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The nature of the interactions between verbal working memory and long-term memory knowledge: a behavioral and neuroimaging investigation

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Thèse présentée par

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En vue de l'obtention du
Doctorat en Sciences Psychologiques et de l'Education

Sous la supervision de
Steve Majerus et Wim Fias

Année académique 2023-2024

Psychologie & Neuroscience Cognitives
PsyNCog
Psychology & Neuroscience of Cognition

Sous la supervision de

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Au sein de l'Unité de Recherches

Psychologie et Neurosciences Cognitives (PsyNCog)
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Summary

The research conducted in this PhD Thesis aimed to determine the nature of the interactions between verbal working memory (WM) and long-term memory (LