenon of context-dependent stimulus processing. For example, many studies examining the neural effects of feature-selective attention present the same stimuli in contexts which require attention to different stimulus features, often finding that the task-relevant feature is preferentially coded (Ritz & Shenhav, 2024; e.g., Jackson et al., 2017). However, the geometry of feature representations across tasks is rarely examined explicitly. One recent study (Flesch et al., 2022) has shown that when different visual features of the same stimulus ('leafiness' vs. 'branchiness' of artificial tree stimuli) are relevant for different tasks, neural representations of stimulus categories in parietal and frontal cortex are orthogonalised across the two tasks, implying independent coding.

This study aims to contrast different forms of category-selective coding in the human brain by establishing the neural basis of categorising two independent stimulus sets according to two orthogonal categorisation rule boundaries, and whether representational adaptations occur when an overlapping stimulus set is used. This study also tested whether EEG is a suitable neuroimaging method for identifying the neural basis of category representation, as previous studies focused on invasive single-neuron methods in non-human primates or other neuroimaging methods. A working memory task was implemented in which participants learned to categorise visual stimuli along two orthogonal category boundaries. After an initial task-learning session, the first EEG session used independent stimulus sets for the two tasks to encourage the development of task-generalised neural category representations that are shared across tasks. This was followed by a second EEG session with the same participants, where new stimuli were added to the task to create conflict and encourage the development of independent representations. In the first EEG session, the stimuli presented for the two categorisation tasks were drawn from non-overlapping areas of a large feature space, meaning

that any given stimulus could only appear in one of the two categorisation tasks, thus avoiding conflict between tasks. In comparison, the new stimuli introduced in the second EEG session were drawn from an overlapping area of the feature space, meaning these stimuli could appear in both tasks and needed to be categorised in two different ways, creating inter-task conflict. This allowed us to observe any changes in category-selective neural representations in the independent stimuli and the overlapping stimuli separately.

We hypothesised that representations would generalise in the first session, and the representations would become more independent when conflicting stimuli were shown in the second session. We found that category-specific patterns generalised across tasks in Session 1, suggesting the presence of multitasking shared neural representations. We also found that these representations became more independent when overlapping stimuli were introduced in Session 2. Both results support our initial hypothesis. However, our results also suggest that the old stimuli continued to be represented by the same multitasking shared representations in Session 2 (despite the presence of the interfering overlapping stimuli). Further analyses suggest that the stimuli closer to the interfering overlapping stimuli within the feature space shifted their category representations compared to stimuli further away in feature space. This 'warping' effect may explain the cross-generalisation found in the old stimuli in Session 2 despite the addition of the new, overlapping stimuli. In sum, we conclude that human category learning can flexibly integrate novel stimuli even when these introduce cross-task conflict.

Methods

Participants

Thirty adults (12 male, 18 female, aged between 19 to 33 years old, M = 22.57, SD = 3.72) with normal or corrected-to-normal vision participated in this study. Participants were recruited from two UK universities and compensated for taking part in this study. An additional four participants were excluded due to poor performance or noisy EEG data.

Materials

Stimuli

The stimuli used in this study were designed to vary across three feature dimensions of size, shape, and colour. The category boundaries for the two tasks were orthogonal 2D planes dividing the feature space such that all three features were required to perform the task perfectly. The stimuli ranged from blue or orange, triangle or circle, and small or large. Individual feature axes were randomly flipped for each participant, so that particular feature combinations were counterbalanced across participants. Stimuli were positioned close to the two category boundaries along five 2D planes that were orthogonal to both category boundaries. The five stimulus-containing planes ran along the long diagonal of the 3D feature space (see Fig. 1c). Each plane contained 16 stimuli spaced equidistantly on a 4x4 grid (see Fig. 1d). Stimuli were drawn from planes 1-3 for Task 1 and from planes 3-5 for Task 2. Therefore, only stimuli from plane 3 were used in both tasks (Session 2). In Session 1, the stimulus sets used for the two tasks were non-overlapping (Task 1: planes 1 and 2, Task 2: planes 4 and 5), and there was no feature overlap between stimuli used for the two tasks (e.g., all stimulus feature values for all stimuli in Task 2 were larger than those for all stimuli in Task 1). Session 2 introduced stimuli from plane 3 in both tasks (while maintaining orthogonal category boundaries), thus creating overlap in the stimulus sets for the two tasks.

Figure 1

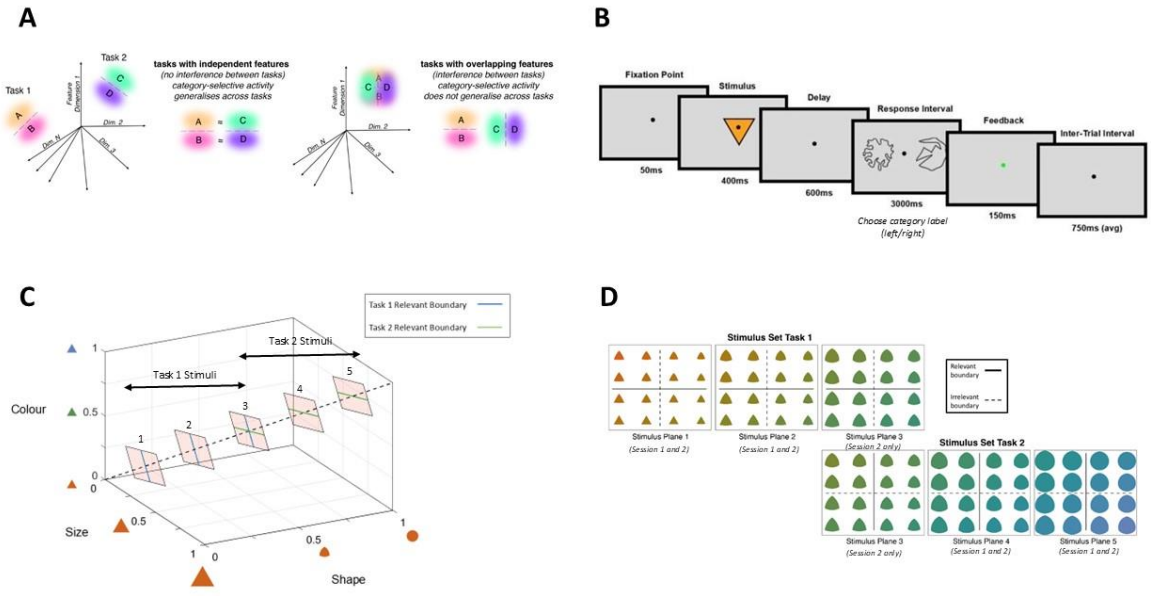


*Figure 1**A**. Hypothesised representation of the tasks split by independent and overlapping features. The tasks with independent features are represented on the left, meaning these are the tasks in which there was no interference. We hypothesised that category-selective activity would generalise across tasks. For the tasks with overlapping features (interference present between the tasks due to stimuli belonging to multiple categories across tasks, illustration on the right), we hypothesised that category-selective activity would not generalise across tasks (therefore specialised). **B**. The stimulus was presented for 400ms followed by a delay period of 600ms. The choice screen was then presented, and participants chose a category label and were given feedback after response or 3000ms (timeout). The fixation point turned from black to green signifying a correct response, or to red signifying incorrect for 150ms. **C**. A 3D representation of the feature space from which the stimuli used for the experiment were drawn. Each axis represents a feature dimension (size, shape, and colour). Stimuli were drawn from five 2D planes which were equally spaced along one long diagonal in the feature*

space. Participants learned to categorise the stimuli using this relevant decision boundary (either into category A/B for Task 1, or category C/D for Task 2). ***D****. The stimuli used in the experiment are shown split by Planes 1-3 for Task 1 and 3-5 for Task 2. The overlapping stimuli are those within Stimulus Plane 3, in which the same stimuli belong to both Task 1 and Task 2. The relevant and irrelevant boundaries are also highlighted for each stimulus plane.*

The stimuli varied from 3° to 7° in size (each degree of visual angle corresponds to 40 pixels on the screen), and the colours were drawn from a segment of an equiluminant colour wheel. The stimulus shape varied from triangular to circular. We created stimulus shapes parametrically by creating three circle segments drawn at a fixed distance (depending on stimulus size) from a central point, with the midpoint of each segment 60º apart from the others. We varied the shape by varying the radius of the imaginary circle from which each segment was drawn. When the radius was equal to the distance to the central point, this produced a circle. As the radius of the segments increased, their curvature decreased, producing straighter lines up to a triangle. We refer to the stimuli used in the initial learning session and in EEG Session 1 as old stimuli and the stimuli introduced in EEG Session 2 (the stimuli from plane 3) as new stimuli.

In Session 2, overlapping stimuli were introduced which occupied the middle of the feature space (plane 3) and could be categorised in both tasks.

The categorisation task involved identifying a stimulus category by choosing the corresponding category label. The category labels were four difficult-to-verbalise arbitrary shapes taken from Endo et al. (2013) and the categories they represented were counterbalanced across participants. Each category in each task was assigned a different label. The labels were presented 4° to the left and right of the fixation point. The labels were

3.75° in height and width. Two labels were displayed per task, representing the two categories within the task.

Apparatus

The initial 16 participants were tested at the University of Oxford. Stimuli were presented on a 24-inch screen with a spatial resolution of 1920 x 1080 pixels, background luminance of 0.5 (grey), refresh rate of 100Hz. Participants were seated approximately 64cm away from the screen and the stimulus presentation was controlled using Psychophysics Toolbox Version 3 (Brainard, 1997) in MATLAB R2015b. EEG data was recorded using EasyCap 61 Ag/AgCl sintered electrodes, a Neuroscan SynAmps RT amplifier, and Curry 7 acquisition software. Eye movements were recorded using an EyeLink 1000 camera, and vertical/horizontal electrooculogram (EOG) electrodes were placed below the left eye and lateral to both eyes. A ground electrode was placed on the left elbow reference electrodes were placed on the left and right mastoids. During recording, the left mastoid was the active reference, which was re-referenced to the average of both mastoid offline.

The data from the remaining 18 participants were collected at the University of Nottingham. Stimuli were presented on a 27-inch screen with a spatial resolution of 2560 x 1440 pixels, background luminance of 0.5 (grey), refresh rate of 100Hz. Stimulus presentation was controlled using Psychophysics Toolbox Version 3 in MATLAB R2021b. EEG data was recorded from 64 electrodes using a BioSemi ActiveTwo EEG system. Eye movements were recorded using an Eyelink 1000 Plus system. Six external electrodes were placed on the participant, including the left and right HEOG, right upper and right lower VEOG, as well as left and right mastoids.

Design

Participants performed two visual categorisation tasks requiring the categorisation of simple abstract stimuli (Fig. 1b). Participants were not told what the two rules were for the two tasks but learnt this via trial-by-trial feedback before EEG recording began. During the EEG sessions the two tasks were performed in separate blocks, with 24 blocks (12 per task) consisting of 96 trials each per session.

The experiment was conducted over three sessions: the initial 'learning' session in which participants learned the different rules for Task 1 and Task 2, the first EEG session involving independent stimulus sets for Task 1 and Task 2, followed by the second EEG session involving the stimuli from the previous session mixed with new overlapping stimuli (stimuli presented in both Task 1 and Task 2, see Fig.2 for a session structure overview). Category boundaries for the two tasks remained the same throughout the experiment for each participant.

Figure 2

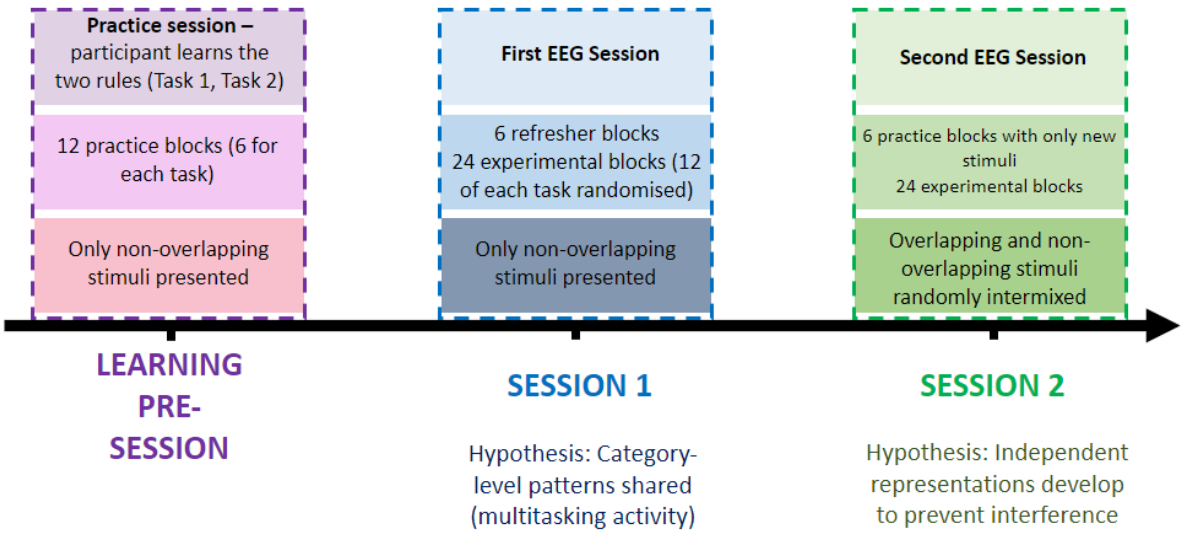


Figure 2. This figure outlines the structure for each session of the experiment including the Learning Session, Session 1, and Session 2. The initial learning session includes a shortened version of the behavioural task where 12 blocks in total are completed (six blocks of each task with its own stimulus set of old stimuli are asked to be categorised, allowing for two rules to be learnt via feedback). The first EEG session began with six refresher blocks (three blocks from T1, three blocks from T2) to remind the participant of the two rules learnt in the previous session. The participant is presented with 24 blocks (12 blocks of each task) of non-overlapping stimulus sets meaning different sets for T1 and for T2. In this session it is predicted that as different stimulus sets will be used for the tasks meaning there is no overlap between the stimuli, category-level patterns will be shared as participants will categorise these stimulus sets using the same multitasking neurons. The second EEG session involved the participant learning how to categorise only the new, overlapping stimuli using the rules learnt in the previous session. The participant has six blocks of learning to categorise only the new stimuli into Task 1 and Task 2. The overlapping stimuli can be categorised into both tasks, but the participant must learn how to categorise that stimulus depending on which task is currently being presented (only one task is presented per block). In this session it is predicted that as overlapping stimuli will be introduced which can now be categorised into both Task 1 and Task 2, independent neural representations will form to deal with this interference between categories.

Procedure

Participants performed a visual categorisation task where stimuli were categorised according to two rules which the participants learnt via feedback which was displayed after each trial. In each block participants responded according to a categorisation rule.

Each trial began after an inter-trial interval (750ms). A fixation point was presented for 50ms before the stimulus was displayed for 400ms. The delay period lasted for 600ms and

was followed by the choice screen. The arrangement of the category labels (left or right of the fixation point) was randomised from trial-to-trial to prevent participants from preparing their response before the onset of the choice screen. The labels were presented 4° to the left and right of the fixation point. The labels were 3.75° in height and width. Participants had 3000ms to respond by pressing either the 'c' key for the category on the left, or the 'm' key for the category on the right. Feedback was given after the response (or after timeout of 3000ms) by changing the fixation colour to green (correct response) or red (incorrect) for 150ms.

In the Learning Session participants completed a short version of the task (12 blocks instead of 24, 6 blocks per task). In this Learning Session, participants learned the rule for Task 1 and for Task 2. The rules were counterbalanced across participants. Participants were told that there are two separate category rules to learn. Task rule learning was blocked (6 blocks of each task) and participants were informed which rule they would be performing in each block. They were also shown example stimuli from each category at the beginning of the task and were explicitly told to pay attention to all three features (shape, size, and colour). In order to progress to the EEG stage, participants were made to repeat the learning sessions until reaching 70% accuracy.

In Session 1, EEG recording was introduced. Participants initially completed 6 refresher blocks (3 blocks of Task 1, 3 blocks of Task 2) to remind themselves of the rules for each task (the rules were the same as those learnt in the previous Learning Session). Once setup was complete for the EEG recording, participants completed 24 blocks (12 blocks of each task consisting of 96 trials per block). The blocks from the two tasks were intermixed and randomised.

In Session 2, the second EEG recording was conducted. Participants applied the previously learnt rules to new stimuli which appeared in both Task 1 and Task 2. The new stimuli occupied the middle of the 3D feature space, meaning they were placed between the original separate stimulus sets for Task 1 and Task 2. Participants initially performed 6 blocks (3 blocks of Task 1, 3 blocks of Task 2) and were asked to categorise only the new stimuli to familiarise themselves. Once the EEG recording began, participants completed 24 blocks (96 trials per block), with the new stimuli and old stimuli mixed at random within each block. Each block still consisted of only one task and the blocks were ordered randomly.

Behavioural Analysis

We calculated mean accuracy and median reaction time on correct trials for each participant per task and session, and separately for old and new stimuli in Session 2. Effects of session, stimulus set (old, new) and task were compared with repeated-measures ANOVA and paired-samples t-tests.

We estimated the decision boundary between categories separately for Session 1, the old stimuli in Session 2, and the new stimuli in Session 2. We fit a logistic regression model to trialwise choice data using maximum likelihood estimation. The model contained two parameters, the decision boundary θ and the slope σ:

$$dv = \cos(\theta)*dv_{Task\ 1} + \sin(\theta)*dv_{Task\ 2},$$

where $dv_{Task\ 1}$ is the relevant decision variable for Task 1 (i.e., the signed distance from the category boundary for Task 1), taking on values of -1.5, -0.5, +0.5, or +1.5 in arbitrary units), $dv_{Task\ 2}$ is the decision variable for Task 2 (the signed distance from the category boundary for Task 2), and θ is the estimated decision boundary angle, dv is the decision variable integrated across relevant and irrelevant information. Boundary angles were calculated by maximum-likelihood estimation of θ, which determines the relative weighting of Task 1 and Task 2

decision variables and therefore the orientation of the participant's subjective decision boundary. We modelled the likelihood of a categorical decision with a sigmoid function with slope σ, estimated using the cumulative normal distribution Φ (and mean μ fixed at 0, corresponding to no bias towards either category):

$$P(\text{resp. category B/D} \mid dv, \sigma) = \Phi\,(dv, \mu, \sigma).$$

For Task 1, the optimal decision boundary is 0°, whereas for Task 2, where the category boundary was orthogonal, the optimal boundary is 90°. We ensured that participants learned separate category boundaries for both tasks by comparing the recovered boundary angles between tasks in each session (and separately for new stimuli in session 2). We also tested whether boundaries differed significantly from their optimal values.

Finally, we reasoned that if participants mapped categories from different tasks onto one another, then categorical information from the currently irrelevant task might exert a bias on the current task. For example, if category A from Task 1 was neurally mapped to category C from Task 2, then during execution of Task 1 a stimulus containing strong evidence for category C might be more likely to lead to an 'A' response (even though evidence for C was irrelevant and orthogonal to evidence for A). This would lead to an increase in the decision boundary angle above 0. Conversely, if category A was mapped instead to category D from Task 2, then evidence for category C should have a repelling effect, decreasing the likelihood of correctly choosing category A. This would lead to a decrease in the decision boundary angle below 0.

Importantly, this effect should be symmetrical: if categories A (from Task 1) and C (from Task 2) are mapped together, then the estimated boundary angle should be shifted in both tasks, but in opposing directions. If this was the case, boundary angle estimates should be anticorrelated across tasks. We tested this using Spearman rank correlations between

boundary angles from the two tasks, separately for each session (and the new stimuli in Session 2).

EEG Preprocessing

EEG data were preprocessed using EEGLab and FieldTrip in MATLAB. The EEG signal was downsampled to 250Hz and referenced to the mean of the right and left mastoids. EEG and EOG channels were bandpass-filtered (EEG: 0.1-45Hz, EOG: 0.1-25Hz). The data were epoched at stimulus onset (from 1s before to 2.2s after stimulus onset). Trials containing eye blinks/movements during stimulus presentation, muscle movements, and drift were manually rejected. The data then underwent Independent Component Analysis (ICA) to further remove any artifacts including muscle movements and eye blinks or eye movements. Lastly, we used semi-automatic rejection using the fieldtrip function 'ft_rejectvisual' to visually inspect and remove any remaining outlying trials.

EEG Analysis

We used multivariate pattern analysis to test the coding principles of category-selective activity in the EEG data. We estimated decodability of a stimulus category using leave-one-block-out cross-validation. We first selected the data from one task and held out one of the 12 task blocks. From the remaining 11 training blocks, we calculated the average response to each category for every time point. For each held-out test trial, we then calculated the Mahalanobis distance to each of the two category averages from the training data. We calculated the noise covariance using the training data. In particular, we first removed the corresponding category average from each trial in the training data and concatenated all time points from 0-1s after stimulus onset along the trial dimension, yielding a trials*time points-by-channels noise matrix, from which we calculated the channel-by-channel covariance using a shrinkage estimator (Ledoit & Wolf, 2004). We calculated a single covariance matrix across

time points assuming that noise covariance was approximately stationary over the relatively short 1s stimulus-to-probe window. This allowed us to calculate a more robust covariance estimate and to significantly speed up the analysis. We used this covariance in the calculation of Mahalanobis distances calculated separately for each time point. We then calculated decodability on each test trial by subtracting the Mahalanobis distance to the same-category average from the other-category-average. We then repeated the procedure, holding out a different block as the test data, until all trials had acted as the test data. We then averaged the distance difference over trials, resulting in a decodability score which measures how well the category of a stimulus can be inferred from the EEG data. We repeated the procedure for both tasks separately. This general decoding approach was modified to test for generalisation across tasks (see next section). Finally, we tested for significance using one-sample t-tests against 0 for each time point and corrected for multiple comparisons using cluster-based permutation tests (based on cluster mass, 10,000 permutations). We additionally calculated the average decodability over a predefined time window of interest (250-750ms after stimulus onset, avoiding stimulus-driven responses from 0-250ms) and calculated significance with one-sample t-tests.

Within-task and Cross-task Decodability

To test our hypothesis that the same category-selective neural activity pattern is shared across different tasks (Hypothesis 1), we adapted the within-task decoding approach described above for cross-task decoding. Within-task decoding involves training a decoder on the EEG data for Task 1 and then testing on Task 1 (or training and testing on Task 2). Cross-task decoding involves training a decoder on the data from Task 1 and then testing it on Task 2. We repeated the above steps except that the means from the training data were calculated on one task, and the test trials were from the other task. Task 1 included categories A vs. B, whereas Task 2 included categories C vs D. We held out one block from each task resulting in

22 blocks remaining to be used as training data. For each task in the training data, we calculated means per category, which yielded 4 means (categories A-D). To make cross-decoding possible, we first needed to identify which category from Task 1 might map onto which category from Task 2. Since we predict that one category from Task 2 is arbitrarily mapped onto either one of the categories from Task 1, this mapping cannot be predicted a priori. In the training data, we identified how categories are mapped across tasks (i.e., whether A≈C and B≈D or A≈D and B≈C) by minimizing the average Mahalanobis distance between cross-task pairs in a pre-defined window from 250-750ms after stimulus onset. Choosing a different window (500-1,000ms) gave largely the same results. We then calculated the distance of individual test trials to the category means from the other task and calculated the distance difference (subtracting the more similar category from the less similar category). Finally, we averaged over the trials and calculated significance as above.

We also hypothesised that when conflicting, overlapping stimuli are introduced, category representations will become independent across tasks to prevent interference (Hypothesis 2). If both Task 1 and Task 2 used the same neural activity patterns to discriminate between categories (showing multitasking activity), the classifier should be able to generalise across tasks. However, if Task 1 and Task 2 rely on independent neural activity patterns, then the decoding should not generalise. As a control, the above analyses were also repeated for the task-irrelevant category boundary (i.e., 90º rotated from the task-relevant category boundary).

Figure 3

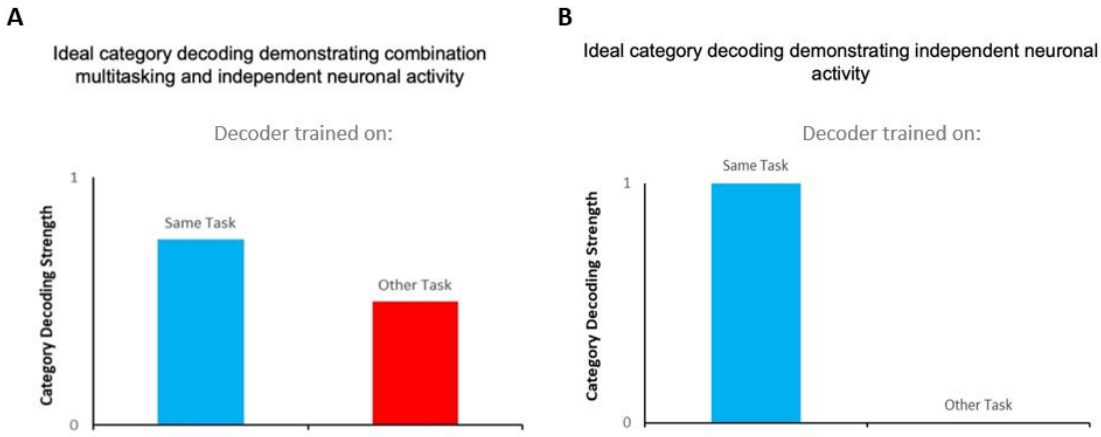


*Figure 3**A**. We expected that under multitasking an idealised decoding result would identify significant cross-task decoding, confirming multitasking activity, with a small drop from within-task decoding, suggesting some independent neural activity. This level of decoding strength for within task (blue) and cross task (red) decoding for the actual EEG data would suggest multitasking activity to be present as the decoding strength for other (cross) task is high, suggesting the same neural population codes for both tasks.* ***B.*** *The idealised category decoding result under exclusively independent neural activity would, by contrast, show high category decoding within task (blue), compared to the cross-task decoding (other task) which is absent. Such a result would suggest that different neural populations code for categories in each task.*

Results

Behavioural Analysis

Participants Treat the Tasks Separately

We first analysed the behavioural response data to identify the average subjective category boundaries of participants. Participants completed both categorisation tasks

adequately in both sessions, with subjective categorisation boundaries appearing to align well with the correct category boundaries (Fig.4). We estimated subjective decision boundaries separately for each task and session. We defined the correct category boundary for Task 1 as a 0º line through the 2D stimulus planes and a 90º line for Task 2 (Figure 4a,b, see also Figure 1c). Overall participant choices showed a clear distinction between the two tasks across both sessions. The heat-maps highlight the clear boundaries for Session 1 and the old stimuli in Session 2, compared to the new stimuli in Session 2 where the category boundaries become less defined. Overall, this suggests participants did treat the tasks separately and did not use a single rule for both tasks.

Figure 4

Heat Maps Showing Category Boundaries Averaged Across Participants

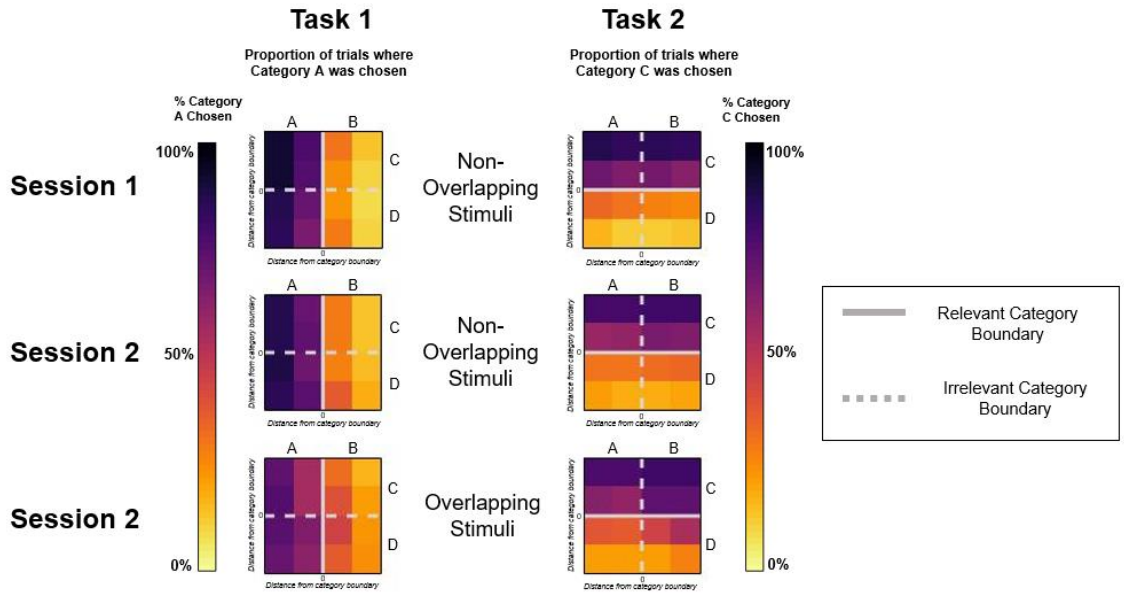


Figure 4. Heat-maps displaying category choices as a function of distance to the task-relevant and irrelevant category boundaries, averaged across all participants for Session 1

Task 1 and Task 2 (old stimuli, i.e., non-overlapping stimuli), Session 2 Task 1 and Task 2 (non-overlapping stimuli), and Session 2 Task 1 and 2 (new stimuli, i.e., overlapping stimuli). The colours represent the proportion of category A (Task 1) or category C (Task 2) choices, ranging from brightest (0%) to darkest (100%). The heat maps show a step change in choices at the relevant category boundaries for the old stimuli for both Tasks 1 and 2 in Session 1 (top row) and Session 2 (second row). While choices to the overlapping stimuli in Session 2 (bottom row) were still clearly distinct across tasks and aligned with the relevant category boundary, they were more variable.

To quantify this pattern we next estimated the decision boundary between categories for Session 1, the old stimuli in Session 2, and the new stimuli in Session 2. For Task 1, the optimal decision boundary is 0 degrees, whereas for Task 2 (where the category boundary is orthogonal), the ideal boundary is 90 degrees. We compared the boundary angles between tasks in each session, as well as testing whether the boundaries were significantly different from their optimal value. This allowed us to ensure whether participants learned separate category boundaries for both tasks.

Using t-tests to compare the decision boundary angles, we found that for Session 1, the Task 1 angle (6.84°±2.53º s.e.m.) was significantly different to the Task 2 angle (84.71±3.14°, $t(29)=17.1$, $p=1.1*10^{-16}$, Cohen's d=-3.1). However, the estimated Task 1 boundary was slightly but significantly above 0° (optimal decision boundary angle for this task, $t(29)=2.7$, $p=.011$, $d=0.49$). The Task 2 boundary did not differ significantly from 90° ($t(29)= -1.68$, $p=.10$, $d=0.31$). Interestingly, in aggregate both boundary angles were biased slightly towards a common diagonal (45º), hinting at the possibility of shared coding driving behaviour to some extent. To explore this possibility systematically, we examined whether

the two boundary estimates for each participant were biased towards the same diagonal. For example, if category A in Task 1 is mapped onto category C in Task 2 and this drives behaviour to some extent, then Task 1 trials that are both A and C should be more likely to be classified as A than Task 1 trials that are both A and D (thus tilting the subjective boundary away from the A/C quadrant, i.e. below 0º). If the same mapping is true for Task 2, the boundary estimate for Task 2 should be pushed in the other direction (i.e., the boundary for Task 2 should also move away from A/C, above 90º). Therefore, both boundary estimates would be biased away from the optimum (0º or 90º) and towards the 135º diagonal. Conversely, if A≈D (and B≈C) the opposite would happen, pushing the subjective boundaries toward the 45º diagonal. Across participants, this should lead to a negative correlation in boundary estimates across tasks. Indeed, we found a significant negative correlation between the boundary estimates across tasks (Spearman's rho=-0.47, p<.001).

We found largely comparable results in Session 2. For Session 2 old stimuli, decision boundaries differed significantly from each other (Task 1 angle -1.60 ±2.18º, Task 2 angle 87.12±7.16º, Task 1 vs 2: t(29)=11.49, p=2.57*10^{-12}, d=-2.10). Neither decision boundary differed from the optimal value (Task 1 vs 0º: t(29)=-0.73, p=0.469, d=-0.13, Task 2 vs 90º: t(29)=0.40, p=0.690, d=0.07). Unlike in Session 1, the negative correlation between decision boundary angles was only marginally significant (rho=-0.35, p=0.058), possibly consistent with a reduction in shared task coding.

We saw the same pattern for the new stimuli presented in Session 2. Again there was a significant difference between decision boundaries (Task 1 angle 0.69±6.42º, Task 2 angle 88.55±10.06º, Task 1 vs 2: t(29)=6.46, p=4.61*10^{-7}, d=-1.18) and neither boundary differed from the optimal value (Task 1 vs 0º: t(29)=0.11, p=0.92, d=0.02, Task 2 vs 90º: t(29)=0.14, p=0.89, d=0.03). There was no correlation between boundary angles (rho=-0.29, p=0.118).

This lack of correlation is broadly in line with increasingly independent coding of tasks once the new overlapping stimuli were introduced.

In sum, estimated decision boundaries were close to optimal and distinct across the two tasks, which shows that participants were successfully able to learn separate decision rules for both Task 1 and Task 2. Furthermore, in Session 1 boundary estimates were correlated across the two tasks, consistent with a shared categorical mapping. In Session 2, boundary estimates were still marginally correlated for old stimuli but uncorrelated for the newly introduced stimuli which created overlap in the stimulus sets across tasks. While this points to a possible reduction in shared task coding, this behavioural measure is indirect and will need to be corroborated by analyses of neural activity.

Figure 5

Estimated category decision boundary angles for Session 1, Session 2 old stimuli and Session 2 new stimuli

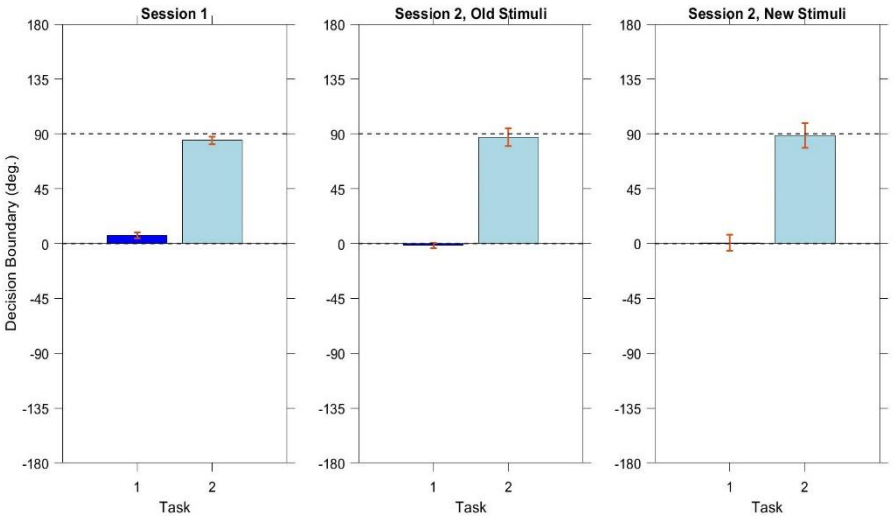


Figure 5. Estimated decision boundary angles were found to be close to their ideal value across the two tasks, suggesting participants learned separate decision rules for Task 1 and

Task 2. The optimal boundary for Task 1 is 0 degrees, compared to 90 degrees for Task 2. Error bars indicate standard error of the mean.

Introduction of Cross-task Conflict Reduces Categorisation Performance

We next tested whether the introduction of overlapping stimuli in Session 2 affected categorisation performance (Figure 6). We conducted a 3x2 within-subjects ANOVA for session (1,2 old, 2 new) and task (1,2) against accuracy. Results displayed a clear main effect for session ($F(2, 58) = 70.60$, $p<.001$, $p\eta^2 = .549$) on accuracy. Accuracy was higher in Session 1 (M=0.79, SD=0.091) than Session 2 old stimuli (M=0.756, SD=0.101) and Session 2 new stimuli (M=0.69, SD=0.106). This suggests participants were more successful at categorising the old stimuli in Session 1 than Session 2, possibly due to the second session introducing the new stimuli and so creating conflict. There was a borderline main effect of Task ($F(1, 29) = 4.36$, $p=.05$), suggesting that while performance was slightly higher for Task 1, there were no drastic differences in performance across tasks. There was a significant interaction between session and task ($F(2, 58) = 12.3$, $p<.001$) because accuracy did not differ between tasks for the new stimuli in Session 2 (see Supplementary Figure S1).

A paired t-test was also conducted for session 1 old stimuli, session 2 old stimuli, and session 2 new stimuli accuracy. Accuracy was higher in Session 1 ($M = 0.791$, $SD = 0.0912$) than for the same stimuli in Session 2 ($M = 0.756.$, $SD = 0.1014$, $t(29) = 4.277$, $p<.001$). Accuracy was also significantly higher for the old stimuli in Session 1 than the new stimuli in Session 2 ($M = 0.693$, $SD = 0.106$, $t(29) = 10.688$, $p<.001$). Finally, in Session 2, the old stimuli showed a significantly higher accuracy than the new stimuli ($t(29) = 8.188$, $p<.001$).

While we did not expect any task effects in reaction time, we also conducted a 3x2 within-subjects ANOVA against reaction time (Figure 6). There was no effect of session (F(2,

58) = 1.99, p =.146, ηp^2 =.033) or task (F(1, 29) = 1.56, p=.222, ηp^2 =.05) and no interaction (F(2, 58) = .240, p =.788, ηp^2 =.004). Reaction times did not differ between Session 1 (M = 0.416, SD = 0.081) and Session 2 old stimuli (M = 0.405, SD = 0.100, t(29) = 0.165, p=0.11) or Session 2 new stimuli (M = 0.419, SD = 0.118, t(29) = 0.270, p=0.789). However, responses to Session 2 old stimuli were significantly faster than to new stimuli RT (t(29) = 3.10, p=0.004), possibly reflecting the greater difficulty of categorising the new stimuli.

Performance was well above chance in both sessions and for old and new stimuli. However, the drop in performance in Session 2, particularly on the new interfering stimuli, could indicate that their introduction succesfully led to conflict between the two tasks. The drop in performance for the old stimuli in Session 2 was interesting because it occurred despite participants undergoing extensive practice (including ~2000 trials in Session 1).

Figure 6

Accuracy and Reaction Time for Session 1 Old Stimuli, Session 2 Old Stimuli, and Session 2 New Stimuli

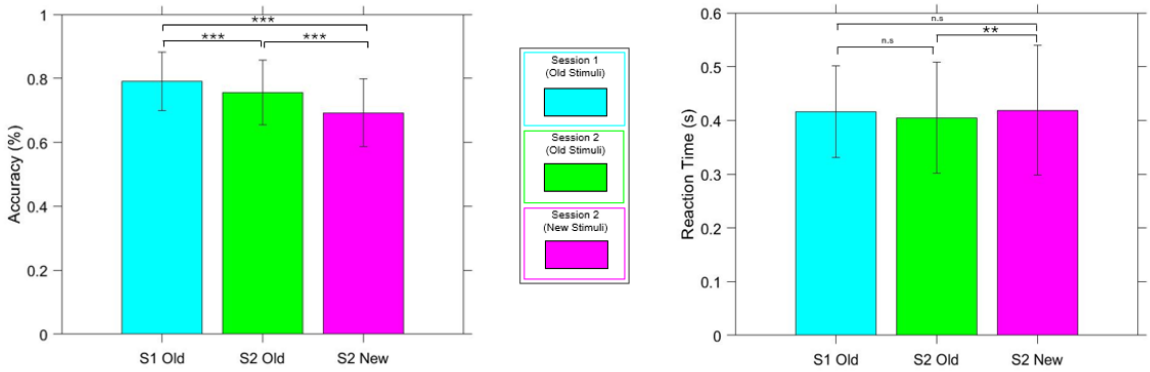


Figure 6. Behavioural analyses explored Session (1, 2 old, 2 new) against both accuracy (left) and reaction time (right). Accuracy was found to be the highest in Session 1, with a significant decline in Session 2 Old, and a further decline in Session 2 New. This suggests the

introduction of the conflicting stimuli (Session 2 New) may contribute to the drop in performance.

Neural Analysis

To examine the link between the introduction of conflicting stimuli resulting in interference, we first need to examine the neural data and find a metric of category selectivity. This was developed by examining the EEG data of Session 1.

Category Selective Neural Patterns Generalise Across Tasks

We analysed the decodability of a stimulus' category from the EEG data. First, we explored within-task and cross-task category decoding for the old stimuli in Session 1 only. For Session 1, we predicted category decoding to generalise across tasks (Figure 3). Within-task decodability was significant (significant cluster window = 50-1000ms, cluster-based permutation test, $p<.001$). Crucially, category decoding also generalised across tasks (cluster window = 264-760ms, $p=.002$). We found the same-task decoding to be significantly better than the cross-task decoding, suggesting that either the cross-task generalisation was not perfect, or other factors (such as sensory differences between the categories), may have influenced the within-task decoding, but not the cross-task decoding (Fig. 7).

Figure 7

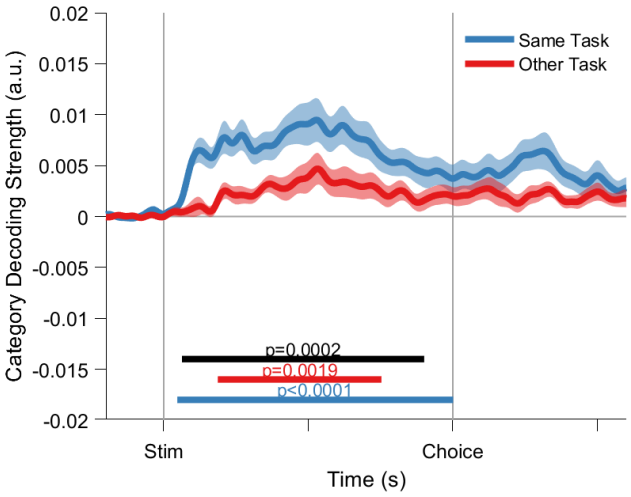


Figure 7. Within-task and Cross-task decoding for the old stimuli presented in Session 1. For the relevant task, a significant presence of within-task ($p<.001$) and cross-task ($p=.002$) decoding is present, as well as a significant difference ($p<.001$).

In theory, category decoding and cross-task generalisation could have been driven by other factors, such as sensory differences between categories. To test for this, we performed a control analysis (Figure 8a) decoding the same stimuli along an orthogonal category boundary (the category boundary from the other task, which was irrelevant on the current task). Within-task decodability was found to be highly significant ($p<.001$, cluster window = 44-860ms). However, cross-task decoding was not significant ($p=.383$), confirming that the cross-task coding was driven by categorisation.

As the within-task category decoding for the irrelevant category boundary was strong, a substantial portion of the within-task decoding (particularly early in the trial) may have been driven by sensory differences between categories. To control for this potential confound, we calculated the difference between the relevant and irrelevant within- and cross-task decoding (Figure 8b). Cross-task decoding was significantly stronger for the relevant vs the irrelevant category boundary found ($p=0.0246$, cluster window = 416-636ms). However, for within-task decoding the difference was only a trend ($p=0.099$). The difference between relevant and irrelevant category decoding was not stronger for cross-task vs within-task decoding ($p=0.526$). Since within-task decoding was substantially reduced after subtracting irrelevant category decoding, a substantial proportion of within-task decoding may indeed have been driven by low-level sensory differences between categories. By contrast, the cross-task decoding remained significant, consistent with cross-task decoding primarily reflecting genuine categorical coding. After subtracting irrelevant category decoding, there was no longer a significant difference between within- and cross-task decoding. This may be a result of the confound of perceptual differences being removed, meaning the category coding

within-task and across-tasks is indistinguishable and therefore consistent with a largely generalising category-selective population.

Figure 8

Within and Cross Task Decoding for the old stimuli within the Relevant and Irrelevant Category in Session 1

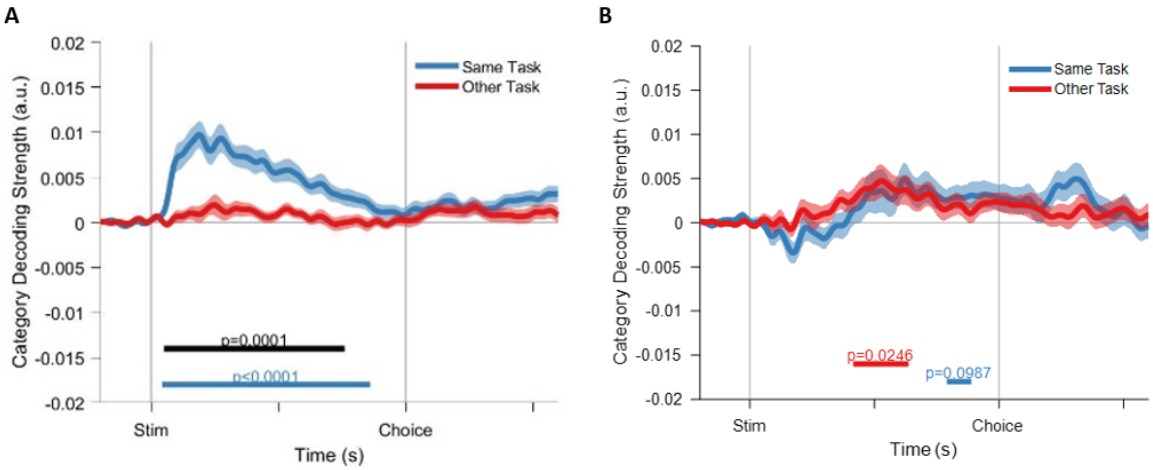


*Figure 8**A**. Within-task and Cross-task decoding for the old stimuli presented in Session 1 for the irrelevant category. For the irrelevant task, within-task decoding is significant (p<.0001) and significantly stronger than cross-task decoding (p=.0001). However, cross-task decoding was not significant (most significant candidate cluster p=.383).* ***B****. Within- and cross-task decoding difference for the relevant minus irrelevant boundary in Session 1. Cross-task decoding difference was significantly larger for the relevant vs irrelevant boundary (p=0.0246), although the difference for within-task decoding was only significant at a trend level (p=0.0987).*

Category Selective Neural Patterns Become Independent After Introduction of Cross-Task Conflict

The drop in behavioural performance for the new, overlapping stimuli Session 2 had suggested an increase in between-task conflict, possibly inducing a shift to independent category coding. We next tested whether a corresponding drop in cross-task generalisation was found.

We analysed the within-task and cross-task decodability for the new, overlapping stimuli only shown in Session 2 (Figure 9). Within-task decodability was significant (cluster window = 88-952ms, $p<.001$). However, cross-task decodability was found to be non-significant (no candidate clusters). Correspondingly, the difference between within-task and cross-task decodability was also significant ($p=.027$). This confirms our hypothesis that in the presence of cross-task conflict, the neural category signal no longer generalises. The absence of cross-task decoding indicates that the categories of new stimuli in Session 2 were independently coded, in contrast to the shared coding in Session 1.

Figure 9

Within and Cross-Task Category Decoding of New Stimuli in Session 2

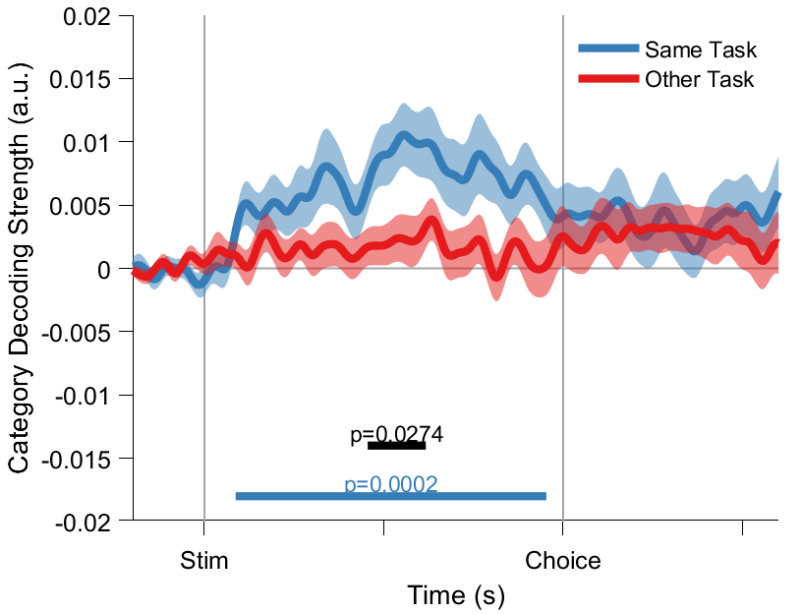


Figure 9. Within and Cross-Task decoding for new, overlapping stimuli presented only in Session 2. Within-task decoding (blue) is significant (p=.0002). Cross-task decoding (red) was not significant, leading to a significant difference between within- and cross-task decoding (p = .0274).

Interestingly, decoding of the irrelevant category was just as strong as the relevant category decoding (Suppl. Fig. S3). We explored the decoding difference between the relevant and irrelevant category in Session 2 for the (new) overlapping stimuli. In contrast to Session 1, neither within- (p=.090) nor cross-task (p=.479) decoding was stronger for the relevant category boundary, indicating that coding of the relevant category was either absent or no stronger than coding of the irrelevant category for new stimuli. Since neither difference (relevant minus irrelevant for either within- or cross-task decoding) was significant, their difference was also not significant (there were no uncorrected p-values <0.05). Interestingly, within-task decoding was slightly better for the irrelevant category (small negative trend around 400ms), although not significant (see Suppl. Fig. 17).

We next explored whether the coding of old stimuli changed in response to the introduction of the new stimuli (Figure 10). As expected, and as with the new stimuli, within-task decodability was significant for the old stimuli in Session 2 (cluster window = 72-1000ms, $p<.001$). However, in contrast to the absence of cross-task decoding for the new stimuli, a strong trend was found for cross-task decodability (cluster window = 384-590ms, $p=.06$), suggesting that cross-task decoding persisted at least in part for the old stimuli.

There was no drop in decoding relative to the previous session for within-task decoding (Figure 10, top left) or for cross-task decoding (Figure 10, top right), consistent with generalised coding persisting into Session 2.

To establish the task-specificity of category decoding, we calculated the cross-task decoding difference between relevant – irrelevant category boundaries for Session 1 and Session 2 old stimuli (Figure 10, bottom right, see Suppl. Fig. S4, S5 for irrelevant category boundary decoding, Suppl. Fig. S18 for difference between relevant and irrelevant category boundary decoding for within-task decoding). The cross-task decoding benefit for relevant category decoding was significant for both Session 1 ($p=.024$, cluster window = 416 – 636ms) and Session 2 ($p=0.026$, cluster window = 756 – 992ms). No significant difference between Session 1 and Session 2 was found ($p=.583$). This suggests that the pure decoding strength was strong enough for the old stimuli in Session 1 and Session 2, as the relevant category signal remained significant despite removing the irrelevant signal. In sum, old stimuli in Session 2 maintained a cross-generalised code, unlike the new stimuli.

Figure 10

Within Task and Cross Task Category Decoding for Old stimuli in Session 1 and Session 2 for relevant task, and decoding difference

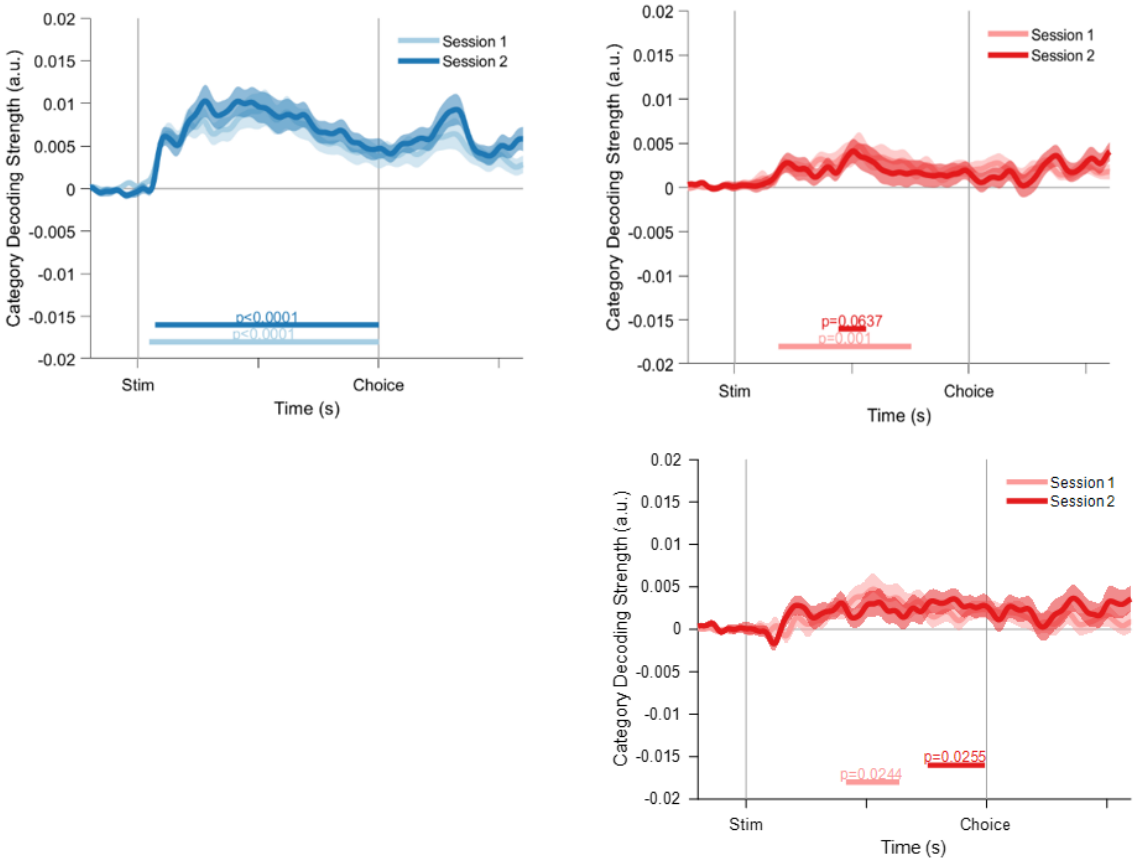


Figure 10. Within- (top left, blue) and cross-task (top right, red) decoding comparing Session 1 and Session 2 category decoding for old stimuli. There is no significant difference between sessions. Cross-task decoding difference for the relevant -irrelevant category boundary (bottom right, red) in Sessions 1 and 2. Both Session 1 and Session 2 exhibited significantly stronger decoding for the task-relevant boundary, with no significant difference between sessions.

We next aimed to simplify the above set of analyses by averaging over the time dimension (250-750ms after stimulus onset). We analysed the category decoding strength for the relevant category boundary (Figure 11) and for the irrelevant category boundary (Suppl. Fig. S2). We conducted one-sample t-tests against 0 and found for the relevant category, Session 1 within-task was highly significant (M = .0079, SD = *.009, t(29)* = 5.11, p=<.001*),* as well as cross-task decoding (M = .0032, SD = .006, $t(29)$ = 3.22, p<.001). For the old stimuli in Session 2, results also showed significant within-task decoding (M = .009, SD = .008, $t(29)$ = 5.87, p<*.001*), and cross-task decoding was marginally significant *(*M = .0023, SD = .006, $t(29)$ = 2.08, p=.05). For the new, overlapping stimuli in Session 2, within-task decoding was significant (M = .0074, SD = .011, $t(29)$ = 3.77, p<.001), with no significant cross-task decoding (M = .0002, SD = .009, $t(29)$ = 0.108, p=.915).

Figure 11

Category Decoding Strength for Relevant Stimuli

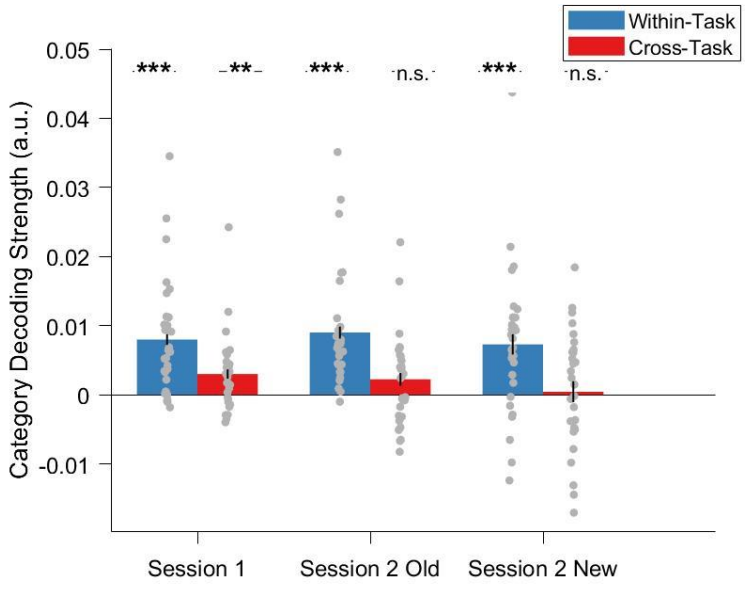


Figure 11. Within and cross category decoding strength split by session and type for the relevant category. Error bars represent standard error of the mean. Grey dots represent individual participants.

In sum, the above results demonstrate that task-relevant categories are coded differently for the new (independent coding) and old (generalized coding) stimuli in Session 2. If the same category-selective pattern had been used for both the old and new stimuli, then both stimulus sets should show cross-generalisation. We propose that the category representation of new stimuli in Session 2 is different from the category pattern for the old stimuli. The different category signals would therefore explain how participants were able to generalise between the tasks for the old stimuli, but not for the new stimuli. To confirm this, we ran the decoder on the old stimuli and tested these on the new stimuli (within the same task) to see whether this would fail to cross-generalise.

New and Old Stimuli Share Categorical Coding

The aim of the next set of analyses was to test whether the old and new stimuli in Session 2 had distinct category-specific neural activity patterns, consistent with the hypothesis that the category of the new stimuli was represented by a distinct neural pattern to avoid between-task interference. We used cross-stimulus generalisation by training a decoder on the old stimuli and seeing if it can generalise to the new stimuli. However, shared perceptual features between the old and new stimulus sets are likely to influence generalisation on some level, possibly confounding the analysis – so we might expect some level of cross-generalisation in the absence of genuinely shared categorical coding. To address this issue, we capitalised on a feature of our stimulus set (Fig. 1c,d): for each task, stimuli were drawn from three 2D planes placed within the 3D feature space. Each of these 2D planes contained 16 stimuli (8 from each category). Since the stimuli introduced in Session 2 were shared across tasks, this led to five stimulus planes in total. The planes were placed at equal intervals on the long diagonal axis of the 3D feature space, so that plane 1 (used only for Task 1) was near one corner of the feature space, plane 2 (used for Task 1) was nearer the centre, plane 3 (new stimuli in Session 2 only, shared between Tasks 1 and 2) occupied the centre, and planes 4 and 5 (Task 2 only) approached the other end of the feature space. This tiling allowed us to compare generalisation from old to new stimuli to the generalisation between different subsets of old stimuli. As the distance between the stimulus planes is equal within the feature space, this should allow for the perceptual similarity between stimuli in plane 2 (old stimuli) vs plane 3 (new) to be roughly comparable to that between plane 2 (old) vs plane 1 (old). A useful comparison would be to train a category decoder on the old stimuli from plane 2, and test how well this generalises to the new stimuli in plane 3 vs the old stimuli in plane 1. This process would then be repeated for Task 2 by training on the old stimuli in plane 4, testing on the new stimuli in plane 3 vs. the old stimuli in plane 5. After averaging these together, this

would allow us to see the strength of generalisation from old to new stimuli and whether the cross-stimulus generalisation is stronger for old-to-old generalisation. This would suggest that the new stimuli have a different type of category coding to the old stimuli. To calculate a ceiling on cross-stimulus generalisation, we also conducted within-stimulus decoding involving training and testing on the same stimulus plane.

Before we conducted the neural analyses, we analysed the behavioural data to further explore whether the stimuli planes closer to the new stimuli in Plane 3 (Plane 2 and 4) had less clearly defined category boundaries than stimuli planes further away in the feature space (Plane 1 and 5). We analysed the behavioural response data split by session, as well as plane (Figure 12). Accuracy appeared to be higher for the stimuli within planes 1 and 5 than planes 2 and 4, where the boundary between categories became less clearly defined (with accuracy even lower for plane 3, see also Fig. 4-6). Overall, the further away the stimulus plane is from Plane 3 (the centre of the feature space), the easier the stimuli become to categorise. More importantly, accuracy was still high across all stimulus planes.

Figure 12

Heat Maps Showing Categorisation Performance Averaged Across Participant per Stimulus Plane

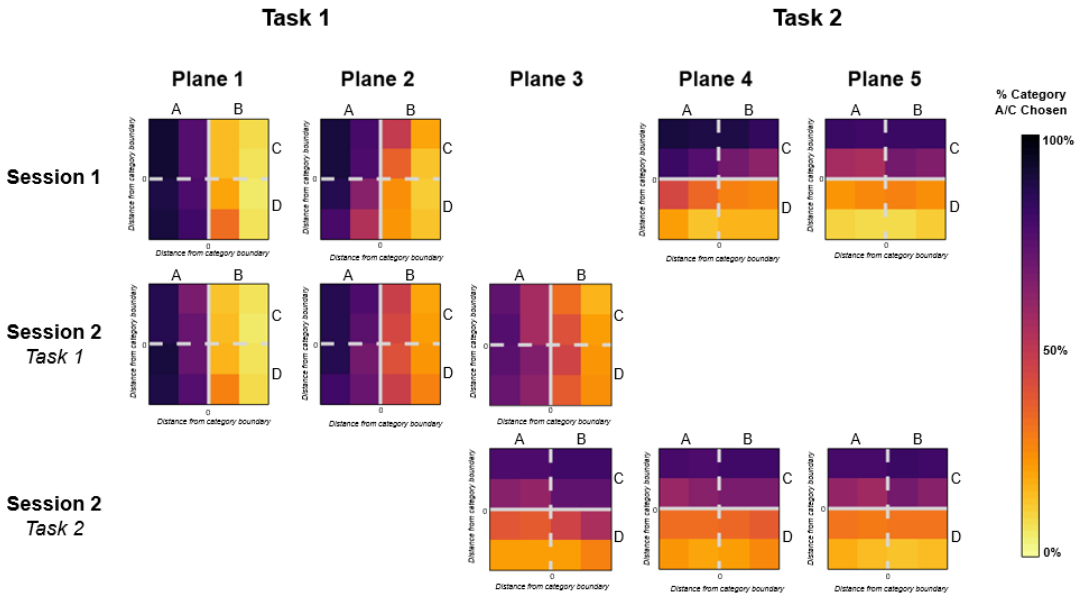


Figure 12. Heat-maps displaying category choices as a function of distance to the task-relevant and irrelevant category boundaries, split by stimulus plane (see Fig. 4 for plotting conventions).

For the neural data, we initially conducted within- and cross-plane decoding for Session 1 to examine generalisation within task before the new stimuli were introduced. For Task 1 this involved training on plane 2 and testing on either plane 2 (Same Plane) or plane 1 (Other Plane), whereas for Task 2 we trained on plane 4 and tested on either plane 4 (Same) or plane 5 (Other). We then averaged Same and Other Plane decoding over the tasks (Fig. 13a, for results split by task, see supplemental Figure S6 and S7). Same-plane decoding was found to be highly significant (p<.001, cluster window 44-1000ms). Cross-plane decoding was also found to be significant (although not as strongly present, p=.01, cluster window 64-288ms). This decoding was at a much earlier timepoint than other categorical decoding we have seen, possibly due to the presence of perceptual similarities and could suggest a later timeframe involves true category signal. A significant difference was also found to be present (p<.001, cluster window 64-968ms).

We then analysed the within- and cross-plane decoding for Session 2 (Fig. 13b, for task split see S8 and S9). Results show a highly significant presence of within-plane decoding (p<.001, cluster window = 64 – 1000ms), as well as a presence of cross-plane decoding (p=.005, cluster window = 188-528ms). A strong significant difference was also found (p<.001, cluster window = 60-1000ms).

Figure 13

Within and Cross Plane Decoding for Session 1 (left) and Session 2 (right) old stimuli

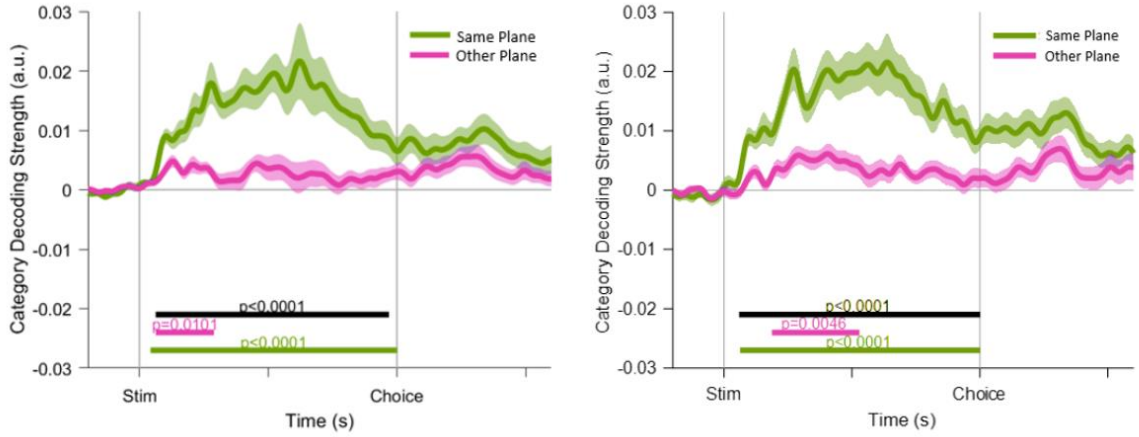


Figure 13. a) Within- (Same Plane) and cross-plane (Other Plane) decoding for Session 1. A highly significant presence of within-plane (p<.001) was found, as well as a significant presence of cross-plane decoding (p=.01) and a significant difference (p<.001). b) Within and Cross-plane decoding for Session 2, old stimuli. Within-plane decoding was found to be highly significant (p<.001), with a clear presence of cross-plane decoding also found (p=.005). A strong significant difference was also found (p<.001).

Given the comparable results in Sessions 1 and 2, we averaged over both sessions (Fig. 14). Cross-generalisation between planes was present, albeit not strongly (p=.002, cluster window = 80-540ms). Within-plane decoding was highly significant (p<.001, cluster window = 52-1000ms) and significantly stronger than cross-plane decoding (p<.001, cluster window = 56-1000ms).

Figure 14

Within- and Cross-Plane Decoding Averaged Over Session 1 and 2

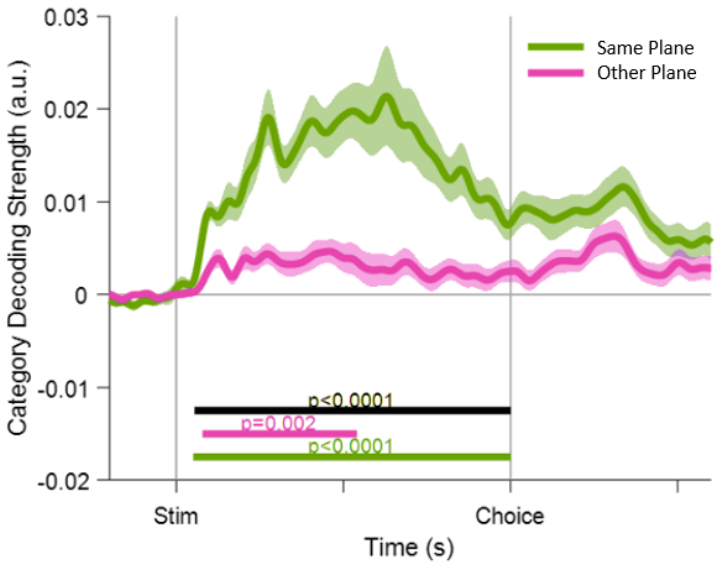


Figure 14. Within- and cross-plane decoding averaged over both session 1 and 2 for the old stimuli. Within-plane ($p<.001$) and cross-plane decoding ($p=.002$) were significant, although within-plane decoding was significantly higher ($p<.001$).

To explore the within- and cross-plane decoding between old and new stimuli, we also analysed the data in Session 2 by training on Stimulus plane 2 (old stimuli) and testing on plane 2 (within-plane) and plane 3 (cross-plane, generalisation from old to new stimuli) for Task 1 (for Task 2, we trained on plane 4 and tested on plane 4 or 3). As before we averaged decoding over both tasks. Both within-plane decoding ($p<.001$, cluster window = 168 – 948ms) and cross-plane decoding ($p=.005$, cluster window = 88 – 416ms) were significant. This suggests an unexpected finding that the new overlapping stimuli cross-generalise to the old stimuli (to a similar extent as old-to-old generalisation). No significant difference between the within-plane and cross-plane decoding was found (most significant candidate cluster $p=.0733$).

Figure 15

Within- and Cross-Plane Decoding from old to new stimuli for Session 2, Averaged over Tasks 1 and 2

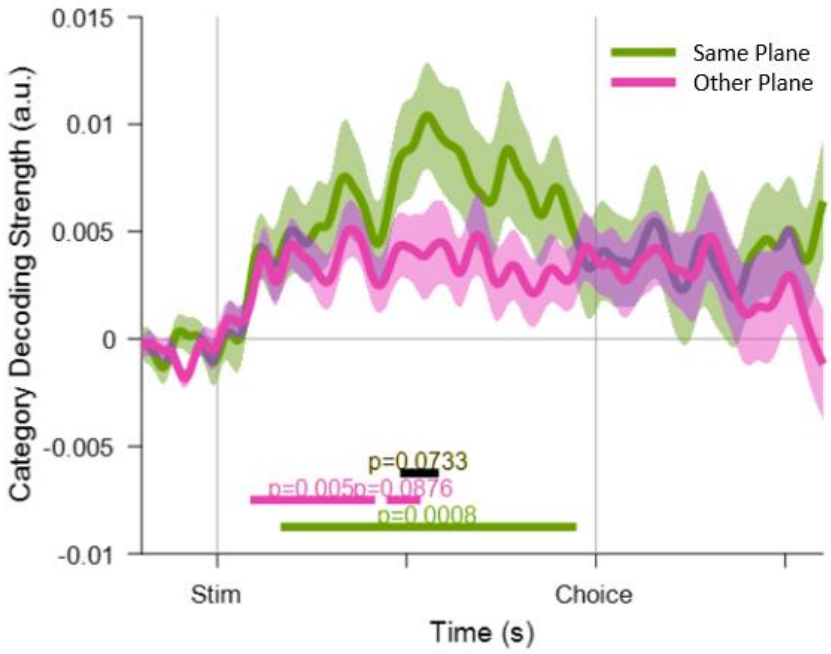


Figure 15. Within and cross-plane decoding in Session 2, training on old stimuli (planes 2, 4) and testing on new stimuli (plane 3). Within-plane decoding (p<.001) cross-plane decoding (p=.005) were significant, suggesting the new, overlapping stimuli cross-generalise to the old stimuli. No significant difference was found (p=.130).

In sum, within-task generalisation from old to new stimuli (Fig. 15) was approximately equal to generalization between subsets of the old stimuli (Fig. 13b), contradicting our hypothesis that new stimuli were represented by a distinct category-selective pattern. This puzzling result seemed to be at odds with the finding that old stimuli generalised across tasks, but new stimuli did not. One way to reconcile these findings is that category representations were not constant within the old stimuli themselves (as indicated by the imperfect generalisation from plane 2 to plane 1, or 4 to 5 in Task 2). If this were the case, then categorical representation might gradually morph along the feature space: so even

though stimuli from plane 1 partially generalise to plane 2, and plane 2 to plane 3, stimuli from distant ends of the feature space for one task (i.e., plane 1 to plane 3) might not generalise. This would then allow both some parts of the stimulus space to generalize between tasks while others do not, and different stimulus sets within a task to generalise. We explored this next.

Distant Old Stimuli Do Not Generalise to New Stimuli

The presence of strong cross-plane decoding from stimulus plane 2 to both planes 3 and 1 was unexpected. We tested the possibility that a complete uniform representation of the category is not created and therefore the categorical code becomes slightly different for stimuli planes 1, 2, and 3, explaining the lack of 'perfect' cross decoding. This would provide an explanation as to why the old stimuli can cross-generalise across tasks, but the new overlapping stimuli cannot (although they can still cross-generalise from old stimuli to the new stimuli within a task). These predictions suggest that generalisation from stimuli planes 1 to 3/5 to 3 should not be as strong as 2 to 3/4 to 3.

We conducted within- and cross-plane decoding analyses for Session 2, Task 1 (training on plane 1 and testing on either plane 1 (within) or plane 3 (cross-plane)). Within-plane decoding was highly significant (p<.001, cluster window 76-1000ms), with no significant clusters found for cross-plane decoding. Within-plane decoding was therefore significantly stronger than cross-plane decoding (p<.001, cluster window = 80 – 884ms).

We also examined within- and cross-plane decoding for Session 2, Task 2 (train on plane 5, test on planes 5 and 3). Again, within-plane decoding was significant (p<.001, cluster window = 64 – 970ms), and cross-plane decoding was not significant (most significant cluster p=.596). Within-plane decoding was stronger than cross-plane decoding (p=.006, cluster window 220-589ms; p=.004, cluster window = 599-1000ms).

We next averaged within- and cross-plane decoding in Session 2 across Tasks 1 and 2 (Fig. 16). Within-plane decoding was found to be highly significant (p<.001, cluster window = 60-1000ms), with no significant clusters found for cross-plane decoding. A strong significant difference was also found (p<.001, cluster window = 64-1000ms).

Figure 16

Within and Cross Decoding for Session 2, averaged over Task 1 and 2 (train on old stimuli from planes 1/5, generalise to new stimuli from plane 3)

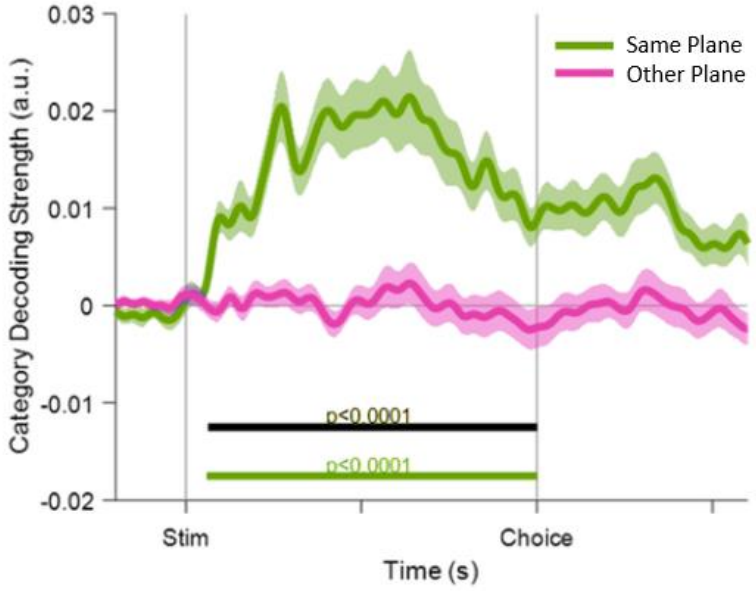


Figure 16. Within- and cross-plane decoding in Session 2 for planes 1, 3 and 5. A highly significant presence of within-task (p<.001) and category difference decoding (p<.001) was found. No significant clusters were found for cross-task decoding.

Finally, we explored within and cross-plane decoding in Session 2 for stimulus planes 1, 3 and 5, but using plane 3 as the training data (Fig. 17). Within-plane decoding was again found to be highly significant (p<.001, cluster window = 88-948ms). No significant clusters

for cross-plane decoding were found, and two significant clusters were found for difference between within- and cross-plane decoding (p=.005, cluster window = 248-649ms; p=.002, cluster window = 683-956ms).

Figure 17

Within and Cross Decoding for Session 2, Averaged over Task 1 and 2 (train on new stimuli form plane 3, test on plane 1/5)

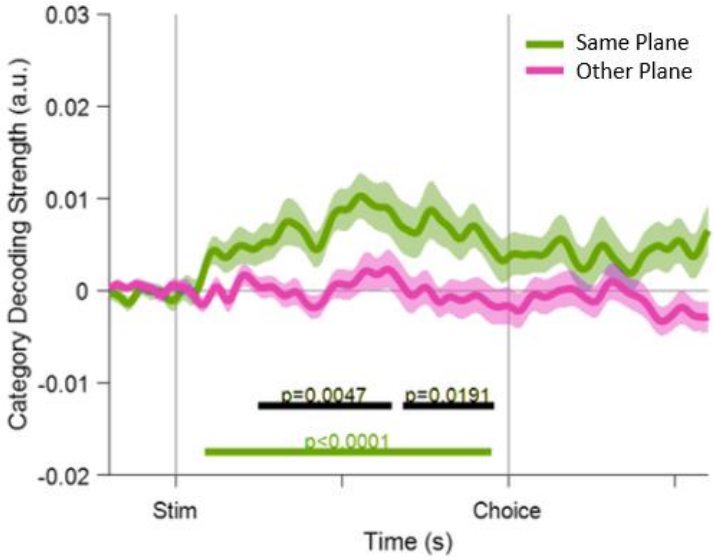


Figure 17. Within and cross-plane decoding in Session 2 for planes 1, 3 and 5, using plane 3 as training data. Significant within-plane decoding was found (p<.001). There were no significant clusters for cross-plane decoding, and two significant clusters for within- vs. cross-plane decoding difference (p=.005, p=.002).

These results provide evidence to suggest that while category membership can be decoded from the new stimuli in stimulus plane 3, it generalises to category coding of nearby old stimuli (planes 2 and 4), it does not cross-generalise to distant old stimuli (planes 1 and 5). There is a clear need to orthogonalise the two tasks when the new overlapping stimuli are

introduced, and it was initially hypothesised that the participants treat the new stimuli as a new task, meaning EEG patterns would not cross-generalise to old stimuli from the same task. However, our analysis showed that this was only true for the most dissimilar stimuli from the same task (i.e., from stimulus planes 1 and 5). It could be proposed that in Session 2, the orthogonal representations for categories of the new overlapping stimuli are warping the existing category representations for planes 2 and 4 (as these are physically more similar to the new stimuli). This could be validated by exploring cross-task generalisation separately for stimulus planes 1 and 5, which should successfully cross-generalise, and for planes 2 and 4, which should not cross-generalise as strongly due to the stimuli being closer to the interfering stimuli from plane 3. A reduction of cross-generalisation in Session 2 also implies that it is lower than in Session 1. To conduct these cross-task analyses, we split the EEG data by plane.

Cross-Task Generalisation Is Driven By the Most Dissimilar Stimuli in the Feature Space

We began by conducting within- and cross-task decoding in Session 1 (as in Fig. 7), but only for stimuli from planes 1 and 5 (Fig. 18 – note that the figure legends for Figs 18-21 erroneously labels the within- and cross-task conditions as within- and cross-plane). Both within-task (p<.001, cluster window = 44-1000ms) cross-task decoding were significant (p=.002, cluster window = 344-884ms). As before, within-task decoding was significantly higher (p<.001, cluster window = 60-768ms).

Figure 18

Within and Cross-Task Decoding for Session 1, Stimuli Planes 1 and 5 (old stimuli)

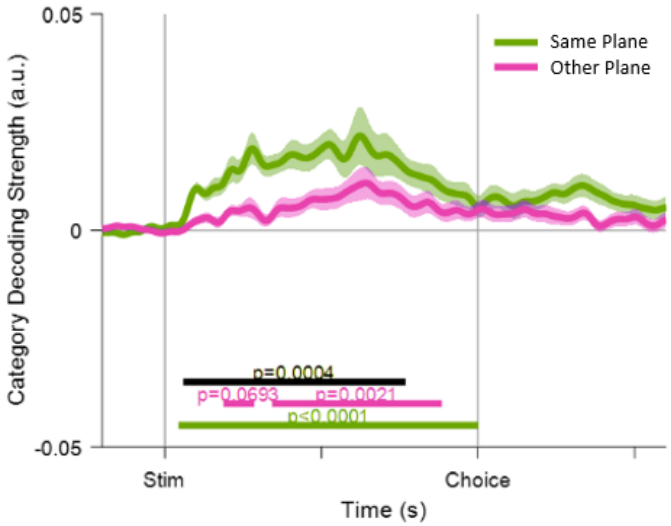


Figure 18. Within and cross-task decoding in Session 1 for stimuli planes 1 and 5. Within-task decoding (p<.001) and cross-task decoding (p=.002) were found to be significant, as well as a significant difference present (p<.001). Note the legend (Same/Other Plane) should read Within/Cross Task.

Within- and cross-task decoding for Session 1 was also conducted exploring stimuli planes 2 and 4 (Fig. 19). Within-task decoding was highly significant (p<.001, cluster window = 76-1000ms). However, cross-task decoding was not significant (p=.479), and a significant difference was found (p<.001, cluster window = 76-908ms). Therefore, even in Session 1 the stimuli closest to the centre of the feature space showed distinct categorical representations for the two tasks.

Figure 19

Within and Cross Task Decoding for Session 1, Stimulus Planes 2 and 4 (old stimuli)

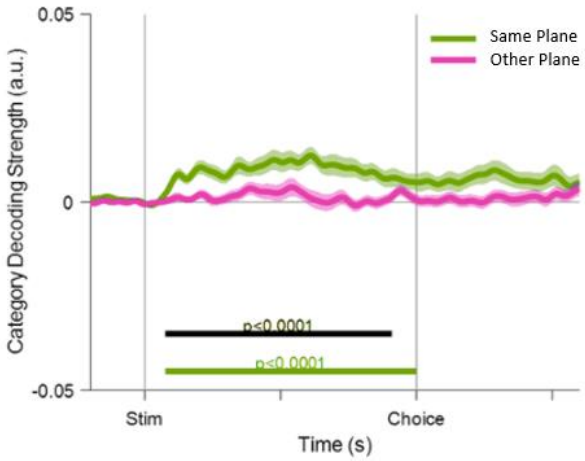


Figure 19. Within and cross-task decoding in Session 1 for planes 2 and 4. Within-task decoding was highly significant (p<.001) and significantly stronger than cross-task decoding (p<.001). However, cross-task decoding was not significant (p=.479).

We next explored the same effects in Session 2, starting with within- and cross-task decoding using stimulus planes 1 and 5 (Fig. 20). Within-task decoding was highly significant (p<.001, cluster window = 60-1000ms) and significantly stronger than cross-task decoding (p<.001, cluster window = 64-1000ms). Cross-task decoding was not significant but exhibited a trend (p=.064).

Figure 20

Within- and Cross-Task Decoding for Session 2, Stimuli Planes 1 and 5 (old stimuli)

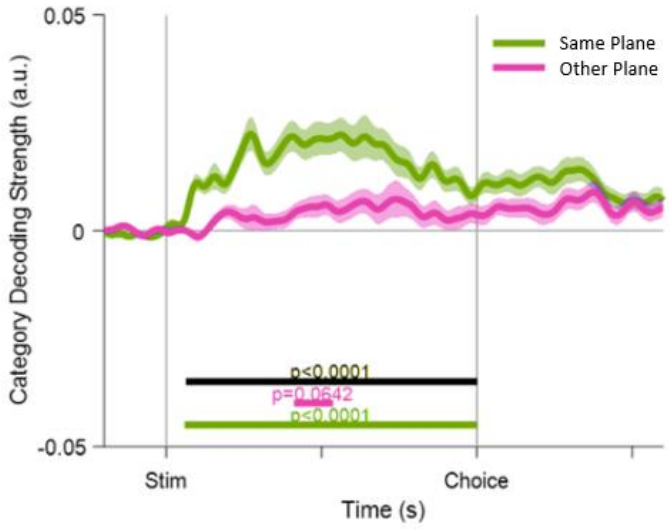


Figure 20. Within- and cross-task decoding in Session 2 for planes 1 and 5. Within-task decoding was statistically significant (p<.001) and significantly stronger than cross-task decoding (p<.001). However, cross-task decoding only trended toward significance (p=.064).

We also explored within and cross-task decoding in Session 2 for planes 2 and 4 (Fig. 21). Again, we found only within-task decoding (p<.001, cluster window 84-1000ms) but no cross-task decoding, with significantly stronger within-task decoding (p=.0017, cluster window 100-701ms; p=.032, cluster window = 743-940ms).

Figure 21

Within- and Cross-Task Decoding for Session 2, Stimulus Planes 2 and 4 (old stimuli)

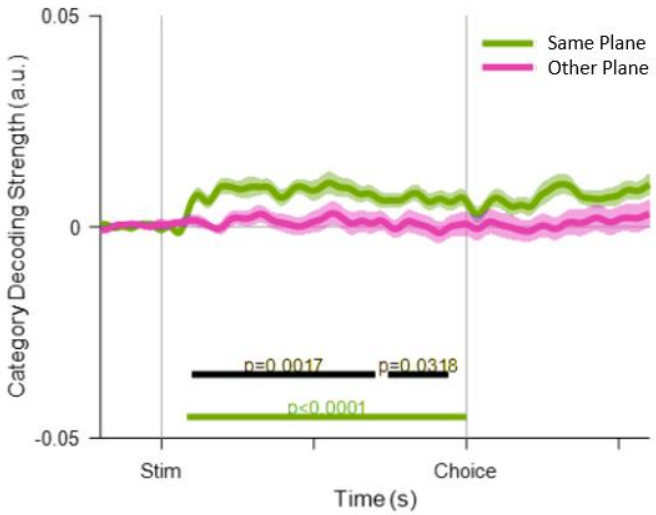


Figure 21. Within- and cross-task decoding in Session 2 for planes 2 and 4. Within-task decoding was statistically significant (p<.001) and significantly stronger than cross-task decoding (p=.0017). Cross-task decoding was not significant (no candidate clusters).

Subtracting decoding of the irrelevant category boundary largely confirmed this pattern of results (Suppl. Figs. S21-S24): Category decoding cross-generalised between tasks only in Session 1 and for stimuli from planes 1 and 5. Overall, this set of results confirmed our suspicion that task-generalisation was restricted to the most distant stimuli in the feature space. However, by training decoders on small subsets of the overall stimulus set, decoding in general may have become noisier (visible in the apparent reduction in within-task decoding), making it difficult to draw strong conclusions from this last set of analyses.

Discussion

The purpose of this study was to uncover whether neural representations of visual stimulus categories can be decoded using EEG, and how these representations adapt to interference between tasks. Our study contributes towards a novel understanding that categorical codes from distinct stimuli can generalise. Previous studies which have explored the mechanistic neural basis of how categorical codes generalise have focused on either primate research (Cromer et al., 2010; Freedman et al., 2001), or artificial neural networks (Chaisangmongkon et al., 2017). We aimed to provide insight into the neural basis of categorisation in humans and how they deal with interference. We hypothesised that representations would generalise in the first session where stimuli were non-overlapping and then become independent when conflicting stimuli were introduced in the second session.

Participants also performed better in Session 1 where only old stimuli were present, compared to Session 2 where overlapping stimuli were introduced, suggesting categorising these overlapping stimuli was more cognitively demanding. However, performance was also poorer in Session 2 for the old stimuli despite having extensive practice on the task and stimulus set. One possibility is that the continued use of a multitasking representation in Session 2 led to conflict which reduced behavioural performance.

Our main analysis was cross-task category decoding in which we trained a decoder on the data from Task 1 and tested it on the data from Task 2 (and vice versa). If both tasks used the same neural activity pattern to discriminate between categories (multitasking activity), then this should manifest in generalisation across tasks. However, if the different tasks rely on independent neural activity patterns, then the decoding should not generalise. In Session 1, category-specific patterns generalised across tasks, suggesting multitasking neural populations represented the two categories in both tasks. We speculate that in Session 1 participants reused the same two neural populations reflecting the two categories for each

task. This supports findings from both Cromer et al. (2010) and Fitzgerald et al. (2011) who demonstrated that neurons are able to multitask and represent multiple category rules, similarly to our results.

In Session 2, we introduced new stimuli which were shared across tasks with the aim of inducing conflict to potentially be resolved by orthogonalising categorical neural patterns. For the new overlapping stimuli found only in Session 2, cross-task decodability was not found, suggesting that these neural representations were independent from one another. This supports our hypothesis of representations becoming independent when conflicting stimuli were introduced in the second session. We suggest that these independent representations were present due to the conflicting overlapping stimuli creating interference. This aligns with evidence from Roy et al. (2010) who found independent neural populations for categories in a task employing orthogonal category boundaries over a shared stimulus set, meaning different neurons represented each category in the two tasks. Roy et al. (2010) suggested that when task demands are high due to overlapping category schemes, neurons become more independent in an attempt to reduce this interference. However, it is important to note that in our task the category decoding was no stronger than the decoding of an irrelevant category boundary, meaning that our apparent category decoding on this stimulus set may have been driven in large part by perceptual differences between stimulus categories. Nonetheless, participants were able to perform this task in the absence of strong category decoding. This may highlight the limits of EEG for resolving category-specific codes distinctly from low-level perceptual codes.

However, cross-task decodability for the old stimuli was also found in Session 2. This suggests that participants continued to use these same representations from Session 1 in Session 2 for the old stimuli, meaning multitasking representations were present. This was not expected as both tasks in Session 2 contained old stimuli intermixed with the new

overlapping stimuli, suggesting some type of conflicting interference would be found. We thought the brain would try to prevent interference by creating independent representations and apply these also to old stimuli. Persistent representations may have been found due to the non-overlapping condition being learned first. This supports Chaisangmongkon et al. (2017) findings of the brain's flexibility and adaptability as they found neural representations were successfully reused in artificial networks, with our results mirroring this finding but in humans. This suggests that new category-selective representations may not be required for each new categorisation task.

Multitasking representations may have been carried forward from Session 1 to Session 2 because of session order. In Session 1 participants completed the tasks with only non-overlapping stimuli, before being introduced to overlapping stimuli in Session 2. For future research, this may be counterbalanced to understand whether the representations would change depending on which session was initially completed. If the new, overlapping stimuli were introduced in the first session, this might result in all stimuli (including the old, non-overlapping) being categorised with separate neural populations and so no cross-generalisation occurring to reduce the risk of miscategorisation. Also, the apparent presence of independent neural populations for the overlapping stimuli in the second session may be a result of the demands of the task. As the second session was more cognitively demanding due to the presence of these new, previously unseen stimuli which presumably created conflict in the already drawn neural category representations, their representation may have gradually become independent over the course of the second session. By contrast, new stimuli that do not overlap may have been more easily integrated into existing categorical representations. In addition, exploring the spatial locations of this categorisation process via fMRI would further provide insight into this mechanism and the neural representations involved. Multivariate analyses could determine whether neural similarity across tasks reflects shared perceptual

features in early visual cortex, or more abstract category representations in higher-order areas. This would clarify whether reduced cross-generalisation occurs due to changes in perceptual coding, higher-level categorical coding, or top-down control mechanisms which modulate how sensory regions represent task-relevant information.

As the continued cross-task generalisation for the old stimuli in Session 2 despite the presence of the overlapping, interfering stimuli was unforeseen, we further investigated this by analysing generalisation of neural codes between old and new stimuli within a task. These analyses suggested that category-selective representations for the new overlapping stimuli are partially neurally distinct (but somewhat overlapping with perceptually similar old stimuli): when decoding using training data from the old stimuli and testing on the new overlapping stimuli, generalisation was successful from the old stimuli adjacent to new stimuli in feature space, while there was no generalisation from the more distant old stimuli. This reduced cross-generalisation for the stimulus planes at the ends of the feature space suggests a gradual shift in category-selective patterns across the feature space.

One possibility is that old stimuli at the far edges of the feature space used a shared category-selective pattern across tasks, but that the category patterns gradually warped as they approached the centre of the feature space, where category representations were orthogonalised to avoid interference. Indeed, upon reanalysis, strong cross-task generalisation appeared to be limited to the stimuli from the edges of the feature space (stimulus planes 1 and 5).

Our results are further supported by behavioural literature which shows a performance deficit when categorising the same stimuli for multiple rules. Literature has shown task performance to deteriorate when stimulus-response mappings are flexibly switched, particularly when stimuli are involved in competing categorical schemes. A classical ‘task

switching' cost is also shown to manifest slower reaction times and reduced performance, which may have proven to be involved in this experiment when participants were forced to switch between categorisation rules (Yeung et al., 2006). This has also been found in paradigms where the same stimuli are reused under different category rules despite persistent practice, suggesting participants are not simply forming associations between the stimulus and category, but task-specific rules (Dreisbach et al., 2007). The significantly poorer performance found in Session 2 for the new stimuli is consistent with this pattern, suggesting that maintaining and selecting categories for multiple tasks creates an additional cognitive demand.

Our findings also emphasise the brain's ability to adaptively code depending on the context of the task, particularly when reusing category schemes under changing task demands. Duan et al. (2024) used MEG to demonstrate when participants categorise the same stimuli for different tasks, the brain is able to transform high-dimensional sensory input into task-relevant representations. This suggests the neural representation of the stimuli is not fixed and can be reconfigured depending on which categorisation rule is active. In our study, we found the new stimuli in Session 2 to form independent neural representations.

Recent computational work from Flesch et al. (2023) also provides important insight into how humans categorise overlapping stimuli. Flesch et al. (2023) developed a neural-network model where tasks were learned on separate stimulus sets and the network developed representations for each task. This means that when learning these separate stimulus sets, the current task was implied by the stimulus and did not need to be separately encoded. By contrast, when the same stimuli were used for both tasks, a separate mechanism was necessary to identify which categorisation rule to apply, which produced orthogonal, task-specific representations to prevent interference between conflicting rules. In Session 1 of our study, participants learned the category boundaries on separate stimulus sets and so the

context was implicitly bound to which stimuli they saw, allowing for efficient categorisation. However, in Session 2, when the new, overlapping stimuli were introduced, the 'context' became flexible, meaning a gating mechanism would be required to identify which categorisation rule to apply. Our data suggests the new overlapping stimuli failed to cross-generalise across tasks and used orthogonal, task-specific representational subspaces to avoid interference. Interestingly, the old, non-overlapping stimuli in Session 2 still displayed cross-generalisation, suggesting their representations did not require re-gating and remained flexible despite being mixed with the new stimuli. This could suggest a mixed strategy where the representations were used, and gating only occurs when necessary.

There is also evidence to suggest category learning reshapes perceptual and neural representations in the visual cortex. Using fMRI, Folstein et al. (2013) demonstrated that after participants learned to categorise stimuli, 'neural discriminability' (reduced adaptability) increased in the visual cortex and became more sensitive to variations in shape relevant for categorisation. Bougou et al. (2024) also recorded spiking activity in the lateral occipital complex and showed that despite the neural representations remaining predominantly 'shape'-feature focused, they also found category-specific encoding. Linear decoders were also successfully able to classify stimulus category, demonstrating that perceptual and category learning modify the structure of neural representations within the visual cortex.

We demonstrated that neural representations underlying visual categorisation in humans are flexible depending on task demands. When category-learning involved the old, non-overlapping stimulus sets, the neural representations were able to generalise across tasks demonstrating a shared, multitasking representation. However, when the stimuli appeared in competing categorisation tasks, category-selective patterns were forced to reformat and create independent representations to mitigate interference. This adaptability suggests the brain is able to reuse stable representations, when possible, but is forced to orthogonalise when faced

with interference which can degrade performance accuracy. This strategy may offer the most efficient balance between flexibility and reusability to conserve resources depending on the task demands. These results contribute to a growing literature which highlights that the human brain is dynamic when approaching categorisation and enables us to face new situations and environments in rapidly and adaptively.

Chapter 3 – Exploring Dual Task Interference in Visual Working Memory

Chapter Summary

Dual-task interference arises when two tasks compete for shared cognitive resources, resulting in impaired behaviour (dual-task costs). Although evidence from human and non-human primate studies suggests interference occurs when multiple tasks rely on overlapping neural populations, either during task execution or in some cases during working memory maintenance, many questions remain unresolved. First, many studies have confounding dual-task demands with increases in overall working memory load, making it unclear whether these costs truly reflect task competition or capacity limits. Second, prioritisation has been shown to improve performance within single tasks, but it is not known whether similar prioritisation occurs during multiple tasks. Third, although extensive practice has been proposed to reduce dual-task cost, it is unclear whether short-term practice can improve the ability to manage these competing representations.

Motivated by these gaps in the literature, we conducted three behavioural experiments to determine whether dual-task costs persist despite controlling for working memory load, whether successful performance depends on dynamic prioritisation of the relevant information, whether this can be reduced with practice. No dual-task costs or prioritisation effects were found once load was controlled, although prioritisation did emerge in a single task (experiment 3). This suggests dual-task costs to reflect memory load rather than true working memory competition between tasks.

General Introduction

When conflicting streams of information are processed at the same time in dual tasks, this generates dual task interference (DTI, Kahneman, 1973). As both tasks draw from the same cognitive resource, this interference decreases accuracy and increases response times

compared to completing the tasks individually (known as dual task cost, DTC, Pashler, 1994). As we often need to dual-task in our daily lives, it is important to know not only what causes this interference, but also whether we can reduce it. Dual task costs usually arise when executing two non-automatic tasks at the same time. This cost appears to arise from reliance on a shared limited resource (Musslick & Cohen, 2021). Alternatively, dual task costs can also arise when two tasks are executed sequentially but require simultaneous maintenance of information in working memory. In this case, the cause of the dual task cost still appears to be interference, but between the representations in the same limited capacity WM store (Fougnie & Marois, 2009).

The study of dual task interference on non-human primates has provided fundamental insight into DTC. Recent behavioural studies suggest that humans and animals exhibit DTI similarly, meaning animal studies can provide insight into how to overcome this interference (Basile & Hampton, 2013). Watanabe and Funahashi (2014) explored working memory-based dual task costs and speculated that the shared resource might be mnemonic representation in dorsolateral pre-frontal cortex. They recorded single neuron activity from the dorsolateral prefrontal cortex of monkeys performing a dual task. The dual task consisted of concurrent spatial attention and spatial working memory tasks. On each trial, a spatial location was cued as a future saccade target and had to be retained across a delay (WM task). Simultaneously, a different location had to be covertly attended to detect a brief colour change (attention task). Importantly, the attention probe occurred before the cue to execute a memory-guided saccade, meaning the monkeys had to prioritise the attention task whilst maintaining the saccade goal. The monkeys exhibited a dual task cost – their response times were slower in the dual-task than in single-task conditions. The authors argued that this was direct evidence of a shared cognitive capacity limitation, and that dual task interference occurred due to two tasks accessing this finite resource which exceeds the total resource

available. Also, these results suggest that DTI arises from competitive interactions between task processing caused by overlapping neural populations. Importantly, this demonstrates that similarly to humans, monkeys also exhibit limited information processing when performing dual tasks. However, this framework was not entirely supported by their data. During the attention task execution phase, WM-related information encoded in dlPFC population activity was reduced, but it reappeared once the attention task was executed and monkeys prepared for the execution of the WM task. Their conclusion was that dual task interference can be minimised by temporarily reducing activity related to the irrelevant task. How this information is retained for later reactivation is unclear, but one possibility is that activity-silent maintenance (Mongillo, 2008; Stokes, 2015) which allows for storage with minimal impact on behaviour or interference with the ongoing task (Buschman, 2021).

It is important to note that these monkeys underwent immense amounts of practice (or overtraining) when learning how to complete the tasks (as humans learn much faster, Mac-Auliffe et al., 2021), with 40 sessions being labelled as ‘quick’ for monkeys when learning a dual-task paradigm (behavioural procedure requiring performing two tasks simultaneously, Watanabe & Funahashi, 2015). It could be suggested that this ‘overtraining’ reduced interference between tasks and therefore decreased the dual task cost effect as the monkeys had become familiar with performing both tasks simultaneously. Importantly, this means that the reduction in task-irrelevant neural activity was also the result of overtraining and not representative of the neural representation of dual-task performance with less practice. This could suggest that these findings are specific to the way in which these non-human primates learn to strategise when completing dual tasks due to the extensive training period.

Previous studies shows that practice can substantially overcome dual task costs (Strobach, 2020). For example, Whitfield and Holdosh (2021) examined how practice reduces DTI using a speech and attention task. Participants in the limited practice group (3

practice blocks) were found to exhibit dual task interference for both the speech and visuomotor attention tasks, compared to participants in the extended practice group (15 practice block over two days) who exhibited little-to-none. Similarly, Agethen and Krause (2012) found that dual-task interference decreased only for a repeatedly practiced pairing of a motor sequencing task with a visuospatial working memory task, but not when the motor task was combined with a novel memory task. This suggests that the practice effects may be task-specific, rather than a general improvement in multitasking. Also, Schumacher et al. (2001) asked participants to perform dual task consisting of a visual-manual task and an auditory verbal choice reaction task. The visual task involved participants manually pressing a key associated with the position of circles presented, whereas the auditory task involved participants responding by saying one, two, or three depending on the pitch of three tones. In the dual task condition the stimuli for both tasks were presented simultaneously. Dual task costs were initially high, however, after extensive practice, were found to be eliminated. This suggests that practice enabled participants to shift from serial processing to a more coordinated response-selected strategy, although this may be specific to visual and auditory dual task situations. However, subsequent work has shown that elimination of DTC is not universal. Liepelt et al. (2011) replicated this study and found high levels of dual-task cost reduction after practice, but when attempting to generalise these findings to an alternative dual-task situation (visual-manual task and an auditory-pedal task), dual task costs did reduce but remained high after practice. These studies provide sufficient evidence to suggest that practice may be a way to eliminate or at least reduce dual task interference.

Although substantial practice has been found to reduce DTC, the mechanisms underlying this improvement remain contested. An influential account from Ruthruff et al. (2003) suggests that ‘extensive practice’ (approx. 2 hours practice, Levy & Pashler, 2001) reduces the resource demands of tasks, and at low levels of practice tasks can only work one

at a time (but this changes at high practice levels). Also, Ruthruff et al. (2003) suggest at low practice levels, individuals schedule tasks in a single channel order, compared to with extensive practice where they learn a 'riskier' parallel scheduling strategy (Schumacher et al., 2001). Ruthruff et al. (2006) proposed that each performance of a task increases the association between the stimulus category and the response, allowing activation of the correct response without drawing on central cognitive resources. Many of the theories surrounding why low levels of practice impair dual task performance suggest that higher levels of practice result in better acquisition of task coordination skills (Strobach & Torsten, 2017). Despite the evidence suggesting that extensive practice can reduce dual task interference, it cannot be eliminated entirely (Ruthruff et al., 2006). Hazeltine et al. (2006) found large 'residual' dual task costs with specific pairings of input and output modalities (auditory-manual and visual-vocal). Overall, the literature indicates that practice can reduce DTI, but it is unclear whether this reflects automatisation of individual tasks, reduced reliance on resources, improved cross-task scheduling, or a combination of these.

Relatively less explored are dual-task costs arising from sequential execution of two tasks that require concurrent storage of task-related information in working memory. Fougnie and Marois (2009) explored the effect of dual task interference with two separate visual working memory tasks (vWM). In a series of three experiments, they investigated whether DTI was the result of interference at the encoding, retrieval, or maintenance stage. Participants were asked to encode two visual arrays but only later instructed which one to retain, and the number of items in each array was manipulated to measure whether interference occurred because a second stimulus array needed to be encoded or merely due to overall capacity limitations. Interference was only present when the total memory load across both arrays exceeded 3-4 items (typical vWM capacity). As the arrays were presented either sequentially or simultaneously, they were able to observe whether interference between

encoding and maintenance stages would impact performance independently of overall WM load (i.e., when the total load was within the participant's WM capacity) and found performance to be the same for both conditions. This suggests interference arises purely at the maintenance stage and only when overall load exceeds the capacity limit. Response order was also manipulated to see whether retrieval of one memory set would affect maintenance of another, but this also had no effect, confirming that interference was the result solely of overall load exceeding capacity in the maintenance phase. This study is crucial as it demonstrates interference arises from limitations on mnemonic maintenance mechanisms, rather than encoding or retrieval of one array drawing resources away from the maintenance of the other array due to attentional overlap of maintenance and encoding/retrieval. It is important to note that the effect of practice on dual task interference with two visual working memory tasks has not yet been explored.

Overall, the human literature on dual-task interference consistently shows that in dual tasks requiring concurrent task execution interference arises from performing multiple tasks simultaneously, while in tasks requiring concurrent maintenance interference arises primarily from the increase in overall mnemonic load (Fougnie & Marois, 2009). While attentional bottleneck theories dominate the field of DTI, studies using visual WM paradigms could show that this interference also arises when mnemonic load exceeds capacity limitations. Extensive practice is also suggested to reduce dual task interference (Ruthruff et al., 2006; Schumacher et al., 2001; Strobach, 2020), but these are thought to depend on specific task situations, with minimal practice leading to no significant improvement (Ruthruff et al., 2003). The ability to overcome dual-task interference has been linked to the development of parallel scheduling and task automatisation. Despite this, dual-task costs are found to still be present even in optimal conditions and after extensive practice (Hazeltine et al., 2006). More

research needs to examine how task structure and learning influence our ability to dual task, particularly within visual working memory.

Watanabe and Funahashi (2014) concluded DTI to partially be minimised by temporarily reducing activity related to the irrelevant task. However, it is unclear how this information is retained for later reactivation. One possibility is 'activity-silent' maintenance (Stokes, 2015), which may allow for storage with minimal impact on behaviour or interference with the ongoing task (Kamiński & Rutishauser, 2020). Whether a similar mechanism is responsible for successful dual task scheduling in humans is unknown. We sought out to explore this phenomenon, and also to answer several questions which the study by Watanabe and Funahashi (2014) left open and we sought to clarify in a set of behavioural experiments.

Firstly, the authors calculated dual task costs by comparing dual with single tasks. However, this confounded dual task with WM load as the dual task condition required keeping two locations in mind, instead of one. The observed dual task cost could therefore be more simply described as a memory load effect. As mentioned above, other work in humans (Fougnie & Marois, 2009; Klingberg T, 1998) has identified maintenance as the likely bottleneck in performing two WM tasks concurrently, making this explanation more likely. We sought to test whether WM dual task costs arise when controlling for memory load.

Secondly, if dual task costs arise primarily due to increased memory load, their mitigation may be due to more successful prioritisation of the relevant memory item. State-based models describe working memory as having varying levels of activation, supporting dynamic prioritisation. For example, Cowan's Embedded-Processes Model suggests working memory to be a set of long-term memory representations which vary in their activation, and the focus of attention only allowing for a single item to be processed efficiently (Cowan,

1999). Oberauer (2002) extends this model by narrowing the framework to suggest a more specific view of how prioritised items are selected and maintained. Importantly, this could explain the pattern of results by Watanabe and Funahashi since several studies have shown that prioritised and unprioritised WM items are stored in different neural patterns, seemingly to minimise interference. One possible mechanism could be activity-silent storage of the unprioritised item (Rose et al., 2016; Wolff et al., 2017), although direct evidence for this mechanism is still being sought. Alternatively, information for both the prioritised and unprioritised tasks could be stored via active firing but in orthogonal or minimally overlapping activity subspaces (Panichello & Buschman, 2021; Xie et al., 2022). Re-examining the Watanabe and Funahashi (2014) results with this in mind shows that there was residual activity related to the currently unprioritised task – whether this was stored in an orthogonal subspace is unknown. Importantly, there is still no evidence for this mechanism in humans. Some work suggests that unprioritised information is still decodable from neural activity patterns in humans, and that its activity patterns overlap with those of prioirtised items (at least partially, Iamshchinina et al., 2021; Muhle-Karbe et al., 2021; Paluch et al., 2025).

Thirdly, monkeys underwent extensive practice (months). This may have fundamentally altered how they performed the dual task and minimised the dual task costs. While there are no studies on practice effects on a dual working memory task (in humans or monkeys), the broader dual-task literature suggests that task interference can be significantly reduced (but not always entirely eliminated) with extensive (hours to days) practice. Since most studies showing activity orthogonalization in WM are based on monkey studies, it is unclear whether this is achieved only with practice. By contrast, WM prioritisation in humans occurs quickly and is robustly observed (Souza & Oberauer, 2016) in a single relatively short

session (typically 1 hour). Whether it requires or improves with practice has not yet been studied.

We therefore sought to address three open questions relating to WM-based dual task costs in humans. Does it exist when controlling for WM load? Does a reduction in DTC rely on dynamic prioritisation of relevant information at the right time? Does this change with practice? To test this, we modified a visual working memory task into a dual WM task requiring dynamic switching between two similar (and therefore likely interfering) tasks. Participants performed a dual visual working memory task involving remembering the location, orientation, and colour of tilted bars, presented sequentially in two arrays (as in Fougnie & Marois, 2009). Participants were asked to determine whether the probed item matched the orientation of the cued item, and in the dual trials, a second item from the other array was also probed. The experiment involved reverse response mapping for the second response, requiring a separate task configuration for the two WM tasks. In brief, across two experiments we observed no evidence for dual task costs once load was controlled. Interestingly, we also saw no evidence for dynamic prioritisation of the relevant task. In a third experiment, we sought to remove the dual task element to see whether dynamic prioritisation re-emerged. We indeed found this to be the case, with one possibility that dual task costs arise because they make prioritisation more difficult, possibly due to increased overall task load.

Chapter 3.1 – Dual-task Interference in Working Memory: Impairments in Temporal Prioritisation Despite Practice

Introduction

This study aims to address how practice reduces dual-task interference using two visual working memory tasks. Our task design was adapted from Watanabe and Funahashi (2014) who used a spatial attention task and spatial memory task in non-human primates. A key aspect of their design was that it did not differentiate dual tasking from an increase in working memory load. This meant that it was unclear whether dual-task interference arose from interference of the secondary task or an increase in memory load. Here we aimed to resolve this ambiguity by independently varying the load for both tasks, allowing us to test whether performance was lower in a dual vs a single task with the same load, and whether increasing the distractor load in a dual task had an additional effect on performance. Addressing this confound was a key motivation for the present study. In our experiment, participants completed a dual visual working memory task where they were asked to remember the orientation of coloured rectangular stimuli for two tasks and respond to two probes in sequence (one probe per task). This allowed for the simultaneous maintenance of working memory information for the two separate tasks but also allowed us to independently vary the memory load for each task to distinguish the load for the currently executed task from the combined load across both tasks. We also included single task conditions. This allowed us to test whether the dual-task condition produced interference once load was taken into account. Additionally, we tested whether any interference reduced with brief practice.

Relatively little work has explored dual-tasking using two working memory tasks, and no studies appear to have examined practice effects (Cocchini et al., 2002; Worden et al., 2016; rather than the well-researched dual-task studies which typically involve performing

two tasks simultaneously, Klingberg T, 1998). Many studies have however studied the effect of a secondary attention-demanding task performed in the retention interval of a working memory task (Ricker & Cowan, 2010; Vergauwe et al., 2009). The insertion of a secondary task reduces working memory recall, and the impairment scales with the amount of time (i.e., cognitive load) taken up in the retention interval by the secondary task (Barrouillet et al., 2004; Vergauwe et al., 2010). This is consistent with the dual-task cost arising because the secondary task prevents attentional refreshing of working memory contents during retention, leading to forgetting. These costs are not universally observed. Some work has failed to replicate this effect, such as Ricker and Vergauwe (2020) who failed to find a load effect in visual working memory when dual-tasking. The nature of working-memory based dual-task costs is therefore not completely resolved yet.

While these studies have not tested practice effects on dual task costs, the related phenomenon of prioritisation in working memory (in single tasks) has been studied extensively and may also shed light on whether practice is needed to reduce costs. Several studies have shown that participants can prioritise one item in working memory when it is cued for retrieval but then flexibly reprioritise a different item for a second response (e.g., Oberauer, 2002; Rerko et al., 2014). This process resembles dual-tasking in that it requires participants to quickly switch from one task-relevant representation to another. Under this re-interpretation, difficulties prioritising a second WM item after recalling a first item could be interpreted as a dual-task or switch cost. Unlike the extensive practice which is required to reduce dual-task costs in traditional paradigms, some research suggests that prioritisation in working memory tasks can require minimal practice as it is so robust, and that it can even be observable within a single session (Souza & Oberauer, 2016). Souza and Oberauer (2016) found that participants exhibited retro-cue benefits from the start of their experimental session despite not having training sessions and participants completing only 12 practice

trials. Berryhill et al. (2012) also suggest that participants are able to adopt a prioritisation strategy spontaneously, meaning that no practice is required. We therefore speculated that WM-based dual-task costs might also be reduced with minimal practice.

Our study aimed to understand the costs when attempting to prioritise one working memory task whilst maintaining another task in mind. We hypothesised that significant dual-task interference would be present, with this cost increasing with the WM load of the secondary task (which we refer to as distractor load). We also hypothesised that this dual-task cost would reduce with practice.

To pre-empt the results, we did not find significant dual-task interference in our experiment. Accuracy did not differ between single and dual-task conditions when accounting for overall memory load, suggesting participants were able to maintain information for two tasks as effectively as a single task (as long as the overall memory load was equivalent). Overall, we can conclude that there is no difference in accuracy when trying to maintain items for two tasks, compared to one task. We can also conclude that no practice effect on accuracy was found. Reaction times were significantly slower for higher target load conditions, suggesting that the increased demand, even within a single task, led to slower responses. We also found that practice partly improved reaction time, with a significant decrease in reaction time in the second half of the experiment. However, practice did not specifically improve performance in relation to distractor load. Therefore, practice did not reduce dual-task interference. We discuss why this unexpected null effect may have occurred. These findings suggest that dual-task costs in visual working memory may not occur as a result of attempting to manage two tasks simultaneously, but rather the overall demands due to memory load.

Methods

Design

This study explored the effects of practice on dual-task interference using a dual visual working memory task. Participants were asked to remember the location, orientation, and colour of tilted bars and after a delay, were probed on one of them with a test stimulus in the centre of the screen. Participants had to decide whether this item matched the orientation of the memory item. In the dual-task trials, a second item from the same array was probed afterwards. Importantly, the response mapping was reversed for the second response (e.g., Task 1: match= left-hand response and mismatch = right-hand response, Task 2: match = right-hand response and mismatch = left-hand response). This created a separate task configuration for the retrieval of the second item. Participants performed single or dual-task conditions. Additionally, we varied the number of stimuli presented on each trial independently for Task 1 and Task 2. Stimuli were presented in different colours for the two probe periods, allowing us to vary how many WM items could be tested by the upcoming probe (target load - relevant information participant must maintain) and how many could be tested by the other probe (distractor load – currently irrelevant information) between 1 and 2 items each on dual-task trials. On single task trials, the target load varied between 1, 2, and 4 items.

A within-subjects design was implemented with the independent variables of Distractor Load (0 = single-task, 1 or 2 = dual-task), Target Load (1 or 2 remembered stimuli, load 4 not analysed here), and Response (1 or 2). The dependent variables recorded were accuracy (measured by the ability to correctly identify whether the probe matched the memory stimulus), and reaction time (the time taken in seconds to respond to the probe). The experimental data were split into first and second half to examine practice effects.

Single Task

The single task condition involved an orientation change detection task in which participants encoded one, two, or four oriented coloured rectangles and had to maintain them until one item was probed. The probe matched one of the cued stimuli in colour, and either had the same orientation as the cued item (match) or was rotated 30° clockwise/counterclockwise (mismatch) and was presented centrally on the screen. Participants performed two different variants of the single task. The single tasks differed in the colour of the memory stimuli and in their response mappings, as for Task 1 participants responded using 'F' key for a match, and 'J' key for a mismatch, compared to Task 2 where the reverse mapping was used ('J' for mismatch, 'F' for match). Assignment of response mapping to tasks was counterbalanced across participants.

Dual-task

In the dual-task condition, stimuli from both tasks were presented together but were probed in sequence and always in the same order (Task 1 was probed first, then Task 2) at the centre of the screen. Across the single and dual-task conditions, two different stimulus colours were associated with each task, meaning that a stimulus of a given colour was only probed in one of the tasks. This allowed participants to anticipate which stimuli from a task would be probed first.

Participants

Twenty-five participants were initially recruited for this study, with four participants being excluded from the analysis due to low accuracy, resulting in twenty-one participants in the final sample (9 male, 12 female) aged between 18-53 years old (M = 22.67, SD = 8.12). Participants were recruited within the University of Nottingham as well as word-of-mouth.

All participants had normal or corrected-to-normal vision. The study followed the guidelines of the University of Nottingham's School of Psychology Ethics Committee.

Materials

This study was created using PsychoPy 2022.2.5 (Peirce et al., 2019). Participants completed the study using PsychoPy presented on an iMac in a quiet room at the University of Nottingham's School of Psychology or using a 13" MacBook Pro 2019 laptop. Both setups used QWERTY keyboard for recording the key responses.

Stimuli

The visual stimuli consisted of rectangles with a randomly generated orientation from 0° to 180 ° and 0.05, 0.25 in size (as a proportion of screen height). Up to four different coloured rectangles were presented on screen simultaneously, with each stimulus presented in a different quadrant of the screen at an eccentricity of approximately 0.28 (as a proportion of screen height). Stimuli could have one of 4 colours, with the colour indicating which task a particular item could be probed on (first or second). The colour mapping was consistent throughout an individual's study but was counterbalanced across participants. The RGB values for the colours used in this experiment were [(0.9588, 0.1863, 0.3294), (0.6059, 0.4961, 0.1059), (0.1804, 0.5588, 0.5490), (0.6961, 0.3922, 0.7196)].

Procedure

Participants were asked to perform a visual working memory dual-task (WM DT). Both dual and single task conditions were randomised within each experimental block.

Task Outline

Participants completed 20 blocks in total with 24 trials per block. Every trial began with a fixation period of 1000ms where participants fixated on a white dot in the centre of the screen (Fig. 1, see S1 and S2 for all single/dual-task combinations). In the dual-task

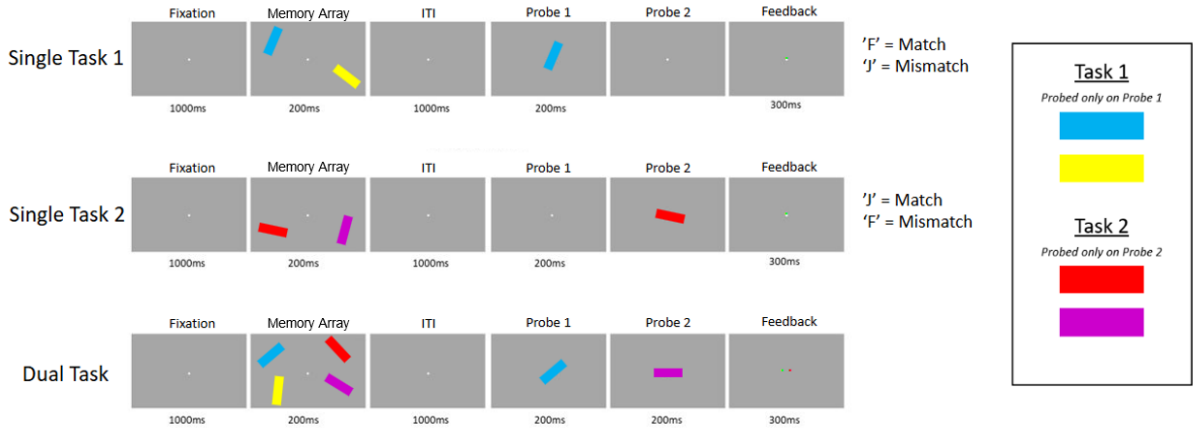
condition, the array of memory stimuli was presented for (200ms). After the memory delay (1000ms), the first probe screen would appear in which one probe stimulus (for Task 1) was presented centrally and matched the colour of one of the Task 1 memory stimuli. It either matched the orientation or was rotated 30° clockwise or anticlockwise (mismatch). After the first response and inter-response delay of 750ms, a second probe stimulus appeared (for Task 2). As different stimulus colours were associated with each task, a stimulus of a given colour was only probed in one of the tasks allowing for the participant to anticipate which stimuli would be probed first and second. This resulted in participants having to switch between the two response mappings in every dual-task trial. At the end of each trial feedback was provided with two feedback dots appearing next to each other for 300ms (left dot corresponding to probe 1 response, and right dot corresponding to probe 2 response) and turning green (correct response) or red (incorrect).

For the single task conditions, one, two, or four different coloured stimuli with random orientations were presented for 200ms. The encoding for the stimuli was the same except all stimulus colours corresponded to one task. Participants had to remember the orientation of the stimuli, and after the memory delay of 1000ms, one stimulus was probed. In dual task trials, one task (e.g., specific response mapping) was always probed first and the other second. Therefore, the delay between the encoding and response for Task 2 was always longer than for Task 1. Importantly, the response to Task 2 was always made after a first response to the other task had been given. In Task 1 single-task trials, the trial ended after the first response. However, to better equate Task 2 single-task trials with their dual-task counterpart, participants made a quick response (by pressing the space bar) to the appearance of a red fixation dot first. This dot appeared only on Task 2 single-task trials and at the time when the probe for Task 1 normally appeared. After the 750ms inter-response interval, the probe to Task 2 then appeared.

Participants received minimal practice (2 blocks consisting of 6 trials from each task) to reduce practice effects before the onset of the experiment. Participants completed 20 blocks in total consisting of 24 trials per block for a total of 480 trials. Halfway between every block and at the end of each block, participants were able to take a break and received feedback on their average accuracy and reaction time.

Figure 1

Example Task Outline for Single and Dual-task Conditions



Note. Task outline for an example trial for Single Task 1, Single Task 2, and Dual-task conditions. For Single Task 1 and Task 2, participants were asked to remember the orientation of different coloured stimuli and then respond whether the probe was a 'match' or a 'mismatch'. In this example, the blue and the yellow stimuli are tied to Single Task 1 whereas the red and pink stimuli are tied to Single Task 2. Therefore, the Single Task 1 has 2 target cues and 0 distractors, as does Single task 2. The Dual-task example shown above has 2 targets and 2 distractors, but the number of targets and distractors on any given trial could vary independently.

Results

Dual-task interference was determined by comparing performance on single task trials with dual-task trials with the same overall memory load. Task difficulty is determined by the Target Load (1 or 2 stimuli), whereas task type is determined by Distractor Load (0 = single task, 1 or 2 = dual-task). Target Load and Distractor Load descriptive statistics for Accuracy (Table A1) and Reaction Time (Table A2) are in the appendices.

No Significant Difference in Accuracy Across Single and Dual-task Conditions

In our experiment we wanted to observe whether visual working memory dual-task costs arise as a result of attempting to execute two tasks, or whether this is due to holding more items in mind. If the DTC were present due to increased load, then we would expect no performance difference between the single and dual-task, meaning only the overall load would influence the accuracy. This would result in the effect of target load being equivalent to the effect of distractor load. If the DTC is due to the cost of executing two tasks, then the effect of distractor load should be significantly larger than target load. Alternatively, if the working memory system is able to prioritise the currently task-relevant memory representation, then the effect of distractor load should be lower than the effect of target load.

In order to test for effects of target load and distractor load, we conducted a 2 x 2 x 3 within-subjects ANOVA for accuracy against Response (1, 2), Target Load (1, 2), and Distractor Load (0, 1, 2). Accuracy was higher on the first Response ($F(1, 20) = 81.62$, $p<.001$, $\eta_p^2 = 0.803$), for the lower Target Load conditions ($F(1, 20) = 22.08$, $p<.001$, $\eta_p^2 = 0.523$) and lower Distractor Load conditions ($F(2, 40) = 4.66$, $p = .016$, $\eta_p^2 = 0.104$). This shows that the overall load of the task is important and items from both tasks compete for shared working memory resources. Also, the effect size of target load was larger than that of distractor load. If dual-task costs were simply due to load effects, then the Target Load and

Distractor Load should have equivalent effects. This suggests prioritisation to protect the relevant items, as target load impaired performance more than distractor load. A significant interaction was found between Response and Distractor Load ($F(2, 40) = 3.84$, $p = .03$, $\eta_p^2 = 0.088$), suggesting distractor load impacted accuracy more for the second response. A significant interaction for Target Load and Distractor Load ($F(2, 40) = 3.49$, $p = .04$, $\eta_p^2 = 0.08$) was also found, although no interaction effect was found between Response and Target Load ($F(1, 20) = 0.617$, $p = .441$, $\eta_p^2 = 0.03$). A three-way interaction effect between Response, Target Load, and Distractor Load was also found ($F(2, 40) = 3.51$, $p = .04$, $\eta_p^2 = 0.081$), suggesting the influence of the target and distractor loads differed between responses.

Crucial to our experiment, we tested the relative effect of Distractor Load on accuracy by comparing conditions with an equal number of items held in working memory but distributed differently across the tasks. The alpha level was Bonferroni-corrected accordingly (adjusted to 0.025). We found when comparing T2D0 (target load = 2, distractor load = 0) and T1D1 (both having an overall WM load of 2, averaged over response 1 and 2), results showed no significant difference ($t(20)=0.902$, $p=.378$, $d = .152$). We also compared T1D2 and T2D1, which also showed no significant difference ($t(20)=1.883$, $p=.074$, $d=.213$).

We next calculated Bayes Factors using Bayesian paired t-tests (Cauchy prior of 0.707) to test for a genuine null effect between the pairs. We found evidence in favour of a null effect for T2D0 vs T1D1 in Response 1 (0.232) and T1D2 vs T2D1 (0.234) for Response 2, and an inconclusive effect for T2D0 vs T1D1 (0.592) in Response 2. While there was evidence for a true effect of T1D2 vs T2D1 in Response 1 (7.417), performance was better in the condition with the higher distractor load (T1D2), indicating successful prioritisation of only the relevant target item.

Reaction Time Increased as Target Load Increased

We also investigated the effect of response, target load, and distractor load on Reaction Time. 2 x 2 x 3 within-subjects ANOVA was also conducted to explore the effects of Response (1, 2), Target Load (1, 2) and Distractor Load (0, 1, 2). Reaction time slowed as Target Load increased ($F(1, 20) = 33.74$, $p<.001$, $\eta_p^2 = 0.628$), but there was no effect of Response ($F(1, 20) = 0.167$, $p = .688$, $\eta_p^2 = 0.01$) or Distractor Load ($F(2, 40) = 1.17$, $p = .322$, $\eta_p^2 = 0.028$). A two-way interaction effect between Response and Distractor Load was also found ($F(2, 40) = 6.77$, $p<.001$, $\eta_p^2 = 0.145$). The interaction was likely driven by the increase in reaction time on the second response in the single task condition with two target items (i.e., T2D0). By contrast, increases in distractor load otherwise led to modest increases in reaction time. There was no interaction between Response and Target Load ($F(1, 20) = 0.512$, $p = .483$, $\eta_p^2 = 0.025$), but there were trend-level interactions between Target Load and Distractor Load ($F(2, 40) = 3.08$, $p = .06$, $\eta_p^2 = 0.07$), and Response, Target Load and Distractor Load ($F(2, 40) = 2.70$, $p = .08$, $\eta_p^2 = 0.063$). These may have also been driven by the increased response time on T2D0 for response 2 (compared to T1D0 on response 2 and T2D0 on response 1).

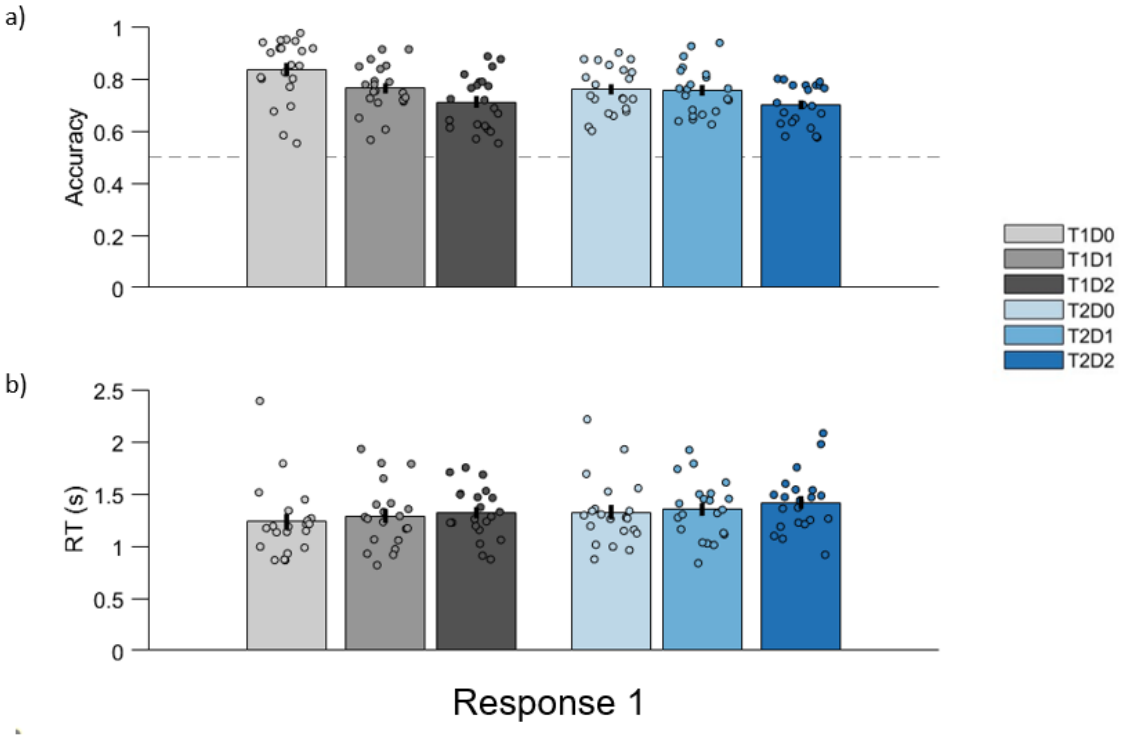
We then compared dual-task costs on reaction time by comparing conditions with an equal number of items held in working memory. If dual-task costs were observed in reaction time, but not accuracy, this could suggest participants attempted to create a trade-off to preserve their accuracy by slowing their responses in an attempt to avoid errors. If dual-task interference was present we would expect both accuracy and reaction time to be impacted, but only finding reaction time costs may also suggest that working memory capacity was not exceeded, as participants were able to maintain the items, but the attentional control processes involved struggled to process both tasks efficiently (e.g., Barrouillet et al., 2004).

Firstly, we conducted a paired samples t-test comparing the reaction time for T1D1 and T2D0 (overall load of 2). We found a significant difference ($t(20)=-5.08$, $p<.001$, $d=.462$), with T2D0 (M= 1.42, SD= .355) having a significantly larger reaction time than T1D1 (M= 1.27, SD= .275). When comparing T1D2 and T2D1 (overall load of 3), no significant difference ($t(20)=1.64$, $p=.0.117$, $d=.076$) was found.

Bayesian paired t-tests revealed weak evidence in favour of a null effect for T2D0 vs T1D1 in Response 1 (0.406), and T1D2 vs T2D1 (0.311) for Response 2. However, results suggest very strong evidence for a true effect of T2D0 vs T1D1 in Response 2 (257.13), and moderate evidence for T2D2 vs T2D1 in Response 1 (3.447).

Figure 2

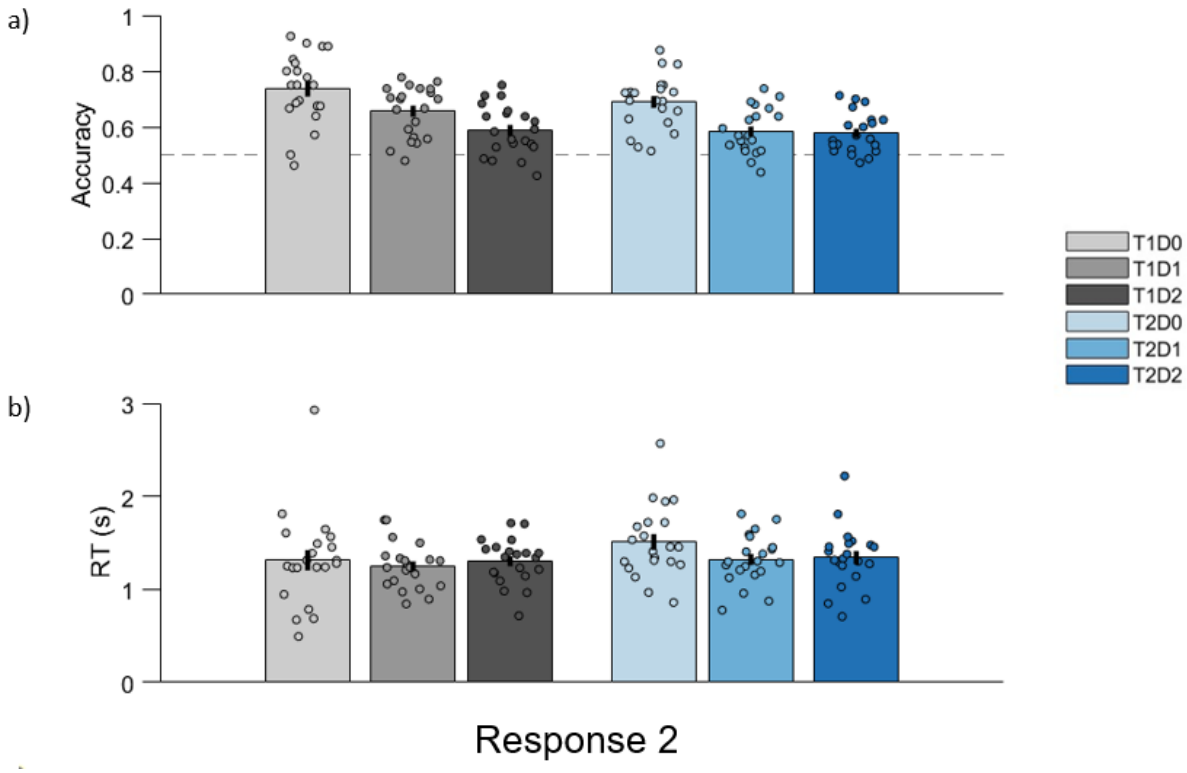
Average Accuracy and Reaction Time (s) for All Target and Distractor Conditions in Response 1



Note. Average accuracy (a) and reaction times (b) of different target and distractor load conditions in Response 1. The different bars illustrate the six different conditions involved in each task with T representing target load, and D representing distractor load (D0 = single task). Increasing distractor load decreases mean accuracy (a) but increases response times. Error bars show the standard error. Dots represent individual participants.

Figure 3

Average Accuracy and Reaction Time (s) for All Target and Distractor Conditions in Response 2



Note. Average accuracy (a) and reaction times (b) of different target and distractor load conditions in Task 2. The different bars illustrate the six different conditions involved in each task with T representing target load, and D representing distractor load (D0 = single task). Increasing distractor load decreases mean accuracy (a) but increases response times. T2 D0 noticeably has the highest reaction time (b) (possibly due to small sample size). Error bars show the standard error.

Practice Did Not Improve Accuracy

To identify a learning effect, the experimental data were split into two halves to allow us to compare participant performance from the start of the experiment to the end of the experiment. This would allow us to see whether a learning effect occurred. A 3 x 2 x 2 x 2 within-subjects ANOVA was conducted on Distractor Load (DL, 0, 1, 2), Experimental Half (1,2), Response (1,2), and Target Load (TL) (1,2). There was no significant difference in participant accuracy in the first half of the experiment compared to the second half of the experiment ($F(1,20)=2.676$, $p=.117$, $np^2= .118$). There was no interaction found with any of the other factors (all $p>.120$).

We also ran post-hoc comparisons using paired samples t-tests to test whether practice reduced dual-task interference. We applied a Bonferroni corrected alpha level of .0125. We calculated the dual-task cost in Half 1 for T1D1 vs T2D0 ($M= .027$, $SD = .093$) and compared this to the corresponding cost in Half 2 ($M= .002$, $SD= .106$) and found no effect ($t(20) =-.881$, $p=.389$), suggesting no reduction in dual-task cost with practice. Similarly, no effect was found when comparing the dual task cost in Half 1 for T2D1 vs T1D2 ($M=.011$, $SD= .075$) to Half 2 ($M= .031$, $SD= .083$, $t(20)=-.745$, $p=.465$).

Reaction Time Reduced Throughout the Experiment

A 3 x 2 x 2 x 2 within-subjects ANOVA was also conducted exploring Distractor Load (DL), Experimental Halves, Response, and Target Load (TL) on Reaction Time. Reaction time in the first half of the experiment (M=1.506, SD=.549) was significantly higher than the second half of the experiment (M=1.292, SD=.257, $F(1,20)$=38.236, p<.001, np^2 = .657). No effect was found between Half and the other factors (all p>.100).

We then conducted post-hoc comparisons in the form of paired-sample t-tests (Bonferroni corrected alpha value of 0.0125) to further explore the above results and determine whether practice improved reaction time. We calculated the dual-task cost in Half 1 for T1D1 vs T2D0 (M= 0.134, SD= 0.197) and compared this to Half 2 to find no effect (M= 0.114, SD= 0.141, $t(20)$=.644, p=.527). Similarly, no effect was observed when comparing the dual-task cost in Half 1 for T2D1 vs T1D2 (M= 0.051, SD= 0.131) to Half 2 (M = 0.058, SD= 0.066, $t(20)$=-.232, p=.819). This suggests that despite participants becoming faster overall, practice did not reduce reaction-time based dual-task costs.

Figure 4

Average Accuracy and Reaction Time for Response 1 and Response 2 in First Half of the Experiment

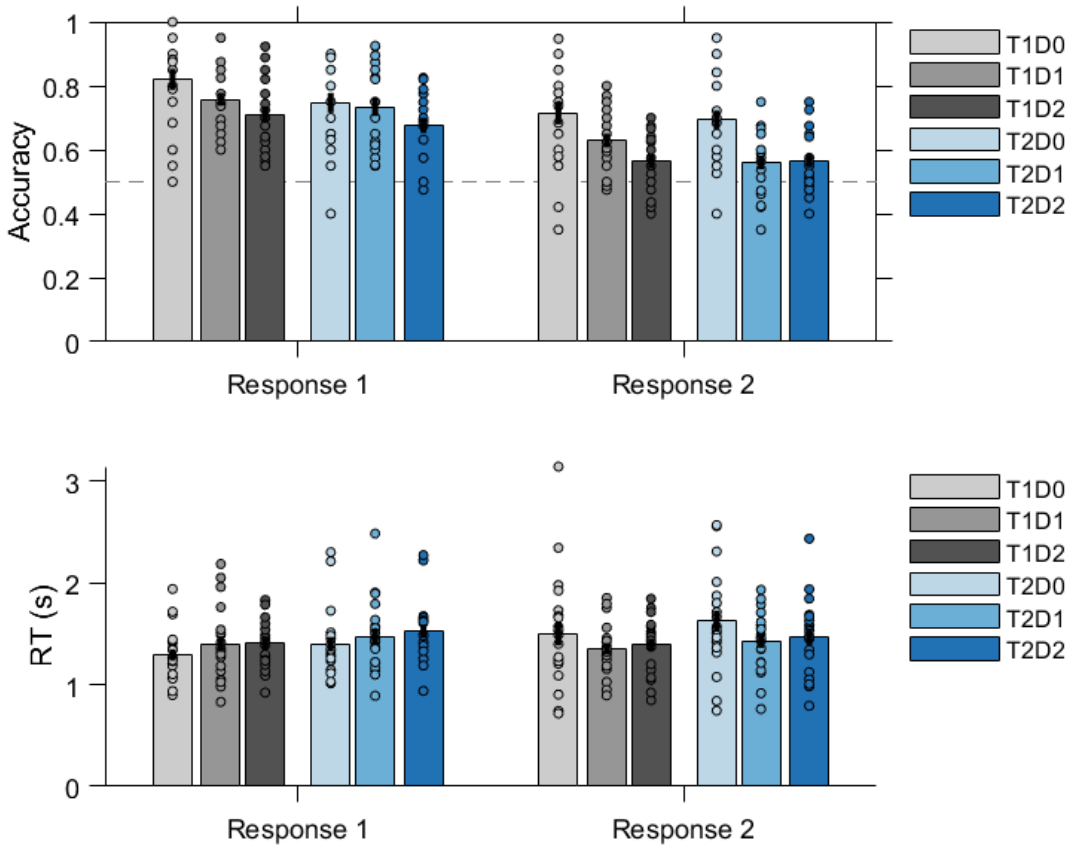
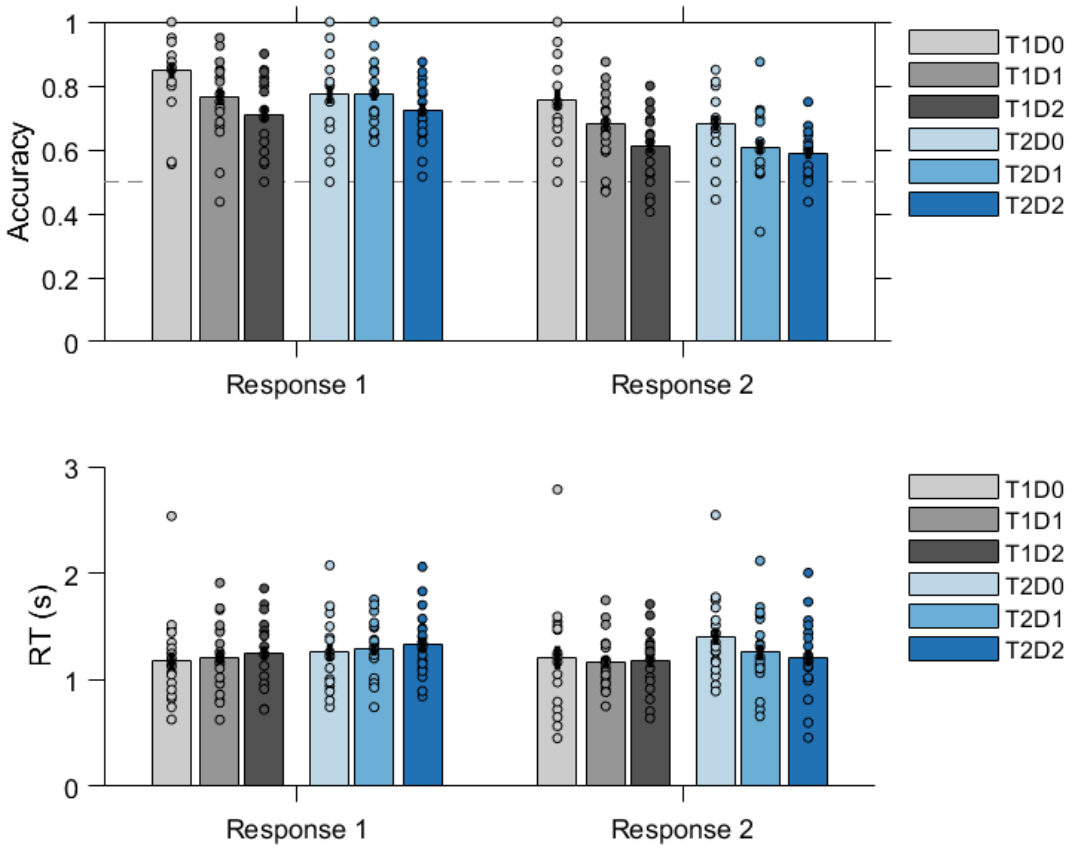


Figure 5.

Average Accuracy and Reaction Time for Response 1 and Response 2 Second Half of the Experiment


Accuracy
1
0.8
0.6
0.4
0.2
0
Response 1
Response 2
T1D0
T1D1
T1D2
T2D0
T2D1
T2D2
RT (s)
3
2
1
0
Response 1
Response 2
T1D0
T1D1
T1D2
T2D0
T2D1
T2D2

Discussion

This study aimed to examine the effects of practice on dual-task interference with visual working memory tasks. A limited number of studies have examined learning effects in dual-task paradigms using visual working memory tasks. We aimed to see whether a visual working memory task involving maintaining two tasks in mind leads to costs due to combined memory load or dual-task interference due to executing two tasks, and whether any interference could be reduced with short-term practice. We developed a dual-task paradigm using two visual working memory tasks to address these questions. Our paradigm used a dual-task made from two near-identical visual WM tasks to maximise the amount of interference. We hypothesised that participants would experience dual-task interference, and that this would increase as the number of distractor stimuli increased. We also hypothesised that a learning effect would be present, meaning DTI would decrease throughout the experiment (measured by an increase in accuracy and a decrease in reaction time). Overall, our findings suggest that dual-task interference was not found and therefore could not be reduced with practice. However, we did find working memory interference as performance reduced as a result of an increase in load.

Our study did not find significant dual-task interference in the typical sense of an increase in reaction time and decrease in accuracy in dual-task conditions compared to single-task conditions once overall memory load was taken into account. We found that participants performed similarly in conditions with matched overall memory demands regardless of whether this was a single or dual-task condition. On the contrary, we found that for the low-load trials (combined load of two items), reaction time showed dual-task facilitation in response 2: participants were slower in a single-task condition with two target items compared to a single-task condition with one target for response 1 and one target for response 2. When overall memory load was two items, no dual-task cost was observed for the first

response, suggesting participants neither had a cost from keeping a prospective second task in mind nor a benefit from being able to prioritise only the currently task-relevant WM item. For the second response, we observed a reaction-time benefit in the dual-task condition, suggesting executing two decisions in succession was faster than responding to one of two possible items in a single task.

We found significant working memory interference across tasks, as accuracy was significantly reduced with increased distractor load, as well as an increase in reaction time when increasing target load. This suggests that in our experiment, apparent dual-task interference is best explained and described as the result of an increase in total working memory load, rather than task switching or cross-task conflict. Ricker and Vergauwe (2020) also failed to find a cognitive load effect in a visual working memory task under dual-task conditions. However, unlike our participants, theirs maintained performance across increasing loads, with no difference in single or dual-task conditions, suggesting that working memory may be more robust to interference than we initially thought.

In addition to a dual-task cost we expected a load-dependent effect on performance. In our experiment, task performance decreased as distractor load and target load increased, further supporting previous findings in which interference increases depending on the overall memory load. For example, Buschman et al. (2011) demonstrated that remembering a single item was strongly represented by neurons in the PFC, but when multiple items were introduced, the representation for the first item decreased. This suggests that as distractor load/target load increased, the neural mechanisms behind encoding for these items struggled to cope. Watanabe and Funahashi (2014) emphasised that the brain may struggle to deal with dual-tasking due to a cognitive capacity limitation of the WM system. Our findings provide evidence to support the idea that this may have been caused by an increase in memory load rather than by the addition of a second task.

We also predicted a practice effect in which dual-task interference would reduce and this would be shown through both an improvement in accuracy and a reduction in response time in dual-task compared to single task trials. Although we did not find significant reduction in dual-task interference across the experiment, it could have been presented early on. However, we found no evidence for this as there was no significant dual-task cost even in the first half of the experiment. This does not rule out even more rapid learning occurring over the first few trials of the experiment. As accuracy did not significantly increase, and practice was not found to improve conditions with higher distractor load, we suggest that despite participants becoming faster throughout the experiment, they did not become more effective at limiting interference from competing memory representations of the irrelevant task.

Although no dual-task interference was found, there are multiple other reasons that could explain why our study did not show a learning effect. Firstly, learning time was very limited (consisting of only an hour) with previous studies suggesting that extensive learning is required to overcome dual-task interference, or show a reduction (Maquestiaux et al., 2008; Whitfield & Holdosh, 2021). The null effect of practice on dual-task interference could be explained by the interference being observed in our experiment was mostly driven by working memory resource limitations, rather than poor strategy. If both tasks were drawing from the same, limited working memory resource, then performance declines are likely once this resource becomes overwhelmed regardless of practice. A lack of improvement in accuracy may also suggest participants were already performing at their maximum capacity, meaning at the start of the experiment they had already reached their ceiling. Our paradigm consisted of two visual working memory tasks. A learning effect for this type of dual-task design has not been examined, with previous studies showing learning effects typically using a combination of auditory and visual task paradigms to separate the input and output of the

task (e.g., Liepelt et al., 2011, who attempted to generalise previous findings from Schumacher et al. (2001) onto different types of dual-task paradigm but failed to). The lack of practice effects here may be due to the tasks being too similar, meaning it is harder to overcome interference as it is greater compared to two dissimilar tasks (Liepelt et al., 2011).

Finally, our task design may have been too complicated to elicit learning effects. Participants may have had a lack of incentive to pay attention to the different task colours and their mappings and instead remembered all the cued stimuli rather than associating the colours with the different tasks and mappings. This could be addressed by simplifying the task design by using only 1 colour per task. This may induce a larger incentive for participants to pay attention to the different colours and may yield a learning effect (information about this follow up study is found below).

Overall, our study found that dual-task interference in visual working memory is better explained by overall memory load, rather than the performance of two tasks. This challenges the classical notion of multitasking costs arising from maintaining concurrent task representations. Exploring simplified mappings between stimuli and tasks or explicit cues in future experiments would allow for participants to be able to compartmentalise more efficiently and better allocate their cognitive resources to the current task, possibly reducing interference even under high-load conditions.

Chapter 3.2 – Exploring Dual Task Interference in Working Memory and ADHD: A Simplified Paradigm Exploring Effects of Cognitive Load on Performance and Relationship to Inattention and Hyperactivity

Introduction

In experiment 1, we tested two opposing predictions: on the one hand, performing a dual WM task could incur costs compared to a single task even when controlling for overall WM load. On the other, once WM load is taken into account, a dual task might in fact improve performance because it allows task-based prioritisation. While we did not find a cost once load was taken into account, we also found no evidence for a task-based prioritisation benefit. This stands in contrast to other forms of prioritisation (based on explicit cueing, e.g., Rerko et al., 2014, or temporal expectation, e.g., van Ede et al., 2017). One possibility is that this in fact indicates a dual-task cost which was cancelled out by the prioritisation benefit. However, this conclusion is difficult to draw from a set of null results. Another, we argue more plausible possibility could be that the complexity of the task led to the null effect. Participants had to remember and use two different response mappings on each trial and needed to remember the associations between four stimulus colours and response order/response mapping. This may have created too much cognitive load, leading to goal neglect, i.e., ignoring some task instructions when the set of instructions becomes too large (Bhandari & Duncan, 2014; Duncan et al., 2008). Additionally, there was no real incentive to prioritise the stimuli relevant to the upcoming response because probed items could always be selected from memory reactively (Braver, 2012) since the colour of the probe stimulus uniquely identified the relevant memory stimulus. Here we aimed to simplify the task by reducing the number of stimulus colours to one per task. Additionally, here we sought to decouple the possible dual-task cost from any possible prioritisation benefit by probing the

two tasks in an unpredictable order that was randomised from trial to trial. Our aim was to test whether in this simplified version we would replicate the lack of dual-task costs observed in experiment 1. In brief, we still found no benefit of dual-task-based prioritisation. Instead we now observed a dual task cost on reaction time. We also found that this cost reduced with brief practice.

A second, orthogonal aim of the experiment was to examine the role of attention-deficit hyperactivity disorder (ADHD). Understanding the deficiencies in mechanisms like ADHD is vital in addressing treatment and theory development (Kofler et al., 2009). ADHD is a neurological disorder typically characterised by difficulties with attention, hyperactivity, as well as impulsiveness (Alderson et al., 2013). The functional working memory model of ADHD proposes that working memory deficits are an important aspect of ADHD (Rapport et al., 2001). This model highlights the importance of working memory to the disorder as those with ADHD typically exhibit increased motor activity in order to increase cortical arousal, which is required for central executive functioning (Rapport et al., 2001). However, many studies have focused on the relationship between ADHD and working memory in children (Caldani et al., 2019; Fabio et al., 2020; Kofler et al., 2020; Orban et al., 2017). ADHD was initially thought to be a childhood disorder, but recent interest has sparked more examination into adults with the disorder, with studies estimating that 4% to 5% of the adult population meet the criteria for the condition (Kessler et al., 2006) and even led to changes in the DSM criteria to reflect adult diagnoses (Kessler et al., 2010). In adulthood, hyperactive behaviours often decline compared to childhood, whereas inattention and impulsivity tend to persist and are more likely to impact cognitive control processes related to working memory tasks (Luo et al., 2019). However, it is unclear to what extent WM deficits are driven by capacity limits vs the ability to select relevant information from WM, and to what extent the latter can potentially compensate for the former. Furthermore, it is unclear whether these deficits are

linked to slowed or impaired task learning. Demonstrating a relationship between ADHD and capacity while taking prioritisation into account would be useful because it could indicate that strategic prioritisation training could be a more viable strategy for improving effective WM capacity than the largely unsuccessful attempts to increase raw WM capacity through training (Holmes et al., 2019).

Deficits in multitasking in ADHD individuals are often linked to impairments in executive control processes, rather than simply storage limitations. Executive functions including planning, inhibition, and goal-directed control are crucial for coordinated behaviour when multiple task demands must be handled (Barkley, 1997). Within working memory, these control processes are important for planning for upcoming task requirements and for prioritising the most relevant information whilst maintaining other information in a secondary state. Both of these processes result in demands on cognitive control, and both are central to the prioritisation mechanisms examined in this study.

Evidence suggests that individuals with ADHD experience difficulties in these forms of control. For example, research has suggested that exaggerated processing bottlenecks are present when individuals with ADHD attempt to manage concurrent task demands (Ewen et al., 2012), as well as deficits in maintaining information not currently relevant but still required for later use ('secondary memory', Gibson et al., 2009). Load-related effects have also been observed, with increases in working memory demands leading to disproportionately greater performance declines in individuals with ADHD compared to controls (Mukherjee et al., 2021). This suggests that ADHD-related working memory difficulties may reflect deficits in the control and prioritisation of stored information, rather than simply capacity limits. Also, if difficulties in ADHD are linked to deficits in scheduling and prioritisation within working memory, then practice with tasks which explicitly require preparing for sequential responses and prioritising relevant representations may actually improve individuals' ability

to develop control strategies. This provides a strong motivation for exploring how short-term practice influences performance in the present task, and whether this differs as a function of ADHD.

As there is limited research exploring adult ADHD and its influence on working memory dual task performance, we aim to address the relationship between the ADHD subscales of inattention and hyperactivity on overall performance when dual tasking. We also aimed to see whether short-term practice would reduce this dual task cost, particularly in those with high levels of ADHD as previous results have suggested WM performance can be significantly improved with training (Klingberg et al., 2002).

We predicted that increasing working memory load would reduce performance, reflected in lower accuracy and increased reaction time. We also predicted a dual-task cost, meaning performance would be worse in the dual-task condition than in the single-task condition when overall memory load was matched. However, as the task structure reduced mapping complexity compared to Experiment 1, we also tested the idea that dual-task performance may instead benefit from task-based prioritisation of the currently relevant stimuli once the probe was presented. We also predicted that performance would improve across the experiment, reflecting short-term learning of task structure and response mappings. We predicted this effect to be larger in the dual-task condition, reflecting participants becoming more efficient at coordinating two tasks. Additionally, we predicted that higher ADHD symptom levels would be associated with greater sensitivity to working memory load and dual-task demands. We also explored whether hyperactivity would relate to accuracy or reaction time, and if practice-related improvements would be reduced in individuals with higher ADHD symptom levels. As we examined a random cohort rather than individuals with an ADHD diagnosis, we are only exploring random variation (which may include individuals with a formal diagnosis of ADHD).

Methods

This experiment was conducted as a follow-up study to the experiment outlined in Chapter 3.1. For details regarding the methods, please refer to Chapter 3.1. This experiment uses a simplified paradigm compared to the previous experiment, as the complexity of the previously used task may have influenced whether a learning effect and dual-task effect was present. Firstly, the number is stimulus colours was reduced from four to two, with one colour assigned to each task, therefore removing the need to remember multiple colour-response order associations. Secondly, response mappings were simplified so that each task retained a consistent mapping within blocks, reducing switching demands compared to Experiment 1 where multiple mappings needed to be tracked concurrently. Thirdly, this design focused on a clearer manipulation of working memory load (1, 2, 4), whilst also keeping the prioritisation structure constant to allow for a more direct test of dual-task costs vs prioritisation benefits.

Design

Participants completed a visual working memory task requiring orientation change detection in PsychoPy (v2023.1.1). Accuracy (correctly identifying whether a probe matched a memory stimulus), and reaction time were measured, with load (1, 2, 4), experimental half (1, 2), condition (single, dual), and task (1, 2) being manipulated. Participants completed 20 blocks in total, 10 of which were dual-task and 10 of which were single-task (counterbalanced to avoid order effects). Load was randomised by trial within each block. Inattention and hyperactivity levels in participants were measured using Adult ADHD Self-Report Scale (ASRS-V1.1, Kessler et al. 2005).

Participants

40 undergraduate students from the University of Nottingham participated in this experiment via an online recruitment scheme and/or word-of-mouth. Participants who were recruited via the scheme were compensated with 1 course credit, and those recruited elsewhere were compensated £10/hr. Two participants were excluded from the final sample due to incomplete task performance, resulting in a final sample of 38 participants (33 female, 5 male) aged 18-21 years old (M = 19.23, SD = 1.03). Participants had corrected or normal vision. The study was conducted in compliance with the University of Nottingham's School of Psychology Ethics procedure.

Participants were not told of the ADHD questionnaire aspect of the study until completing the questionnaire after completing the WM task to avoid influencing their responses. The ADHD questionnaire scores varied across participants with approximately equal proportions of high and low scores as defined by Kessler et al. (2005).

Stimuli

The visual stimuli used in the experiment were identical to those in Experiment 1, with the exception that only two colours were used. Stimuli were rectangular bars with a random orientation from 0° to 180° and 0.05, 0.25 in size (in proportion to screen height). The bars were coloured pink (255, 105, 180) and blue (0, 255, 255). The mapping of colour to task (which colour corresponded to Task 1 vs Task 2) was counterbalanced across participants to avoid biases related to colour preference. A black fixation cross was presented at the centre of the screen on each trial, with feedback presented in the form of a single green or red dot (for correct or incorrect responses, respectively) in the centre of the screen for the single task and two dots positioned to the left and right of fixation for the first task (-0.025,

0.0, x/y coordinates in units of screen height) and second task (+0.025, 0.0) in the dual-task condition.

Procedure

Participants were asked to complete a visual working memory task involving single-task and dual-task conditions. Participant demographics including sex, age, and handedness were recorded before the experiment began. Participants were instructed how to conduct the experiment and then read through an introductory slideshow consisting of detailed instructions. Participants first completed four practice blocks of 8 trials each, consisting of two single-task blocks and two dual-task blocks.

Single Task

The single-task condition involved an orientation change detection task where participants encoded one, two, or four oriented same-coloured rectangles which were maintained until one of the items was probed. The probe stimulus was presented in the same location as one of the memory stimuli and matched its colour. The probe either had the same orientation as the probed memory item (match) or was rotated 30° clockwise/anticlockwise (mismatch). Feedback was presented in the centre of the screen. Each block consisted of a single task, meaning the colour of the stimuli and the response mapping were the same throughout the block. Participants were presented with the response mapping rule before the block began, which could either be the ‘F’ key for match and ‘J’ key for mismatch in Task 1, or ‘J’ for match and ‘F’ for mismatch in Task 2. Assignment of response mappings to tasks was counterbalanced across participants.

Dual Task

The dual-task condition involved either two or four oriented stimuli consisting of two colours (pink and blue) which were presented in random corners of the screen

simultaneously. For the load-two condition, one stimulus of each colour was presented, whereas in the load-four condition, two of each colour were presented. Each trial required two sequential responses, one for each task (colour). The probe displays were presented one at a time. Importantly, the order in which the two colours were probed was randomised on a trial-by-trial basis. Participants did not know in advance whether the blue or pink stimulus would be tested first on a given trial. This ensured participants could not prepare only one task set in advance so that both stimulus sets were maintained in working memory.

The probe consisted of two items (one of each colour) and feedback was presented in the form of two coloured dots indicating a correct response (green), or incorrect (red). The response mapping for each colour remained consistent throughout the task and was identical to the corresponding single-task blocks. Participants were required to switch between the two response mappings within a trial, but these mappings themselves did not change. Percentage accuracy and reaction time was also presented to participants at the end of each block.

Task Outline

Figure 1 displays trial outline details. Every trial began with a fixation period of 1000ms where participants were instructed to maintain fixation.

In the single-task condition, the memory stimuli (one, two, or four same-coloured rectangular stimuli) appeared on screen for 200ms. After stimulus offset, a blank delay of 1000ms followed. A single probe was then presented at the location of one of the memory items and remained on screen for 200ms. This either matched the original orientation or was rotated 30° clockwise or anticlockwise. Participants had 4000ms from probe onset to respond using the task-specific response mapping. The probe was visible until a response was made (or the response window time elapsed). Feedback was presented after every trial with either a

red dot for incorrect, or green for correct for 300ms and an inter-trial interval (ITI) was presented for 1000ms before the next trial began.

In the dual task condition the memory stimuli consisted of two items (one of each colour, load 2) or four items (two of each colour, load 4). After stimulus offset, a blank delay period for 1000ms followed. After this, the probe 1 was presented and corresponded to one of the two colours and appeared at the location of a memory item for that colour set. The probe remained for 200ms and the order of colour probing was randomised on each trial so participants could not predict which task would be tested first. Participants had 4000ms from onset of probe to respond. Following the first response, a second blank delay was presented for 500ms. Probe 2 was then presented for 200ms and corresponded to the other colour (task) and required the alternative response mapping. Combined feedback was then provided for 300ms with two coloured dots (left dot corresponding to response 1, and right dot corresponding to response 2).

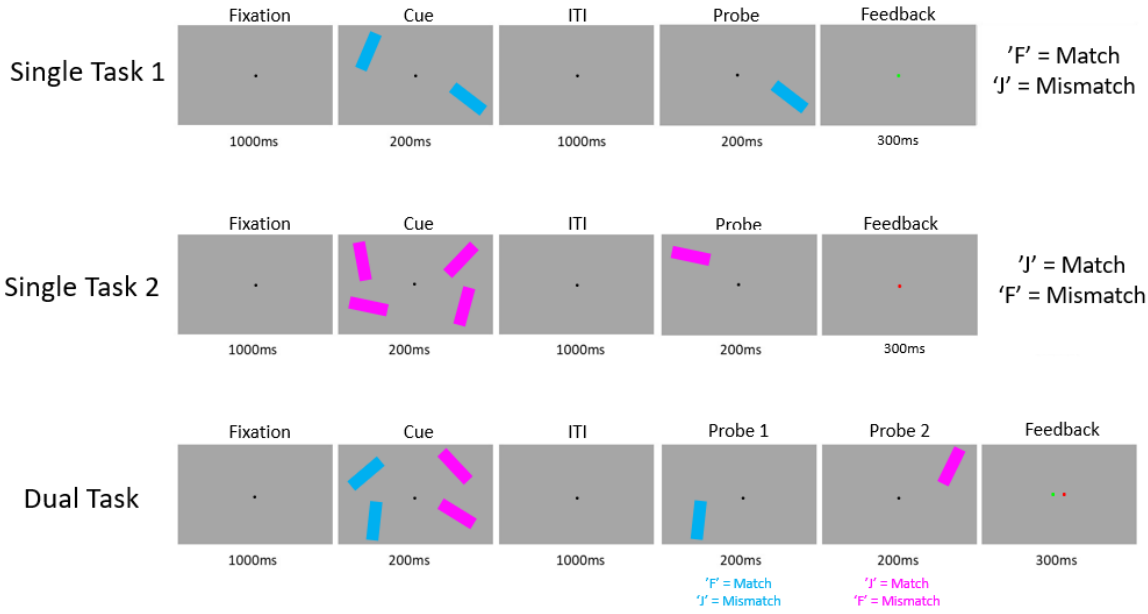
20 blocks were presented in total consisting of 24 trials each, totalling 480 trials for the whole experiment. 10 blocks were of the single task condition (5 blocks of pink stimuli, 5 blocks of blue stimuli), and 10 blocks of dual task condition. At the end of each block participants were able to take a break which was manually ended by pressing the spacebar key. The experiment lasted approximately 1 hour. Once participants reached the end of the study, they were shown a screen thanking them for their participation.

After completing the working memory task participants were provided with the ADHD questionnaire. The ASRS-V1.1 questionnaire (Kessler et al., 2005) consists of 18 questions exploring symptoms of ‘Inattention’ and ‘Hyperactivity’. The questionnaire included six questions focused on ‘Hyperactivity’, for example “How often do you fidget or squirm with your hands and feet when you have to sit down for a long time?” Twelve

questions focused on ‘Inattention’, such as “How often are you distracted by activity or noise around you?” Participants were asked to respond by ticking a box on a Likert scale (‘Never’, ‘Rarely’, ‘Sometimes’, ‘Often’, and ‘Very Often’). Participants were not told the questions were specific to ADHD to avoid bias, but they were made aware of this in the debrief form. The questionnaire took 5-10 minutes on average to complete and once completed, participants were provided with the debrief form and asked if they had any questions remaining. For the full list of questions, please refer to Appendix A.

Figure 1

Task Outline for Single and Dual Task Conditions



Note. Task outline for Single Task 1, Single Task 2, and Dual Task conditions. For Single Task 1 and Task 2, participants were asked to remember the orientation of same-coloured stimuli and then respond when being probed whether this was a ‘match’ or a ‘mismatch’ in

terms of orientation.

Results

A 2x2x2 within-subjects ANOVA was conducted to explore Experimental Half (1, 2), Condition (Single, Dual) and Load (2, 4), on Accuracy and Reaction Time (Figure 1). We only included the first response from the dual task trials. Performance was averaged across the two response mappings. The results are outlined below and post-hoc results were Bonferroni corrected (see Appendix B for full results).

No Dual-Task Cost Observed in Accuracy

We found no significant main effect of Condition ($F(1,37) = .265$, $p = .61$, $\eta_p^2 = .007$), suggesting there was no significant difference in accuracy in the single task condition compared to the dual task condition, and therefore no evidence of dual-task cost.

In contrast, there was a large main effect of Load ($F(1, 37) = 246.18$, $p < .001$, $\eta_p^2 = .869$), with lower accuracy in load 4 than load 2. Accuracy was found to be slightly higher in the second half of the experiment ($M = .758$, $SD = .103$) than the first half ($M = .739$, $SD = .112$, $F(1,37) = 4.214$, $p = .047$, $\eta_p^2 = .102$).

No significant interactions were found involving Condition (all $p \geq .495$) meaning although accuracy declined with increasing load, this load effect did not differ between the single- and dual-task conditions and was consistent across the two halves of the experiment.

Dual-Task Cost Observed in Reaction Time

Reaction Time analysis revealed a significant main effect of Condition ($F(1,37) = 9.38$, $p=.004$, $\eta_p^2 = .809$), with slower responses in the dual-task condition ($M = 1.158$, SD

= .263) compared to the single-task condition (M = .807, SD = .157, $t(37) = 12.52$, $p<.001$), suggesting the presence of a dual-task cost.

A main effect of Load ($F(1,37) = 48.77$, $p<.001$, $\eta_p^2 = .569$) was also found for Reaction Time, with post-hoc analysis revealing participants took longer in the higher load condition (M = 1.03, SD = .230) than the lower load condition (M = .937, SD = .190).

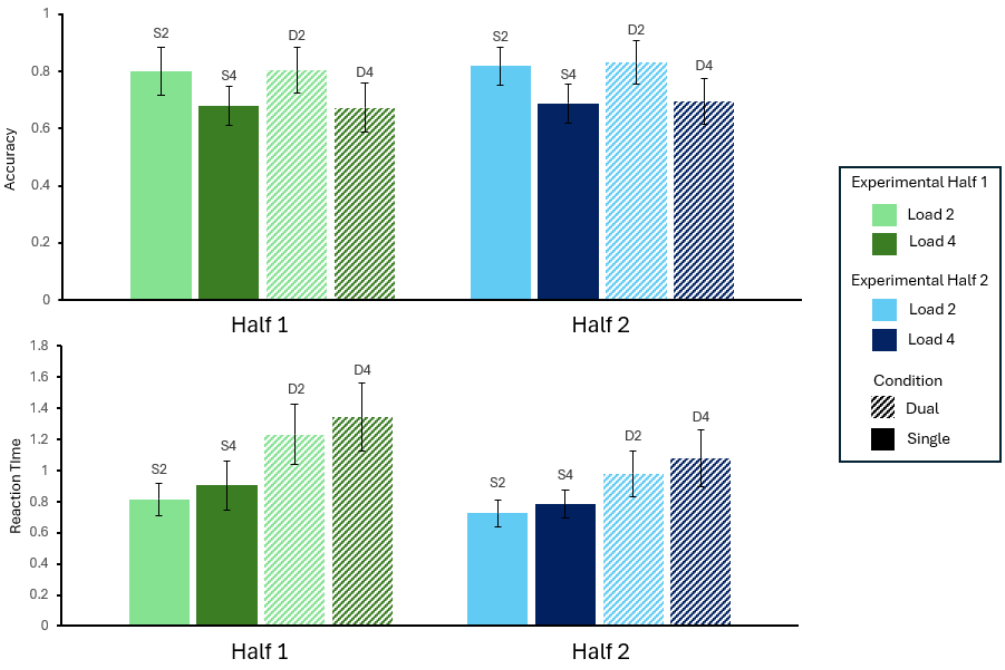
Dual-Task Reaction Time Costs Reduced with Practice

Importantly, for reaction time we also found a significant interaction between Half and Condition ($F(1,37) = 22.94$, $p<.001$, $\eta_p^2 = .383$), indicating that the effect of half was different in the dual vs single condition. Post-hoc analysis revealed reaction time to be higher in Half 1 single task (M = .859, SD = .187) than Half 2 single task (M = .754, SD = .127, $t(37) = 5.654$, $p<.001$). This was also found for the dual task condition, in which the reaction time was higher in the first half (M = 1.29, SD = .292) than the second half (M = 1.029, SD = .234, $t(37) = 8.881$, $p<.001$). The interaction was thus driven by a greater improvement in the dual task condition, indicating that dual-task reaction time cost was reduced with practice.

We found no significant two-way interaction between Condition and Load ($F(1,37)$ = 2.728, p = .107, η_p^2 = .069), indicating that the increase in reaction time associated with higher load was comparable for the single- and dual-task conditions. No significant three-way interaction for Reaction Time was found between Condition, Load and Experimental Half ($F(1,37)$ = .180, p = .674, η_p^2 = .005).

Figure 1

Accuracy and Reaction Time for Single and Dual Tasks in Experimental Half 1 and 2



Note. Accuracy and Reaction Time split by Experimental Half, Load, and Condition.

ADHD Analyses

We next examined the effect of ADHD on performance. We used three different measures of ADHD symptoms: ADHD type (low, high), and covariates of the ADHD traits Inattention and Hyperactivity. We conducted mixed-effects ANOVA to explore the interaction of ADHD type with the within-subject variables of Experimental Half, Condition, and Load. We conducted mixed-effects ANCOVA to measure the effect of the continuous variables Inattention and Hyperactivity. To group participants into their respective groups of 'high' or 'low' ADHD score, we firstly observed Part A (questions 1-6). This section of the ASRS-V.1 Questionnaire (Kessler et al., 2005) was used to assess participants combined scores on inattention and hyperactivity. A score of 4+ (scored at least 'Sometimes' or 'Often', depending on the question) out of a total of six questions in this section was scored 'high' (Adler et al., 2019). Part B of the questionnaire was scored out of 12. To score participants on

the subscales of Inattention and Hyperactivity, responses to specific questions contributed to the different subscales (Inattention questions = 1-4, 7, 12; Hyperactivity questions= 5-6, 13-18). This scoring follows recommendations by Adler et al. (2019), where in a clinical setting high scores would indicate symptoms consistent with possible ADHD which would warrant follow-up investigation. However, this is not the same as an ADHD diagnosis. Out of our total sample of 38 participants, 18 belonged to the high ADHD trait group.

ADHD Did Not Influence Overall Accuracy

We conducted a mixed-design ANOVA to explore the within-subjects variables of Experimental Half (1, 2), Condition (single, dual), Load (2, 4) and the between-subjects variable of ADHD Group (low, high) on accuracy and reaction time.

No significant main effect was found for ADHD group on accuracy ($F(1, 36) = 3.166$, $p = .084$, $\eta_p^2 = .081$) suggesting overall performance accuracy did not differ between high and low ADHD participants (Fig. 2).

Importantly, no significant interactions were found between group and Condition ($F(1, 36) = .145$, $p = .706$, $\eta_p^2 = .004$) or Half ($F(1,36) = .206$, $p = .653$, $\eta_p^2 = .006$). This suggests ADHD traits did not influence dual-task effects on accuracy or modulate practice-related improvements over time. Likewise, there was no interaction between ADHD group and Load ($F(1, 36) = .001$, $p = .970$, $\eta_p^2 = .0000403$) or three-way interactions between Half, Load, and ADHD group ($F(1, 36) = 3.091$, $p = .087$, $\eta_p^2 = .079$). No significant interactions were found between Half, Condition, and ADHD group ($F(1, 36) = .157$, $p = .694$, $\eta_p^2 = .004$), Load, Condition, and ADHD group ($F(1, 36) = 1.067$, $p = .308$, $\eta_p^2 = .029$), or Half, Load, Condition, and ADHD Group ($F(1, 36) = .024$, $p = .878$, $\eta_p^2 = .00066$).

ADHD Traits Exacerbated Load-Related Slowing in Reaction Time

No significant main effect was found for ADHD group on overall reaction time either ($F(1, 36) = 1.513$, $p = .227$, $\eta_p^2 = .040$, Fig. 2). However, a significant interaction between Load and ADHD group was found ($F(1, 36) = 6.658$, $p = .014$, $\eta_p^2 = .156$). This suggests a significant difference in the load effect on reaction time between ADHD groups. Post-hoc analysis suggests individuals in the high ADHD group took longer to respond in Load 4 ($M = 1.081$, $SD = .239$) than Load 2 ($M = .958$, $SD = .339$, $t(37) = 7.033$, $p<.001$). Participants from the low ADHD group also had higher reaction times for Load 4 ($M = .98$, $SD = .212$), than Load 2 ($M = .919$, $SD = .194$, $t(37) = 3.66$, $p = .005$), but the load effect was much smaller (approximately 60ms compared to ~120ms in the high ADHD group). There was no significant difference for the Load 2 condition between high ADHD ($M = .958$, $SD = .339$) and low ADHD individuals ($M = .919$, $SD = .194$, $t(37) = .757$, $p = .454$), but a trend in the Load 4 condition (high ADHD: $M = 1.081$, $SD = .239$, low ADHD: $M = .98$, $SD = .212$, $t(37) = 2.764$, $p = .054$), suggesting that ADHD symptoms mainly impacted performance at high load.

ADHD Did Not Influence Dual-Task Costs

ADHD group did not significantly interact with Condition for reaction time ($F(1,36) = 0.21$, $p = .652$, $\eta_p^2 = .006$. This indicates that dual-task cost in reaction time was similar for both high and low ADHD participants. The interaction between Condition, Load, and ADHD group was also not significant, ($F(1,36) = .715$, $p = .404$, $\eta_p^2 = .019$), demonstrating ADHD traits did not differentially affect dual-task performance as load increased.

ADHD Did Not Modulate Practice Effects

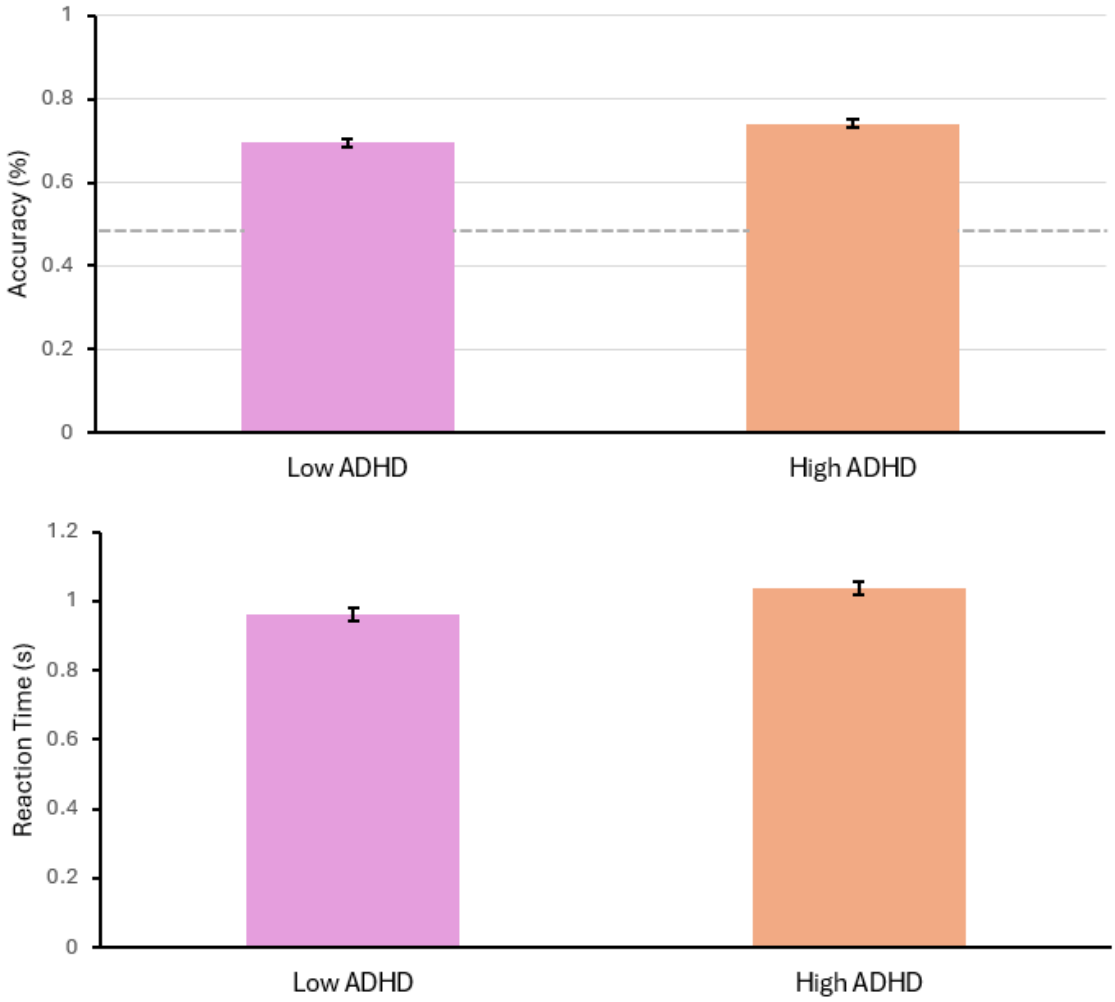
There was no significant interaction between Experimental Half and ADHD for reaction time ($F(1,36) = 2.618$, $p = .114$, $\eta_p^2 = .068$). This indicates both groups showed

comparable reductions in reaction times across the experiment. No three-way interactions were found between Half, Condition, and ADHD ($F(1,36) = .641$, $p = .429$, $\eta_p^2 = .017$), Half, Load, and ADHD, ($F(1,36) = .086$, $p = .771$, $\eta_p^2 = .002$) and there was no four-way interaction between Half, Condition, Load, and ADHD ($F(1,36) = .374$, $p = .545$, $\eta_p^2 = .010$).

In sum, these results suggest overall ADHD group had no effect on accuracy meaning both low and high group ADHD scorers had comparable performance. For reaction time, load effects were influenced by ADHD group. There were no practice effect differences between participants with high or low ADHD scores.

Figure 2

Low/High ADHD Accuracy and Reaction Time



Note. Accuracy and Reaction Time Data for low and high ADHD groups (error bars are SEM).

ADHD Inattention and Hyperactivity Subscales had no influence on Performance

We next ran a mixed-ANCOVA with added covariates of inattention and hyperactivity to explore their interactions with Experimental Half (1, 2), Condition (single, dual), and Load (2,4). 4).

No significant main effect was found for Inattention ($F(1,34) = 1.522$, $p = .226$, $\eta_p^2 = .043$) or Hyperactivity ($F(1,34) = .032$, $p = .859$, $\eta_p^2 = .000946$) on accuracy.

No Evidence of Subscale Influence on Dual-Task Effects on Accuracy

The Inattention and Condition interaction was not significant ($F(1,34) = 1.02$, $p = .321$, $\eta_p^2 = .029$, indicating inattention did not influence the difference in accuracy between single and dual task conditions.

Hyperactivity and Condition interaction was also not significant, ($F(1,34) < .001$, $p = .989$, $\eta_p^2 < .001$). We also examined three-way interaction effects between Inattention, Condition, and Load to uncover whether Inattention influenced dual-task costs once load increased. We found no significant effect for accuracy ($F(1,34) = .062$, $p = .805$, $\eta_p^2 = .002$). For Hyperactivity, we also found no significant interaction for accuracy ($F(1,34) = 1.963$, $p = .170$, $\eta_p^2 = .055$). This suggests that neither subscale influenced how load affected dual-task performance.

Hyperactivity but not Inattention Influenced Practice Effects on Accuracy

No interaction effect was found between Inattention and Half ($F(1, 34) = .08$, $p = .775$, $\eta_p^2 = .002$. However, an effect between hyperactivity and Half ($F(1, 34) = 5.10$, $p = .030$, $\eta_p^2 = .130$) was found although this did not interact with task condition or load.

There was no significant interaction effect between Inattention, Condition, and Experimental Half ($F(1,34) = .112$, $p = .740$, $\eta_p^2 = .003$). We also did not find a significant interaction in the accuracy data for Hyperactivity ($F(1,34) = .355$, $p = .555$, $\eta_p^2 = .010$). This suggests that symptom severity did not influence practice-related improvements differently across task conditions.

ADHD Subscales Do Not Predict Reaction Time Performance

For reaction time, we also found no significant main effect for Inattention ($F(1, 34) = .592$, $p = .447$, $\eta_p^2 = .017$), or Hyperactivity ($F(1, 34) = .417$, $p = .523$, $\eta_p^2 = .012$). There were no significant interactions between Inattention and Condition ($F(1,34) = 1.79$, $p = .190$, $\eta_p^2 = .050$) or Hyperactivity and Condition ($F(1, 34) < 0.001$, $p = .988$, $\eta_p^2 < .001$). No three-way interactions were found for Inattention, Condition, and Load ($F(1, 34) = 2.543$, $p = .120$, $\eta_p^2 = .070$) or Hyperactivity, Condition, and Load ($F(1, 34) = .736$, $p = .397$, $\eta_p^2 = .021$).

However, there was a significant interaction between Inattention and Half ($F(1, 34) = 6.45$, $p = .016$, $\eta_p^2 = .160$), and there was a trend towards an interaction with condition ($F(1, 34) = 3.84$, $p = .058$, $\eta_p^2 = .102$). The Hyperactivity and Half interaction was not significant ($F(1, 34) = .05$, $p = .833$, $\eta_p^2 = .001$).

The Inattention and Load Interaction was not significant ($F(1,34) = 1.75$, $p = .194$, $\eta_p^2 = .049$), and neither was Hyperactivity and Load ($F(1, 34) = .72$, $p = .403$, $\eta_p^2 = .021$.

In sum, ADHD symptoms did not strongly modulate dual-task performance or practice effects.

Discussion

Our study aimed to examine the influence of load on working memory performance and dual task demands, whether short-term practice successfully reduces said interference, whilst also exploring the effects of ADHD. This study was conducted to build on findings from Chapter 3.1, in which a more complex dual-task design was implemented. Using a simplified version of the task, we were able to test whether the absence of apparent dual-task costs in the previous experiment was genuine, or whether it was caused by the high task demands of the previous design.

Our visual memory task again did not elicit dual-task interference or dual-task cost in accuracy despite the increase in working memory load. However, we now did find a dual-task cost for reaction time, suggesting the addition of another task resulted in slower responses (even after accounting for overall WM load) but their accuracy remained stable. This dual-task cost on reaction time was comparable on Load 2 and Load 4 trials. We also found evidence to suggest improved reaction time in the second half of the experiment due to short-term practice and specifically a reduction in the dual-task cost, as well as a modest improvement in accuracy. Finally, we found no significant effects of ADHD group, or subscale (inattention and hyperactivity) on dual task costs or practice effects, although an interaction was found between load and ADHD group for reaction time, possibly suggesting some sensitivity to cognitive demands for higher ADHD individuals.

We found a presence of dual-task cost in reaction time, but not accuracy, in our experiment, suggesting participants were able to maintain their accuracy when performing the dual-task condition but the cognitive load imposed by having to shift attention between both tasks resulted in slower reaction times. These results provide an alternative explanation to the results of Watanabe and Funahashi (2014), who found monkeys to exhibit behavioural interference in the presence of a dual task. Although Watanabe and Funahashi (2014) found a

decrease in accuracy when dual-tasking (possibly caused by the working memory load confound) which we failed to find, both studies found an increase in reaction time in the dual-task condition compared to the single-task condition. It is important to note that the discrepancies in findings between our results and those of Watanabe and Funahashi (2014) may be due to their study using non-human primates whereas we explored the working memory interference effect in humans. Also, our study still supports theories suggesting dual-tasking negatively impacts executive functions and attentional resources shown through the increase in reaction time. The absence of a decrease in accuracy may be a result of participants focusing more on prioritising the correct answer of the task rather than speed.

However, the absence of a dual-task cost on accuracy raises the question of whether cues are required to successfully improve performance when dual-tasking. Our experiment did not use cues to aid in shifting between task sets, which has been found to significantly improve working memory performance (Berryhill et al., 2012). Surprisingly, we did not find accuracy to decline despite the absence of these cues, possibly suggesting participants were forced to find a more conservative response strategy and again focused on accuracy rather than reaction time. It may be possible that our working memory system is able to maintain these multiple representations with a limited reduction in accuracy if the task demands are within capacity limits.

Importantly, our results provide evidence in support of a practice effect. Performance improved over the course of the experiment, with reaction time decreasing and accuracy modestly but non-significantly increasing. Crucially, there was an interaction between experimental half and condition for reaction time. Although reaction time improved across the experiment for both conditions, the improvement was larger in the dual-task condition. This suggests that dual-task reaction time cost can be improved with brief practice, which contrasts with the dual-task literature which typically reports DTI is highly resistant to

training. However, as no interaction between experimental half and condition was found for accuracy, practice may have primarily speeded selection of the task-relevance response mapping without improving task-specific memory maintenance or selection. This supports evidence from Ruthruff et al. (2003), who suggest minimal practice does not significantly change dual task interference, and 'extensive' practice is required.

In terms of ADHD findings, previous literature has shown that inattention drives working memory deficits in individuals with ADHD (Lui & Tannock, 2007). Rogers et al. (2011) found inattention to result in poor performance in auditory-verbal tasks, as well as visuospatial working memory tasks. Therefore, we expected to find high inattention individuals to perform significantly worse, particularly when dual-tasking. Despite this literature, we found no significant effect of inattention on accuracy or reaction time. This may have occurred due to the task demands in our simplified design not being difficult enough to result in attention control mechanism deficits or alternatively, participants were not significantly impaired (which is unsurprising as we found no dual-task cost).

We also examined the effect of hyperactivity, which is much less commonly investigated in working memory literature than inattention. However, Barkley (1997) suggests behavioural disinhibition can impact executive functioning. This effect may have been difficult to observe in our experiment as participants were constrained in their ability to be impulsive or hyperactive, meaning they physically weren't able to disrupt task performance. Since trials were short and the task repetitive, we may have been less likely to find a relationship to hyperactivity.

It is important to consider that we did not specifically recruit individuals with a clinical diagnosis of ADHD but instead relied on a brief self-report. This may have minimised group differences even though we saw substantial variation in self-reported

symptom severity. Also, our ADHD measure was a self-reported questionnaire, and although the ASRS-V1.1 (Kessler et al., 2005) is a validated and successful measure in predicting diagnosis (Green et al., 2019), it may be subjective to reporting bias. Finally, our task design may not have required higher-order executive functions due to its relative simplicity, meaning ADHD-impairments were not present because they are detectable only in more cognitively demanding tasks.

The majority of ADHD studies of executive function have focused on childhood populations rather than adulthood, suggesting adults may respond to these working memory tasks differently and develop strategies which allow them to compensate, even if these ADHD deficits still exist. Importantly, applying these findings to real-life dual-tasking scenarios, such as driving, could provide an opportunity to allow insight into how to enhance this performance and which tasks could impact those with ADHD.

In conclusion, our study successfully demonstrates that WM dual-tasking impacts reaction time. The lack of DTC on accuracy conversely highlights the flexibility of working memory. Despite there being no large impact of ADHD traits on performance, the observed load-related difference could suggest individuals with higher ADHD symptoms may be more sensitive to higher cognitive demands. In terms of the significant practice effects, it is important to consider whether the demands of the task were sufficient enough to elicit a large practice effect, and whether this was influenced by the task complexity. Future research exploring the effects of retrocues on visual working memory prioritisation, as well as possibly simplifying the task further could allow for a clearer effect to be shown in terms of learning. Also, exploring the load patterns using clinical ADHD populations may clarify the relationship between ADHD symptoms and working memory performance under multitasking conditions.

Chapter 3.3 – The Effect of Cognitive Load and Short-term Practice on Working Memory Prioritisation in ADHD

Introduction

Chapters 3.1 and 3.2 investigated dual-task interference in visual working memory by exploring performance change when participants are required to simultaneously maintain and process two tasks. This paradigm allowed us to investigate capacity limitations and interference effects, but it failed to clearly separate task interference from prioritisation effects within working memory, as performance deficits may have reflected general dual-task costs rather than limitations in item prioritisation (especially chapter 3.1). To address this, the current study simplified the paradigm by changing the dual-task element to a dual-response, single-task design. This allowed us to test whether participants prioritise multiple items when the response order is predictable, and when attentional resources need to be re-allocated between items across responses in sequence. This design enabled us to directly investigate how cognitive load and short-term practice influence performance in a WM paradigm requiring prioritisation of multiple items. Importantly, this shift in task demands also allowed us to re-evaluate ADHD effects, and in particular hyperactivity, which previously failed to influence working memory in Chapter 3.2. Since the new paradigm emphasised prioritisation of information across sequential responses, we expected potential hyperactivity-related deficits to emerge more clearly.

Primarily, our aim was to investigate how increasing distractor load (and therefore overall load) and short-term practice affect working memory prioritisation. Also, we examined whether individuals with high ADHD traits show reduced prioritisation and practice effects (especially under increased cognitive demands), and whether the traits of inattention and hyperactivity differentially influence performance. We implemented a dual-

response visual working memory paradigm in which participants encoded items belonging to two colour sets and responded in sequence to probes from each set. This allowed participants to prioritise one set of items in anticipation of the probe, whilst maintaining the remaining items for subsequent retrieval. This task allowed us to manipulate memory load and response, therefore increasing demands on attentional shifting and prioritisation within working memory. Also, we examined whether performance improved over the session, reflecting short-term practice. Finally, we explored whether individual differences in inattentive and hyperactive ADHD traits impact cognitive load and prioritisation.

We hypothesised that increasing working memory load would impair prioritisation, leading to reduced accuracy and slower reaction time prioritisation benefits. We also hypothesised that performance would improve in the second half of the experiment, reflecting short-term practice effects. We also hypothesised that higher ADHD traits and inattention and hyperactivity scores would be associated with poorer performance (particularly under high load and dual response conditions).

Methods

The present experiment employed a similar paradigm to that used in Chapter 3.2. However, the current chapter uses a modified design to focus on item prioritisation and sequencing responses by simplifying the task from two response mappings to a single response mapping across both responses on each trial. The design rationale and differences from Chapter 3.2 are highlighted below.

Participants

60 participants were recruited for this experiment using opportunity sampling from the University of Nottingham. Eleven participants were excluded from the final dataset due to incomplete data or poor performance (below chance, 50%), resulting in a final sample of 49 individuals. Participant ages ranged from 18-23 years old (*M*=19.11, *SD*=1.25), with 44 female, 2 male, and 3 not reporting their gender. We used the same self-report questionnaire to identify ADHD symptoms. 26 participants were grouped as 'high ADHD', and 23 as 'low ADHD'. Participants had normal or corrected-to-normal vision. All participants provided informed written consent.

Materials

The study was conducted in a quiet room using a Windows PC and keyboard. The study was conducted using PsychoPy v2024.2.1 (Peirce et al., 2019). Participants sat approximately 70cm from the screen.

The stimuli used in the experiment were rectangular bars of pink (255,105,180) and blue (0,255,255) with the same stimulus dimensions as in chapters 3.1 and 3.2. Participants were told prior to the experiment to respond using 'F' and 'J' on the keyboard (e.g., 'F' for match, 'J' for mismatch, which was counterbalanced across participants). A black fixation dot (0,0,0) appeared at the centre of the screen. Participants were told to focus on the fixation dot throughout the duration of the experiment.

Participants were also asked to complete the Adult ADHD Self-Report Scale (ASRS v.1.1, Kessler, 2015). Refer to Chapter 3.2 for details regarding the scale.

Design

A mixed-effects visual working memory paradigm was employed to examine the impact of memory load and capacity when prioritising task-relevant information by using a change detection task. The task consisted of load manipulation (load 2 or load 4 memory stimuli) and a prioritisation manipulation (all items relevant for first response vs. a subset of items relevant for the first response, with remaining items tested on a second response).

The single response condition involved a single probe in the same location as one of the memory stimuli. Participants were required to judge whether the probe matched the orientation of the corresponding memory stimulus. In the dual-response condition, participants were required to respond sequentially to two probes. Importantly, the response order was determined by stimulus colour and was announced at the beginning of each block (e.g., pink first, or blue first), allowing participants to anticipate which memory item would be tested first. This design required participants to prioritise the memory item associated with the first response, whilst also maintaining the remaining item(s) for retrieval on the second response.

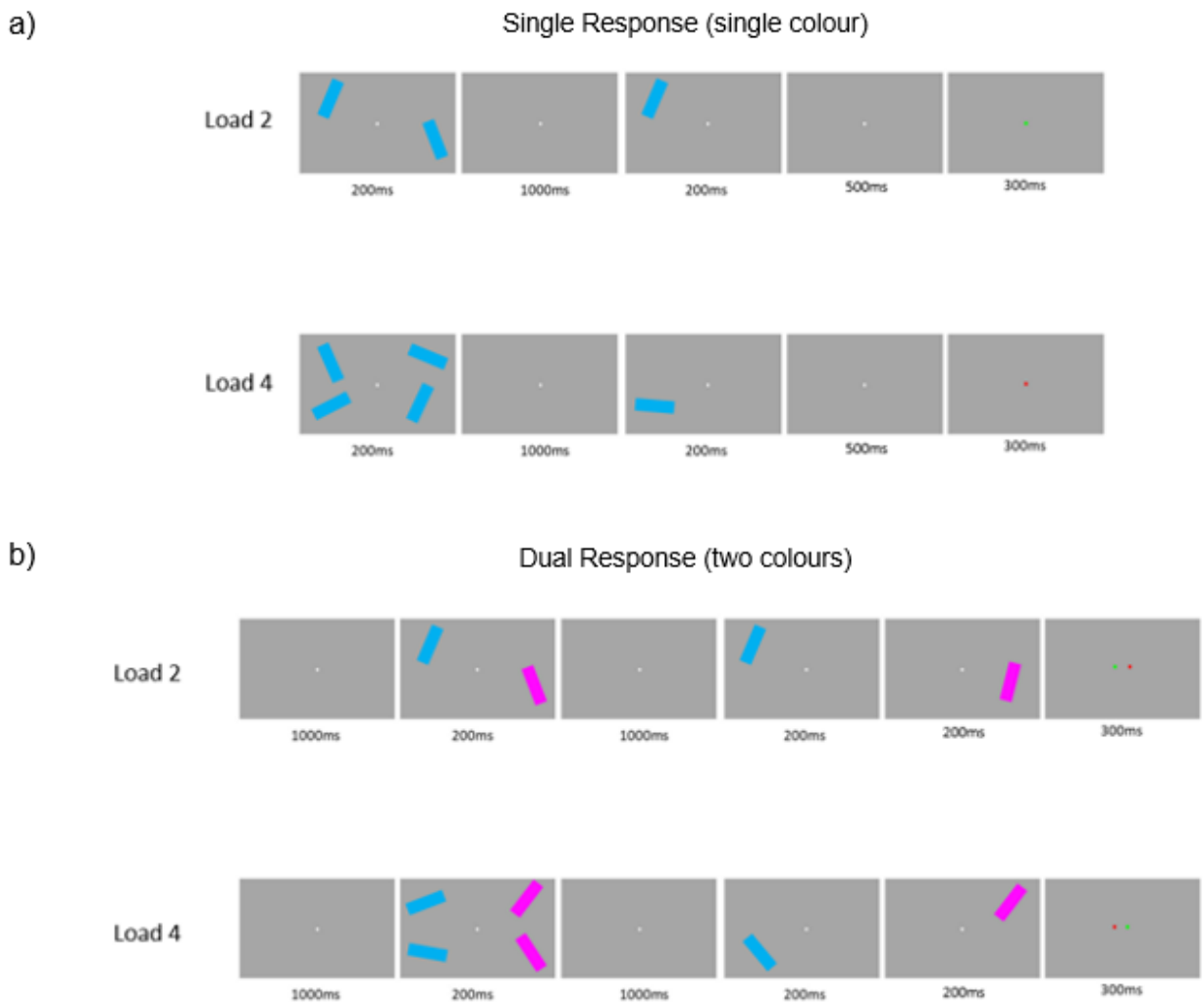
By informing participants of the response order, the task allowed participants to allocate attentional resources to the maintained representations that were relevant to the upcoming response. This also allowed us to assess individuals' ability to prioritise relevant information.

The response order was counterbalanced across blocks and announced at the beginning of the block, with either the pink or blue item(s) probed first. Accuracy (correct identification of probe as match/mismatch to memory stimulus), and reaction time were the dependent variables. Between-subject variables were ADHD group (high/low) and ADHD trait (inattention, hyperactivity). Within-subjects variables were load (2,4), experimental half

(1, 2), and task (single response, dual response). Participants completed 20 blocks in total (10 single response, 10 dual response), with block order counterbalanced across participants.

Figure 1.

Single and Dual Task Outline



Note. Figure 1a displays the task outline for the single task (involving a single colour only). Each trial contained either a total load of 2 (two stimuli of single colour) or load 4 (all four stimuli of the same colour). Blocks with blue or pink stimuli were presented in different blocks. Figure 1b displays the dual response (two colour) trial condition in which either a

total load of 2 (one stimulus of each colour) or load 4 (two stimuli of each colour) could be displayed.

Procedure

Participants were required to complete four task conditions involving encoding the orientation of either two or four rectangular stimuli randomly oriented between 0-180 degrees.

Firstly, participants completed four short practice blocks, before completing the full experiment involving 20 experimental blocks (10 single response, 10 dual response) presented in a randomized order. Each block included 24 trials, meaning 480 trials in total. The stimuli were presented for 200ms, followed by a 1000ms retention interval. A probe stimulus then appeared for 200ms in the same location as the probed memory stimulus and either matched its orientation or was rotated 30 degrees clockwise/counterclockwise. Participants were required to respond using the 'F' and 'J' keys to indicate match and mismatch (response mapping was counterbalanced across participants).

Feedback was then provided as the fixation dot changed from black to either green (indicating correct), or red (incorrect). For dual response trials, two feedback dots were displayed simultaneously (left dot = first response, right dot = second response). The interval between the first response and the onset of the second probe stimulus was 750ms. The inter-trial interval was 500ms and consisted of a blank screen. At the end of each block, participants received a summary of their average accuracy and reaction time. The experiment lasted approximately 1 hour.

Once the experiment was completed, participants completed the Adult ADHD self-report scale questionnaire (ASRS V1.1, Kessler et al., 2005).

Results

The aim of this experiment was to determine whether participants can prioritise task-relevant items in our visual working memory paradigm, and how this is affected by increased load and ADHD traits, hyperactivity and inattention.

All analyses listed below use within-subjects factors of Experimental Half (first half, second half), Condition (single response, dual response), and Load (2, 4). We focused mainly on the first response in the dual response blocks to match the single and dual response conditions.

Prioritisation Improves Accuracy and Reduces Load Effect

Higher Accuracy when Task-Relevant Items are Prioritised

A within-subjects ANOVA with Experimental Half, Condition, and Load was conducted on accuracy and revealed a significant main effect of Condition ($F(1,48) = 23.12$, $p<.001$, $\eta_p^2 = .325$), with accuracy higher in the dual-response condition ($M = .807$, $SD = .079$) than the single-response condition ($M = .770$, $SD = .087$). This effect is consisted with our hypothesis that participants can prioritise the items required for the first response in the dual-response condition, leading to improved accuracy compared to a single-response condition with the same load.

Also, a significant main effect of Experimental Half was found ($F(1,48) = 13.04$, $p<.001$, $\eta_p^2= .214$), suggesting improved accuracy in the second half of the experiment ($M = .800$, $SD = .078$) compared to the first half ($M = .777$, $SD = .088$), showing a general practice effect (see Appendix A for all condition-wise means and ANOVA effects).

Accuracy Decreases with Increased Load, but Less in the Dual-Response Condition

A strong main effect of Load was found ($F(1,48) = 558.42$, $p<.001$, $\eta_p^2 = .921$), with higher accuracy in the Load 2 condition ($M = .861$, $SD = .078$) than the Load 4 condition ($M = .716$, $SD = .089$), suggesting that increasing memory load impairs performance.

Importantly, a significant interaction between Condition and Load was observed, ($F(1,48) = 7.591$, $p=.008$, $\eta_p^2 = .137$), indicating that the effect of load on accuracy differed between the single and dual response conditions.

Post-hoc paired sample t-tests (Bonferroni corrected alpha level 0.0083) demonstrated that in the single-response condition, accuracy was significantly higher for Load 2 ($M = .852$, $SD = .080$) than Load 4 ($M = .690$, $SD = .095$, $t(48) = 17.14$, $p<.001$). For the dual-response condition, accuracy was also significantly higher for Load 2 ($M = .871$, $SD = .076$) than Load 4 ($M = .744$, $SD = .083$, $t(48) = 15.14$, $p<.001$), but the decline was significantly smaller. This interaction suggests that despite accuracy declining with increased load in both conditions, prioritisation diminished the impact of increased load in the dual-response condition.

No significant interactions were found between Experimental Half and Condition ($F(1,48) = .512$, $p=.478$, $\eta_p^2 = .011$), Experimental Half and Load ($F(1,48) = .913$, $p=.344$, $\eta_p^2 = .019$), or the three-way interaction ($F(1,48) = .090$, $p=.766$, $\eta_p^2 = .002$). Therefore prioritisation benefits and load effects were unaffected by practice.

Reaction Time Improves with Practice, but is Sensitive to Load

No Overall Dual-Response Cost in Reaction Time

A parallel within-subjects ANOVA was also conducted on reaction time, with Experimental Half, Condition, and Load as factors (Appendix B). A significant main effect of Experimental Half was found ($F(1,48) = 114.13$, $p<.001$, $\eta_p^2 = .704$), with faster responses in the second half of the experiment (M = .680, SD = .122) than the first half (M = .783, SD

= .152). A significant main effect of Load was also observed, ($F(1,48) = 122.6$, $p<.001$, $\eta_p^2 = .719$), with slower responses in the Load 4 condition (M = .767, SD = .144) than Load 2 (M = .696, SD = .130).

In contrast to Experiment 3.2, no significant main effect of Condition was found ($F(1,48) = .376$, $p = .542$, $\eta_p^2 = .008$), implying the dual-response condition did not produce an overall reaction time cost when the probed stimulus set could be anticipated.

Increasing Load Further Slows Responses in the Dual-Response Condition

A significant interaction between Condition and Load was observed ($F(1,48) = 27.65$, $p<.001$, $\eta_p^2 = .365$), suggesting the effect of load on reaction time differed between single and dual response conditions. Post-hoc paired-samples t-tests (Bonferroni corrected) revealed that in the single response condition, reaction time was significantly faster for Load 2 ($M = .704$, $SD = .120$) than Load 4 ($M = .754$, $SD = .130$, $t(48) = 6.49$, $p<.001$). Similarly, in the dual-response condition, reaction time was significantly faster for Load 2 ($M = .689$, $SD = .139$) than Load 4 ($M = .780$, $SD = .155$, $t(48) = 12.54$, $p<.001$). The significant interaction reflects that load-related slowing of reaction time was more pronounced in the dual-response condition, suggesting that maintaining and prioritising multiple items puts greater demands on attentional control processes. It may also point to a speed-accuracy tradeoff in the Load 4 dual-response condition.

Also, no significant interactions were found between Experimental Half and Condition ($F(1,48) = .111$, $p=.740$, $\eta_p^2 = .002$), Experimental Half and Load ($F(1,48) = .824$, $p=.369$, $\eta_p^2 = .017$), or the three-way interaction ($F(1,48) = .006$, $p=.937$, $\eta_p^2 = .0001$).

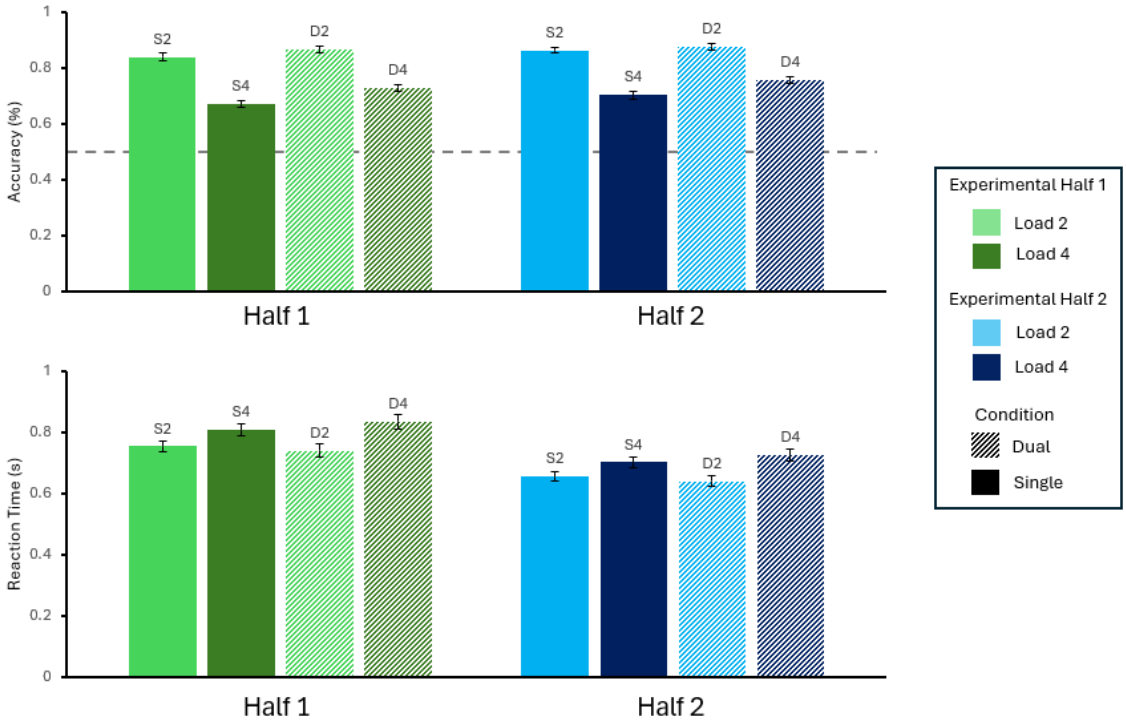
Prioritisation Benefits Accuracy and Eliminates Response Costs

Overall, these findings demonstrate that participants successfully used response order information to prioritise task-relevant items in working memory, leading to higher accuracy

in the dual-response condition and reduced impact of load. Despite increasing load slowing responses, no overall reaction time cost was associated with the dual response condition, suggesting that prioritisation after reducing the task to a single response mapping reduced the cost of maintaining more items. Also, reaction time was improved with practice and increased with load. Figure 2 displays average accuracy and reaction time data for the Response Conditions split for Experimental Half 1 and Half 2.

Figure 2.

Average Accuracy and Reaction Time split across all conditions



Note. Accuracy and Reaction Time data for Experimental Half 1 and Half 2, Load 2 and 4, and Single Task and Dual Task conditions. Participant accuracy was found to be higher in the dual task condition rather than the single task condition, with accuracy increasing in the second half of the experiment. Reaction time was also found to improve in the second half of the experiment. Error bars are SEM.

ADHD Traits Do Not Affect Accuracy, but Impact Reaction Time Under Load

No Difference in Accuracy Between High and Low ADHD Groups

To examine the effect of ADHD traits on prioritisation performance, a mixed effects ANOVA was conducted on accuracy with Experimental Half, Condition, and Load as within-subjects factors and ADHD group (high, low) as a between-subjects factor (Appendix C).

No significant main effect of ADHD group was found ($F(1,48) = 0.537$, p=.467, η_p^2= .011), and no significant interactions were found between ADHD group and Experimental Half ($F(1,48) = 2.94$, p= .093, η_p^2= .059), Condition ($F(1,48) = .689$, p = .411, η_p^2= .014), and Load ($F(1,48) = .696$, p = .408, η_p^2= .015). No significant three- or four-way interactions were observed (all p>.11), demonstrating that ADHD severity did not influence accuracy or the ability to prioritise task-relevant items.

ADHD Severity Influences Reaction Time Across Load and Response Conditions

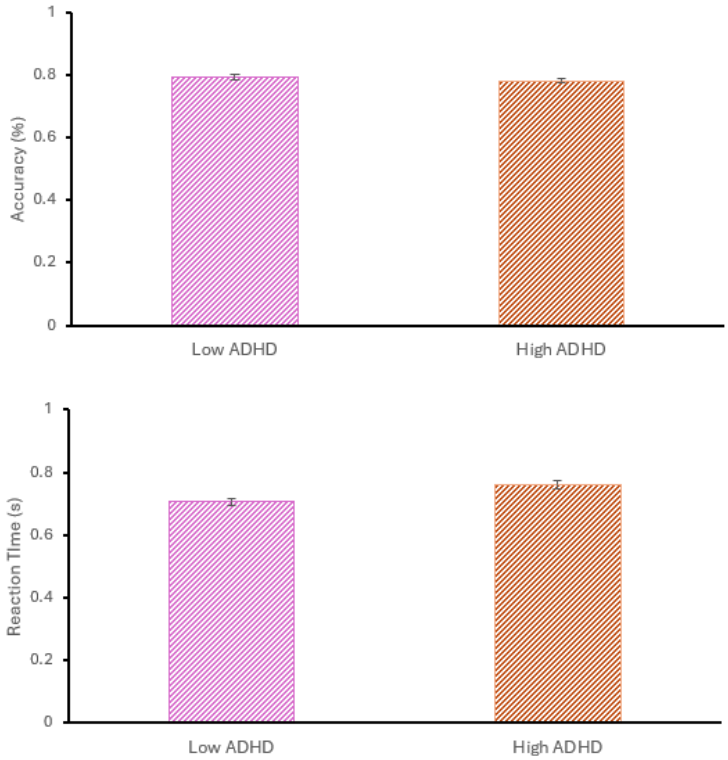
The mixed-effects ANOVA was then repeated for reaction time and found no significant main effect of ADHD group ($F(1,48) = 2.39$, p = .129, η_p^2= .048). However, a significant interaction between ADHD group and Condition was observed ($F(1,48) = 4.79$, p = .034, η_p^2= .093). In the high ADHD group, reaction times were marginally slower in the dual response condition (M = .772, SD = .160) than the single response condition (M = .750, SD = .129), whereas in the low group, responses were numerically but non-significantly faster in the dual response condition (M = .701, SD = .130) compared to the single response condition (M = .712, SD = .128). Individuals in the high ADHD group may therefore have required longer response times in the dual response condition to gain a prioritisation benefit in accuracy.

In addition, we found a significant three-way interaction between ADHD group, Load, and Condition ($F(1,48) = 8.525$, $p = .005$, $\eta_p^2 = .154$). This interaction indicates that the effect of load and condition on reaction time differed by ADHD severity.

Post-hoc paired-samples t-tests (Bonferroni corrected) showed that in the high ADHD group, reaction time was slower in the dual-response Load 4 condition ($M = .82$, $SD = .167$) than the dual-response Load 2 condition ($M = .724$, $SD = .149$, $t(48) = 9.01$, $p<.001$). The reaction time difference in the single-response conditions also differed between Load 4 ($M = .766$, $SD = .148$) and Load 2 ($M = .734$, $SD = .122$, $t(48) = 2.99$, $p=.004$), but the load effect was much smaller. In the low ADHD group, reaction time was significantly slower in the single-response Load 4 condition ($M = .744$, $SD = .129$) than the single-response Load 2 condition ($M = .679$, $SD = .114$, $t(48) = 4.54$, $p<.001$). Low ADHD participants also performed slower in the dual-response Load 4 condition ($M = .744$, $SD = .136$) than the Load 2 condition ($M = .658$, $SD = .124$, $t(48) = 6.233$, $p<.001$). Unlike the high ADHD group, load effects were comparable between single- and dual-response conditions. These results suggests that ADHD severity influences how efficiently participants can prioritise and manage increased load, particularly under the increased prioritization demands of the dual-response condition.

Figure 3.

Accuracy and Reaction Time for Low ADHD and High ADHD scorers



Note. Accuracy and Reaction Time for Low ADHD and High ADHD group.

Hyperactivity, but Not Inattention, Reduces Benefit of Prioritisation

To examine ADHD subtypes, inattention and hyperactivity scores were entered as covariates in a mixed-effects ANCOVA. For accuracy, no significant main effects were found for Inattention ($F(1,48) = 1.11$, $p = .277$, $\eta_p^2 = .026$), or Hyperactivity ($F(1,48) = 2.399$, $p = .128$, $\eta_p^2 = .051$). However, a significant interaction between Condition and Hyperactivity was found ($F(1,48) = 6.02$, $p = .018$, $\eta_p^2 = .118$), suggesting higher hyperactivity was associated with a reduced accuracy benefit in the dual-response condition. For reaction time, no significant main effects were found for Inattention or Hyperactivity (all $p > .11$).

Discussion

In this study, we examined how cognitive load and ADHD-related traits influence the prioritisation of information within a visual working memory task that required either a single response or two sequential responses. We also explored whether performance during these tasks could be improved through short-term practice. Our results demonstrate that increasing cognitive load impaired working memory performance, whereas short-term practice led to improvements in both accuracy and response speed over time. Although overall ADHD severity did not predict performance differences, we did find trait specific differences associated with hyperactivity. These findings reinforce the flexibility of working memory in adapting to task demands through prioritisation and learning.

An important finding of this study was that performance was higher in the dual-response condition compared to the single-response condition, particularly for accuracy. This appears to contradict previous literature which highlights the performance costs when attempting to perform multiple tasks concurrently (Pashler, 1994). However, it is important to note that our experiment did not involve performing two independent tasks and instead focused on participants completing a single visual working memory task that required maintaining multiple items and responding sequentially. The dual-response element allowed participants to prioritise only working memory items which were relevant for the upcoming probe (i.e., only the pink items) while maintaining the other items in a deprioritised state (Olivers et al., 2011).

While accuracy and reaction times improved in the second half, practice did not particularly improve the dual-response benefit. This suggests that priorisation appeared early on and remained stable throughout the session. Therefore, no extensive practice is required for prioritisation in this task. It is unclear why prioritisation was not a viable strategy in the first two experiments.

When exploring ADHD, there were no overall differences between high and low ADHD participants for accuracy or reaction time. This might suggest that ADHD severity did not impact performance. However, individuals with high ADHD responded slower especially in the higher load dual-response condition, suggesting that these complex task situations are more demanding for this group. Participants with lower ADHD traits instead had modestly faster reaction times in the dual-response conditions, suggesting a greater ability to allocate attentional resources. These results support the idea that ADHD is associated with difficulties in maintaining the focus of attention on information within working memory, particularly whilst having to divide attention (Kofler et al., 2011). This may result in ADHD individuals not being able to focus on and process currently relevant information effectively. However, we did not find broader accuracy deficits, suggesting that prioritisation may still remain mostly intact, with performance differences more notable in processing efficiency rather than representational reliability.

Inattention and Hyperactivity subscales of ADHD were explored in relation to accuracy and reaction time. Inattention scores were not associated with differences in accuracy or reaction time, whereas higher hyperactivity scores were found to be associated with reduced accuracy as a function of response condition. This suggests hyperactivity (rather than inattention) is more associated with performance deficits in the presence of high task demands, with hyperactivity known to cause impulsive, erratic behaviour (Gibbins et al., 2010), possibly increasing likelihood of errors when forced to manage multiple representations. Although inattention is typically emphasised in working memory literature due to its prevalence in ADHD individuals (Salvi et al., 2019), our findings suggest that hyperactivity-related traits may also play a role in performance under prioritisation demands. This is particularly relevant due to having real-life implications, with ADHD having a prevalence of almost 7% globally in the adult population (Song et al., 2021), and multitasking

being an everyday task. It is important to address the influences of this condition on everyday life as addressing the impacts of specific subscales would enable an improvement in not only diagnosis, but also treatment.

Several limitations should be considered when interpreting these results. Accuracy levels in some conditions (particularly lower load conditions) were approaching ceiling performance for some participants. This again may have reduced our ability to detect subtle effects of prioritisation, practice, or even individual differences. This could be addressed by increasing task difficulty using smaller orientation differences or shorter encoding times. Also, despite performance improving across experimental halves, suggesting short-term learning, our study failed to identify improvements that were specific to prioritisation. To address this, we could include further manipulations such as changing the response mappings mid-experiment, to isolate which cognitive processes are sensitive to short-term practice. Additionally, it may be interesting to expand this study to more complex real-life demands as prioritisation in everyday life often requires maintaining information across a variety of tasks and under time constraints. Additionally, our task focused on visual working memory, meaning extending this paradigm to verbal, auditory, or cross-modal working memory tasks could determine whether the prioritisation and practice effects found are specific to visuospatial representations, particularly as some research has suggested practice effects are different in verbal working memory tasks (Kirschen et al., 2005; McEvoy et al., 1998). Also, future research could explore the focus of attention in relation to ADHD as it is suspected these individuals may not be able to prioritise valuable information in working memory, such as by holding different items as having different values (Atkinson et al., 2025). Here we found that individual with high self-reported ADHD symptoms still exhibited prioritization benefits. Exploring the neural mechanisms underlying the prioritisation and maintenance of items within working memory, as well as how these are influenced by changing task demands

would also be interesting to explore. Recent theory suggests that prioritised WM contents may rely on sustained activity, while synaptic plasticity mechanisms may be enough to support unprioritised working memory (Kamiński & Rutishauser, 2020; Manohar et al., 2019). Exploring the neural correlates of this process would further allow us to understand the interference which arises when multiple items are being maintained within working memory and how neural interference could explain behavioural performance limitations.

In summary, across Experiments 3.1-3.3, we investigated whether prioritisation benefits emerge in visual working memory. Experiments 3.1 and 3.2 provided little evidence that prioritisation improved performance under more complex dual-task conditions, suggesting that when task demands are high and coordination requirements increase, the ability to flexibly prioritise may be constrained. Experiment 3.3 addressed this by simplifying the structure of the task whilst retaining sequential responding. Under these conditions, clear prioritisation benefits emerged. Notably, the prioritisation benefit was larger for Load 4 (5.4%) than Load 2 (1.9%), suggesting prioritisation may be more beneficial when working memory demands are greatest. This also suggests that the absence of prioritisation effects in Experiments 3.1 and 3.2 may be due to excessive task complexity and coordination demands, rather than the inability to prioritise. We successfully observed reliable short-term practice effects in Experiment 3.3, with improvements in accuracy and reaction time. As practice did not singularly enhance the prioritisation benefit, this suggests that prioritisation was implemented early and was stable throughout the experiment, rather than gradually. This suggests prioritisation to be flexibly applied when task demands require it, however this depends on the overall cognitive load and task structure. Regarding ADHD-traits, overall symptom severity did not predict impairments in accuracy. However, hyperactivity was found to interact with task condition in reaction time and was associated with reduced accuracy under high demand conditions. This indicates that despite prioritisation mechanisms

remaining largely intact in individuals with high ADHD traits, processing efficiency and performance under complex/high-load conditions may be selectively vulnerable. This chapter demonstrates that prioritisation in working memory is sensitive to task structure and load, meaning when demands are manageable, prioritisation provides clear performance advantages (particularly under high working memory load), but these diminish when tasks impose coordination demands. These findings clarify conditions under which prioritisation enhances working memory performance and demonstrates that individual differences can influence how effectively performance is maintained in demanding situations.

Chapter 4 – Does Training Help Distinguish Prioritised Working Memory Representations via Subspace Orthogonalisation? A Preregistration.

Chapter Summary

This chapter outlines a pre-registered EEG experiment examining how training influences the representational relationship between prioritised and unprioritised working memory items. Previous evidence suggests prioritisation may involve gain-based enhancement or reformatting into more orthogonal subspaces, but learning effects have not been explored. Effector-specific maintenance of working memory representations may further support training-based orthogonalisation. Here we propose to distinguish between these possibilities with a study using a two-item task with a priority cue and a manipulation of response effector configuration. Simulated results demonstrate that our analysis plan can distinguish gain changes from reduced representational overlap. This study will explore whether extended training reduces cross-condition generalisation between prioritised and unprioritised items as a result of orthogonalisation between items, and whether these changes can predict reduced behavioural interference, bridging experience-dependent changes in neural coding to performance benefits in working memory.

Introduction

Working memory (WM) allows for the temporary retention of information yet its capacity is limited to only a small number of items. The source of this capacity limit has been debated for decades (Fougnie & Marois, 2011). Among several explanations for capacity limitations (Baddeley, 1986; Cowan, 2001, 2012; Luck & Vogel, 1997; Oberauer et al., 2016), two prominent proposals are that either WM relies on a fixed number of memory slots, or that multiple items interfere with one another through competitive interactions. In the slot-based accounts, representations can be maintained independently until available slots are filled. Alternatively, capacity limits may arise from mutual interference between concurrently held items, with competition for shared neural resources occurring even before item capacity is reached.

Early computational models of WM proposed that the storage of simple features in WM (e.g., spatial locations maintained across a delay) can be implemented via persistent firing of tuned memory cells in an attractor state (Amit & Brunel, 1997; Compte, 2006). When multiple memory items are encoded within the same attractor population, their representations have reduced precision and, if the items are similar enough, repel each other or even merge into a single attractor bump (Edin et al., 2009; Wei et al., 2012). These models have assumed that when multiple items are encoded within the same neural population, this creates inter-item competition.

Consistent with this single-population account, empirical work suggests competitive interactions between concurrently stored items in WM, including spiking patterns of prefrontal neurons in non-human primates (Buschman et al., 2011) and in BOLD activation patterns in visual and parietal regions in humans (Sprague et al., 2016). However, more recent work suggests that multiple WM contents can be simultaneously encoded within the same overall neural population whilst occupying relatively orthogonal activity dimensions.

For example, when multiple spatial locations are maintained for a sequential WM task, activity in the PFC can represent items in distinct subspaces depending on their position in the sequence (Chen et al., 2024; Tian et al., 2024; Xie et al., 2022). In a sequential WM task performed by mice, medial PFC activity encoded future goal locations in independent slot-like activity patterns (El-Gaby et al., 2024). Similarly, non-spatial stimuli features can be maintained in orthogonal patterns when encountered at different spatial locations (Wolff et al., 2020), potentially relying on spatially organised representations in sensory brain regions. Modelling work has shown that relatively simple networks can learn to maintain information in largely independent activity subspaces (Botvinick & Plaut, 2006; Bouchacourt & Buschman, 2019; Wang et al., 2025).

To optimise the limited capacity of WM, we can prioritise items that are likely to be relevant for an upcoming action (Cowan, 2000; Griffin & Nobre, 2003; Oberauer, 2002). The neural mechanism of item prioritisation in the brain is still poorly understood. Recent work has proposed that unprioritised items may be maintained in activity-silent states that minimally impact behaviour (Lewis-Peacock et al., 2012; Rose et al., 2016; Stokes, 2015; Wolff et al., 2017). Others suggest that prioritisation reflects an activity boost for prioritised items, potentially at the expense of unprioritised items (Schneegans & Bays, 2017; Sprague et al., 2016; Watanabe & Funahashi, 2014), resulting in reduced but persistent activity of unprioritised items (Barbosa et al., 2021).

Alternatively, prioritised WM contents could be maintained in a representational format which is independent from other concurrently stored contents via rotation into an orthogonal activity subspace or, by representing them in a different brain area (Christophel et al., 2018). Panichello and Buschman (2021) recorded activity of neurons in the prefrontal and parietal cortex of macaques performing a colour WM task and found that priority cues led to rotation of the cued content into a subspace that was orthogonal to both the uncued item

representation and the pre-cue activity patterns. Computational models of WM prioritisation have reproduced this mechanism (Piwek et al., 2023; Wan et al., 2020, 2022, 2024; Whittington et al., 2025). A key consequence of orthogonalisation is that a readout mechanism tuned only to the prioritised subspace can retrieve the prioritised WM content without interference from other concurrently held items. The presence of orthogonalisation can be identified using cross-condition generalisation. A multivariate pattern classifier trained to decode the prioritised/cued item should generalise poorly to unprioritised/uncued representations (if orthogonal). Alternatively, a prioritisation-based boost of activity without changing the representational format should lead to positive cross-condition generalisation. Finally, suppression of the unprioritised item (inverting its population activity pattern) could yield negative cross-condition generalisation (Stokes et al., 2020). However, unlike orthogonalisation, it is unclear how these mechanisms would prevent interference from unprioritised WM representations without disrupting maintenance of the unprioritized items.

The majority of human neuroimaging WM prioritisation studies have not provided clear support for prioritisation-by-orthogonalisation. Some studies found that unprioritised WM contents are not decodable, preventing direct tests of orthogonalisation (LaRocque et al., 2013; Lewis-Peacock et al., 2012). Studies that successfully found decoding of both prioritised and unprioritised items have found positive cross-generalisation (Iamshchinina et al., 2021; Muhle-Karbe et al., 2021) or negative cross-generalisation (van Loon et al., 2018; Yu et al., 2020).

A recent study using human single-unit recordings provides a potential solution to the inconsistent findings above (Paluch et al., 2025). In a 2-item visual WM task requiring prioritisation of one of the items, medial temporal lobe neurons were more active when a preferred stimulus was prioritised, but still fired above baseline when it was unprioritised (compared to when it was not maintained at all). This pattern was also reflected at the neural

population level because activity contained a shared activity subspace between both the prioritised and unprioritised item representations. Importantly, population activity also contained separate subspaces that were unique to the prioritised and unprioritised items alone. This combination of shared and unique representational subspaces could explain the positive cross-generalisation in some human studies, whilst still allowing for priority-dependent separation in others.

However, the existence of both shared and unique subspaces does not explain why some studies in overtrained animals often report near-complete orthogonality between representations (Panichello & Buschman, 2021; Tian et al., 2024; Xie et al., 2022). One possibility is that extensive task practice leads to neural WM representations that are increasingly optimised for selective readout, producing stronger orthogonalisation. Humans with minimal training may only achieve partial orthogonalisation (Muhle-Karbe et al., 2021; Paluch et al., 2025). Overtraining humans has also been found to lead neural task representations to more closely resemble those of extensively trained non-human primates (Takagi et al., 2021), but the effect of training on neural orthogonalisation has not yet been explored.

A growing body of research suggests that working memory representations can reflect prospective action plans, and that it is not simply a sensory buffer but interacts dynamically with motor preparation mechanisms. It is suggested that what we remember is influenced by how we plan to use this information. Boettcher et al. (2021) showed that the neural representation of a remembered stimulus changes when its associated response effector is known, with distinct motor preparatory activity emerging early in the delay period. This suggests that working memory maintenance incorporates effector-specific planning, linking sensory representations to the motor system. Similarly, Gresch et al. (2025) found retrospective cues to elicit effector-specific shifts in neural activity. Prioritisation of one item

was found to involve preparatory activity in motor networks specific to the anticipated response. This suggests that prioritisation may not only amplify the representation of cued items, but may also embed anticipatory motor codes which differentiate items at the prospective action level. Henderson et al. (2022) also showed that when working memory items are associated with distinct action goals, their representations become more separable in sensorimotor networks. This was manifested as distinct patterns of motor planning activity, suggesting action-specific representation can help partition items and may reduce interference between them.

These findings imply that response preparation contributes to how WM representations are coded in the brain. If competing working memory items are mapped onto the same effector (e.g., both planned responses use the same hand), then their neural codes may be more overlapping, increasing the chance of interference. Conversely, if items are associated with different effectors (e.g., one response with the left hand and one with the right hand), then their sensorimotor representations may be more distinct. This could potentially induce representational separation or orthogonalisation, not simply within perceptual coding but through effector-specific motor planning. At the neural level, this predicts that different-effector response blocks should show reduced cross-condition generalisation between prioritised and unprioritised representations relative to the same effector blocks, particularly prior to extended training. If this is observed, it would suggest that effector specific coding contributes to representational independence. Alternatively, if different effectors fail to significantly reduce cross-generalisation, this would suggest that orthogonalisation arises primarily within the sensory or higher-order cognitive systems, which are independent of response planning.

We propose that training on a visual working memory prioritisation task will reduce cross-condition generalisation between prioritised and unprioritised contents, without

necessarily changing overall decoding of either representation. This pattern would provide support for the prioritisation-by-orthogonalisation hypothesis. Alternatively, if prioritisation is primarily achieved by strengthening activity of the prioritised item at the expense of the unprioritised representation, we should expect a shift in decoding, with an increase in decoding of the prioritised and a decrease in decoding of the unprioritised item. Importantly, both patterns could be the result of training. Nevertheless, we predict that only the reduced cross-condition generalisation will be associated with reduced interference from the unprioritised item, as measured by performance on prioritised trials approaching performance on one-item trials.

Figure 1

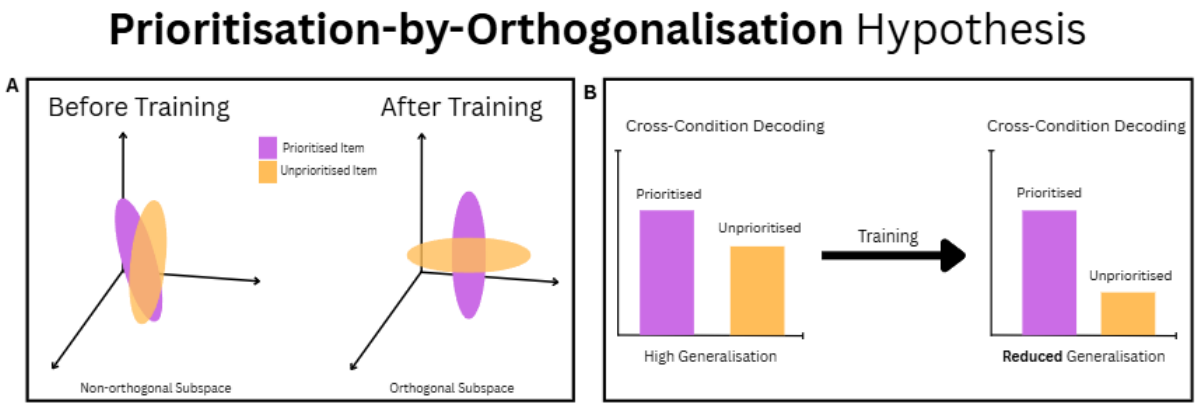


Figure 1. Representation of the prioritisation-by-orthogonalisation hypothesis. A. Before training (left), neural representations of the prioritised and unprioritised working memory items occupy partially overlapping activity subspaces, leading to cross-condition generalisation and interference. After training (right), the representation of the unprioritised item is rotated to an orthogonal neural subspace relative to the prioritised item. B. This reduced representational overlap results in a diminished cross-condition generalisation (bars represent decoding after training a classifier on prioritised items only). The overall decoding of each item may remain stable.

Methods

Design

This study will employ a within-subjects design to explore how training influences neural representations of prioritised and unprioritised items in visual working memory. Participants will complete a visual working memory paradigm involving two-items requiring prioritisation of one item for immediate retrieval whilst maintaining a second item for later. Participants will complete two EEG recordings: one pre-training and one post-training. Participants will complete 10 hours of training on the same task between these EEG sessions. This training will allow us to assess whether repeated exposure to prioritisation demands leads to changes in the representational structure of working memory contents.

During the task, two visual stimuli will be presented sequentially at the same spatial location. Two memory stimuli will vary in colour, either blue or pink. A priority retro-cue will be presented after encoding to indicate which item will be probed first, requiring participants to prioritise this item whilst maintaining the other item in an unprioritised state, which will allow for direct comparison between the prioritised and unprioritised representations. After the first response the previously unprioritised item will be probed. The probe stimuli will consist of bars presented at fixation with orientations sampled randomly from 0-180° and independent of the memory orientations. Participants will have to judge whether the probe is rotated clockwise or counterclockwise compared to the corresponding memory item. Importantly, probe orientations will be uncorrelated with the memory orientations to ensure that the orientation decoding during the probe window (200-400ms) reflects the reinstatement of the remembered item (rather than sensory-driven responses to the probe). Response mappings will be counterbalanced across participants and feedback will be provided following each trial.

We will also manipulate response effector configuration across blocks. This will mean in some blocks, both responses will be made using the same hand, while in other blocks the first and second response will be made with different hands. This manipulation allows us to test whether effector-specific coding contributes to the separation of prioritised and unprioritised working memory representation by reducing response-level competition between item representations.

We will measure the neural decoding accuracy for the prioritised and unprioritised items, as well as condition cross-generalisation between prioritised and unprioritised representations using MVPA of the EEG data. Accuracy and reaction time will also be recorded to assess behavioural training effects, and whether changes in neural representational overlap are associated with a reduction in behavioural interference from the unprioritised items. The design allows us to test whether training reduces the representational overlap between prioritised and unprioritised working memory items, and if this is consistent with prioritisation-by-orthogonalisation. We will also test whether neural interference is reduced by using different response effectors to recall the prioritised and unprioritised items.

Figure 2

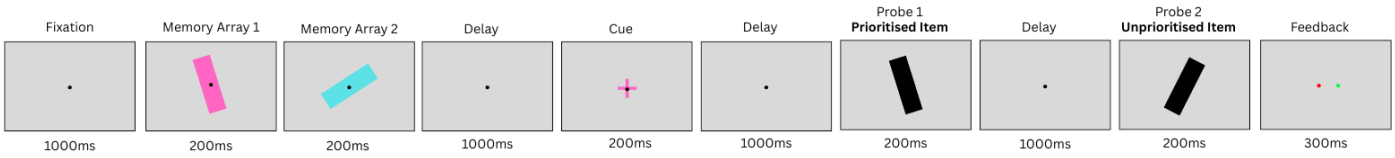


Figure 2. Two memory stimuli (differing in colour and orientation) will be presented sequentially at fixation (for 200ms each) to maximise spatial overlap between representations. This will be followed by a delay period of 1000ms. The retrocue will then be presented for 200ms and indicate which item will be probed first. This is followed by another delay of 1000ms. The first probe will then be presented for 200ms (or until response) and will

always be the prioritised item. Following another delay period of 1000ms, the second probe will then be presented for 200ms (or until response, the second probe will always be the unprioritised item). Feedback is then provided for both probes, with the fixation point turning from black to green signifying a correct response, or to red signifying incorrect.

Participants

We plan to recruit 45 healthy adult participants from the University of Nottingham. Participants will have normal or corrected-to-normal vision and will provide written informed consent in accordance with University of Nottingham ethical guidelines.

The planned sample size was determined using an a priori power analysis based on effect sizes from a prior EEG study of visual working memory decoding. Specifically, we used cross-decoding estimated from Muhle-Karbe et al. (2021), which closely resembles the primary neural measure of interest in our study (cross-generalisation between prioritised and unprioritised working memory representations). In this dataset, cross-decoding from prioritised to unprioritised representations in the 200-400ms window following probe onset yielded a mean decoding value of 0.0279 (SD = 0.0431), corresponding to an effect size of Cohen's d = 0.65. A power analysis for a within-subjects comparison (two-tailed, $\alpha = .05$, power = .80) indicates a required sample of 24 participants for a similar effect. As we aim to detect changes in cross-decoding following training, and as EEG data are prone to participant loss due to artifacts, we increased this estimate. Participants will be excluded if they fail to complete both EEG sessions, have excessive EEG artifacts after preprocessing, and/or poor task performance (suggesting failure to engage with the task and leading to near-chance accuracy).

Materials

The experiment will be programmed and presented using PsychoPy (Peirce et al., 2019) and presented on a 27-inch monitor (2560 x 1440 resolution, background luminance = 0.5, grey) with a refresh rate of 100Hz. The memory stimuli will consist of rectangular bars presented centrally on the screen with an orientation sampled from a continuous space across 0-180°. The bars will be displayed at fixation to maximise representational overlap and minimise spatial separation (Wolff et al., 2020).

Procedure

This study will include three phases: the first pre-training EEG session, a 10-hour training phase, and a second post-training EEG session. During each EEG session, participants will complete the two-item visual working memory task. Participants will complete 25 blocks in total with 60 trials per block.

Response effector configuration will also be manipulated across blocks. In blocks with the same effector, both responses will be made using the same response hand. In different-effector blocks, the first and second responses will be made using different hands. Block order will be counterbalanced across participants and sessions.

Between the EEG sessions, participants will be asked to complete 10 hours of training on the working memory task. Training will be completed across multiple sessions and the task will include the same prioritisation demands and response structure but will not include any EEG recording. This training phase will increase the participants familiarity with the task structure and prioritisation demands, allowing us to test whether extended practice leads to changes in the neural representations of prioritised and unprioritised working memory contents.

Figure 3.

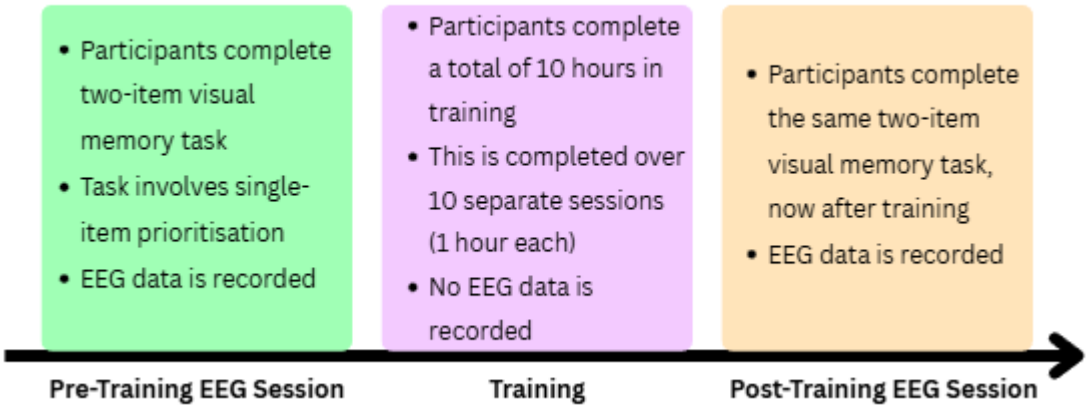


Figure 3. Structure for each session of the experiment including the Pre-Training EEG Session, the Training Session, and the Post-Training EEG Session. The initial Pre-Training EEG Session involves participants completing the experiment whilst EEG data are recorded. Participants will then complete a total of 10 hours of training, spread over 10 sessions. Following this, participants will complete a second EEG session post-training, involving the same visual working memory task.

EEG Recording

EEG data will be recorded using a BioSemi ActiveTwo EEG system from 64 scalp electrodes. Eye movements will be recorded using an EyeLink 1000 Plus system. Six external electrodes will be placed on the participant, including left and right HEOG, right upper and lower VEOG, and left and right mastoids.

Data Analysis Plan

EEG Preprocessing

EEG preprocessing will follow the same steps described in Chapter 2. The continuous EEG data will be visually inspected to identify recording issues (extreme drift, disconnected

channels). Data will then be downsampled to 250Hz and re-referenced to the average of left and right mastoids.

The EEG channels will be bandpass filtered (0.1-40Hz) to reduce drift and high-frequency noise, but preserve event-related activity needed for decoding. EOG channels will be bandpass filtered between 0.1-25Hz. Bad channels (identified by flat-lining, high-frequency noise or extreme variance) will be removed prior to ICA. After ICA and artefact correction, these removed channels will be interpolated. Participants will be excluded if more than 10 of the 64 scalp electrodes (15%) are identified as bad prior to interpolation in either session. Data will then be epoched and the primary epochs for decoding will be time-locked to memory stimulus onset and through to the encoding and maintenance period, as well as the probe window (200-400ms). Baseline correction will be applied prior to multivariate decoding and will be performed for stimulus-locked and probe-locked epochs from -200 to 0ms window.

Prior to ICA, epochs containing artefacts will be identified through visual inspection and removed. This will prevent large artefacts from biasing ICA decomposition. This will include trials with muscle noise and movement artefacts. This will be a combination of manual inspection and automation. Automated trial rejection will be applied to continuous data epoched around memory stimulus onset (-200 to 1500ms) and trials will be marked for rejection if a scalp channel exceeds ±100 μV or if low-frequency drifts exceed 0.5Hz threshold limits. Flagged channels will then be visually inspected to confirm artefactual contamination and manual inspection of unflagged trials will be conducted to identify large muscle artefacts or movement artefacts not detected automatically. ICA will then be performed on the concatenated epochs to further remove artefacts. Prior to ICA, data may be high-pass filtered at 1Hz to improve decomposition stability. Components showing blinks,

saccades, and muscle artefacts will be identified using scalp topography, component time-course and power spectrum characteristics. Artefact components will be removed.

Following ICA correction, remaining noisy trials will then be identified using FieldTrip's semi-automatic visual rejection tool (ft_rejectvisual). Trial-wise variance across channels will be computed, and trials exceeding the ±3 standard deviations ($z > |3|$) from the participants mean variance will be marked for rejection. Trials will be removed if they contain residual artefacts and the final number of trials per condition and session will be reported. Participants will need to have a minimum of 70% of trials in both sessions to be included in the analysis. Also, eye-tracking data will be used as a secondary check to confirm fixation compliance of participants.

EEG Analysis

We will use an established method of orientation decoding in EEG data (Muhle-Karbe et al., 2021; Myers et al., 2026; Wolff et al., 2020a; Wolff et al., 2020b) to test the coding of prioritised and unprioritised working memory representations in EEG activity patterns. We will explore within-condition decoding of prioritised and unprioritised stimulus orientations, and cross-decoding between prioritised and unprioritised representations. This will be conducted separately for the pre-training and post-training EEG sessions, and will be compared across sessions and response effector configuration blocks (same effector, different effectors).

Decoding will be performed using a Mahalanobis distance approach and analyses will be conducted separately for each time point. We will use cross-validation by splitting the data into a training set (90% of task blocks) and a test set (remaining 10%). For the within-condition decoding, trials from the training set will be grouped according to the orientation of the prioritised item or the unprioritised item. Stimulus orientations will be binned into 16

non-overlapping orientation bins from 0-180°. We will compute the average EEG pattern for each orientation bin at each time point. We will then subtract from each training trial the corresponding orientation-bin mean to calculate residual signals on each trial after removing orientation-specific signal. This will allow us to estimate the noise covariance of the training data, separately for each time point, using a shrinkage estimator (Ledoit & Wolf, 2004). We will then compute the Mahalanobis distance between each held-out test trial pattern and each of the orientation-bin averages.

For each test trial, the vector of 16 distances will be shifted circularly so that the centre bin corresponds to the bin containing the test trial orientation. The distance vector will be inverted so that larger values mean greater similarity. We will compute a decoding index using a cosine-weighted sum of the distance vector (Sprague et al., 2016; Wolff et al., 2017). The training-test split will then be repeated until all trials have been used as the test set. Trial-wise decoding time courses will be averaged to yield a decoding time course per participant and condition and will be tested using one-sample t-tests at each time point. We will also used cluster-based permutation tests to correct for multiple tests.

To test the cross-condition generalisation of prioritised and unprioritised representations, we will train the decoder on one representational state and test on the other. Prioritised-to-unprioritised cross-decoding will involve training the trials by the prioritised item orientation and testing them using the unprioritised item orientation. Unprioritised-to-prioritised cross-decoding will involve training trials on the unprioritised item orientation, and testing on the prioritised item orientation. Reduced cross-decoding after training and preserved within-condition decoding will suggest reduced overlap between representational formats, consistent with increased orthogonalisation.

Expected Results

We expect to find training to improve overall performance with an increase in accuracy and reduction in reaction time across sessions. If training results in more efficient prioritisation, then performance for the prioritised probe should be less affected by needing to maintain the second item. This should result in improved prioritised accuracy, faster prioritised reaction time after training, and reduced costs when maintaining the unprioritised item. We also expect effector configuration to influence this. If effector-specific coding is involved in the separation of neural representations, then different-effector blocks should result in reduced interference compared to same-effector blocks (especially prior to training). However, post-training we expect a smaller difference between the effector conditions if practice does in fact promote the separation of representations even in the same-effector blocks.

We also expect decodability of both the prioritised and unprioritised items to be present in the EEG signal, with stronger decoding found for the prioritised item. Under prioritisation-by-orthogonalisation, training should lead to a reduction in cross-condition generalisation between prioritised and unprioritised representations (without needing reduced decoding strength of the unprioritised item). Therefore, we expect a pattern consistent with stable/improved within-condition decoding of both items, with a reduction in cross-decoding.

Alternatively, training could produce increased decoding of the prioritised item and decreased decoding of the unprioritised item, and a resulting reduction in cross-decoding in both directions.

If reduced cross-generalisation is linked to a reduction in interference, then participants who show a larger decrease in cross-condition generalisation following training should also show larger behavioural improvements (greater increases in prioritised accuracy

and/or greater reductions in reaction time). We will therefore test the correlation between Also, if effector-specific coding contributes to increased independence, then this relationship may be stronger in different-effector blocks.

Simulations

To test whether our proposed analysis approach can identify increased orthogonalisation and differentiate it from a reduction in decoding of the unprioritised item, we simulated neural activity patterns and submitted them to our cross-decoding analysis. Our aim was to simulate data containing neural activity patterns corresponding to a prioritised ('cued') and unprioritised ('uncued') WM item. Following the results of Paluch et al., 2025, we assumed that three distinct populations encode the two items: one population exclusively encodes the cued item, one population exclusively encodes the uncued item, and a shared population encodes both items in an overlapping code. Because we are interested in changes to the uncued item, for simplicity we ignored the cued-exclusive population. We therefore created one population subspace for the uncued item, and one shared subspace encoding both the cued and the uncued item.

Each stimulus was encoded as a two-dimensional vector encoding the cosine and sine of the stimulus orientation. This stimulus vector was then projected into a higher dimensional space representing the distributed activity pattern across 60 EEG sensors. To this end, we created a 2x60 matrix of random weights. The first row of this matrix (1x60) was drawn from a standard normal distribution. The second row was drawn from a standard normal distribution with the constraint that it was uncorrelated with the first row, ensuring that the resulting projection into the 60-dimensional activity space remained 2-dimensional. We created one 2x60 weight matrix $\mathbf{w}_{\text{unique}}$ to represent the uncued-only subspace, and another matrix $\mathbf{w}_{\text{shared}}$ to represent the shared subspace.

We simulated activity patterns as the weighted sum of (1) the cued item projected into the shared activity subspace, (2) the uncued item projected into the shared subspace, and (3) the uncued item projected into the unique subspace. We added noise drawn from a standard normal distribution at each timepoint, resulting in activity

$$r_{t,\theta_{cued},\theta_{uncued}}$$
$$= [\cos(\theta_{cued})\ \sin(\theta_{cued})]\, w_{shared} \quad + [\cos(\theta_{uncued})\ \sin(\theta_{uncued})] w_{shared} a_{uncued} a_{shared}$$
$$+ [\cos(\theta_{uncued})\ \sin(\theta_{uncued})] w_{unique} a_{uncued} (1 - a_{shared}) + \eta_t$$

where $\mathbf{r}_{t,\theta cued,\theta uncued}$ is the 60-dimensional activity pattern at timepoint *t* with stimulus orientations θ_{cued} and θ_{uncued}, a_{uncued} is the relative amplitude of the uncued item representation (as a proportion of the strength of the cued representation, ranging from 0 to 1), a_{shared} is the relative amplitude of the uncued item in the shared subspace (ranging from 0 to 1), and η_t is random noise for each at timepoint *t*.

We simulated a standard experiment by creating 30 artificial 'participants', each defined by different weight matrices $\mathbf{w}_{shared}$ and $\mathbf{w}_{unique}$. For each 'participant' we simulated 2,000 trials, with the uncued and cued orientation on each trial drawn from a uniform circular distribution. Data were spatially smoothed by convolving the data with a Gaussian kernel of 2-channel width.

We then decoded the cued and uncued orientation from the simulated data. To assess the effect of subspace overlap we additionally cross-decoded between the cued and uncued orientations, i.e., we trained a decoder to identify the cued orientation and tested how well it generalised to decoding the uncued orientation.

Decoding analyses were conducted using all simulated channels and were conducted separately for each time point. We calculated the average response of the simulated EEG data across all 60 channels to different stimulus orientations and calculated the Mahalanobis-distance-based decoding measure described above. Additionally, we examined cross-decoding from cued to uncued orientations by sorting the training trials into orientation bins according to their cued orientation and then centering the tuning curve on the bin nearest the uncued orientation on each test trial. To cross-decode from uncued to cued orientations we did the opposite (sort training trials by uncued orientation and centre on the bin nearest the cued orientation on each test trial).

Simulation Results

We simulated two potential effects of training: First, we modelled a change in the amplitude of the uncued orientation signal a_{uncued} (relative to the cued orientation), ranging from 0 (i.e., no representation of the uncued orientation at all) to 1 (same amplitude as the cued orientation. Second, we orthogonally varied the relative amount of uncued signal amplitude in the shared subspace a_{shared} (relative to the subspace uniquely coding the uncued item), again ranging from 0 (unique coding only) to 1 (shared coding only).

Figure 4 shows the effect of varying both parameters on decoding of the cued and uncued orientation and on cross-decoding (cued-to-uncued and vice versa). In general, an increase in the shared subspace (increased a_{shared}) led to reductions in decoding of the cued and uncued item (top two panels, presumably due to increased interference between overlapping representations in the shared subspace) but to improved cross-decoding between the two (bottom two panels). An increase in decoding of the uncued item (increased a_{uncued}) led to a concomitant reduction in decoding of the cued item (and increase in cross-decoding from uncued to cued item), provided the subspace overlap was sufficient.

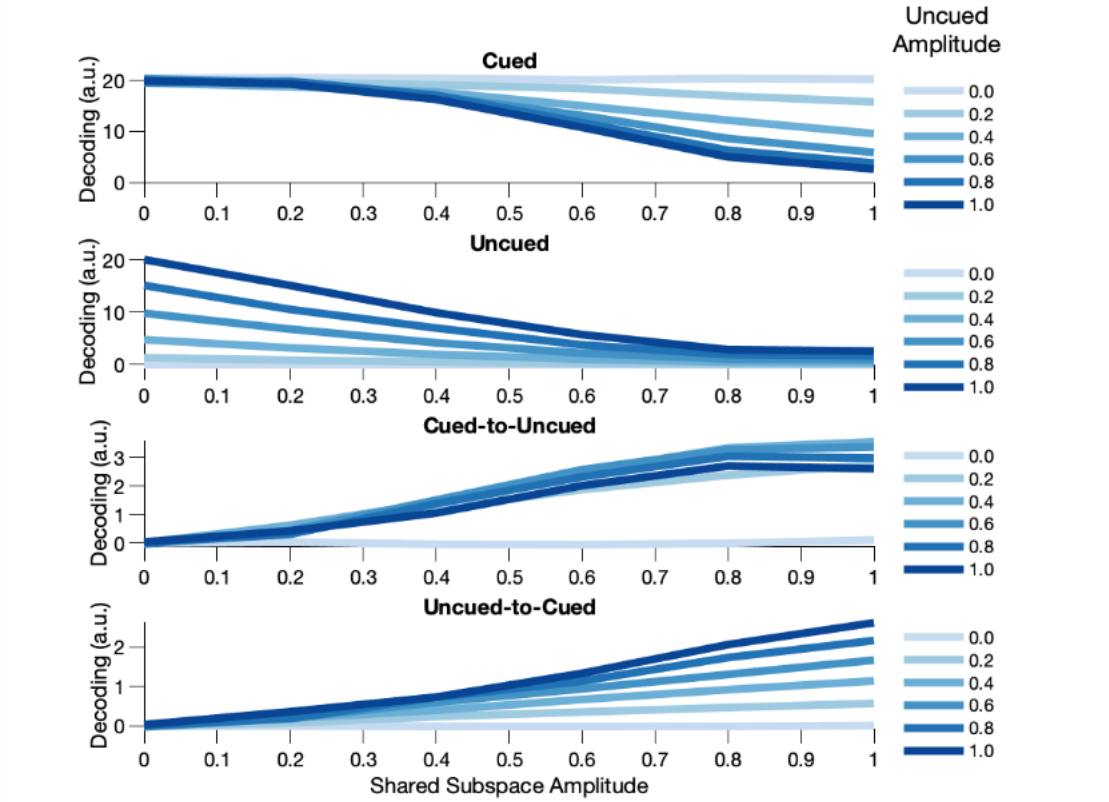


Figure 4. Simulated cross-decoding results for a range of uncued decoding amplitudes a_{uncued} *(different lines) and a range of relative amplitudes in the shared subspace* a_{shared} *(increasing along x-axis).*

We next examined separately the two putative training effects of reducing subspace overlap and of reducing relative decoding of the uncued item by regressing each change against decoding of each measure. A reduction in subspace overlap between the cued and uncued item (i.e., reduction along the x-axis in Figure 4) with no change in overall uncued decoding magnitude led to an increase in decoding of both the cued and uncued decoding, while cross-decoding (in either direction, i.e., from cued to uncued and from uncued to cued) was reduced (Figure 5, left panel). The cross-decoding reduction was especially pronounced in the Cued-to-Uncued direction (possibly owing to the better training signal of the cued item leading to higher cross-decoding, see Figure 4).

By contrast, an overall reduction in decoding of the uncued item (with no change in overlap, i.e., moving vertically from a dark blue line to a lighter blue line in Figure 4) leads to a *reduction* in decoding of the uncued item, an increase in decoding of the cued item, and comparable reductions in cross-decoding from uncued to cued and cued to uncued items. In other words, across the four measures the two effects produce dissociable patterns of change.

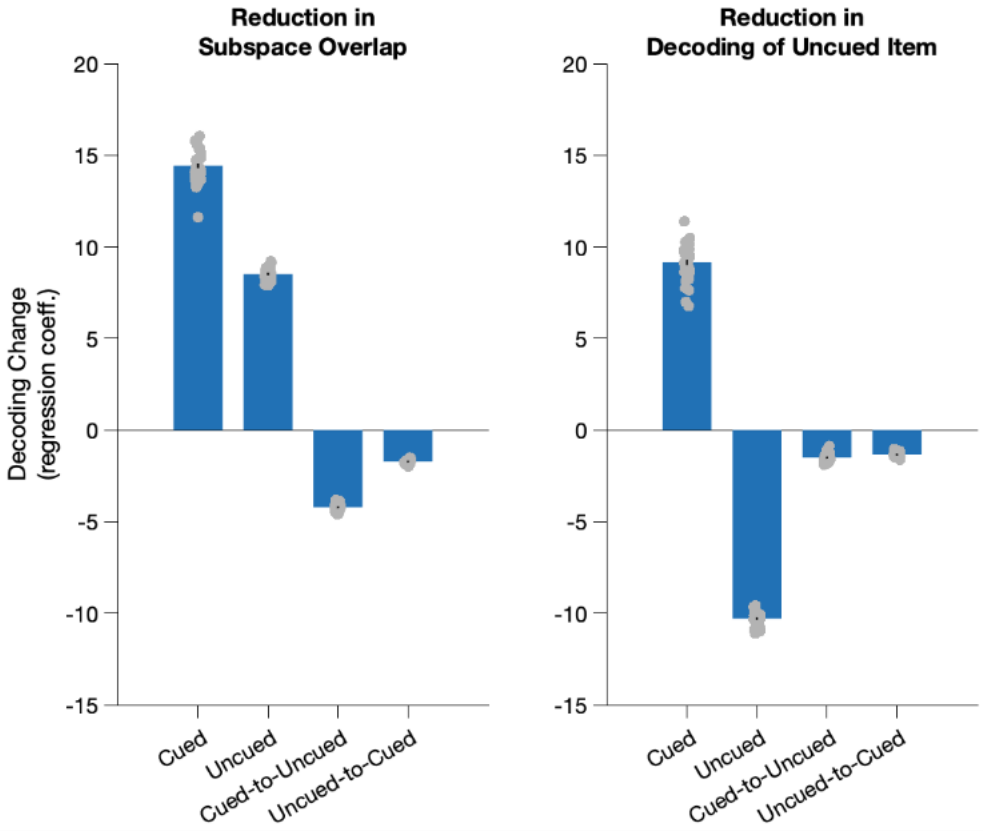


Figure 5. Dissociable effects of changes in subspace overlap vs reduced decoding. A reduction in subspace overlap improves overall decoding of both cued and uncued items and reduces cross-decoding (left panel). By contrast, a reduction in decoding of the uncued item reduced decoding of the uncued item, with a smaller effect on cross-decoding (right panel).

These simulated results suggest that the proposed within- and cross-decoding approach can identify the distinct changes which may occur after training, namely reduced representational overlap between prioritised and unprioritised items (reduced cross-condition generalisation alongside maintained or improved within-condition decoding) and reduced representational strength of unprioritised item (reduction in the decoding of uncued item).

Significance

This pre-registered experiment is designed to explore how training could improve the brain's ability to resolve interference within working memory when multiple items are concurrently maintained but vary in priority. We aim to examine whether neural representations become increasingly independent through experience using extended practice and effector manipulation, and whether this depends partly on response preparation. Reduced cross-condition generalisation after training would suggest prioritisation can be achieved by orthogonalising representations.

General Conclusion

This thesis aimed to examine how working memory prioritises information under capacity limits and how the brain manages this information under conditions which introduce competition such as conflicting categorisation rules, conflicting response mappings, or prioritisation requirements. Collectively, our findings indicate that performance limitations are better explained by interference between representations can be resolved under different tasks demands, rather than the idea of a fixed capacity limit.

A recurring theme found throughout this thesis is that neural and cognitive representations are flexible. Chapter 2 demonstrated that neural category representations in humans adapted selectively when interference was introduced. For independent stimulus sets, neural representations generalised across tasks, consistent with multitasking representations. However, when stimulus-level conflict was introduced, these representations reorganised themselves to reduce cross-task generalisation. Importantly, previously learned representations remained mostly unchanged, suggesting that the cognitive system preserves efficient solutions when possible and only introduces separation when necessary.

Chapter 3 further extends this into visual working memory, showing that increases in load and changes in response demands modulate performance consistent with interference-based accounts. Prioritisation benefits were most evident when response mappings were structured in a consistent way, whereas more complex response demands appeared to reduce these effects. Crucially, short-term practice led to overall improvements in accuracy and reaction time. However, practice did not reduce the load effect, suggesting that whilst participants became more efficient at performing the task, short-term learning did not alter the degree of interference between maintained representations. Individual differences related to ADHD traits were also observed. Whilst overall performance did not differ with self-reported ADHD severity, specific effects of hyperactivity emerged under demanding conditions. Across

experiments, load was consistently found to be detrimental to performance. However, when task demands allowed for efficient prioritisation (such as Experiment 3.3), we found benefits to emerge under higher load, and ADHD-related differences were most prominent in demanding conditions. This suggests that performance reflects an interaction between storage demands and control processes, rather than simply capacity limitations.

This supports the idea that representations are not fully ‘shared’ or fully ‘independent’, but instead are flexibly organised depending on task structure, learning, and task goals. This helps clarify contradictory previous findings, suggesting that representations are reused when effective, but become more distinct when interference poses an issue. This thesis highlights the importance of considering interference, prioritisation, and representational structure when exploring limitations of cognition. Rather than focusing on the number of items which can be held or processed, future research may benefit from exploring how information is structured, protected, and transformed as task demands change.

References

Aben, B., Stapert, S., & Blokland, A. (2012). About the distinction between working memory and short-term memory. Frontiers in psychology, 3, 301. https://doi.org/10.3389/fpsyg.2012.00301

Adam, K. C. S., Awh, E., & Serences, J. T. (2025). Distributed and drifting signals for working memory load in human cortex. bioRxiv : the preprint server for biology, 2025.09.15.676305. https://doi.org/10.1101/2025.09.15.676305

Adams, E. J., Nguyen, A. T., & Cowan, N. (2018). Theories of Working Memory: Differences in Definition, Degree of Modularity, Role of Attention, and Purpose. Language, Speech, and Hearing Services in Schools, 49(3), 340-355. https://doi.org/10.1044/2018_LSHSS-17-0114

Adler, L. A., Faraone, S. V., Sarocco, P., Atkins, N., & Khachatryan, A. (2019). Establishing US norms for the Adult ADHD Self-Report Scale (ASRS-v1. 1) and characterising symptom burden among adults with self-reported ADHD. International journal of clinical practice, 73(1), e13260. https://doi.org/10.1111/ijcp.13260

Agethen, M., & Krause, D. (2012). Reduced dual task interference in multiple repeated dual-task tests: Automatization or task integration?. Current Research in Motor Control IV, 8.

Alderson, R. M., Kasper, L. J., Hudec, K. L., & Patros, C. H. (2013). Attention-deficit/hyperactivity disorder (ADHD) and working memory in adults: a meta-analytic review. Neuropsychology, 27(3), 287. https://doi.org/10.1037/a0032371

Alleman, M., Panichello, M. F., Buschman, T. J., & Johnston, W. J. (2024). The neural basis of swap errors in working memory. Proceedings of the National Academy of Sciences, 121(33), e2401032121. https://doi.org/10.1073/pnas.2401032121

Amit, D. J., & Brunel, N. (1997). Dynamics of a recurrent network of spiking neurons before and following learning. Network: Computation in Neural Systems, 8(4), 373-404. https://doi.org/10.1088/0954-898X_8_4_003

Andersen, R. A., & Cui, H. (2009). Intention, action planning, and decision making in parietal-frontal circuits. Neuron, 63(5), 568-583. https://doi.org/10.1016/j.neuron.2009.08.028

Arterberry, M. E., & Bornstein, M. H. (2002). Infant perceptual and conceptual categorization: The roles of static and dynamic stimulus attributes. Cognition, 86(1), 1-24. https://doi.org/10.1016/S0010-0277(02)00108-7

Atkinson, A. L., Pinheiro Sanchez, B., Warburton, M., Allmark, H., & Allen, R. J. (2025). The Ability to Direct Attention in Working Memory Is Not Impaired in Adults With Symptoms of ADHD. Journal of Attention Disorders, 10870547251330039. https://doi.org/10.1177/10870547251330039

Atkinson, R. C., & Shiffrin, R. M. (1968). Human memory: A proposed system and its control processes. In K. W. Spence & J. T. Spence (Eds.), The psychology of learning and motivation (Vol. 2, pp. 89-195). Academic Press. https://doi.org/10.1016/S0079-7421(08)60422-3

Baddeley, A. D. (2000). The episodic buffer: A new component of working memory? Trends in Cognitive Sciences, 4(11), 417-423. https://doi.org/10.1016/S1364-6613(00)01538-2

Baddeley, A. (1992). Working memory: The interface between memory and cognition. Journal of cognitive neuroscience, 4(3), 281-288. https://doi.org/10.1162/jocn.1992.4.3.281

Baddeley, A. (2003). Working memory and language: An overview. Journal of communication disorders, 36(3), 189-208. https://doi.org/10.1016/S0021-9924(03)00019-4

Baddeley, A. (2007). Working memory, thought, and action (Vol. 45). OuP Oxford.. https://doi.org/10.1093/acprof:oso/9780198528012.001.0001

Baddeley, A. (2010). Working memory. Current Biology, 20(4), R136-R140. https://doi.org/10.1016/j.cub.2009.12.014

Baddeley, A. (2012). Working memory: Theories, models, and controversies. Annual review of psychology, 63(1), 1-29. https://doi.org/10.1146/annurev-psych-120710-100422

Baddeley, A. D. (1997). Human memory: Theory and practice. psychology press. https://doi.org/10.3109/09593989709036469

Baddeley, A. D., & Hitch, G. (1974). Working memory. In The Psychology of learning and motivation/The psychology of learning and motivation (pp. 47-89). https://doi.org/10.1016/S0079-7421(08)60452-1

Barbosa, J., Lozano-Soldevilla, D., & Compte, A. (2021). Pinging the brain with visual impulses reveals electrically active, not activity-silent, working memories. *PLOS Biology*, *19*(10), e3001436. https://doi.org/10.1371/journal.pbio.3001436

Barkley, R. A. (1997). Behavioral inhibition, sustained attention, and executive functions: constructing a unifying theory of ADHD. Psychological bulletin, 121(1), 65. https://doi.org/10.1037/0033-2909.121.1.65

Barrouillet, P., Bernardin, S., & Camos, V. (2004). Time constraints and resource sharing in adults' working memory spans. Journal of experimental psychology: General, 133(1), 83. https://doi.org/10.1037/0096-3445.133.1.83

Basile, B. M., & Hampton, R. R. (2013). Recognition errors suggest fast familiarity and slow recollection in rhesus monkeys. Learning & Memory, 20(8), 431-437. https://doi.org/10.1101/lm.029223.112

Bays, P. M. (2015). Spikes not slots: noise in neural populations limits working memory. Trends in cognitive sciences, 19(8), 431-438. https://doi.org/10.1016/j.tics.2015.06.004

Berryhill, M. E., Richmond, L. L., Shay, C. S., & Olson, I. R. (2012). Shifting Attention among Working Memory Representations: Testing Cue Type, Awareness, and Strategic Control. Quarterly Journal of Experimental Psychology, 65(3), 426-438. https://doi.org/10.1080/17470218.2011.604786

Bhandari, A., & Duncan, J. (2014). Goal neglect and knowledge chunking in the construction of novel behaviour. Cognition, 130(1), 11-30. https://doi.org/10.1016/j.cognition.2013.08.013

Binder, J. R., Desai, R. H., Graves, W. W., & Conant, L. L. (2009). Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. Cerebral cortex (New York, N.Y. : 1991), 19(12), 2767-2796. https://doi.org/10.1093/cercor/bhp055

Boettcher, S. E. P., Gresch, D., Nobre, A. C., & van Ede, F. (2021). Output planning at the input stage in visual working memory. Science Advances, 7(9), eabe8212. https://doi.org/10.1126/sciadv.abe8212

Botvinick, M. M., & Plaut, D. C. (2006). Short-term memory for serial order: a recurrent neural network model. Psychological review, 113(2), 201. https://doi.org/10.1037/0033-295X.113.2.201

Bouchacourt, F., & Buschman, T. J. (2019). A flexible model of working memory. Neuron, 103(1), 147-160. https://doi.org/10.1016/j.neuron.2019.04.020

Bougou, V., Vanhoyland, M., Bertrand, A., Van Paesschen, W., Op De Beeck, H., Janssen, P., & Theys, T. (2024). Neuronal tuning and population representations of shape and category in human visual cortex. Nature communications, 15(1), 4608. https://doi.org/10.1038/s41467-024-49078-3

Brainard, D. H. (1997). The Psychophysics Toolbox. Spatial Vision, 10(4), 433-436. https://doi.org/10.1163/156856897X00357

Braver T. S. (2012). The variable nature of cognitive control: a dual mechanisms framework. Trends in cognitive sciences, 16(2), 106-113. https://doi.org/10.1016/j.tics.2011.12.010

Broadbent, D. P., Giorgia D'Innocenzo, Ellmers, T. J., Parsler, J., Szameitat, A. J., & Bishop, D. T. (2023). Cognitive load, working memory capacity and driving performance: A preliminary fNIRS and eye tracking study. Transportation Research Part F Traffic Psychology and Behaviour, 92, 121-132. https://doi.org/10.1016/j.trf.2022.11.013

Brunoni, A. R., & Vanderhasselt, M. A. (2014). Working memory improvement with non-invasive brain stimulation of the dorsolateral prefrontal cortex: a systematic review and meta-analysis. Brain and cognition, 86, 1-9. https://doi.org/10.1016/j.bandc.2014.01.008

Buchsbaum, B. R. (2016). Working memory and language. In Neurobiology of language (pp. 863-875). Academic Press. https://doi.org/10.1016/B978-0-12-407794-2.00069-9

Buschman, T. J. (2021). Balancing Flexibility and Interference in Working Memory. Annual Review of Vision Science, 7(1), 367-388. https://doi.org/10.1146/annurev-vision-100419-104831

Buschman, T. J., Siegel, M., Roy, J. E., & Miller, E. K. (2011). Neural substrates of cognitive capacity limitations. Proceedings of the National Academy of Sciences, 108(27), 11252-11255. https://doi.org/10.1073/pnas.1104666108

Cairo, T. A., Liddle, P. F., Woodward, T. S., & Ngan, E. T. (2004). The influence of working memory load on phase specific patterns of cortical activity. Cognitive Brain Research, 21(3), 377-387. https://doi.org/10.1016/j.cogbrainres.2004.06.014

Caldani, S., Razuk, M., Septier, M., Barela, J. A., Delorme, R., Acquaviva, E., & Bucci, M. P. (2019). The Effect of Dual Task on Attentional Performance in Children With ADHD. Frontiers in integrative neuroscience, 12, 67. https://doi.org/10.3389/fnint.2018.00067

Carruthers, P. (2013). Evolution of working memory. Proceedings of the National Academy of Sciences, 110(supplement_2), 10371-10378. https://doi.org/10.1073/pnas.1301195110

Chai, W. J., Abd Hamid, A. I., & Abdullah, J. M. (2018). Working memory from the psychological and neurosciences perspectives: a review. Frontiers in psychology, 9, 401. https://doi.org/10.3389/fpsyg.2018.00401

Chaisangmongkon, W., Swaminathan, S. K., Freedman, D. J., & Wang, X. J. (2017). Computing by robust transience: how the fronto-parietal network performs sequential, category-based decisions. Neuron, 93(6), 1504-1517. https://doi.org/10.1016/j.neuron.2017.03.002

Chein, J. M., Moore, A. B., & Conway, A. R. (2011). Domain-general mechanisms of complex working memory span. Neuroimage, 54(1), 550-559. https://doi.org/10.1016/j.neuroimage.2010.07.067

Chen, J., Zhang, C., Hu, P., Min, B., & Wang, L. (2024). Flexible control of sequence working memory in the macaque frontal cortex. Neuron, 112(20), 3502-3514.e6. https://doi.org/10.1016/j.neuron.2024.07.024

Christophel, T. B., Hebart, M. N., & Haynes, J. D. (2012). Decoding the contents of visual short-term memory from human visual and parietal cortex. Journal of Neuroscience, 32(38), 12983-12989. https://doi.org/10.1523/JNEUROSCI.0184-12.2012

Christophel, T. B., Klink, P. C., Spitzer, B., Roelfsema, P. R., & Haynes, J. D. (2017). The distributed nature of working memory. Trends in cognitive sciences, 21(2), 111-124. https://doi.org/10.1016/j.tics.2016.12.007

Cocchini, G., Logie, R. H., Della Sala, S., MacPherson, S. E., & Baddeley, A. D. (2002). Concurrent performance of two memory tasks: evidence for domain-specific working memory systems. Memory & cognition, 30(7), 1086-1095. https://doi.org/10.3758/BF03194326

Collette, F., Hogge, M., Salmon, E., & Van der Linden, M. (2006). Exploration of the neural substrates of executive functioning by functional neuroimaging. Neuroscience, 139(1), 209-221. https://doi.org/10.1016/j.neuroscience.2005.05.035

Collins, A., & Koechlin, E. (2012). Reasoning, learning, and creativity: frontal lobe function and human decision-making. PLoS biology, 10(3), e1001293. https://doi.org/10.1371/journal.pbio.1001293

Compte, A. (2006). Computational and in vitro studies of persistent activity: edging towards cellular and synaptic mechanisms of working memory. Neuroscience, 139(1), 135-151. https://doi.org/10.1016/j.neuroscience.2005.06.011

Conway, A. R., Kane, M. J., Bunting, M. F., Hambrick, D. Z., Wilhelm, O., & Engle, R. W. (2005). Working memory span tasks: A methodological review and user's guide. Psychonomic bulletin & review, 12, 769-786. https://doi.org/10.3758/BF03196772

Coolidge, F. L. (2023). Parietal lobe expansion, its consequences for working memory, and the evolution of modern thinking. Elsevier EBooks, 181-194. https://doi.org/10.1016/B978-0-323-99193-3.00002-7

Cotton, K., Sandry, J., & Ricker, T. J. (2024). The Effects of Mind-Wandering, Cognitive Load, and Task Engagement on Working Memory Performance in Remote Online Experiments. Experimental Psychology, 70(5), https://doi.org/10.1027/1618-3169/a000599

Courtney, S. M., Ungerleider, L. G., Keil, K., & Haxby, J. V. (1997). Transient and sustained activity in a distributed neural system for human working memory. Nature, 386(6625), 608-611. https://doi.org/10.1038/386608a0

Cowan N. (2001). The magical number 4 in short-term memory: a reconsideration of mental storage capacity. The Behavioral and brain sciences, 24(1), 87-185. https://doi.org/10.1017/S0140525X01003922

Cowan N. (2010). The Magical Mystery Four: How is Working Memory Capacity Limited, and Why?. Current directions in psychological science, 19(1), 51-57. https://doi.org/10.1177/0963721409359277

Cowan N. (2014). Working Memory Underpins Cognitive Development, Learning, and Education. Educational psychology review, 26(2), 197-223. https://doi.org/10.1007/s10648-013-9246-y

Cowan N. An embedded-processes model of working memory. In: Miyake A, Shah P, editors. Models of Working Memory: Mechanisms of Active Maintenance and Executive Control. Cambridge, UK: Cambridge University Press; 1999. pp. 62-101. https://doi.org/10.1017/CBO9781139174909.006

Cowan, N. (1988). Evolving conceptions of memory storage, selective attention, and their mutual constraints within the human information-processing system. Psychological bulletin, 104(2), 163. https://doi.org/10.1037/0033-2909.104.2.163

Cowan, N. (1996). Short-term memory, working memory, and their importance in language processing. Topics in language disorders, 17(1), 1-18. https://doi.org/10.1097/00011363-199611000-00003

Cowan, N. (1998). Attention and memory: An integrated framework. Oxford University Press. https://doi.org/10.1093/acprof:oso/9780195119107.001.0001

Cowan, N. (1999). An embedded-processes model of working memory. Models of working memory: Mechanisms of active maintenance and executive control, 20(506), 1013-1019. https://doi.org/10.1017/CBO9781139174909.006

Cowan, N. (2005). Working Memory Capacity (1st ed.). Psychology Press. https://doi.org/10.4324/9780203342398

Cowan, N. (2008). Chapter 20 What are the differences between long-term, short-term, and working memory? Progress in Brain Research, 323-338. https://doi.org/10.1016/S0079-6123(07)00020-9

Cromer, J. A., Roy, J. E., & Miller, E. K. (2010). Representation of Multiple, Independent Categories in the Primate Prefrontal Cortex. Neuron, 66(5), 796-807. https://doi.org/10.1016/j.neuron.2010.05.005

Cuenen, A., Jongen, E. M., Brijs, T., Brijs, K., Houben, K., & Wets, G. (2016). Effect of a working memory training on aspects of cognitive ability and driving ability of older drivers: Merits of an adaptive training over a non-adaptive training. Transportation research part F: traffic psychology and behaviour, 42, 15-27. https://doi.org/10.1016/j.trf.2016.06.012

Curtis, C. E., & D'Esposito, M. (2003). Persistent activity in the prefrontal cortex during working memory. Trends in cognitive sciences, 7(9), 415-423.. https://doi.org/10.1016/S1364-6613(03)00197-9

Daneman, M., & Carpenter, P. A. (1980). Individual differences in working memory and reading. Journal of verbal learning and verbal behavior, 19(4), 450-466. https://doi.org/10.1016/S0022-5371(80)90312-6

Daroff, R. B., & Aminoff, M. J. (2014). Encyclopedia of the neurological sciences. Academic press.

DeGutis, J., & D'Esposito, M. (2007). Distinct mechanisms in visual category learning. Cognitive, Affective, & Behavioral Neuroscience, 7(3), 251-259. https://doi.org/10.3758/CABN.7.3.251

Dellu-Hagedorn, F. (2006). Relationship between impulsivity, hyperactivity and working memory: a differential analysis in the rat. Behavioral and Brain Functions, 2, 1-18. https://doi.org/10.1186/1744-9081-2-10

Derrfuss, J., Ekman, M., Hanke, M., Tittgemeyer, M., & Fiebach, C. J. (2017). Distractor-resistant short-term memory is supported by transient changes in neural stimulus representations. Journal of Cognitive Neuroscience, 29(9), 1547-1565. https://doi.org/10.1162/jocn_a_01141

Desimone, R. (1998). Visual attention mediated by biased competition in extrastriate visual cortex. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 353(1373), 1245-1255. https://doi.org/10.1098/rstb.1998.0280

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. Annual review of neuroscience, 18(1), 193-222. https://doi.org/10.1146/annurev.ne.18.030195.001205

D'Esposito, M., & Postle, B. R. (1999). The dependence of span and delayed-response performance on prefrontal cortex. Neuropsychologia, 37(11), 1303-1315. https://doi.org/10.1016/S0028-3932(99)00021-4

D'Esposito, M., & Postle, B. R. (2015). The cognitive neuroscience of working memory. Annual review of psychology, 66(1), 115-142. https://doi.org/10.1146/annurev-psych-010814-015031

D'Esposito, M., Postle, B. R., & Rypma, B. (2000). Prefrontal cortical contributions to working memory: evidence from event-related fMRI studies. Experimental brain research, 133(1), 3-11. https://doi.org/10.1007/s002210000395

Diamond, A. (2013). Executive functions. Annual Review of Psychology, 64, 135-168. https://doi.org/10.1146/annurev-psych-113011-143750

Diester, I., & Nieder, A. (2007). Semantic associations between signs and numerical categories in the prefrontal cortex. PLoS biology, 5(11), e294. https://doi.org/10.1371/journal.pbio.0050294

Dreisbach, G., Goschke, T., & Haider, H. (2007). The role of task rules and stimulus-response mappings in the task switching paradigm. Psychological research, 71(4), 383-392. https://doi.org/10.1007/s00426-005-0041-3

Duan, Y., Zhan, J., Gross, J., Ince, R. A., & Schyns, P. G. (2024). Pre-frontal cortex guides dimension-reducing transformations in the occipito-ventral pathway for categorization behaviors. Current Biology, 34(15), 3392-3404. https://doi.org/10.1016/j.cub.2024.06.050

Duncan, J., Parr, A., Woolgar, A., Thompson, R., Bright, P., Cox, S., Bishop, S., & Nimmo-Smith, I. (2008). Goal neglect and Spearman's g: competing parts of a complex task. Journal of experimental psychology. General, 137(1), 131-148. https://doi.org/10.1037/0096-3445.137.1.131

Duncan, J., Schramm, M., Thompson, R., & Dumontheil, I. (2012). Task rules, working memory, and fluid intelligence. Psychonomic bulletin & review, 19, 864-870. https://doi.org/10.3758/s13423-012-0225-y

Ebbinghaus, H. (1885). Über das gedächtnis: untersuchungen zur experimentellen psychologie. Duncker & Humblot.

El-Gaby, M., Harris, A. L., Whittington, J. C. R., Dorrell, W., Bhomick, A., & Behrens, T. E. J. (2024). A cellular basis for mapping behavioural structure. Nature, 625, 1050-1057. https://doi.org/10.1038/s41586-024-08145-x

Ellmers, T. J., Cocks, A. J., Doumas, M., Williams, A. M., & Young, W. R. (2016). Gazing into thin air: the dual-task costs of movement planning and execution during adaptive gait. PloS one, 11(11), e0166063. https://doi.org/10.1371/journal.pone.0166063

Endo, N., Saiki, J., Nakao, Y., & Saito, H. (2003). Perceptual judgments of novel contour shapes and hierarchical descriptions of geometrical properties. Japanese Journal of Psychology. https://doi.org/10.4992/jjpsy.74.346

Engel, A. K., Fries, P., & Singer, W. (2001). Dynamic predictions: oscillations and synchrony in top-down processing. Nature Reviews Neuroscience, 2(10), 704-716. https://doi.org/10.1038/35094565

Engle, R. W. (2002). Working memory capacity as executive attention. Current directions in psychological science, 11(1), 19-23. https://doi.org/10.1111/1467-8721.00160

Engle, R. W., Tuholski, S. W., Laughlin, J. E., & Conway, A. R. A. (1999). Working memory, short-term memory, and general fluid intelligence: a latent-variable approach. Journal of experimental psychology. General, 128(3), 309-331. https://doi.org/10.1037//0096-3445.128.3.309

Eriksen, B. A., & Eriksen, C. W. (1974). Effects of noise letters upon the identification of a target letter in a nonsearch task. Perception & psychophysics, 16(1), 143-149. https://doi.org/10.3758/BF03203267

Ester, E. F., Serences, J. T., & Awh, E. (2009). Spatially global representations in human primary visual cortex during working memory maintenance. Journal of Neuroscience, 29(48), 15258-15265. https://doi.org/10.1523/JNEUROSCI.4388-09.2009

Ester, E. F., Sprague, T. C., & Serences, J. T. (2015). Parietal and frontal cortex encode stimulus-specific mnemonic representations during visual working memory. Neuron, 87(4), 893-905. https://doi.org/10.1016/j.neuron.2015.07.013

Ewen, J. B., Moher, J. S., Lakshmanan, B. M., Ryan, M., Xavier, P., Crone, N. E., … Mahone, E. M. (2012). Multiple Task Interference is Greater in Children With ADHD. Developmental Neuropsychology, 37(2), 119-133. https://doi.org/10.1080/87565641.2011.632459

Eysenck, M. W., & Calvo, M. G. (1992). Anxiety and performance: The processing efficiency theory. Cognition & emotion, 6(6), 409-434. https://doi.org/10.1080/02699939208409696

Eysenck, M. W., Derakshan, N., Santos, R., & Calvo, M. G. (2007). Anxiety and cognitive performance: attentional control theory. Emotion, 7(2), 336. https://doi.org/10.1037/1528-3542.7.2.336

Fabio, R. A., Bianco, M., Caprì, T., Marino, F., Ruta, L., Vagni, D., & Pioggia, G. (2020). BMC Psychiatry, 20(1). https://doi.org/10.1186/s12888-020-02677-y

Fang, W., Jiang, X., Chen, J., Zhang, C., & Wang, L. (2025). Oscillatory control over representational geometry of sequence working memory in macaque frontal cortex. Current Biology, 35(7), 1495-1507. https://doi.org/10.1016/j.cub.2025.02.031

Feredoes, E., Heinen, K., Weiskopf, N., Ruff, C., & Driver, J. (2011). Causal evidence for frontal involvement in memory target maintenance by posterior brain areas during distracter interference of visual working memory. Proceedings of the National Academy of Sciences of the United States of America, 108(42), 17510-17515. https://doi.org/10.1073/pnas.1106439108

Fitzgerald, J. K., Freedman, D. J., & Assad, J. A. (2011). Generalized associative representations in parietal cortex. Nature neuroscience, 14(8), 1075-1079. https://doi.org/10.1038/nn.2878

Flesch, T., Balaguer, J., Dekker, R., Nili, H., & Summerfield, C. (2018). Comparing continual task learning in minds and machines. Proceedings of the National Academy of Sciences, 115(44), E10313-E10322. https://doi.org/10.1073/pnas.1800755115

Flesch, T., Juechems, K., Dumbalska, T., Saxe, A., & Summerfield, C. (2022). Orthogonal representations for robust context-dependent task performance in brains and neural networks. Neuron, 110(7), 1258-1270.e11. https://doi.org/10.1016/j.neuron.2022.01.005

Flesch, T., Nagy, D. G., Saxe, A., & Summerfield, C. (2023). Modelling continual learning in humans with Hebbian context gating and exponentially decaying task signals. PLoS computational biology, 19(1), e1010808. https://doi.org/10.1371/journal.pcbi.1010808

Folstein, J. R., Palmeri, T. J., & Gauthier, I. (2013). Category learning increases discriminability of relevant object dimensions in visual cortex. Cerebral cortex (New York, N.Y. : 1991), 23(4), 814-823. https://doi.org/10.1093/cercor/bhs067

Fougnie, D. (2008). The relationship between attention and working memory. New research on short-term memory, 1, 45.

Fougnie, D., & Marois, R. (2009). Dual-task interference in visual working memory: a limitation in storage capacity but not in encoding or retrieval. Attention, perception & psychophysics, 71(8), 1831-1841. https://doi.org/10.3758/APP.71.8.1831

Fougnie, D., & Marois, R. (2011). What limits working memory capacity? Evidence for modality-specific sources to the simultaneous storage of visual and auditory arrays. Journal of experimental psychology. Learning, memory, and cognition, 37(6), 1329-1341. https://doi.org/10.1037/a0024834

Freedman, D. J., & Assad, J. A. (2006). Experience-dependent representation of visual categories in parietal cortex. Nature, 443(7107), 85-88. https://doi.org/10.1038/nature05078

Freedman, D. J., Riesenhuber, M., Poggio, T., & Miller, E. K. (2001). Categorical representation of visual stimuli in the primate prefrontal cortex. Science (New York, N.Y.), 291(5502), 312-316. https://doi.org/10.1126/science.291.5502.312

Frisch, S., Förstl, S., Legler, A., Schöpe, S., & Goebel, H. (2012). The interleaving of actions in everyday life multitasking demands. Journal of neuropsychology, 6 2, 257-69 . https://doi.org/10.1111/j.1748-6653.2012.02026.x

Funahashi, S. (2006). Prefrontal cortex and working memory processes. Neuroscience, 139(1), 251-261. https://doi.org/10.1016/j.neuroscience.2005.07.003

Funahashi, S. (2017). Working memory in the prefrontal cortex. Brain sciences, 7(5), 49. https://doi.org/10.3390/brainsci7050049

Funahashi, S., Bruce, C. J., & Goldman-Rakic, P. S. (1989). Mnemonic coding of visual space in the monkey's dorsolateral prefrontal cortex. Journal of neurophysiology, 61(2), 331-349. https://doi.org/10.1152/jn.1989.61.2.331

Fuster, J. M. (2001). The prefrontal cortex-an update: time is of the essence. Neuron, 30(2), 319-333. https://doi.org/10.1016/S0896-6273(01)00285-9

Fuster, J. M., & Alexander, G. E. (1971). Neuron activity related to short-term memory. Science (New York, N.Y.), 173(3997), 652-654. https://doi.org/10.1126/science.173.3997.652

Fuster, J. M., & Jervey, J. P. (1982). Neuronal firing in the inferotemporal cortex of the monkey in a visual memory task. Journal of Neuroscience, 2(3), 361-375. https://doi.org/10.1523/JNEUROSCI.02-03-00361.1982

Garner, K. G., & Dux, P. E. (2015). Training conquers multitasking costs by dividing task representations in the frontoparietal-subcortical system. Proceedings of the National Academy of Sciences, 112(46), 14372-14377. https://doi.org/10.1073/pnas.1511423112

Garner, K. G., & Dux, P. E. (2023). Knowledge generalization and the costs of multitasking. Nature Reviews Neuroscience, 24(2), 98-112. https://doi.org/10.1038/s41583-022-00653-x

Gibbins, C., Weiss, M. D., Goodman, D. W., Hodgkins, P. S., Landgraf, J. M., & Faraone, S. V. (2010). ADHD-hyperactive/impulsive subtype in adults. Mental illness, 2(1), e9. https://doi.org/10.4081/mi.2010.e9

Gibson, B. S., Gondoli, D. M., Flies, A. C., Dobrzenski, B. A., & Unsworth, N. (2009). Application of the Dual-Component Model of Working Memory to ADHD. Child Neuropsychology, 16(1), 60-79. https://doi.org/10.1080/09297040903146958

Gilchrist AL, Cowan N, Naveh-Benjamin M. Working memory capacity for spoken sentences decreases with adult aging: Recall of fewer, but not smaller chunks in older adults. Memory. (2008);16:773-787 https://doi.org/10.1080/09658210802261124

Gluck, M. A., Poldrack, R. A., & Kéri, S. (2008). The cognitive neuroscience of category learning. Neuroscience and biobehavioral reviews, 32(2), 193-196. https://doi.org/10.1016/j.neubiorev.2007.11.002

Goldman-Rakic, P. S. (1987). Circuitry of Primate Prefrontal Cortex and Regulation of Behavior by Representational Memory. Comprehensive Physiology, 373-417. https://doi.org/10.1002/cphy.cp010509

Green, J. G., DeYoung, G., Wogan, M. E., Wolf, E. J., Lane, K. L., & Adler, L. A. (2019). Evidence for the reliability and preliminary validity of the Adult ADHD Self-Report Scale v1.1 (ASRS v1.1) Screener in an adolescent community sample. International journal of methods in psychiatric research, 28(1), e1751. https://doi.org/10.1002/mpr.1751

Gresch, D., Behnke, L., Van Ede, F., Nobre, A. C., & Boettcher, S. E. (2025). Neural dynamics of reselecting visual and motor contents in working memory after external interference. Journal of Neuroscience, 45(18). https://doi.org/10.1523/JNEUROSCI.2347-24.2025

Griffin, I. C., & Nobre, A. C. (2003). Orienting attention to locations in internal representations. Journal of cognitive neuroscience, 15(8), 1176-1194. https://doi.org/10.1162/089892903322598139

Gurnani, H., & Cayco Gajic, N. A. (2023). Signatures of task learning in neural representations. Current opinion in neurobiology, 83, 102759. https://doi.org/10.1016/j.conb.2023.102759

Harrison, S. A., & Tong, F. (2009). Decoding reveals the contents of visual working memory in early visual areas. Nature, 458(7238), 632-635. https://doi.org/10.1038/nature07832

Hazeltine, E., Ruthruff, E., & Remington, R. W. (2006). The role of input and output modality pairings in dual-task performance: Evidence for content-dependent central interference. Cognitive psychology, 52(4), 291-345. https://doi.org/10.1016/j.cogpsych.2005.11.001

Henderson, M. M., Rademaker, R. L., & Serences, J. T. (2022). Flexible utilization of spatial- and motor-based codes for the storage of visuo-spatial information. eLife, 11, e75688. https://doi.org/10.7554/eLife.75688

Heninger, W. G., Dennis, A. R., & Hilmer, K. M. (2006). Research note: Individual cognition and dual-task interference in group support systems. Information Systems Research, 17(4), 415-424. https://doi.org/10.1287/isre.1060.0102

Hervey, A. S., Epstein, J. N., & Curry, J. F. (2004). Neuropsychology of adults with attention-deficit/hyperactivity disorder: a meta-analytic review. Neuropsychology, 18(3), 485. https://doi.org/10.1037/0894-4105.18.3.485

Hilla, Y., Peylo, C., & Sauseng, P. (2025). Prefrontal working memory activity slots support sequence memory similar to hippocampal long-term memory position recall. Neuron, 113(2), 189-191. https://doi.org/10.1016/j.neuron.2024.12.022

Hitch, G. J., & Baddeley, A. D. (1976). Verbal reasoning and working memory. The Quarterly Journal of Experimental Psychology, 28(4), 603-621. https://doi.org/10.1080/14640747608400587

Holmes, J., Woolgar, F., Hampshire, A., & Gathercole, S. E. (2019). Are Working Memory Training Effects Paradigm-Specific?. Frontiers in psychology, 10, 1103. https://doi.org/10.3389/fpsyg.2019.01103

Iamshchinina, P., Christophel, T. B., Gayet, S., & Rademaker, R. L. (2021). Essential considerations for exploring visual working memory storage in the human brain. Visual Cognition, 29(7), 425-436. https://doi.org/10.1080/13506285.2021.1915902

Impact of Task Similarity and Training Regimes on Cognitive Transfer and InterferenceN. Menghi, S. Vigano', W. J. Johnston, S. Elnagar, S. Fusi, F. C. DoellerbioRxiv 2025.09.22.677779; https://doi.org/10.1101/2025.09.22.677779

Jackson, J., Rich, A. N., Williams, M. A., & Woolgar, A. (2017). Feature-selective attention in frontoparietal cortex: multivoxel codes adjust to prioritize task-relevant information. Journal of cognitive neuroscience, 29(2), 310-321. https://doi.org/10.1162/jocn_a_01039

Jackson, K., Shaw, T., & Helton, W. (2022). The effects of dual-task interference on visual search and verbal memory. Ergonomics, 66, 125 - 135. https://doi.org/10.1080/00140139.2022.2061053

Jackson, M. C., & Raymond, J. E. (2008). Familiarity enhances visual working memory for faces. Journal of Experimental Psychology: Human Perception and Performance, 34(3), 556. https://doi.org/10.1037/0096-1523.34.3.556

Jacobsen, C. F., Elder, J. H., & Haslerud, G. M. (1936). Studies of cerebral function in primates (Vol. 13, No. 1, pp. 101-112). Johns Hopkins Press. https://doi.org/10.1037/h0056632

James, W. (1890). The Principles Of Psychology Volume II By William James (1890). Henry Holt and Company. https://doi.org/10.1037/10538-000

Jiang, X., Bradley, E., Rini, R. A., Zeffiro, T., Vanmeter, J., & Riesenhuber, M. (2007). Categorization training results in shape- and category-selective human neural plasticity. Neuron, 53(6), 891-903. https://doi.org/10.1016/j.neuron.2007.02.015

Johnson, M. K., McMahon, R. P., Robinson, B. M., Harvey, A. N., Hahn, B., Leonard, C. J., ... & Gold, J. M. (2013). The relationship between working memory capacity and broad measures of cognitive ability in healthy adults and people with schizophrenia. Neuropsychology, 27(2), 220. https://doi.org/10.1037/a0032060

Johnson, R. (2014). The Neural Basis of Deception and Credibility Assessment. Elsevier EBooks, 217-300. https://doi.org/10.1016/B978-0-12-394433-7.00006-3

Kahneman, D. (1973). Attention and effort (Vol. 1063, pp. 218-226). Englewood Cliffs, NJ: Prentice-Hall.

Kamiński, J., & Rutishauser, U. (2020). Between persistently active and activity-silent frameworks: novel vistas on the cellular basis of working memory. Annals of the New York Academy of Sciences, 1464(1), 64-75. https://doi.org/10.1111/nyas.14213

Kane, M. J., & Engle, R. W. (2000). Working-memory capacity, proactive interference, and divided attention: limits on long-term memory retrieval. Journal of Experimental Psychology: Learning, Memory, and Cognition, 26(2), 336. https://doi.org/10.1037//0278-7393.26.2.336

Kane, M. J., Bleckley, M. K., Conway, A. R., & Engle, R. W. (2001). A controlled-attention view of working-memory capacity. Journal of experimental psychology: General, 130(2), 169. https://doi.org/10.1037/0096-3445.130.2.169

Kessler, R. C., Adler, L., Ames, M., Demler, O., Faraone, S., Hiripi, E., Howes, M. J., Jin, R., Secnik, K., Spencer, T., Ustun, T. B., & Walters, E. E. (2005). The World Health Organization Adult ADHD Self-Report Scale (ASRS): a short screening scale for use in the general population. Psychological medicine, 35(2), 245-256. https://doi.org/10.1017/S0033291704002892

Kessler, R. C., Adler, L., Barkley, R., Biederman, J., Conners, C. K., Demler, O., ... & Zaslavsky, A. M. (2006). The prevalence and correlates of adult ADHD in the United States: results from the National Comorbidity Survey Replication. American Journal of psychiatry, 163(4), 716-723. https://doi.org/10.1176/ajp.2006.163.4.716

Kessler, R. C., Green, J. G., Adler, L. A., Barkley, R. A., Chatterji, S., Faraone, S. V., ... & Van Brunt, D. L. (2010). Structure and diagnosis of adult attention-deficit/hyperactivity disorder: analysis of expanded symptom criteria from the Adult ADHD Clinical Diagnostic Scale. Archives of general psychiatry, 67(11), 1168-1178. https://doi.org/10.1001/archgenpsychiatry.2010.146

Kim, C., Kroger, J. K., Calhoun, V. D., & Clark, V. P. (2015). The role of the frontopolar cortex in manipulation of integrated information in working memory. Neuroscience letters, 595, 25-29. https://doi.org/10.1016/j.neulet.2015.03.044

Kirschen, M. P., Chen, S. A., Schraedley-Desmond, P., & Desmond, J. E. (2005). Load-and practice-dependent increases in cerebro-cerebellar activation in verbal working memory: an fMRI study. Neuroimage, 24(2), 462-472. https://doi.org/10.1016/j.neuroimage.2004.08.036

Klingberg T. (1998). Concurrent performance of two working memory tasks: potential mechanisms of interference. Cerebral cortex (New York, N.Y. : 1991), 8(7), 593-601. https://doi.org/10.1093/cercor/8.7.593

Klingberg, T. (2010). Training and plasticity of working memory. Trends in cognitive sciences, 14(7), 317-324. https://doi.org/10.1016/j.tics.2010.05.002

Klingberg, T., Forssberg, H., & Westerberg, H. (2002). Training of Working Memory in Children With ADHD. Journal of Clinical and Experimental Neuropsychology, 24(6), 781-791. https://doi.org/10.1076/jcen.24.6.781.8395

Koenigs, M., Barbey, A. K., Postle, B. R., & Grafman, J. (2009). Superior parietal cortex is critical for the manipulation of information in working memory. The Journal of neuroscience, 29(47), 14980-14986. https://doi.org/10.1523/JNEUROSCI.3706-09.2009

Kofler, M. J., Rapport, M. D., Bolden, J., Sarver, D. E., & Raiker, J. S. (2009). Journal of Abnormal Child Psychology, 38(2), 149-161. https://doi.org/10.1007/s10802-009-9357-6

Kofler, M. J., Rapport, M. D., Bolden, J., Sarver, D. E., Raiker, J. S., & Alderson, R. M. (2011). Working memory deficits and social problems in children with ADHD. Journal of abnormal child psychology, 39, 805-817. https://doi.org/10.1007/s10802-011-9492-8

Kolb, B., and Wishaw, I. Q. (2009). Fundamentals of Human Neuropsychology. New York: Worth Publishers.

Kondo, H., Osaka, N., & Osaka, M. (2004). Cooperation of the anterior cingulate cortex and dorsolateral prefrontal cortex for attention shifting. Neuroimage, 23(2), 670-679. https://doi.org/10.1016/j.neuroimage.2004.06.014

Ku, Y. (2018). Selective attention on representations in working memory: cognitive and neural mechanisms. PeerJ, 6. https://doi.org/10.7717/peerj.4585

Kubota, K. I. S. O. U., Iwamoto, T. A. K. A. S. H. I. G. E., & Suzuki, H. (1974). Visuokinetic activities of primate prefrontal neurons during delayed-response performance. Journal of Neurophysiology, 37(6), 1197-1212. https://doi.org/10.1152/jn.1974.37.6.1197

Lara, A. H., & Wallis, J. D. (2015). The Role of Prefrontal Cortex in Working Memory: A Mini Review. Frontiers in Systems Neuroscience, 9. https://doi.org/10.3389/fnsys.2015.00173

LaRocque, J. J., Lewis-Peacock, J. A., Drysdale, A. T., Oberauer, K., & Postle, B. R. (2013). Decoding attended information in short-term memory: an EEG study. Journal of cognitive neuroscience, 25(1), 127-142. https://doi.org/10.1162/jocn_a_00305

Lavie, N., Hirst, A., De Fockert, J. W., & Viding, E. (2004). Load theory of selective attention and cognitive control. Journal of experimental psychology: General, 133(3), 339. https://doi.org/10.1037/0096-3445.133.3.339

Lebedev, M. A., Messinger, A., Kralik, J. D., & Wise, S. P. (2004). Representation of attended versus remembered locations in prefrontal cortex. PLoS biology, 2(11), e365. https://doi.org/10.1371/journal.pbio.0020365

Ledoit, O., & Wolf, M. (2004). A well-conditioned estimator for large-dimensional covariance matrices. Journal of multivariate analysis, 88(2), 365-411. https://doi.org/10.1016/S0047-259X(03)00096-4

Lee, J. J., Krumin, M., Harris, K. D., & Carandini, M. (2022). Task specificity in mouse parietal cortex. Neuron, 110(18), 2961-2969. https://doi.org/10.1016/j.neuron.2022.07.017

Levy, J., & Pashler, H. (2001). Is dual-task slowing instruction dependent?. Journal of Experimental Psychology: Human Perception and Performance, 27(4), 862. https://doi.org/10.1037//0096-1523.27.4.862

Lewis-Peacock, J. A., Drysdale, A. T., Oberauer, K., & Postle, B. R. (2012). Neural evidence for a distinction between short-term memory and the focus of attention. Journal of cognitive neuroscience, 24(1), 61-79. https://doi.org/10.1162/jocn_a_00140

Li, Y., Hu, X., Yu, Y., Zhao, K., Saalmann, Y. B., & Wang, L. (2017). Feedback from human posterior parietal cortex enables visuospatial category representations as early as primary visual cortex. Brain and behavior, 8(1), e00886. https://doi.org/10.1002/brb3.886

Libby, A., & Buschman, T. J. (2021). Rotational dynamics reduce interference between sensory and memory representations. Nature neuroscience, 24(5), 715-726. https://doi.org/10.1038/s41593-021-00821-9

Liebe, S., Hoerzer, G. M., Logothetis, N. K., & Rainer, G. (2012). Theta coupling between V4 and prefrontal cortex predicts visual short-term memory performance. Nature neuroscience, 15(3), 456-462. https://doi.org/10.1038/nn.3038

Liepelt, R., Strobach, T., Frensch, P., & Schubert, T. (2011). Improved intertask coordination after extensive dual-task practice. Quarterly Journal of Experimental Psychology, 64(7), 1251-1272. https://doi.org/10.1080/17470218.2010.543284

Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. Nature, 390(6657), 279-281. https://doi.org/10.1038/36846

Luck, S. J., & Vogel, E. K. (2013). Visual working memory capacity: from psychophysics and neurobiology to individual differences. Trends in Cognitive Sciences, 17(8), 391-400. https://doi.org/10.1016/j.tics.2013.06.006

Lui, M., & Tannock, R. (2007). Working memory and inattentive behaviour in a community sample of children. Behavioral and Brain Functions, 3(1), 12-12. https://doi.org/10.1186/1744-9081-3-12

Luna, D., & Kim, H. M. C. (2009). How much was your shopping basket? Working memory processes in total basket price estimation. Journal of Consumer Psychology, 19(3), 346-355. https://doi.org/10.1016/j.jcps.2009.03.003

Luo, X., Guo, J., Liu, L., Zhao, X., Li, D., Li, H., ... & Sun, L. (2019). The neural correlations of spatial attention and working memory deficits in adults with ADHD. NeuroImage: Clinical, 22, 101728. https://doi.org/10.1016/j.nicl.2019.101728

Mac-Auliffe, D., Chatard, B., Petton, M., Croizé, A. C., Sipp, F., Bontemps, B., ... & Lachaux, J. P. (2021). The dual-task cost is due to neural interferences disrupting the optimal spatio-temporal dynamics of the competing tasks. Frontiers in Behavioral Neuroscience, 15, 640178. https://doi.org/10.3389/fnbeh.2021.640178

Manohar, S. G., Zokaei, N., Fallon, S. J., Vogels, T. P., & Husain, M. (2019). Neural mechanisms of attending to items in working memory. Neuroscience & Biobehavioral Reviews, 101, 1-12. https://doi.org/10.1016/j.neubiorev.2019.03.017

Manor, I., Vurembrandt, N., Rozen, S., Gevah, D., Weizman, A., & Zalsman, G. (2012). Low self-awareness of ADHD in adults using a self-report screening questionnaire. European psychiatry : the journal of the Association of European Psychiatrists, 27(5), 314-320. https://doi.org/10.1016/j.eurpsy.2010.08.013

Maquestiaux, F., Laguë-Beauvais, M., Bherer, L., & Ruthruff, E. (2008). Bypassing the central bottleneck after single-task practice in the psychological refractory period paradigm: Evidence for task automatization and greedy resource recruitment. Memory & Cognition, 36(7), 1262-1282. https://doi.org/10.3758/MC.36.7.1262

Mariette, Katya Olmos-Solis, Johannes Jacobus Fahrenfort, & Olivers, C. N. (2018). Current and future goals are represented in opposite patterns in object-selective cortex. ELife, 7. https://doi.org/10.7554/eLife.38677

Mathis, M. W., Rotondo, A. P., Chang, E. F., Tolias, A. S., & Mathis, A. (2024). Decoding the brain: From neural representations to mechanistic models. Cell, 187(21), 5814-5832. https://doi.org/10.1016/j.cell.2024.08.051

McEvoy, L. K., Smith, M. E., & Gevins, A. (1998). Dynamic cortical networks of verbal and spatial working memory: effects of memory load and task practice. Cerebral cortex (New York, NY: 1991), 8(7), 563-574. https://doi.org/10.1093/cercor/8.7.563

Menghi, N., Johnston, W. J., Vigano', S., Hinrichs, M. A. B., Maess, B., Fusi, S., & Doeller, C. F. (2025). The effects of task similarity during representation learning in brains and

neural networks. Nature Communications. https://doi.org/10.1038/s41467-025-66849-8

Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. Annual review of neuroscience, 24, 167-202. https://doi.org/10.1146/annurev.neuro.24.1.167

Miller, E. K., Li, L., & Desimone, R. (1993). Activity of neurons in anterior inferior temporal cortex during a short-term memory task. Journal of Neuroscience, 13(4), 1460-1478. https://doi.org/10.1523/JNEUROSCI.13-04-01460.1993

Miller, G. A. (1956). The magical number seven, plus or minus two: Some limits on our capacity for processing information. Psychological review, 63(2), 81. https://doi.org/10.1037/h0043158

Miller, G. A., Galanter, E., & Pribram, K. H. (1960). Plans and the structure of behavior. https://doi.org/10.1037/10039-000

Miyake, A., Friedman, N. P., Emerson, M. J., Witzki, A. H., Howerter, A., & Wager, T. D. (2000). The unity and diversity of executive functions and their contributions to complex "frontal lobe" tasks: A latent variable analysis. Cognitive psychology, 41(1), 49-100. https://doi.org/10.1006/cogp.1999.0734

Mongillo, G., Barak, O., & Tsodyks, M. (2008). Synaptic theory of working memory. Science (New York, N.Y.), 319(5869), 1543-1546. https://doi.org/10.1126/science.1150769

Muhle-Karbe, P. S., Myers, N. E., & Stokes, M. G. (2021). A Hierarchy of Functional States in Working Memory. Journal of Neuroscience, 41(20), 4461-4475. https://doi.org/10.1523/JNEUROSCI.3104-20.2021

Mukherjee, P., Hartanto, T., Ana-Maria Iosif, Dixon, J. F., Hinshaw, S. P., Murat Pakyurek, van, Guyer, A. E., McClure, S. M., Schweitzer, J. B., & Fassbender, C. (2021). Neural basis of working memory in ADHD: Load versus complexity. NeuroImage Clinical, 30, 102662-102662. https://doi.org/10.1016/j.nicl.2021.102662

Musslick, S., & Cohen, J. D. (2021). Rationalizing constraints on the capacity for cognitive control. Trends in cognitive sciences, 25(9), 757-775. https://doi.org/10.1016/j.tics.2021.06.001

Musslick, S., Saxe, A. M., Ozcimder, K., Dey, B., Henselman, G., & Cohen, J. D. (2017). Multitasking Capability Versus Learning Efficiencyin Neural Network Architectures. In Proceedings of the Annual Meeting of the Cognitive Science Society (Vol. 39).

Myers, N. E., Stokes, M. G., & Muhle-Karbe, P. S. (2026). Human Beta Oscillations Reflect Magnitude and Fidelity of Priority Shifts in Working Memory. Journal of Neuroscience. https://doi.org/10.1523/JNEUROSCI.1548-25.2026

Myers, N. E., Stokes, M. G., & Nobre, A. C. (2017). Prioritizing information during working memory: beyond sustained internal attention. Trends in cognitive sciences, 21(6), 449-461. https://doi.org/10.1016/j.tics.2017.03.010

Nairne, J. S., & Neath, I. (2012). Sensory and working memory. Handbook of Psychology, Second Edition, 4. https://doi.org/10.1002/9781118133880.hop204015

Nee, D. E., Brown, J. W., Askren, M. K., Berman, M. G., Demiralp, E., Krawitz, A., & Jonides, J. (2013). A meta-analysis of executive components of working memory. Cerebral cortex (New York, N.Y. : 1991), 23(2), 264-282. https://doi.org/10.1093/cercor/bhs007

Ngiam, W. X., Brissenden, J. A., & Awh, E. (2019). "Memory compression" effects in visual working memory are contingent on explicit long-term memory. Journal of Experimental Psychology: General, 148(8), 1373. https://doi.org/10.1037/xge0000649

Nijboer, M., Borst, J. P., Van Rijn, H., & Taatgen, N. A. (2016). Driving and multitasking: the good, the bad, and the dangerous. Frontiers in psychology, 7, 1718. https://doi.org/10.3389/fpsyg.2016.01718

Noonan, M. P., Walton, M. E., Behrens, T. E. J., Sallet, J., Buckley, M. J., & Rushworth, M. F. S. (2010). Separate value comparison and learning mechanisms in macaque medial and lateral orbitofrontal cortex. Proceedings of the National Academy of Sciences, 107(47), 20547-20552. https://doi.org/10.1073/pnas.1012246107

Norris D. (2017). Short-term memory and long-term memory are still different. Psychological bulletin, 143(9), 992-1009. https://doi.org/10.1037/bul0000108

Oberauer K. (2009). Interference between storage and processing in working memory: Feature overwriting, not similarity-based competition. Memory & cognition, 37(3), 346-357. https://doi.org/10.3758/MC.37.3.346

Oberauer, K. (2002). Access to information in working memory: exploring the focus of attention. Journal of Experimental Psychology: Learning, Memory, and Cognition, 28(3), 411. https://doi.org/10.1037/0278-7393.28.3.411

Oberauer, K., & Lin, H. Y. (2017). An interference model of visual working memory. Psychological review, 124(1), 21. https://doi.org/10.1037/rev0000044

Oberauer, K., Awh, E., & Sutterer, D. W. (2017). The role of long-term memory in a test of visual working memory: Proactive facilitation but no proactive interference. Journal of Experimental Psychology: Learning, Memory, and Cognition, 43(1), 1. https://doi.org/10.1037/xlm0000302

Oberauer, K., Farrell, S., Jarrold, C., & Lewandowsky, S. (2016). What limits working memory capacity?. Psychological bulletin, 142(7), 758. https://doi.org/10.1037/bul0000046

Oberauer., K (2019). Working Memory and Attention - A Conceptual Analysis and Review. Journal of Cognition, 2(1). https://doi.org/10.5334/joc.58

Oh, S. H., & Kim, M. S. (2004). The role of spatial working memory in visual search efficiency. Psychonomic bulletin & review, 11, 275-281. https://doi.org/10.3758/BF03196570

Olivers, C. N., Peters, J., Houtkamp, R., & Roelfsema, P. R. (2011). Different states in visual working memory: When it guides attention and when it does not. Trends in cognitive sciences, 15(7), 327-334. https://doi.org/10.1016/j.tics.2011.05.004

Olshausen, B. A., & Field, D. J. (1996). Emergence of simple-cell receptive field properties by learning a sparse code for natural images. Nature, 381(6583), 607-609. https://doi.org/10.1038/381607a0

Orban, S. A., Rapport, M. D., Friedman, L. M., Eckrich, S. J., & Kofler, M. J. (2017). Journal of Abnormal Child Psychology, 46(4), 713-727. https://doi.org/10.1007/s10802-017-0338-x

Osaka, M., Osaka, N., Kondo, H., Morishita, M., Fukuyama, H., Aso, T., & Shibasaki, H. (2003). The neural basis of individual differences in working memory capacity: an fMRI study. NeuroImage, 18(3), 789-797. https://doi.org/10.1016/S1053-8119(02)00032-0

Owen, A. M., Evans, A. C., & Petrides, M. (1996). Evidence for a two-stage model of spatial working memory processing within the lateral frontal cortex: a positron emission tomography study. Cerebral cortex (New York, N.Y. : 1991), 6(1), 31-38. https://doi.org/10.1093/cercor/6.1.31

Owen, A. M., McMillan, K. M., Laird, A. R., & Bullmore, E. (2005). N-back working memory paradigm: a meta-analysis of normative functional neuroimaging studies. Human brain mapping, 25(1), 46-59. https://doi.org/10.1002/hbm.20131

Pacheco-Estefan, D., Fellner, M.-C., Kunz, L., Zhang, H., Reinacher, P., Roy, C., ... & Axmacher, N. (2024). Maintenance and transformation of representational formats during working memory prioritization. Nature Communications, 15, 52541. https://doi.org/10.1038/s41467-024-52541-w

Palmer, J. (1990). Attentional limits on the perception and memory of visual information. Journal of Experimental Psychology: Human perception and performance, 16(2), 332. https://doi.org/10.1037//0096-1523.16.2.332

Paluch, K., Magnuski, M., Średniawa, W., Ivanovski, D., Rysz, A., Służewska-Niedźwiedź, M., ... & Kamiński, J. (2025). Unattended working memory items are coded by persistent activity in human medial temporal lobe neurons. Nature Human Behaviour, 9(10), 2099-2113. https://doi.org/10.1038/s41562-025-02235-0

Panichello, M. F., & Buschman, T. J. (2021). Shared mechanisms underlie the control of working memory and attention. Nature, 592(7855), 601-605. https://doi.org/10.1038/s41586-021-03390-w

Pashler, H. (1994). Dual-task interference in simple tasks: data and theory. Psychological bulletin, 116(2), 220. https://doi.org/10.1037/0033-2909.116.2.220

Pashler, H. (1994). Graded capacity-sharing in dual-task interference?. Journal of Experimental Psychology: Human Perception and Performance, 20(2), 330. https://doi.org/10.1037//0096-1523.20.2.330

Pasternak, T., Lui, L. L., & Spinelli, P. M. (2015). Unilateral prefrontal lesions impair memory-guided comparisons of contralateral visual motion. Journal of Neuroscience, 35(18), 7095-7105. https://doi.org/10.1523/JNEUROSCI.5265-14.2015

Peirce, J. W., Gray, J. R., Simpson, S., MacAskill, M. R., Höchenberger, R., Sogo, H., Kastman, E., Lindeløv, J. (2019). PsychoPy2: experiments in behavior made easy. Behavior Research Methods. https://doi.org/10.3758/s13428-018-01193-y

Petrides, M. (1996). Specialized systems for the processing of mnemonic information within the primate frontal cortex. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 351(1346), 1455-1462. https://doi.org/10.1098/rstb.1996.0130

Petrides, M., & Pandya, D. N. (1984). Projections to the frontal cortex from the posterior parietal region in the rhesus monkey. Journal of Comparative neurology, 228(1), 105-

116.
https://doi.org/10.1002/cne.902280110

Piwek, E. P. (2023). Neural mechanisms for flexible behaviour in humans and artificial neural networks (Doctoral dissertation, University of Oxford).

Plummer, P., & Eskes, G. (2015). Measuring treatment effects on dual-task performance: a framework for research and clinical practice. Frontiers in human neuroscience, 9, 225. https://doi.org/10.3389/fnhum.2015.00225

Poldrack, R. A., & Packard, M. G. (2002). Competition among multiple memory systems: converging evidence from animal and human brain studies. Neuropsychologia, 41(3), 245-251. https://doi.org/10.1016/S0028-3932(02)00157-4

Postle, B. R. (2005). Working memory as an emergent property of the mind and brain. Neuroscience, 139(1), 23-38. https://doi.org/10.1016/j.neuroscience.2005.06.005

Postle, B. R., Druzgal, T. J., & D'Esposito, M. (2003). Seeking the neural substrates of visual working memory storage. Cortex, 39(4-5), 927-946. https://doi.org/10.1016/S0010-9452(08)70871-2

Pratt, N., Willoughby, A., & Swick, D. (2011). Effects of working memory load on visual selective attention: behavioral and electrophysiological evidence. Frontiers in human neuroscience, 5, 57. https://doi.org/10.3389/fnhum.2011.00057

Qi, S., Zeng, Q., Luo, Y., Duan, H., Ding, C., Hu, W., & Li, H. (2014). Impact of working memory load on cognitive control in trait anxiety: An ERP study. PLoS One, 9(11),

e111791.
https://doi.org/10.1371/journal.pone.0111791

Rademaker, R. L., Chunharas, C., & Serences, J. T. (2019). Coexisting representations of sensory and mnemonic information in human visual cortex. Nature neuroscience, 22(8), 1336-1344. https://doi.org/10.1038/s41593-019-0428-x

Rainer, G., Asaad, W. F., & Miller, E. K. (1998). Selective representation of relevant information by neurons in the primate prefrontal cortex. Nature, 393(6685), 577-579. https://doi.org/10.1038/31235

Rainer, G., Rao, S. C., & Miller, E. K. (1999). Prospective coding for objects in primate prefrontal cortex. Journal of Neuroscience, 19(13), 5493-5505. https://doi.org/10.1523/JNEUROSCI.19-13-05493.1999

Rapport, M. D., Chung, K. M., Shore, G., & Isaacs, P. (2001). A conceptual model of child psychopathology: Implications for understanding attention deficit hyperactivity disorder and treatment efficacy. Journal of Clinical Child & Adolescent Psychology, 30(1), 48-58. https://doi.org/10.1207/S15374424JCCP3001_6

Recarte, M. A., & Nunes, L. M. (2003). Mental workload while driving: effects on visual search, discrimination, and decision making. Journal of experimental psychology: Applied, 9(2), 119. https://doi.org/10.1037/1076-898X.9.2.119

Recarte, M. A., & Nunes, L. M. (2003). Mental workload while driving: effects on visual search, discrimination, and decision making. Journal of experimental psychology: Applied, 9(2), 119. https://doi.org/10.1037/1076-898X.9.2.119

Rerko, L., Souza, A. S., & Oberauer, K. (2014). Retro-cue benefits in working memory without sustained focal attention. Memory & cognition, 42(5), 712-728. https://doi.org/10.3758/s13421-013-0392-8

Reynolds, J. H., Chelazzi, L., & Desimone, R. (1999). Competitive mechanisms subserve attention in macaque areas V2 and V4. The Journal of neuroscience : the official journal of the Society for Neuroscience, 19(5), 1736-1753. https://doi.org/10.1523/JNEUROSCI.19-05-01736.1999

Ricker, T. J., & Cowan, N. (2010). Loss of visual working memory within seconds: the combined use of refreshable and non-refreshable features. Journal of experimental psychology: Learning, memory, and cognition, 36(6), 1355. https://doi.org/10.1037/a0020356

Ricker, T. J., & Vergauwe, E. (2020). Consistent failure to produce a cognitive load effect in visual working memory using a standard dual-task procedure. Journal of Cognition, 3(1), 15. https://doi.org/10.5334/joc.108

Rigotti, M., Barak, O., Warden, M. R., Wang, X. J., Daw, N. D., Miller, E. K., & Fusi, S. (2013). The importance of mixed selectivity in complex cognitive tasks. Nature, 497(7451), 585-590. https://doi.org/10.1038/nature12160

Ritz, H., & Shenhav, A. (2024). Orthogonal neural encoding of targets and distractors supports multivariate cognitive control. Nature Human Behaviour, 8(5), 945-961. https://doi.org/10.1038/s41562-024-01826-7

Rogers, M., Hwang, H., Toplak, M., Weiss, M., & Tannock, R. (2011). Inattention, working memory, and academic achievement in adolescents referred for attention deficit/hyperactivity disorder (ADHD). Child Neuropsychology, 17(5), 444-458. https://doi.org/10.1080/09297049.2010.544648

Rose, N. S., LaRocque, J. J., Riggall, A. C., Gosseries, O., Starrett, M. J., Meyering, E. E., & Postle, B. R. (2016). Reactivation of latent working memories with transcranial magnetic stimulation. Science (New York, N.Y.), 354(6316), 1136-1139. https://doi.org/10.1126/science.aah7011

Roux, F., & Uhlhaas, P. J. (2014). Working memory and neural oscillations: alpha-gamma versus theta-gamma codes for distinct WM information?. Trends in cognitive sciences, 18(1), 16-25. https://doi.org/10.1016/j.tics.2013.10.010

Roy, J. E., Riesenhuber, M., Poggio, T., & Miller, E. K. (2010). Prefrontal cortex activity during flexible categorization. Journal of Neuroscience, 30(25), 8519-8528. https://doi.org/10.1523/JNEUROSCI.4837-09.2010

Rushworth, M. F., Nixon, P. D., Eacott, M. J., & Passingham, R. E. (1997). Ventral prefrontal cortex is not essential for working memory. Journal of Neuroscience, 17(12), 4829-4838. https://doi.org/10.1523/JNEUROSCI.17-12-04829.1997

Ruthruff, E., Hazeltine, E., & Remington, R. (2006). What causes residual dual-task interference after practice?. Psychological Research, 70, 494-503. https://doi.org/10.1007/S00426-005-0012-8.

Ruthruff, E., Johnston, J. C., & Van Selst, M. (2001). Why practice reduces dual-task interference. Journal of Experimental Psychology: Human Perception and Performance, 27(1), 3. https://doi.org/10.1037/0096-1523.27.1.3

Ruthruff, E., Johnston, J. C., Van Selst, M., Whitsell, S., & Remington, R. (2003). Vanishing dual-task interference after practice: Has the bottleneck been eliminated or is it merely latent?. Journal of Experimental Psychology: Human Perception and Performance, 29(2), 280. https://doi.org/10.1037/0096-1523.29.2.280

Ruthruff, E., Pashler, H. E., & Hazeltine, E. (2003). Dual-task interference with equal task emphasis: Graded capacity sharing or central postponement?. Perception & Psychophysics, 65(5), 801-816. https://doi.org/10.3758/BF03194816

Ruthruff, E., Van Selst, M., Johnston, J. C., & Remington, R. (2006). How does practice reduce dual-task interference: Integration, automatization, or just stage-shortening?. Psychological research, 70, 125-142. https://doi.org/10.1007/s00426-004-0192-7

Sachdev, P., & Kruk, J. (1996). Restlessness: the anatomy of a neuropsychiatric symptom. Australian and New Zealand journal of psychiatry, 30(1), 38-53. https://doi.org/10.3109/00048679609076071

Sakai, K., Rowe, J. B., & Passingham, R. E. (2002). Active maintenance in prefrontal area 46 creates distractor-resistant memory. Nature neuroscience, 5(5), 479-484. https://doi.org/10.1038/nn846

Salazar, R. F., Dotson, N. M., Bressler, S. L., & Gray, C. M. (2012). Content-specific fronto-parietal synchronization during visual working memory. Science, 338(6110), 1097-1100. https://doi.org/10.1126/science.1224000

Salvi, V., Migliarese, G., Venturi, V., Rossi, F., Torriero, S., Viganò, V., Cerveri, G., & Mencacci, C. (2019). ADHD in adults: clinical subtypes and associated characteristics. Rivista di psichiatria, 54(2), 84-89. https://doi.org/10.1708/3142.31249

Saults, J. S., & Cowan, N. (2007). A central capacity limit to the simultaneous storage of visual and auditory arrays in working memory. Journal of Experimental Psychology: General, 136(4), 663. https://doi.org/10.1037/0096-3445.136.4.663

Schmidt, B. K., Vogel, E. K., Woodman, G. F., & Luck, S. J. (2002). Voluntary and automatic attentional control of visual working memory. Perception & psychophysics, 64(5), 754-763. https://doi.org/10.3758/BF03194742

Schneegans, S., & Bays, P. M. (2017). Neural architecture for feature binding in visual working memory. Journal of Neuroscience, 37(14), 3913-3925. https://doi.org/10.1523/JNEUROSCI.3493-16.2017

Schoechlin, C., & Engel, R. R. (2005). Neuropsychological performance in adult attention-deficit hyperactivity disorder: Meta-analysis of empirical data. Archives of Clinical

Neuropsychology, 20(6), 727-744. https://doi.org/10.1016/j.acn.2005.04.005

Schubert, T., Kübler, S., & Strobach, T. (2024). A mechanism underlying improved dual-task performance after practice: Reviewing evidence for the memory hypothesis. Psychonomic Bulletin & Review, 31(5), 2005-2021. https://doi.org/10.3758/s13423-024-02498-0

Schumacher, E. H., Seymour, T. L., Glass, J. M., Fencsik, D. E., Lauber, E. J., Kieras, D. E., & Meyer, D. E. (2001). Virtually perfect time sharing in dual-task performance: Uncorking the central cognitive bottleneck. Psychological science, 12(2), 101-108. https://doi.org/10.1111/1467-9280.00318

Schweppe, J., & Rummer, R. (2014). Attention, working memory, and long-term memory in multimedia learning: An integrated perspective based on process models of working memory. Educational Psychology Review, 26, 285-306. https://doi.org/10.1007/s10648-013-9242-2

Scoville, W. B., & Milner, B. (1957). Loss of recent memory after bilateral hippocampal lesions. Journal of neurology, neurosurgery, and psychiatry, 20(1), 11. https://doi.org/10.1136/jnnp.20.1.11

Seger, C. A., & Miller, E. K. (2010). Category Learning in the Brain. Annual Review of Neuroscience, 33(1), 203-219. https://doi.org/10.1146/annurev.neuro.051508.135546

Serences, J. T., Ester, E. F., Vogel, E. K., & Awh, E. (2009). Stimulus-specific delay activity in human primary visual cortex. Psychological science, 20(2), 207-214. https://doi.org/10.1111/j.1467-9280.2009.02276.x

Shallice, T., & Warrington, E. K. (1970). Independent functioning of verbal memory stores: A neuropsychological study. Quarterly journal of experimental psychology, 22(2), 261-273. https://doi.org/10.1080/00335557043000203

Shiffrin, R. M., & Atkinson, R. C. (1969). Storage and retrieval processes in long-term memory. Psychological review, 76(2), 179. https://doi.org/10.1037/h0027277

Simmering, V. R. (2016). Monographs of the Society for Research in Child Development, 81(3), 7-24. https://doi.org/10.1111/mono.12249

Simons, D. J., & Levin, D. T. (1997). Change blindness. Trends in cognitive sciences, 1(7), 261-267. https://doi.org/10.1016/S1364-6613(97)01080-2

Sisakhti, M., Sachdev, P. S., & Batouli, S. A. H. (2021). The effect of cognitive load on the retrieval of long-term memory: An fMRI study. Frontiers in Human Neuroscience, 15, 700146. https://doi.org/10.3389/fnhum.2021.700146

Smith, E. E., & Jonides, J. (1997). Working memory: a view from neuroimaging. Cognitive psychology, 33(1), 5-42. https://doi.org/10.1006/cogp.1997.0658

Song, P., Zha, M., Yang, Q., Zhang, Y., Li, X., Rudan, I., & Global Health Epidemiology Reference Group (GHERG) (2021). The prevalence of adult attention-deficit hyperactivity disorder: A global systematic review and meta-analysis. Journal of global health, 11, 04009. https://doi.org/10.7189/jogh.11.04009

Souza, A. S., & Oberauer, K. (2016). In search of the focus of attention in working memory: 13 years of the retro-cue effect. Attention, Perception, & Psychophysics, 78, 1839-1860. https://doi.org/10.3758/s13414-016-1108-5

Souza, A. S., Rerko, L., & Oberauer, K. (2016). Getting more from visual working memory: Retro-cues enhance retrieval and protect from visual interference. Journal of Experimental Psychology: Human Perception and Performance, 42(6), 890. https://doi.org/10.1037/xhp0000192

Sperduti, M., Makowski, D., & Piolino, P. (2016). The protective role of long-term meditation on the decline of the executive component of attention in aging: a preliminary cross-sectional study. Aging, Neuropsychology, and Cognition, 23(6), 691-702. https://doi.org/10.1080/13825585.2016.1159652

Sprague, T. C., Ester, E. F., & Serences, J. T. (2016). Restoring latent visual working memory representations in human cortex. Neuron, 91(3), 694-707. https://doi.org/10.1016/j.neuron.2016.07.006

Sprague, Thomas C., Ester, Edward F., & Serences, John T. (2014). Reconstructions of Information in Visual Spatial Working Memory Degrade with Memory Load. Current Biology, 24(18), 2174-2180. https://doi.org/10.1016/j.cub.2014.07.066

Stokes M. G. (2015). 'Activity-silent' working memory in prefrontal cortex: a dynamic coding framework. Trends in cognitive sciences, 19(7), 394-405. https://doi.org/10.1016/j.tics.2015.05.004

Stokes, M. G., Kusunoki, M., Sigala, N., Nili, H., Gaffan, D., & Duncan, J. (2013). Dynamic coding for cognitive control in prefrontal cortex. Neuron, 78(2), 364-375. https://doi.org/10.1016/j.neuron.2013.01.039

Stokes, M. G., Muhle-Karbe, P. S., & Myers, N. E. (2020). Theoretical distinction between functional states in working memory and their corresponding neural states. Visual Cognition, 28(5-8), 420-432. https://doi.org/10.1080/13506285.2020.1825141

Strobach, T. (2020). The dual-task practice advantage: Empirical evidence and cognitive mechanisms. Psychonomic bulletin & review, 27(1), 3-14. https://doi.org/10.3758/s13423-019-01619-4

Strobach, T., & Torsten, S. (2017). Mechanisms of practice-related reductions of dual-task interference with simple tasks: data and theory. Advances in cognitive psychology, 13(1), 28. https://doi.org/10.5709/acp-0204-7

Swan, G., & Wyble, B. (2014). The binding pool: A model of shared neural resources for distinct items in visual working memory. Attention, Perception, & Psychophysics, 76(7), 2136-2157. https://doi.org/10.3758/s13414-014-0633-3

Szameitat, A. J., Schubert, T., Muller, K., and von Cramon, D. Y. (2002).Localization of executive functions in dual-task performance with fMRI.J. Cogn. Neurosci. 14, 1184-1199. https://doi.org/10.1162/089892902760807195

Takagi, Y., Hunt, L. T., Woolrich, M. W., Behrens, T. E., & Klein-Flügge, M. C. (2021). Adapting non-invasive human recordings along multiple task-axes shows unfolding of

spontaneous and over-trained choice. Elife, 10, e60988. https://doi.org/10.7554/eLife.60988.sa2

Teng, C., & Postle, B. R. (2024). Investigating the roles of the visual and parietal cortex in representing content versus context in visual working memory. eNeuro, 11(2), ENEURO.0270-20.2024. https://doi.org/10.1523/ENEURO.0270-20.2024

Thalmann, M., Souza, A., & Oberauer, K. (2019). How Does Chunking Help Working Memory?. Journal of Experimental Psychology: Learning, Memory, and Cognition, 45, 37-55. https://doi.org/10.1037/xlm0000578

Tian, Z., Chen, J., Zhang, C., Min, B., Xu, B., & Wang, L. (2024). Mental programming of spatial sequences in working memory in the macaque frontal cortex. Science, 385(6667), 1437-1444. https://doi.org/10.1126/science.adp6091

Todd, J. J., & Marois, R. (2004). Capacity limit of visual short-term memory in human posterior parietal cortex. Nature, 428(6984), 751-754. https://doi.org/10.1038/nature02466

Tsubomi, Hiroyuki, Keisuke Fukuda, Katsumi Watanabe, and Edward K. Vogel. "Neural limits to representing objects still within view." Journal of Neuroscience 33, no. 19 (2013): 8257-8263. https://doi.org/10.1523/JNEUROSCI.5348-12.2013

van Ede, F., Niklaus, M., & Nobre, A. C. (2017). Temporal expectations guide dynamic prioritization in visual working memory through attenuated α oscillations. Journal of Neuroscience, 37(2), 437-445. https://doi.org/10.1523/JNEUROSCI.2272-16.2016

van Loon, A. M., Olmos-Solis, K., Fahrenfort, J. J., & Olivers, C. N. L. (2018). Current and future goals are represented in opposite patterns in object-selective cortex. eLife, 7, e38677. https://doi.org/10.7554/eLife.38677

VanRullen, R., & Thorpe, S. J. (2001). The time course of visual processing: from early perception to decision-making. Journal of cognitive neuroscience, 13(4), 454-461. https://doi.org/10.1162/08989290152001880

Vergauwe, E., Barrouillet, P., & Camos, V. (2009). Visual and spatial working memory are not that dissociated after all: a time-based resource-sharing account. Journal of Experimental Psychology: Learning, Memory, and Cognition, 35(4), 1012. https://doi.org/10.1037/a0015859

Vergauwe, E., Barrouillet, P., & Camos, V. (2010). Do mental processes share a domain-general resource?. Psychological science, 21(3), 384-390. https://doi.org/10.1177/0956797610361340

Vogel, E. K., & Machizawa, M. G. (2004). Neural activity predicts individual differences in visual working memory capacity. Nature, 428(6984), 748-751. https://doi.org/10.1038/nature02447

Vogel, E. K., McCollough, A. W., & Machizawa, M. G. (2005). Neural measures reveal individual differences in controlling access to working memory. Nature, 438(7067), 500-503. https://doi.org/10.1038/nature04171

Vogel, E., Machizawa, M. Neural activity predicts individual differences in visual working memory capacity. Nature 428, 748-751 (2004). https://doi.org/10.1038/nature02447

Vogel, P., Hahn, J., Duvarci, S., & Sigurdsson, T. (2022). Prefrontal pyramidal neurons are critical for all phases of working memory. Cell reports, 39(2). https://doi.org/10.1016/j.celrep.2022.110659

Voytek, B., & Knight, R. T. (2010). Prefrontal cortex and basal ganglia contributions to visual working memory. Proceedings of the National Academy of Sciences, 107(42), 18167-18172. https://doi.org/10.1073/pnas.1007277107

Wager, T. D., & Smith, E. E. (2003). Neuroimaging studies of working memory: Cognitive Affective & Behavioral Neuroscience, 3(4), 255-274. https://doi.org/10.3758/cabn.3.4.255 https://doi.org/10.3758/CABN.3.4.255

Wan, Q., Menendez, J. A., Postle, B. R., & Yu, Q. (2021). Priority-based remapping of content representations in visual working memory. PLOS Computational Biology, 17(6), e1009062. https://doi.org/10.1371/journal.pcbi.1009062

Wan, Q., Menendez, J. A., Postle, B. R., & Yu, Q. (2023). Priority-based transformations of representational formats in visual working memory. Journal of Cognitive Neuroscience, 35(12), 2116-2132. https://doi.org/10.1162/jocn_a_02166

Watanabe, K., & Funahashi, S. (2014). Neural mechanisms of dual-task interference and cognitive capacity limitation in the prefrontal cortex. Nature neuroscience, 17(4), 601-611. https://doi.org/10.1038/nn.3667

Watanabe, K., & Funahashi, S. (2015). A dual-task paradigm for behavioral and neurobiological studies in nonhuman primates. Journal of neuroscience methods, 246, 1-12. https://doi.org/10.1016/j.jneumeth.2015.03.006

Wei, H., & Zhou, R. (2020). High working memory load impairs selective attention: EEG signatures. Psychophysiology, 57(11). https://doi.org/10.1111/psyp.13643

Wei, Z., Wang, X. J., & Wang, D. H. (2012). From distributed resources to limited slots in multiple-item working memory: a spiking network model with normalization. Journal of Neuroscience, 32(33), 11228-11240. https://doi.org/10.1523/JNEUROSCI.0735-12.2012

Wen, Z., & Schwieter, J.W. (2022). Toward an Integrated Account of Working Memory and Language. https://doi.org/10.31234/osf.io/6m3ryWhitney, D., & Levi, D. M. (2011). Visual crowding: a fundamental limit on conscious perception and object recognition. Trends in cognitive sciences, 15(4), 160-168. https://doi.org/10.1016/j.tics.2011.02.005

Whitfield, J. A., & Holdosh, S. R. (2021). Practice mediates bidirectional dual-task interference when performing a novel sequential nonword repetition task. Journal of Speech, Language, and Hearing Research, 64(6), 1904-1917. https://doi.org/10.1044/2021_JSLHR-20-00605

Whittington, J. C., Dorrell, W., Behrens, T. E., Ganguli, S., & El-Gaby, M. (2025). A tale of two algorithms: Structured slots explain prefrontal sequence memory and are unified with hippocampal cognitive maps. Neuron, 113(2), 321-333. https://doi.org/10.1016/j.neuron.2024.10.017

Wixted, J. T. (2023). Atkinson and Shiffrin's (1968) influential model overshadowed their contemporary theory of human memory. Journal of Memory and Language, 104471-104471. https://doi.org/10.1016/j.jml.2023.104471

Wolff, M. J., & Akyürek, E. G. (2025). Variable processing shifts during perceptual acceleration: Evidence from temporal integration. BioRxiv (Cold Spring Harbor Laboratory). https://doi.org/10.1101/2025.02.12.637809

Wolff, M. J., Jochim, J., Akyürek, E. G., & Stokes, M. G. (2017). Dynamic hidden states underlying working-memory-guided behavior. Nature neuroscience, 20(6), 864-871. https://doi.org/10.1038/nn.4546

Wolff, M. J., Jochim, J., Akyürek, E. G., Buschman, T. J., & Stokes, M. G. (2020). Drifting codes within a stable coding scheme for working memory. PLoS Biology, 18(3), e3000625-e3000625. https://doi.org/10.1371/journal.pbio.3000625

Wolff, M. J., Kandemir, G., Stokes, M. G., & Akyürek, E. G. (2020). Unimodal and bimodal access to sensory working memories by auditory and visual impulses. Journal of Neuroscience, 40(3), 671-681. https://doi.org/10.1523/JNEUROSCI.1194-19.2019

Wood, G., Hartley, G., Furley, P. A., & Wilson, M. R. (2016). Working memory capacity, visual attention and hazard perception in driving. Journal of Applied Research in Memory and Cognition, 5(4), 454-462. https://doi.org/10.1016/j.jarmac.2016.04.009

Woodman, G. F., & Luck, S. J. (2004). Visual search is slowed when visuospatial working memory is occupied. Psychonomic bulletin & review, 11, 269-274. https://doi.org/10.3758/BF03196569

Worden, T. A., Mendes, M., Singh, P., & Vallis, L. A. (2016). Measuring the effects of a visual or auditory Stroop task on dual-task costs during obstacle crossing. Gait & posture, 50, 159-163. https://doi.org/10.1016/j.gaitpost.2016.08.033

Xie, Y., Hu, P., Li, J., Chen, J., Song, W., Wang, X.-J., Yang, T., Stanislas Dehaene, Tang, S., Min, B., & Wang, L. (2022). Geometry of sequence working memory in macaque prefrontal cortex. Science, 375(6581), 632-639. https://doi.org/10.1126/science.abm0204

Xu, Y. (2017). Reevaluating the sensory account of visual working memory storage. Trends in Cognitive Sciences, 21(10), 794-815. https://doi.org/10.1016/j.tics.2017.06.013

Xu, Y. (2024). The human posterior parietal cortices orthogonalize the representation of different streams of information concurrently coded in visual working memory. PLOS Biology, 22(11), e3002915. https://doi.org/10.1371/journal.pbio.3002915

Xu, Y., & Chun, M. M. (2006). Dissociable neural mechanisms supporting visual short-term memory for objects. Nature, 440(7080), 91-95. https://doi.org/10.1038/nature04262

Xu, Y., & Chun, M. M. (2007). Visual grouping in human parietal cortex. Proceedings of the national academy of sciences, 104(47), 18766-18771. https://doi.org/10.1073/pnas.0705618104

Xu, Z., Adam, K. C. S., Fang, X., & Vogel, E. K. (2018). The reliability and stability of visual working memory capacity. Behavior Research Methods, 50(2), 576-588. https://doi.org/10.3758/s13428-017-0886-6

Yeung, N., Nystrom, L. E., Aronson, J. A., & Cohen, J. D. (2006). Between-task competition and cognitive control in task switching. The Journal of neuroscience : the official journal of the Society for Neuroscience, 26(5), 1429-1438. https://doi.org/10.1523/JNEUROSCI.3109-05.2006

Yu, Q., & Postle, B. R. (2021). The neural codes underlying internally generated representations in visual working memory. Journal of Cognitive Neuroscience, 33(6), 1142-1157. https://doi.org/10.1162/jocn_a_01702

Yu, Q., Teng, C., & Postle, B. R. (2020). Different states of priority recruit different neural representations in visual working memory. PLOS Biology, 18(6), e3000769. https://doi.org/10.1371/journal.pbio.3000769

Appendices

Chapter 3.1 – Dual-task Interference in Working Memory: Impairments in Temporal Prioritisation Despite Practice

Appendix A - Descriptive Statistics

Table A1

Descriptive Statistics displaying Accuracy Means and SD of Target Load and Distractor Load for Response 1 and Response 2

Response	*Target Load*	*Distractor Load*	*N*	*Mean*	*SD*
R1	*T1*	*D0*	*21*	*0.834*	*0.121*
		D1	*21*	*0.763*	*0.091*
		D2	*21*	*0.711*	*0.103*
	T2	*D0*	*21*	*0.759*	*0.091*
		D1	*21*	*0.756*	*0.094*
		D2	*21*	*0.700*	*0.079*
R2	*T1*	*D0*	*21*	*0.737*	*0.127*
		D1	*21*	*0.656*	*0.092*
		D2	*21*	*0.588*	*0.089*
	T2	*D0*	*21*	*0.689*	*0.097*
		D1	*21*	*0.584*	*0.082*
		D2	*21*	*0.578*	*0.073*

Table A2

Descriptive Statistics displaying Reaction Time Means and SD of Task Load and Distractor Load for Response 1 and Response 2

Response	*Target Load*	*Distractor Load*	*N*	*Mean*	*SD*
R1	*T1*	*D0*	*21*	*1.233*	*0.349*
		D1	*21*	*1.288*	*0.301*
		D2	*21*	*1.321*	*0.247*
	T2	*D0*	*21*	*1.324*	*0.320*
		D1	*21*	*1.350*	*0.278*
		D2	*21*	*1.418*	*0.284*
R2	*T1*	*D0*	*21*	*1.313*	*0.505*
		D1	*21*	*1.247*	*0.248*
		D2	*21*	*1.301*	*0.243*
	T2	*D0*	*21*	*1.509*	*0.390*
		D1	*21*	*1.320*	*0.268*
		D2	*21*	*1.341*	*0.327*

Chapter 3.2 – Exploring Dual Task Interference in Working Memory and ADHD: A Simplified Paradigm Exploring Effects of Cognitive Load on Performance and Relationship to Inattention and Hyperactivity

Appendix A - ASRS-v.1.1 Questionnaire

Adult ADHD Self-Report Scale (ASRS-v1.1) Symptom Checklist

Patient Name		Today's Date					
Please answer the questions below, rating yourself on each of the criteria shown using the scale on the right side of the page. As you answer each question, place an X in the box that best describes how you have felt and conducted yourself over the past 6 months. Please give this completed checklist to your healthcare professional to discuss during today's appointment.			Never	Rarely	Sometimes	Often	Very Often
1. How often do you have trouble wrapping up the final details of a project, once the challenging parts have been done?							
2. How often do you have difficulty getting things in order when you have to do a task that requires organization?							
3. How often do you have problems remembering appointments or obligations?							
4. When you have a task that requires a lot of thought, how often do you avoid or delay getting started?							
5. How often do you fidget or squirm with your hands or feet when you have to sit down for a long time?							
6. How often do you feel overly active and compelled to do things, like you were driven by a motor?							
							Part A
7. How often do you make careless mistakes when you have to work on a boring or difficult project?							
8. How often do you have difficulty keeping your attention when you are doing boring or repetitive work?							
9. How often do you have difficulty concentrating on what people say to you, even when they are speaking to you directly?							
10. How often do you misplace or have difficulty finding things at home or at work?							
11. How often are you distracted by activity or noise around you?							
12. How often do you leave your seat in meetings or other situations in which you are expected to remain seated?							
13. How often do you feel restless or fidgety?							
14. How often do you have difficulty unwinding and relaxing when you have time to yourself?							
15. How often do you find yourself talking too much when you are in social situations?							
16. When you're in a conversation, how often do you find yourself finishing the sentences of the people you are talking to, before they can finish them themselves?							
17. How often do you have difficulty waiting your turn in situations when turn taking is required?							
18. How often do you interrupt others when they are busy?							
							Part B

Adult ADHD Self-Report Scale (ASRS-v1.1) Symptom Checklist Instructions

The questions on the back page are designed to stimulate dialogue between you and your patients and to help confirm if they may be suffering from the symptoms of attention-deficit/hyperactivity disorder (ADHD).

Description: The Symptom Checklist is an instrument consisting of the eighteen DSM-IV-TR criteria. Six of the eighteen questions were found to be the most predictive of symptoms consistent with ADHD. These six questions are the basis for the ASRS v1.1 Screener and are also Part A of the Symptom Checklist. Part B of the Symptom Checklist contains the remaining twelve questions.

Instructions:

Symptoms

1. Ask the patient to complete both Part A and Part B of the Symptom Checklist by marking an X in the box that most closely represents the frequency of occurrence of each of the symptoms.

2. Score Part A. If four or more marks appear in the darkly shaded boxes within Part A then the patient has symptoms highly consistent with ADHD in adults and further investigation is warranted.

3. The frequency scores on Part B provide additional cues and can serve as further probes into the patient's symptoms. Pay particular attention to marks appearing in the dark shaded boxes. The frequency-based response is more sensitive with certain questions. No total score or diagnostic likelihood is utilized for the twelve questions. It has been found that the six questions in Part A are the most predictive of the disorder and are best for use as a screening instrument.

Impairments

1. Review the entire Symptom Checklist with your patients and evaluate the level of impairment associated with the symptom.

2. Consider work/school, social and family settings.

3. Symptom frequency is often associated with symptom severity, therefore the Symptom Checklist may also aid in the assessment of impairments. If your patients have frequent symptoms, you may want to ask them to describe how these problems have affected the ability to work, take care of things at home, or get along with other people such as their spouse/significant other.

History

1. Assess the presence of these symptoms or similar symptoms in childhood. Adults who have ADHD need not have been formally diagnosed in childhood. In evaluating a patient's history, look for evidence of early-appearing and long-standing problems with attention or self-control. Some significant symptoms should have been present in childhood, but full symptomology is not necessary.

Chapter 3.3 – The Effect of Cognitive Load and Short-term Practice on Working Memory Prioritisation in ADHD

Appendix A – Within-subjects ANOVA for Experimental Half, Condition and Load, against Accuracy

Descriptives

Half	Condition	Load	N	Mean	SD	SE	Coefficient of variation
H1	Single	2	49	0.840	0.090	0.013	0.107
		4	49	0.672	0.091	0.013	0.135
	Dual	2	49	0.865	0.079	0.011	0.092
		4	49	0.730	0.092	0.013	0.125
H2	Single	2	49	0.863	0.070	0.010	0.081
		4	49	0.704	0.098	0.014	0.139
	Dual	2	49	0.877	0.072	0.010	0.082
		4	49	0.757	0.073	0.010	0.096

Within Subjects Effects

Cases	Sum of Squares	df	Mean Square	F	p	η^2_p
Half	0.055	1	0.055	13.040	< .001	0.214
Residuals	0.203	48	0.004			
Condition	0.138	1	0.138	23.121	< .001	0.325
Residuals	0.286	48	0.006			
Load	2.080	1	2.080	558.420	< .001	0.921
Residuals	0.179	48	0.004			
Half ✻ Condition	0.002	1	0.002	0.512	0.478	0.011
Residuals	0.164	48	0.003			
Half ✻ Load	0.004	1	0.004	0.913	0.344	0.019
Residuals	0.208	48	0.004			
Condition ✻ Load	0.032	1	0.032	7.591	0.008	0.137
Residuals	0.203	48	0.004			
Half ✻ Condition ✻ Load	3.180×10^{-4}	1	3.180×10^{-4}	0.090	0.766	0.002
Residuals	0.170	48	0.004			

Note. Type III Sum of Squares

Post Hoc Comparisons - Half

		Mean Difference	SE	t	Cohen's d	p_{bonf}
H1	H2	-0.024	0.007	-3.611	-0.284	< .001***

*** p < .001

Note. Results are averaged over the levels of: Load, Condition

Post Hoc Comparisons - Condition

		Mean Difference	SE	t	Cohen's d	p_{bonf}
Single	Dual	-0.038	0.008	-4.808	-0.449	< .001***

*** p < .001

Note. Results are averaged over the levels of: Load, Half

Post Hoc Comparisons - Load

		Mean Difference	SE	t	Cohen's d	p_{bonf}
2	4	0.146	0.006	23.631	1.742	< .001***

*** p < .001

Note. Results are averaged over the levels of: Condition, Half

Post Hoc Comparisons - Half ✻ Condition

		Mean Difference	SE	t	Cohen's d	p_{bonf}
H1, Single	H2, Single	-0.028	0.009	-3.089	-0.334	0.020*
	H1, Dual	-0.042	0.009	-4.677	-0.499	< .001***
	H2, Dual	-0.061	0.011	-5.740	-0.732	< .001***
H2, Single	H1, Dual	-0.014	0.010	-1.422	-0.165	0.970
	H2, Dual	-0.033	0.011	-3.147	-0.398	0.017*
H1, Dual	H2, Dual	-0.019	0.009	-2.262	-0.233	0.169

* p < .05, *** p < .001

Note. P-value adjusted for comparing a family of 6

Note. Results are averaged over the levels of: Load

Post Hoc Comparisons - Condition ✻ Load

		Mean Difference	SE	t	Cohen's d	p_{bonf}
Single, 2	Dual, 2	-0.019	0.008	-2.288	-0.232	0.159
	Single, 4	0.164	0.010	17.144	1.958	< .001***
	Dual, 4	0.108	0.009	11.972	1.293	< .001***
Dual, 2	Single, 4	0.183	0.011	16.997	2.190	< .001***
	Dual, 4	0.128	0.008	15.141	1.525	< .001***

Post Hoc Comparisons - Condition ✻ Load

		Mean Difference	SE	t	Cohen's d	p_{bonf}
Single, 4	Dual, 4	-0.056	0.012	-4.770	-0.665	< .001***

* p < .05, *** p < .001

Note. P-value adjusted for comparing a family of 6

Note. Results are averaged over the levels of: Half

Appendix B - Within-subjects ANOVA for Experimental Half, Condition and Load, against Reaction Time

Descriptives

Half	Condition	Load	N	Mean	SD	SE	Coefficient of variation
H1	Single	2	49	0.753	0.127	0.018	0.169
		4	49	0.807	0.144	0.021	0.179
	Dual	2	49	0.739	0.155	0.022	0.209
		4	49	0.834	0.177	0.025	0.212
H2	Single	2	49	0.655	0.113	0.016	0.172
		4	49	0.701	0.116	0.017	0.166
	Dual	2	49	0.638	0.123	0.018	0.193
		4	49	0.725	0.133	0.019	0.183

Within Subjects Effects

Cases	Sum of Squares	df	Mean Square	F	p	η^2_p
Half	1.051	1	1.051	114.134	< .001	0.704
Residuals	0.442	48	0.009			
Condition	0.002	1	0.002	0.376	0.542	0.008
Residuals	0.286	48	0.006			
Load	0.485	1	0.485	122.601	< .001	0.719
Residuals	0.190	48	0.004			
Half ✻ Condition	2.410×10^{-4}	1	2.410×10^{-4}	0.111	0.740	0.002
Residuals	0.104	48	0.002			
Half ✻ Load	0.002	1	0.002	0.824	0.369	0.017
Residuals	0.107	48	0.002			
Condition ✻ Load	0.042	1	0.042	27.646	< .001	0.365
Residuals	0.072	48	0.002			
Half ✻ Condition ✻ Load	7.666×10^{-6}	1	7.666×10^{-6}	0.006	0.937	1.298×10^{-4}
Residuals	0.059	48	0.001			

Note. Type III Sum of Squares

Post Hoc Comparisons - Half

		Mean Difference	SE	t	Cohen's d	p_{bonf}
H1	H2	0.104	0.010	10.683	0.753	< .001***

*** p < .001

Note. Results are averaged over the levels of: Load, Condition

Post Hoc Comparisons - Condition

		Mean Difference	SE	t	Cohen's d	p_{bonf}
Single	Dual	-0.005	0.008	-0.614	-0.035	0.542

*** p < .001

Note. Results are averaged over the levels of: Load, Half

Post Hoc Comparisons - Load

		Mean Difference	SE	t	Cohen's d	p_{bonf}
2	4	-0.070	0.006	-11.073	-0.512	< .001***

*** p < .001

Note. Results are averaged over the levels of: Condition, Half

Post Hoc Comparisons - Half ✻ Condition

		Mean Difference	SE	t	Cohen's d	p_{bonf}
H1, Single	H2, Single	0.102	0.010	10.485	0.742	< .001***
	H1, Dual	-0.006	0.010	-0.625	-0.046	1.000
	H2, Dual	0.099	0.012	8.211	0.719	< .001***
H2, Single	H1, Dual	-0.108	0.013	-8.435	-0.788	< .001***
	H2, Dual	-0.003	0.008	-0.407	-0.023	1.000
H1, Dual	H2, Dual	0.105	0.012	8.964	0.765	< .001***

*** p < .001

Note. P-value adjusted for comparing a family of 6

Note. Results are averaged over the levels of: Load

Post Hoc Comparisons - Condition ✻ Load

		Mean Difference	SE	t	Cohen's d	p_{bonf}
Single, 2	Dual, 2	0.016	0.008	1.928	0.115	0.359
	Single, 4	-0.050	0.008	-6.485	-0.362	< .001***
	Dual, 4	-0.075	0.010	-7.315	-0.547	< .001***
Dual, 2	Single, 4	-0.066	0.010	-6.659	-0.477	< .001***
	Dual, 4	-0.091	0.007	-12.540	-0.662	< .001***

Post Hoc Comparisons - Condition ⁎ Load

		Mean Difference	SE	t	Cohen's d	p_{bonf}
Single, 4	Dual, 4	-0.025	0.009	-2.752	-0.185	0.050*

* p < .05, *** p < .001

Note. P-value adjusted for comparing a family of 6

Note. Results are averaged over the levels of: Half

Appendix C – Mixed-subjects ANOVA for Experimental Half, Condition, Load, and ADHD group, against Accuracy.

Descriptives

Half	Condition	Load	ADHD	N	Mean	SD	SE	Coefficient of variation
H1	Single	2	High	23	0.835	0.095	0.020	0.113
			Low	26	0.844	0.087	0.017	0.103
		4	High	23	0.669	0.068	0.014	0.102
			Low	26	0.674	0.109	0.021	0.161
	Dual	2	High	23	0.849	0.063	0.013	0.074
			Low	26	0.880	0.090	0.018	0.103
		4	High	23	0.705	0.084	0.018	0.119
			Low	26	0.752	0.094	0.018	0.125
H2	Single	2	High	23	0.860	0.059	0.012	0.068
			Low	26	0.866	0.080	0.016	0.092
		4	High	23	0.703	0.094	0.020	0.134
			Low	26	0.705	0.103	0.020	0.146
	Dual	2	High	23	0.886	0.058	0.012	0.065
			Low	26	0.868	0.083	0.016	0.095
		4	High	23	0.749	0.073	0.015	0.098
			Low	26	0.764	0.073	0.014	0.095

Within Subjects Effects

Cases	Sum of Squares	df	Mean Square	F	p	η^2_p
Half	0.058	1	0.058	14.297	< .001	0.233
Half ✻ ADHD	0.012	1	0.012	2.935	0.093	0.059
Residuals	0.191	47	0.004			
Condition	0.135	1	0.135	22.401	< .001	0.323
Condition ✻ ADHD	0.004	1	0.004	0.689	0.411	0.014
Residuals	0.282	47	0.006			
Load	2.081	1	2.081	555.212	< .001	0.922
Load ✻ ADHD	0.003	1	0.003	0.696	0.408	0.015
Residuals	0.176	47	0.004			
Half ✻ Condition	0.001	1	0.001	0.394	0.533	0.008
Half ✻ Condition ✻ ADHD	0.008	1	0.008	2.561	0.116	0.052
Residuals	0.156	47	0.003			
Half ✻ Load	0.004	1	0.004	0.854	0.360	0.018
Half ✻ Load ✻ ADHD	5.194×10^{-4}	1	5.194×10^{-4}	0.117	0.733	0.002
Residuals	0.208	47	0.004			
Condition ✻ Load	0.030	1	0.030	7.229	0.010	0.133

Within Subjects Effects

Cases	Sum of Squares	df	Mean Square	F	p	η^2_p
Condition ✻ Load ✻ ADHD	0.005	1	0.005	1.200	0.279	0.025
Residuals	0.198	47	0.004			
Half ✻ Condition ✻ Load	2.735×10^{-4}	1	2.735×10^{-4}	0.076	0.785	0.002
Half ✻ Condition ✻ Load ✻ ADHD	4.238×10^{-4}	1	4.238×10^{-4}	0.117	0.734	0.002
Residuals	0.170	47	0.004			

Note. Type III Sum of Squares

Between Subjects Effects

Cases	Sum of Squares	df	Mean Square	F	p	η^2_p
ADHD	0.014	1	0.014	0.537	0.467	0.011
Residuals	1.258	47	0.027			

Note. Type III Sum of Squares

Post Hoc Comparisons - ADHD ✻ Half

		Mean Difference	SE	t	Cohen's d	p_{bonf}
High, H1	Low, H1	-0.023	0.019	-1.202	-0.277	1.000
	High, H2	-0.035	0.009	-3.771	-0.423	0.003**
	Low, H2	-0.037	0.018	-2.045	-0.436	0.279
Low, H1	High, H2	-0.012	0.018	-0.693	-0.146	1.000
	Low, H2	-0.013	0.009	-1.509	-0.159	0.828
High, H2	Low, H2	-0.001	0.016	-0.067	-0.013	1.000

** p < .01, *** p < .001

Note. P-value adjusted for comparing a family of 6

Note. Results are averaged over the levels of: Load, Condition

Post Hoc Comparisons - ADHD ✻ Condition

		Mean Difference	SE	t	Cohen's d	p_{bonf}
High, Single	Low, Single	-0.006	0.019	-0.297	-0.067	1.000
	High, Dual	-0.031	0.011	-2.679	-0.365	0.061
	Low, Dual	-0.049	0.018	-2.683	-0.588	0.060
Low, Single	High, Dual	-0.025	0.018	-1.366	-0.298	1.000
	Low, Dual	-0.044	0.011	-4.060	-0.521	0.001**
High, Dual	Low, Dual	-0.019	0.018	-1.054	-0.223	1.000

** p < .01, *** p < .001

Post Hoc Comparisons - ADHD ✲ Condition

		Mean Difference	SE	t	Cohen's d	p_{bonf}

Note. P-value adjusted for comparing a family of 6
Note. Results are averaged over the levels of: Load, Half

Post Hoc Comparisons - ADHD ✲ Load

		Mean Difference	SE	t	Cohen's d	p_{bonf}
High, 2	Low, 2	-0.007	0.017	-0.399	-0.083	1.000
	High, 4	0.151	0.009	16.746	1.804	< .001***
	Low, 4	0.134	0.018	7.577	1.598	< .001***
Low, 2	High, 4	0.158	0.018	8.937	1.887	< .001***
	Low, 4	0.141	0.008	16.587	1.681	< .001***
High, 4	Low, 4	-0.017	0.018	-0.967	-0.207	1.000

*** p < .001
Note. P-value adjusted for comparing a family of 6
Note. Results are averaged over the levels of: Condition, Half

Appendix D – Mixed-subjects ANOVA for Experimental Half, Condition, Load, and ADHD group, against Reaction Time.

Descriptives

Half	Condition	Load	ADHD	N	Mean	SD	SE	Coefficient of variation
H1	Single	2	High	23	0.788	0.130	0.027	0.165
			Low	26	0.723	0.118	0.023	0.164
		4	High	23	0.818	0.156	0.032	0.190
			Low	26	0.797	0.135	0.027	0.170
	Dual	2	High	23	0.781	0.167	0.035	0.214
			Low	26	0.701	0.134	0.026	0.192
		4	High	23	0.886	0.194	0.041	0.220
			Low	26	0.789	0.149	0.029	0.189
H2	Single	2	High	23	0.679	0.114	0.024	0.168
			Low	26	0.635	0.110	0.022	0.174
		4	High	23	0.713	0.111	0.023	0.155
			Low	26	0.691	0.122	0.024	0.177
	Dual	2	High	23	0.666	0.130	0.027	0.195
			Low	26	0.614	0.113	0.022	0.185
		4	High	23	0.754	0.140	0.029	0.186
			Low	26	0.699	0.122	0.024	0.175

Within Subjects Effects

Cases	Sum of Squares	df	Mean Square	F	p	η^2_p
Half	1.061	1	1.061	116.055	< .001	0.712
Half ✻ ADHD	0.012	1	0.012	1.348	0.252	0.028
Residuals	0.430	47	0.009			
Condition	0.003	1	0.003	0.593	0.445	0.012
Condition ✻ ADHD	0.026	1	0.026	4.791	0.034	0.093
Residuals	0.260	47	0.006			
Load	0.478	1	0.478	120.537	< .001	0.719
Load ✻ ADHD	0.003	1	0.003	0.861	0.358	0.018
Residuals	0.186	47	0.004			
Half ✻ Condition	3.704×10^{-4}	1	3.704×10^{-4}	0.174	0.679	0.004
Half ✻ Condition ✻ ADHD	0.004	1	0.004	1.759	0.191	0.036
Residuals	0.100	47	0.002			
Half ✻ Load	0.002	1	0.002	0.781	0.381	0.016
Half ✻ Load ✻ ADHD	1.042×10^{-4}	1	1.042×10^{-4}	0.046	0.831	9.758×10^{-4}
Residuals	0.107	47	0.002			

Within Subjects Effects

Cases	Sum of Squares	df	Mean Square	F	p	η^2_p
Condition ✻ Load	0.044	1	0.044	33.910	< .001	0.419
Condition ✻ Load ✻ ADHD	0.011	1	0.011	8.525	0.005	0.154
Residuals	0.061	47	0.001			
Half ✻ Condition ✻ Load	2.968×10^{-5}	1	2.968×10^{-5}	0.024	0.876	5.192×10^{-4}
Half ✻ Condition ✻ Load ✻ ADHD	0.002	1	0.002	1.582	0.215	0.033
Residuals	0.057	47	0.001			

Note. Type III Sum of Squares

Between Subjects Effects

Cases	Sum of Squares	df	Mean Square	F	p	η^2_p
ADHD	0.290	1	0.290	2.394	0.129	0.048
Residuals	5.702	47	0.121			

Note. Type III Sum of Squares

Post Hoc Comparisons - ADHD ✻ Condition

		Mean Difference	SE	t	Cohen's d	p_{bonf}
High, Single	Low, Single	0.038	0.033	1.151	0.281	1.000
	High, Dual	-0.022	0.011	-2.031	-0.164	0.288
	Low, Dual	0.049	0.036	1.359	0.360	1.000
Low, Single	High, Dual	-0.060	0.036	-1.666	-0.445	0.614
	Low, Dual	0.011	0.010	1.035	0.079	1.000
High, Dual	Low, Dual	0.071	0.039	1.831	0.524	0.441

*** p < .001

Note. P-value adjusted for comparing a family of 6

Note. Results are averaged over the levels of: Load, Half

Post Hoc Comparisons - ADHD ✻ Condition ✻ Load

		Mean Difference	SE	t	Cohen's d	p_{bonf}
High, Single, 2	Low, Single, 2	0.055	0.032	1.687	0.403	1.000
	High, Dual, 2	0.010	0.012	0.802	0.071	1.000
	Low, Dual, 2	0.076	0.035	2.181	0.560	0.959
	High, Single, 4	-0.032	0.011	-2.990	-0.237	0.124
	Low, Single, 4	-0.011	0.034	-0.315	-0.079	1.000

Post Hoc Comparisons - ADHD ✲ Condition ✲ Load

		Mean Difference	SE	t	Cohen's d	p_{bonf}
	High, Dual, 4	-0.086	0.015	-5.762	-0.637	< .001***
	Low, Dual, 4	-0.011	0.037	-0.287	-0.078	1.000
Low, Single, 2	High, Dual, 2	-0.045	0.035	-1.281	-0.332	1.000
	Low, Dual, 2	0.021	0.011	1.879	0.157	1.000
	High, Single, 4	-0.087	0.034	-2.554	-0.641	0.391
	Low, Single, 4	-0.065	0.010	-6.457	-0.482	< .001***
	High, Dual, 4	-0.141	0.037	-3.761	-1.040	0.013*
	Low, Dual, 4	-0.065	0.014	-4.629	-0.481	< .001***
High, Dual, 2	Low, Dual, 2	0.066	0.037	1.774	0.489	1.000
	High, Single, 4	-0.042	0.014	-3.047	-0.309	0.106
	Low, Single, 4	-0.020	0.036	-0.558	-0.150	1.000
	High, Dual, 4	-0.096	0.011	-9.012	-0.708	< .001***
	Low, Dual, 4	-0.020	0.039	-0.514	-0.149	1.000
Low, Dual, 2	High, Single, 4	-0.108	0.036	-2.977	-0.798	0.129
	Low, Single, 4	-0.087	0.013	-6.708	-0.639	< .001***
	High, Dual, 4	-0.162	0.040	-4.098	-1.197	0.005**
	Low, Dual, 4	-0.086	0.010	-8.634	-0.638	< .001***
High, Single, 4	Low, Single, 4	0.021	0.035	0.608	0.159	1.000
	High, Dual, 4	-0.054	0.012	-4.395	-0.400	0.002**
	Low, Dual, 4	0.022	0.038	0.563	0.159	1.000
Low, Single, 4	High, Dual, 4	-0.076	0.039	-1.955	-0.558	1.000
	Low, Dual, 4	7.464×10^{-5}	0.012	0.006	5.508×10^{-4}	1.000
High, Dual, 4	Low, Dual, 4	0.076	0.041	1.827	0.559	1.000

* p < .05, ** p < .01, *** p < .001

Note. P-value adjusted for comparing a family of 28

Note. Results are averaged over the levels of: Half

Appendix E – Inattention and Hyperactivity Analyses

Accuracy:

Descriptives

Half	Condition	Load	ADHD	N	Mean	SD	SE	Coefficient of variation
H1	Single	2	High	23	0.835	0.095	0.020	0.113
			Low	26	0.844	0.087	0.017	0.103
		4	High	23	0.669	0.068	0.014	0.102
			Low	26	0.674	0.109	0.021	0.161
	Dual	2	High	23	0.849	0.063	0.013	0.074
			Low	26	0.880	0.090	0.018	0.103
		4	High	23	0.705	0.084	0.018	0.119
			Low	26	0.752	0.094	0.018	0.125
H2	Single	2	High	23	0.860	0.059	0.012	0.068
			Low	26	0.866	0.080	0.016	0.092
		4	High	23	0.703	0.094	0.020	0.134
			Low	26	0.705	0.103	0.020	0.146
	Dual	2	High	23	0.886	0.058	0.012	0.065
			Low	26	0.868	0.083	0.016	0.095
		4	High	23	0.749	0.073	0.015	0.098
			Low	26	0.764	0.073	0.014	0.095

Within Subjects Effects

Cases	Sum of Squares	df	Mean Square	F	p	η^2_p
Half	0.003	1	0.003	0.610	0.439	0.013
Half ∗ Inattentive	7.417×10^{-5}	1	7.417×10^{-5}	0.018	0.894	3.984×10^{-4}
Half ∗ Hyperactive	0.005	1	0.005	1.176	0.284	0.025
Half ∗ ADHD	0.002	1	0.002	0.370	0.546	0.008
Residuals	0.186	45	0.004			
Condition	5.206×10^{-4}	1	5.206×10^{-4}	0.095	0.759	0.002
Condition ∗ Inattentive	1.046×10^{-5}	1	1.046×10^{-5}	0.002	0.965	4.240×10^{-5}
Condition ∗ Hyperactive	0.033	1	0.033	6.019	0.018	0.118
Condition ∗ ADHD	0.013	1	0.013	2.292	0.137	0.048
Residuals	0.247	45	0.005			
Load	0.246	1	0.246	67.438	< .001	0.600
Load ∗ Inattentive	0.007	1	0.007	1.884	0.177	0.040
Load ∗ Hyperactive	0.008	1	0.008	2.178	0.147	0.046
Load ∗ ADHD	0.004	1	0.004	1.040	0.313	0.023

Within Subjects Effects

Cases	Sum of Squares	df	Mean Square	F	p	η^2_p
Residuals	0.164	45	0.004			
Half ✻ Condition	0.001	1	0.001	0.408	0.526	0.009
Half ✻ Condition ✻ Inattentive	0.004	1	0.004	1.186	0.282	0.026
Half ✻ Condition ✻ Hyperactive	4.582×10^{-4}	1	4.582×10^{-4}	0.136	0.714	0.003
Half ✻ Condition ✻ ADHD	0.009	1	0.009	2.692	0.108	0.056
Residuals	0.152	45	0.003			
Half ✻ Load	5.130×10^{-4}	1	5.130×10^{-4}	0.113	0.739	0.002
Half ✻ Load ✻ Inattentive	4.928×10^{-4}	1	4.928×10^{-4}	0.108	0.744	0.002
Half ✻ Load ✻ Hyperactive	0.002	1	0.002	0.395	0.533	0.009
Half ✻ Load ✻ ADHD	0.002	1	0.002	0.516	0.476	0.011
Residuals	0.205	45	0.005			
Condition ✻ Load	5.146×10^{-4}	1	5.146×10^{-4}	0.121	0.730	0.003
Condition ✻ Load ✻ Inattentive	1.780×10^{-5}	1	1.780×10^{-5}	0.004	0.949	9.263×10^{-5}
Condition ✻ Load ✻ Hyperactive	0.005	1	0.005	1.272	0.265	0.027
Condition ✻ Load ✻ ADHD	0.004	1	0.004	1.008	0.321	0.022
Residuals	0.192	45	0.004			
Half ✻ Condition ✻ Load	0.001	1	0.001	0.298	0.588	0.007
Half ✻ Condition ✻ Load ✻ Inattentive	0.003	1	0.003	0.944	0.336	0.021
Half ✻ Condition ✻ Load ✻ Hyperactive	0.001	1	0.001	0.309	0.581	0.007
Half ✻ Condition ✻ Load ✻ ADHD	0.002	1	0.002	0.605	0.441	0.013
Residuals	0.166	45	0.004			

Note. Type III Sum of Squares

Between Subjects Effects

Cases	Sum of Squares	df	Mean Square	F	p	η^2_p
Inattentive	0.028	1	0.028	1.110	0.298	0.024
Hyperactive	0.061	1	0.061	2.399	0.128	0.051
ADHD	0.031	1	0.031	1.212	0.277	0.026
Residuals	1.140	45	0.025			

Note. Type III Sum of Squares

Reaction Time

Descriptives

Half	Condition	Load	ADHD	N	Mean	SD	SE	Coefficient of variation
H1	Single	2	High	23	0.788	0.130	0.027	0.165
			Low	26	0.723	0.118	0.023	0.164
		4	High	23	0.818	0.156	0.032	0.190
			Low	26	0.797	0.135	0.027	0.170
	Dual	2	High	23	0.781	0.167	0.035	0.214
			Low	26	0.701	0.134	0.026	0.192
		4	High	23	0.886	0.194	0.041	0.220
			Low	26	0.789	0.149	0.029	0.189
H2	Single	2	High	23	0.679	0.114	0.024	0.168
			Low	26	0.635	0.110	0.022	0.174
		4	High	23	0.713	0.111	0.023	0.155
			Low	26	0.691	0.122	0.024	0.177
	Dual	2	High	23	0.666	0.130	0.027	0.195
			Low	26	0.614	0.113	0.022	0.185
		4	High	23	0.754	0.140	0.029	0.186
			Low	26	0.699	0.122	0.024	0.175

Within Subjects Effects

Cases	Sum of Squares	df	Mean Square	F	p	η^2_p
Half	0.172	1	0.172	18.779	< .001	0.294
Half ✻ ADHD	0.017	1	0.017	1.863	0.179	0.040
Half ✻ Inattentive	5.990×10^{-4}	1	5.990×10^{-4}	0.065	0.799	0.001
Half ✻ Hyperactive	0.014	1	0.014	1.572	0.216	0.034
Residuals	0.412	45	0.009			
Condition	0.005	1	0.005	0.854	0.360	0.019
Condition ✻ ADHD	1.140×10^{-4}	1	1.140×10^{-4}	0.021	0.886	4.596×10^{-4}
Condition ✻ Inattentive	0.012	1	0.012	2.133	0.151	0.045
Condition ✻ Hyperactive	8.905×10^{-4}	1	8.905×10^{-4}	0.162	0.690	0.004
Residuals	0.248	45	0.006			
Load	0.039	1	0.039	9.578	0.003	0.175
Load ✻ ADHD	0.003	1	0.003	0.696	0.409	0.015
Load ✻ Inattentive	9.054×10^{-4}	1	9.054×10^{-4}	0.220	0.642	0.005
Load ✻ Hyperactive	9.565×10^{-5}	1	9.565×10^{-5}	0.023	0.880	5.153×10^{-4}

Within Subjects Effects

Cases	Sum of Squares	df	Mean Square	F	p	η^2_p
Residuals	0.186	45	0.004			
Half ✻ Condition	5.235×10^{-4}	1	5.235×10^{-4}	0.245	0.623	0.005
Half ✻ Condition ✻ ADHD	1.116×10^{-4}	1	1.116×10^{-4}	0.052	0.820	0.001
Half ✻ Condition ✻ Inattentive	3.397×10^{-6}	1	3.397×10^{-6}	0.002	0.968	3.527×10^{-5}
Half ✻ Condition ✻ Hyperactive	0.004	1	0.004	1.729	0.195	0.037
Residuals	0.096	45	0.002			
Half ✻ Load	0.002	1	0.002	0.721	0.400	0.016
Half ✻ Load ✻ ADHD	3.177×10^{-4}	1	3.177×10^{-4}	0.136	0.715	0.003
Half ✻ Load ✻ Inattentive	2.320×10^{-4}	1	2.320×10^{-4}	0.099	0.755	0.002
Half ✻ Load ✻ Hyperactive	6.841×10^{-4}	1	6.841×10^{-4}	0.292	0.592	0.006
Residuals	0.105	45	0.002			
Condition ✻ Load	0.003	1	0.003	2.453	0.124	0.052
Condition ✻ Load ✻ ADHD	0.002	1	0.002	1.808	0.185	0.039
Condition ✻ Load ✻ Inattentive	6.408×10^{-5}	1	6.408×10^{-5}	0.047	0.829	0.001
Condition ✻ Load ✻ Hyperactive	1.972×10^{-5}	1	1.972×10^{-5}	0.015	0.905	3.230×10^{-4}
Residuals	0.061	45	0.001			
Half ✻ Condition ✻ Load	7.453×10^{-4}	1	7.453×10^{-4}	0.597	0.444	0.013
Half ✻ Condition ✻ Load ✻ ADHD	0.002	1	0.002	1.693	0.200	0.036
Half ✻ Condition ✻ Load ✻ Inattentive	2.228×10^{-4}	1	2.228×10^{-4}	0.179	0.675	0.004
Half ✻ Condition ✻ Load ✻ Hyperactive	5.152×10^{-4}	1	5.152×10^{-4}	0.413	0.524	0.009
Residuals	0.056	45	0.001			

Note. Type III Sum of Squares

Between Subjects Effects

Cases	Sum of Squares	df	Mean Square	F	p	η^2_p
ADHD	0.111	1	0.111	0.927	0.341	0.020
Inattentive	0.051	1	0.051	0.425	0.518	0.009
Hyperactive	0.308	1	0.308	2.569	0.116	0.054
Residuals	5.387	45	0.120			

Note. Type III Sum of Squares

Supplemental Figures

Chapter 2 – The Neural Basis of Generalisation and Conflict Resolution in Categorisation

Figure S1

Accuracy and Reaction Time Split by Session and Task

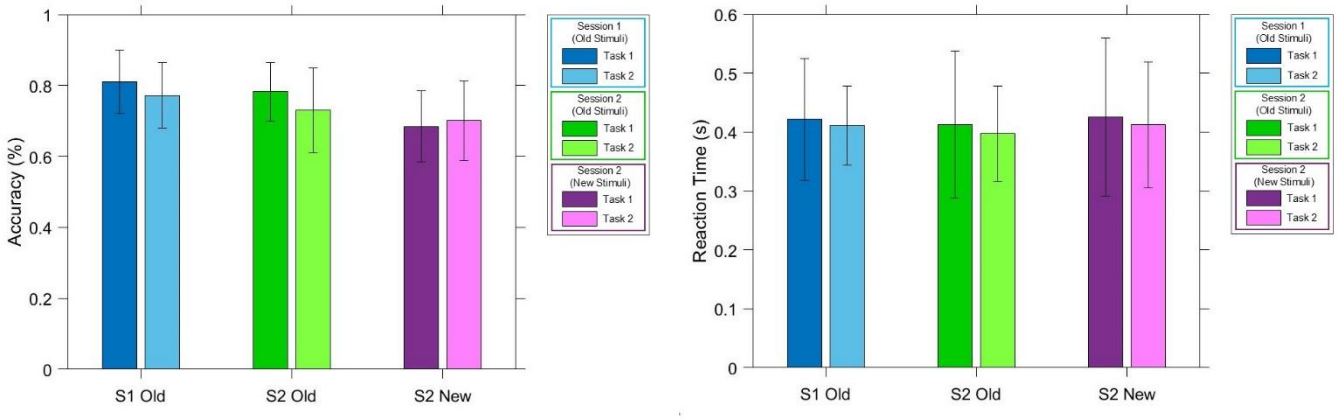


Figure S1. Accuracy (left) and Reaction Time (right) for Session 1 old stimuli, Session 2 old stimuli, and Session 2 new (overlapping stimuli). A 3x2 ANOVA indicated a significant main effect of session ($F(2, 58) = 70.6$, $p<.001$. A significant interaction effect between session and task was also found ($F(2, 58) = 12.3$, $p<.001$), with no main effect of task ($F(1, 29) = 4.36$, $p=.05$). Reaction time displayed no significant main effects for session ($F(2, 58) = 1.99$, $p=.146$) and Task ($F(1, 29) = 1.56$, $p=.222$), and no significant interaction effect ($F(2, 58) = .24$, $p=.788$). Error bars are SEM.

Figure S2

Category Decoding Strength for Session 1 and 2, Split by New/Old stimuli for the Irrelevant Category

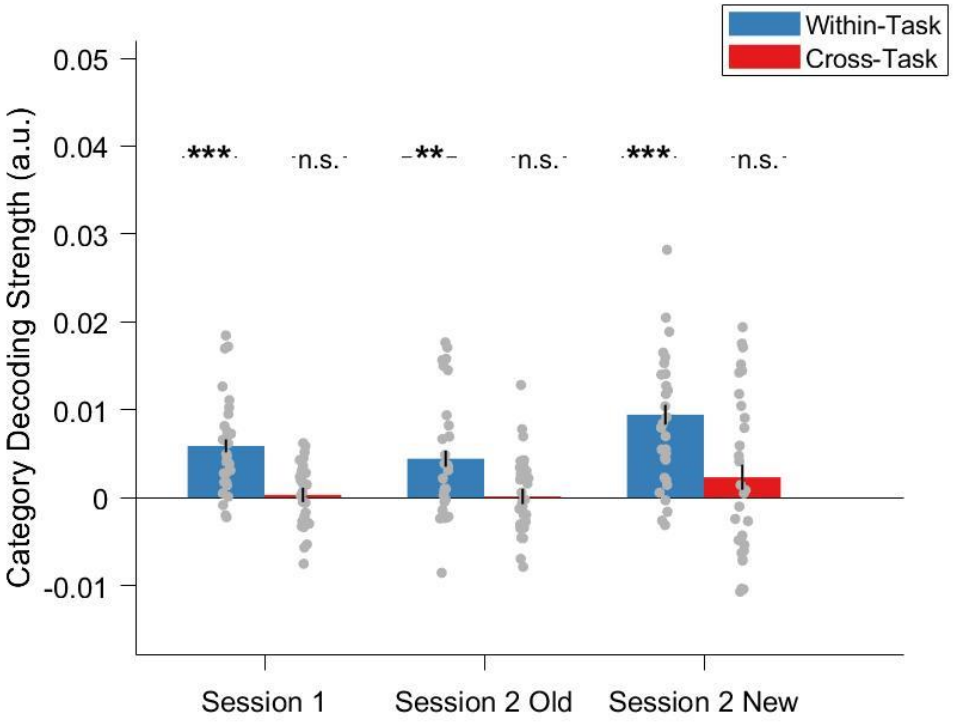


Figure S2. Irrelevant category decoding strength for Session 1 (old stimuli), Session 2 old stimuli, and Session 2 new (overlapping stimuli) averaged over time. T-test results suggest for Session 1, within-task decoding (M = .0059, SD = .0054) was found to be highly significant (t(29) = 5.93, p<.001), with no significant presence found for cross-task decoding (M = .0003, SD = .0036), (t(29) = 0.474, p=.639). For Session 2 (old), within-task decoding was found to be significant (M =.0044, SD = .0069), (t(29) = 3.52, p=.002), with no significant cross-task decoding found (M = .0001, SD = .0045), t(29) = .162, p = .873). For the overlapping stimuli found in Session 2, within-task decoding was found to be highly significant (M = .0094, SD = .009), t(29) = 5.72, p<.001), whereas cross-task decoding (M = .0023, SD = .009) was not found to be significant (t(29) = 1.35, p=.186). Error bars are SEM.

Figure S3

Within and Cross Decoding for Session 2, overlapping stimuli for the Irrelevant Category

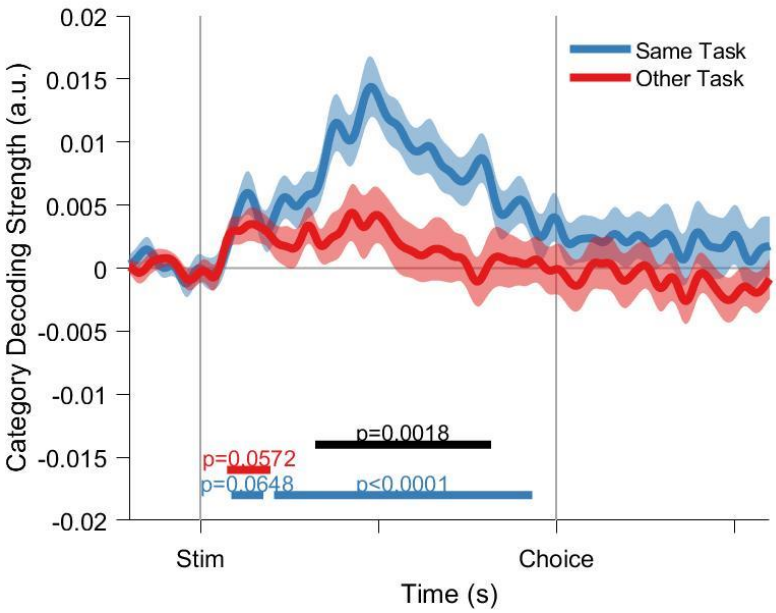


Figure S3. Irrelevant within and cross-task decoding for Session 2, overlapping stimuli. Within-task decoding was found to be highly significant (p<.001, cluster window = 208-932ms), whereas cross-task decoding was not found to be significant (p=.115). A significant difference was found (p=.002, cluster window = 324-816ms).

Figure S4

Within Decoding for Session 1 and Session 2 for old stimuli for the irrelevant category

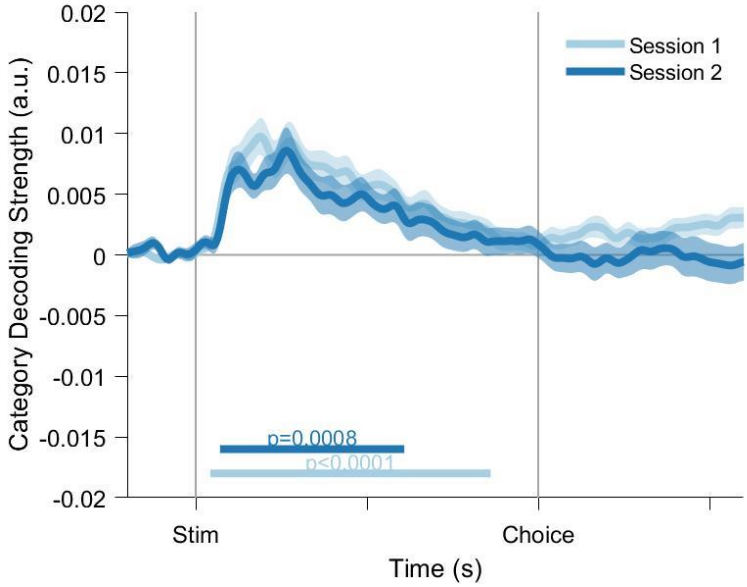


Figure S4. Irrelevant within-task decoding for Session 1 and Session 2 (old stimuli only). Results found a significant presence of within-task decoding in both Session 1 (p<.001, cluster window 44-860ms), and Session 2 (p<.001, cluster window = 72-608ms). No significant difference was found (p=.223).

Figure S5

Cross Decoding for Session 1 and Session 2, old stimuli for the irrelevant category

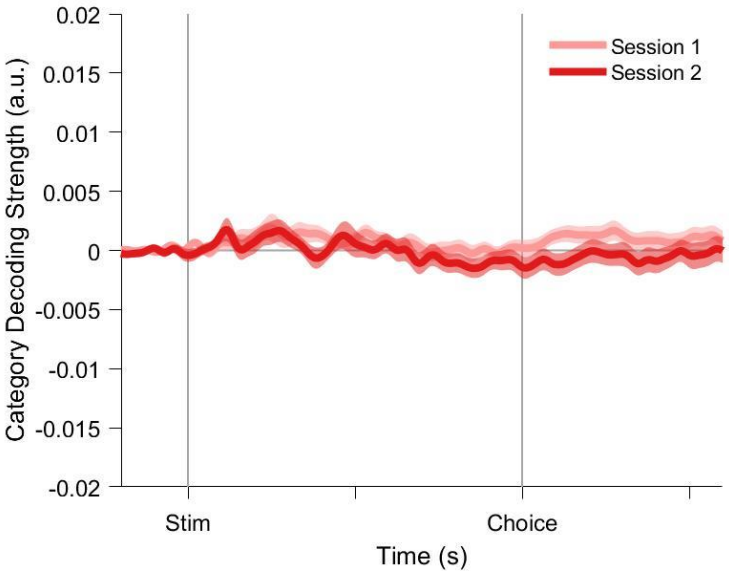


Figure S5. Irrelevant cross-task decoding for Session 1 and Session 2 (old stimuli only). Results indicate no significant presence of cross-task decoding in Session 1 (p=.372) or Session 2 (p=.255), and no significant difference found (no significant clusters).

Figure S6

Within- and Cross-Plane Decoding for Session 1, Task 1 (Stimulus Planes 1 and 2, old stimuli)

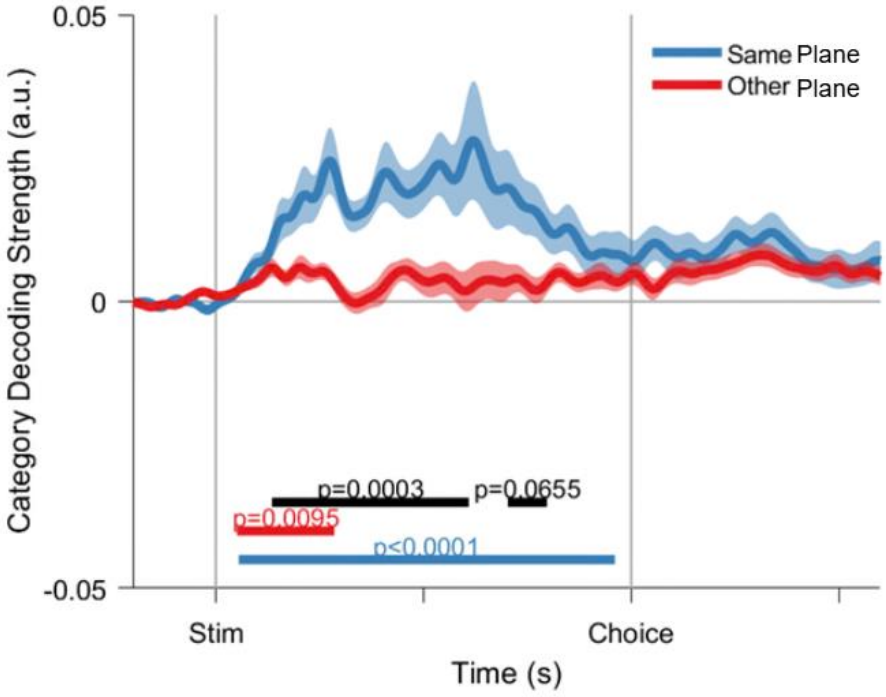


Figure S6.

Within- and cross-plane decoding for Session 1 (stimuli planes 1 and 2), using training data from plane 2. Results suggest a strong presence of within task decoding (p<.001, cluster window = 56-960ms), as well as cross task decoding (p=.001, cluster window = 52 – 284ms). A significant difference was also found (p<.001, cluster window = 136-609ms).

Figure S7

Within and Cross Decoding for Session 1, Task 2 (Stimulus Planes 4 and 5, old stimuli)

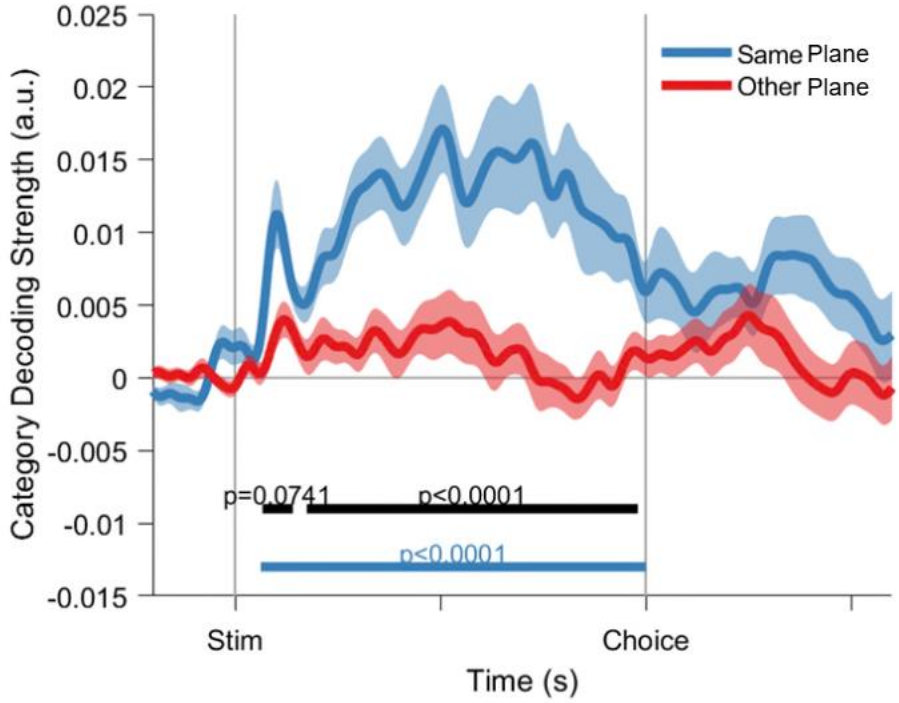


Figure S7. Within and Cross-plane decoding for Session 2 (planes 4 and 5), using training data from plane 4. Results show significant within-task decoding (p<.001, cluster window = 64 – 1000ms) but no cross-task decoding (most significant candidate cluster p=.199). A significant difference was also found (p<.001, cluster window = 176-980ms).

Figure S8

Within and Cross Decoding for Session 2, Task 1 (Stimulus Plane 1 and 2, old stimuli), (Training Data Planes 1/3/5)

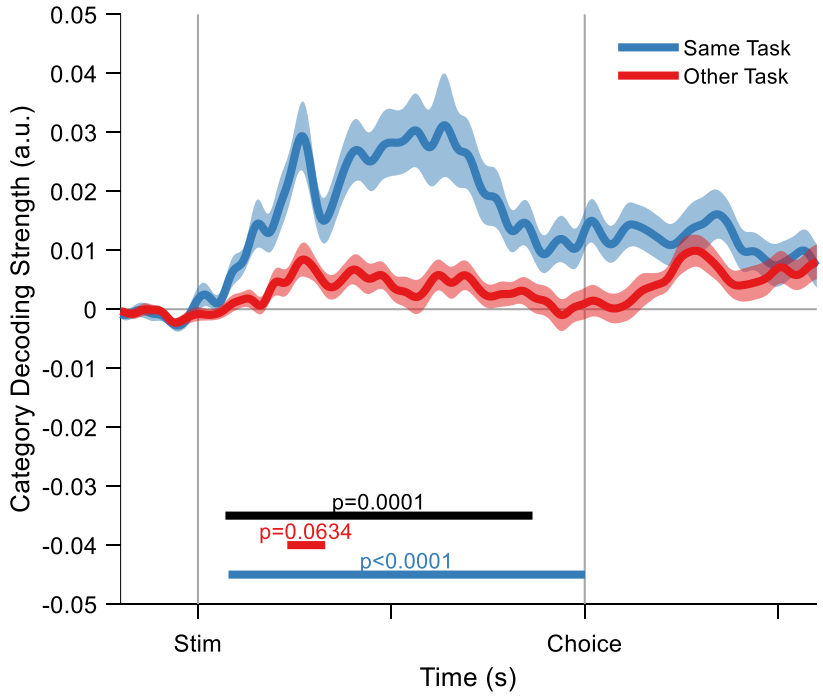


Figure S8. Within and cross-task decoding for Session 2 (stimuli planes 1 and 2), using training data from planes 1, 3 and 5. Within-task decoding was found to be highly significant (p<.001, cluster window = 80-1000ms), with no significant cross-task decoding found (p=.187). A significant difference was also found (p<.001, cluster window = 72-864ms).

Figure S9

Within and Cross Decoding for Session 2, Task 2 (Stimulus Planes 4 and 5, old stimuli), (Training Data Planes 1/3/5)

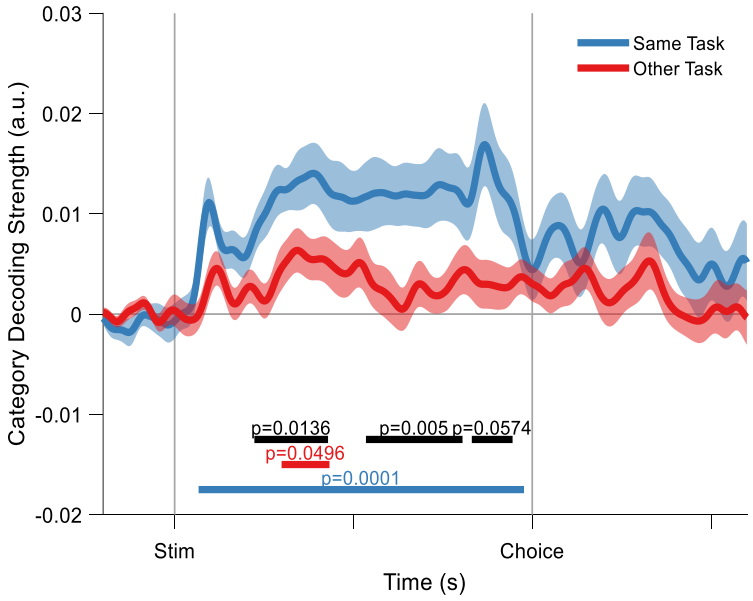


Figure S9. Within and cross-task decoding for Session 2 (stimuli planes 4 and 5), using training data from planes 1, 3 and 5). Within-task decoding was found to be highly significant (p<.001, cluster window = 68-970ms), with no cross-decoding found (p=.05). A significant difference was also found (p=.01, cluster window = 224-429ms and p=.005, cluster window = 535-804ms).

Figure S10

Cross Decoding for Session 2, Averaged over Task 1 (Stimulus Planes 1, 2, and 3) (overlapping and old stimuli), (Training Data Planes 1/3/5)

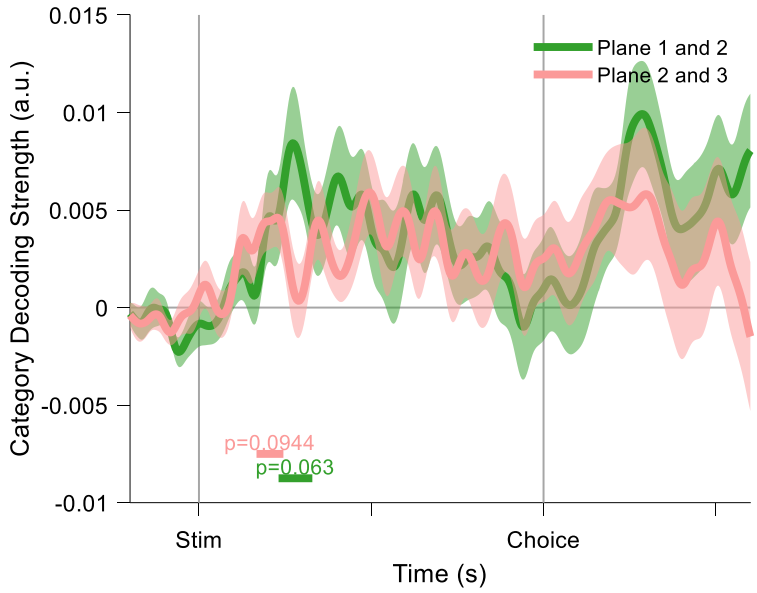


Figure S10. Cross-task decoding for Session 2 (stimuli planes 1, 2 and 3), using training data from planes 1, 3 and 5. Green line indicates cross-decoding for planes 1 and 2, and the pink line indicates cross-decoding for plane 2 and 3. Cross-task decoding was not found to be significant for plane 1 and 2 (p=.194) or 2 and 3 (p=.234), with no significant difference found (p=.234).

Figure S11

Cross Decoding for Session 2, Averaged over Task 2 (Stimulus Planes 3, 4, and 5) (overlapping and old stimuli), (Training Data Planes 1/3/5)

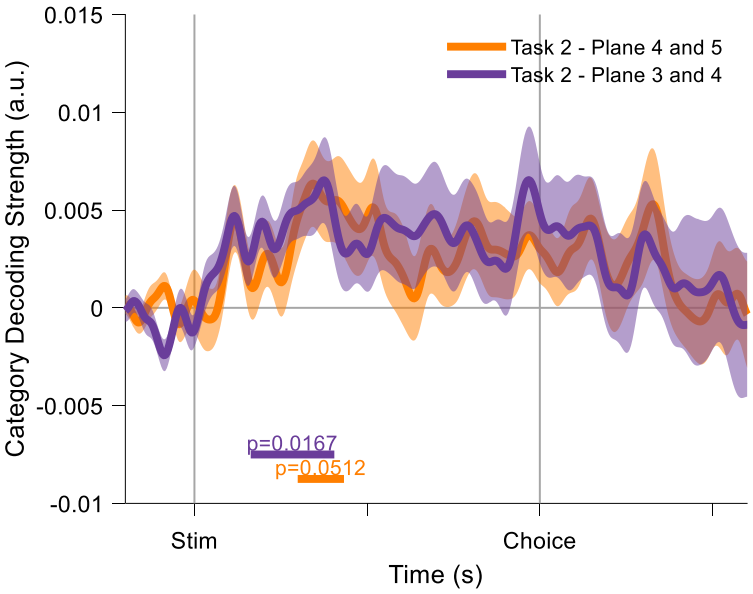


Figure S11. Cross-task decoding for Session 2 (stimuli planes 3, 4 and 5), using training data from planes 1, 3 and 5. The orange line indicates cross-task decoding for planes 4 and 5, whereas the purple line indicates cross-task decoding for planes 3 and 4. Cross-task decoding was found to be significant for planes 3 and 4 (p=.017, cluster window 164-404ms), with no significant decoding found for plane 4 and 5 (p=.156), and no significant difference found (no significant clusters).

Figure S12

Irrelevant Within and Cross Decoding for Session 1, Stimulus Planes 1 and 5 (old stimuli)

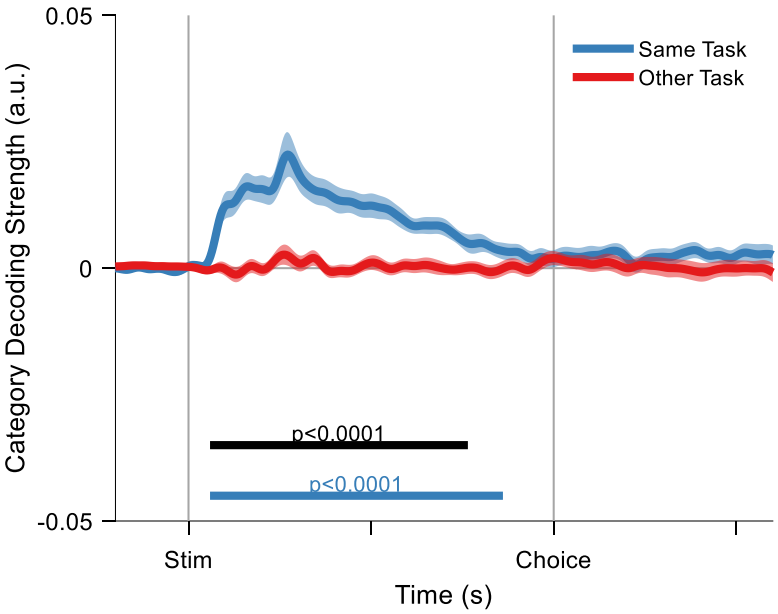


Figure S12. Irrelevant within and cross-task decoding for Session 1 (stimuli planes 1 and 5). Within-task decoding was found to be highly significant (p<.001, cluster window 60-860ms), with no significant cross-task decoding found. A significant difference was also found (p<.001, cluster window 60-764ms).

Figure S13

Irrelevant Within and Cross Decoding for Session 1, Stimulus Planes 2 and 4, old stimuli

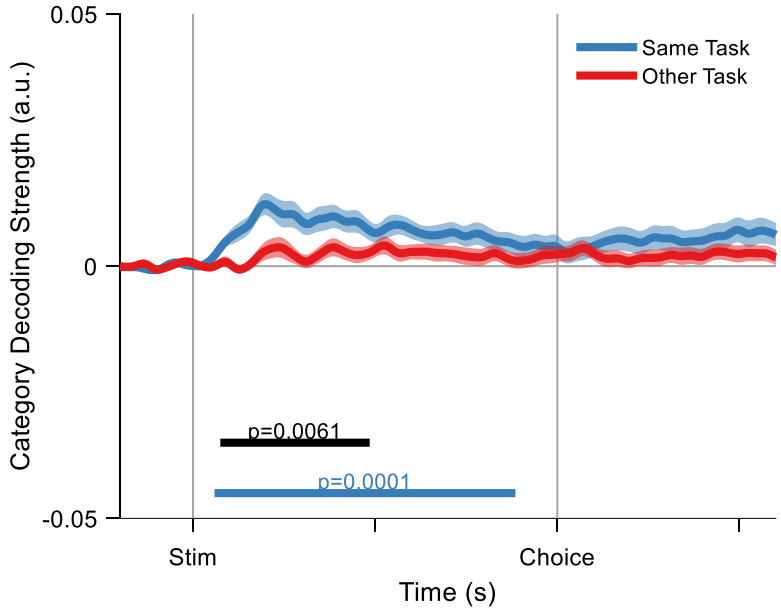


Figure S13. Irrelevant within and cross-task category decoding for Session 1 (planes 2 and 4). Within-task decoding was found to be significant (p<.001, cluster window = 60-884ms). Cross-task decoding was not found to be significant (p=.272). A significant difference in decoding strength was also found (p=.006, cluster window = 76-484ms).

Figure S14

Irrelevant Within and Cross Decoding for Session 2, Stimulus Planes 1 and 5, old stimuli

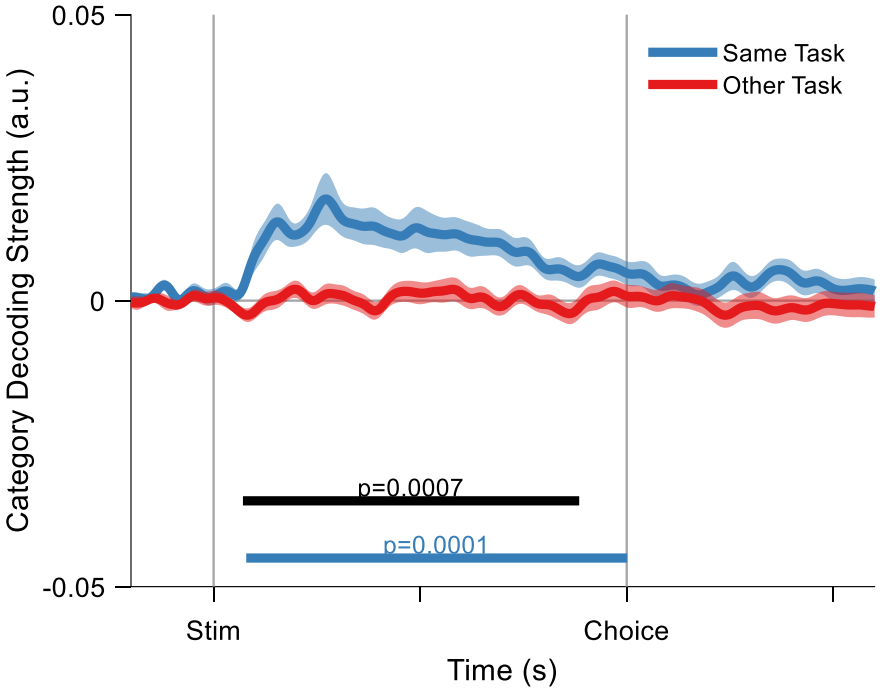


Figure S14. Irrelevant within and cross-task decoding for Session 2 (stimuli planes 1 and 5). Within-task decoding was found to be highly significant (p<.001, cluster window = 80-1000ms). No significant cross-task decoding was found (p=.520), and a significant difference between the decoding types was also found (p<.001, cluster window 72-884ms).

Figure S15

Irrelevant Within and Cross Decoding for Session 2, Stimulus Planes 2 and 4, old stimuli

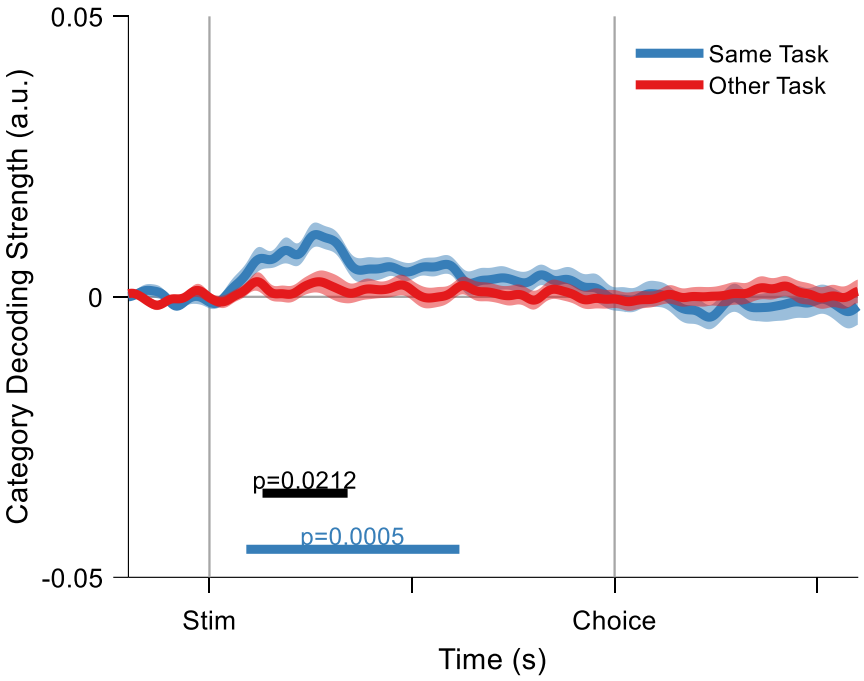


Figure S15. Irrelevant within and cross-decoding for Session 2 (stimuli planes 2 and 4). Within-task decoding was found to be highly significant (p<.001, cluster window = 92-616ms), with no cross-task decoding found. A significant difference was also found (p=.021, cluster window = 132-340ms).

Figure S16

Irrelevant Within and Cross Decoding for Session 2, Stimulus Plane 3 (overlapping stimuli)

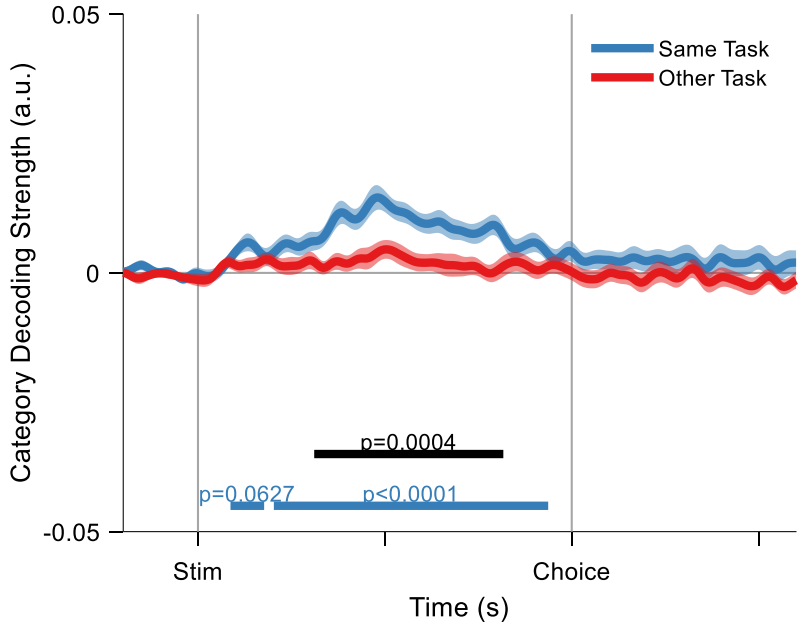


Figure S16. Irrelevant within and cross-task decoding for Session 2, plane 3 new, (overlapping stimuli). Within-task decoding was found to be significant (p<.001, cluster window = 204-936ms). No cross-task decoding was found (p=.239), and a significant difference was also found (p<.001, 312-816ms).

Figure S17

Relevant – Irrelevant Within Task and Cross Task Decoding Difference in Session 2 For the Overlapping Stimuli

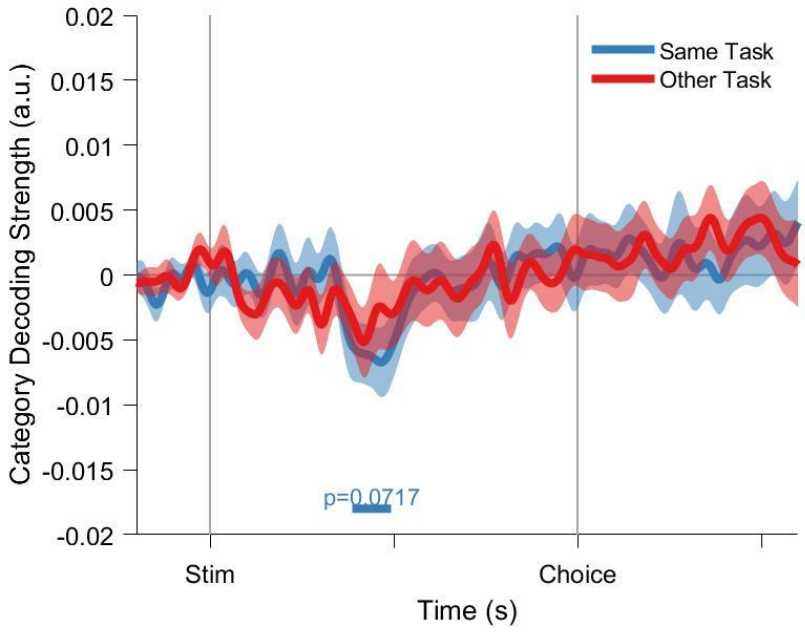


Figure S17. The decoding difference between within and cross task for Session 2, overlapping (new) stimuli. No significant presence of within or cross task decoding was found, as well as no significant difference.

Figure S18

Within and Cross-Task Decoding Difference in Relevant – Irrelevant task for Session 2, Old stimuli

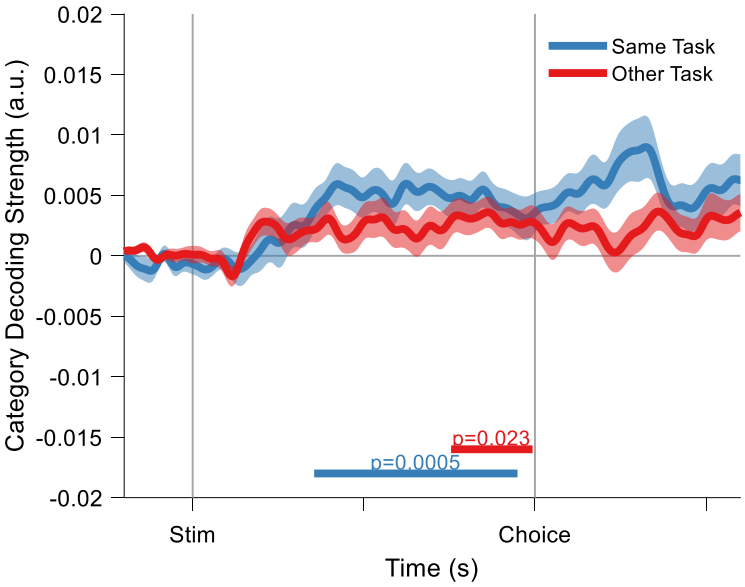


Figure S18. Within and cross-task decoding difference found in Session 2 for the old stimuli. A highly significant presence of within task decoding was found (p<.001), as well as a significant presence of cross-task decoding (p=.023). No significant difference was found.

Figure S19

Within and Cross Decoding for Session 2, Task 1 (Stimulus Planes 1 and 3), (Training Data Planes 1 and 5)

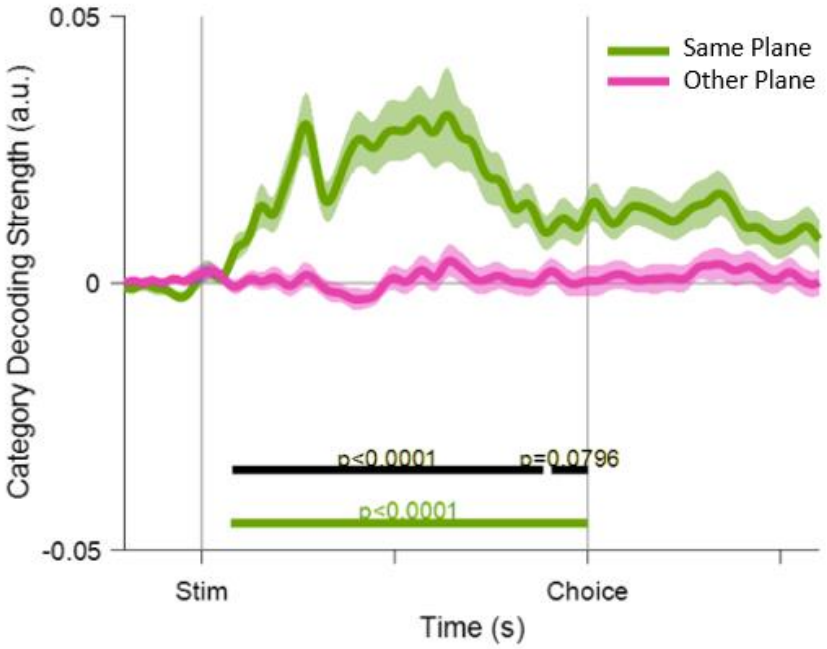


Figure S19. Within and cross-plane decoding for Session 2, planes 1 and 3. Within-plane decoding was highly significant (p<.001), although no cross-plane decoding was found. A significant difference between within and cross-plane decoding was also found (p<.001).

Figure S20

Within and Cross Decoding for Session 2, Task 2 (Stimulus Planes 3 and 5), (Training Data Stimulus Planes 1 and 5).

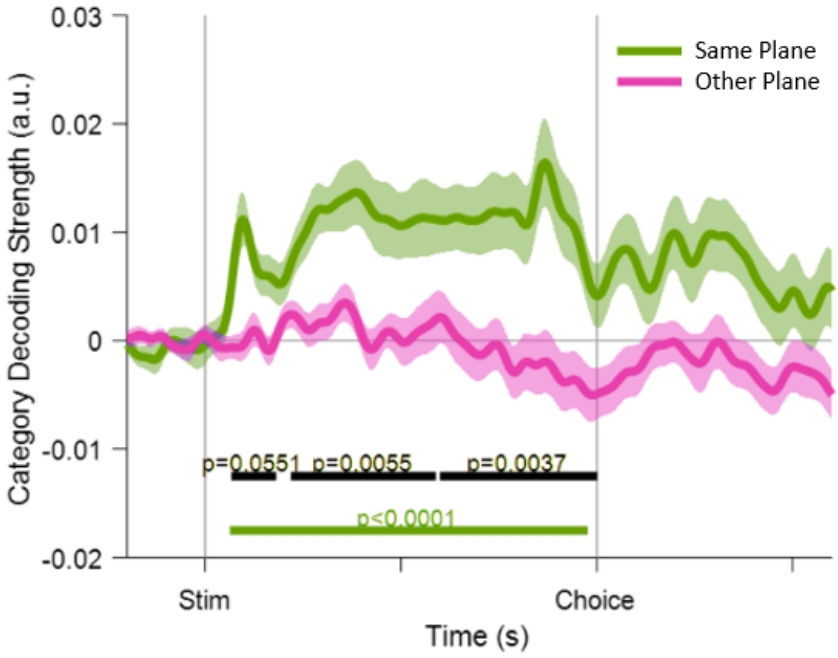


Figure S20. Within and cross-plane decoding in Session 2, Task 2. Within-plane decoding was found to be highly significant (p<.001) with no significant cross-plane decoding found (p=.596). Two significant cluster windows were found for difference between within and cross-plane decoding (p=.006, p=.004).

We calculated the difference in within and category decoding strength for the relevant and irrelevant tasks. Firstly, we calculated the difference for within and cross-plane decoding in Session 1, planes 1 and 5. Within-plane decoding was found to be significant (p=.003, cluster window = 592-976ms). Cross-plane decoding was also found to be significant (p=.004, cluster window = 372-856ms). No significant difference was found (p=.07).

Figure S21

Within and Cross Decoding Difference for Session 1, Stimulus Planes 1 and 5 (old stimuli)

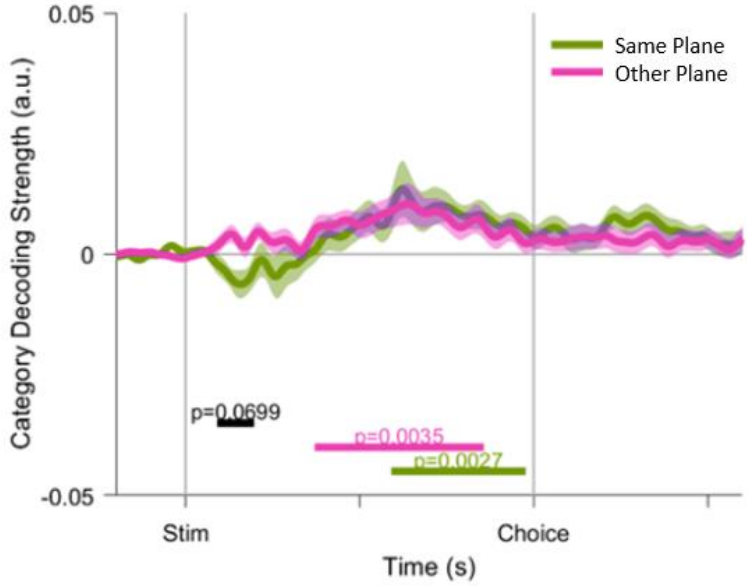


Figure S21. Within and cross-plane decoding difference in Session 1 for planes 1 and 5. Within-plane (p=.003) and cross-plane decoding (p=.004) were found to be significant. No significant difference was found.

We then calculated the within and cross decoding difference in session 1 for planes 2 and 4. No significant presence for within-plane decoding (p=.331), cross-plane decoding (no significant clusters), or significant difference (p=.270) was found.

Figure S22

Within and Cross Decoding for Session 1, Stimulus Planes 2 and 4 (old stimuli)

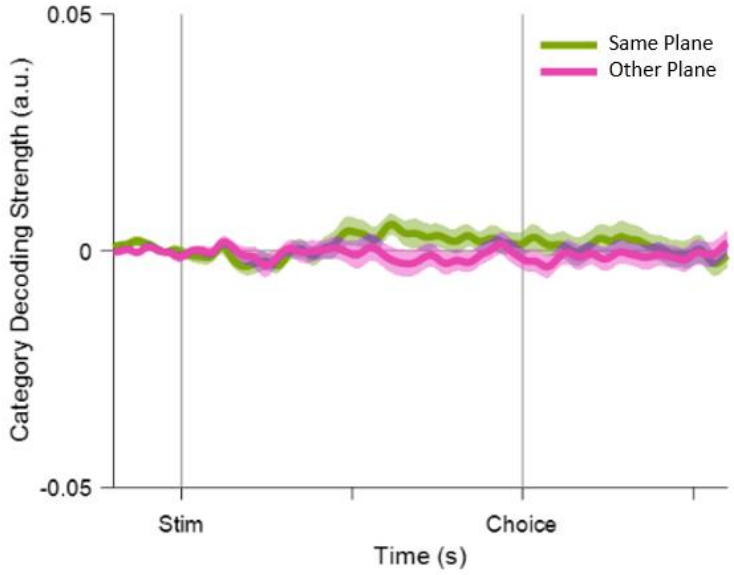


Figure S22. Within and cross-plane decoding in Session 1 for stimuli planes 2 and 4. No significant within-plane decoding, cross-plane decoding, or decoding difference was found.

We then calculated the within and cross-plane decoding difference for Session 2 stimuli planes 1 and 5. Within-plane decoding was found to be significant (p=.005, cluster window = 616-924ms). Cross-plane decoding (p=.409) and decoding difference (p=.380) were not found to be significant.

Figure S23

Within and Cross Decoding for Session 2, Stimulus Planes 1 and 5 (old stimuli)

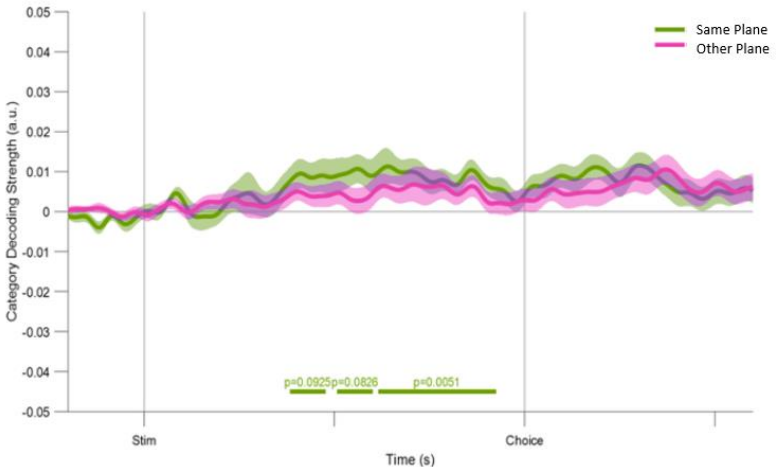


Figure S23. Within and cross-plane decoding in Session 2 for planes 1 and 5. Within-plane decoding was found to be significant (p=.005), with no significant presence of cross-task decoding (p=.409) and no significant difference (p=.380).

Within and cross-task decoding difference for Session 2 planes 2 and 4 were also conducted and found no significant within-plane decoding (*p*=.443), cross-plane decoding, or decoding difference (no significant clusters were found).

Figure S24

Within and Cross Decoding for Session 2, Stimulus Planes 2 and 4 (old stimuli)

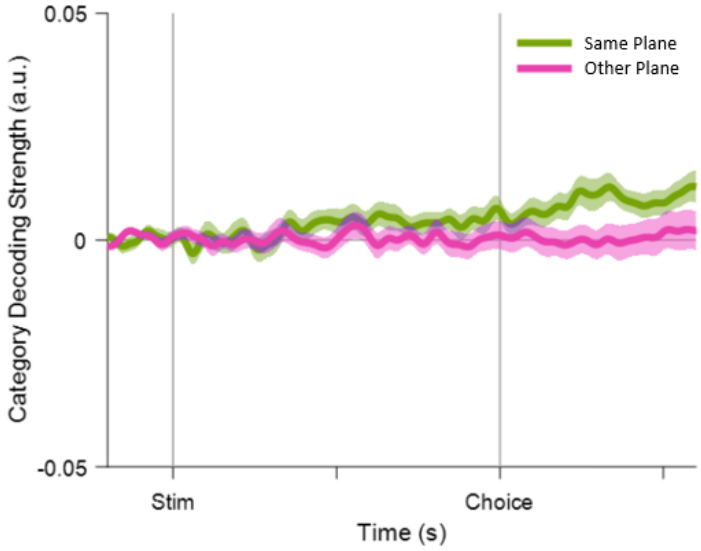


Figure S24. Within and cross-plane decoding in Session 2 for planes 2 and 4. No within, cross-plane, or decoding difference was found.

Chapter 3.1 – Dual-task Interference in Working Memory: Impairments in Temporal Prioritisation Despite Practice

Figure S1.

Additional example of single task condition

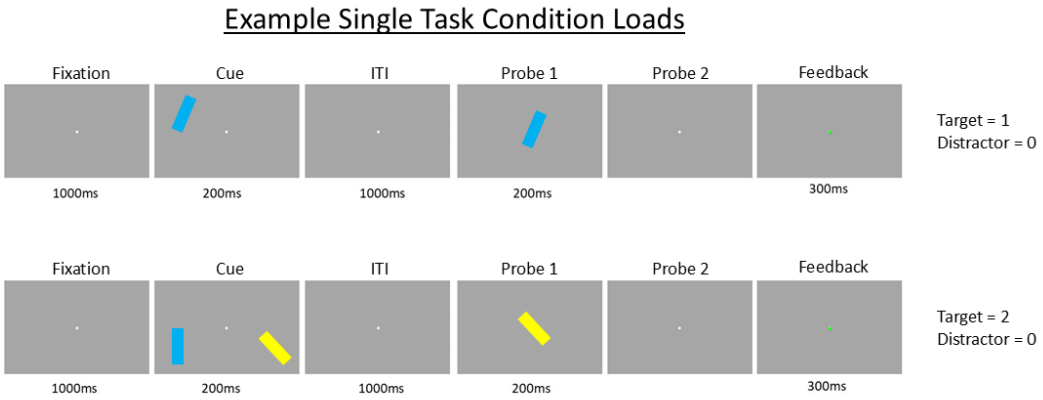


Figure 1 - Example single task condition displaying a blue rectangular stimuli as the initial cue, followed by the probe stimuli (both displayed for 200ms). This example involves a target stimuli of 1, and a distractor stimuli of 0. The second row displays a trial involving two target stimuli and 0 distractor stimuli, with a blue and yellow rectangular stimuli being cued, with only the yellow probed.

Figure S2.

Additional example of Dual-task condition trial

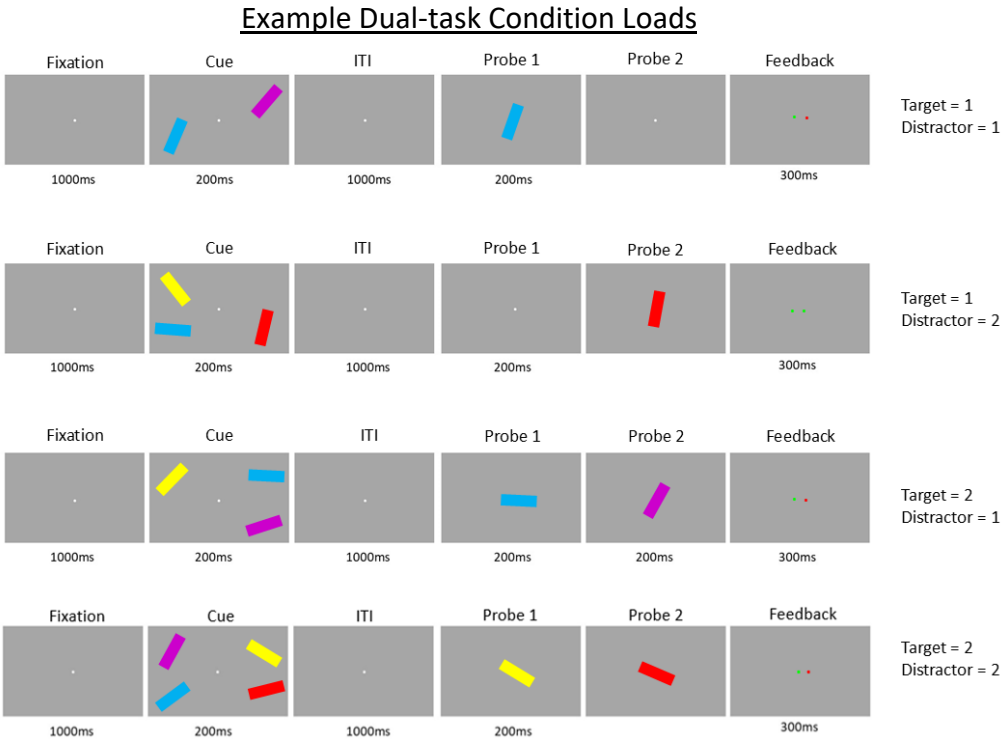


Figure S2. – This figure displays all the possible examples of dual-condition trials. The first row shows a 1 target stimuli and 1 distractor stimuli, with a blue and purple rectangular stimulus as cues, and only the blue stimuli as probe 1 and no probe 2. The second row displays 1 target stimuli and 2 distractor stimuli, with a blue, yellow and red rectangular stimuli shown as cues, but no probe 1 displayed and only the red stimuli shown in probe 2. The third row displays 2 target stimuli and 1 distractor stimuli, with a yellow, purple, and blue stimulus cued, followed by the blue stimuli probed first, and the purple stimulus probed second. The final row displays all 4 coloured stimuli (purple, yellow, blue, and red). This shows a target of 2 and distractor of 2, with the yellow stimulus probed first and red stimulus probed second.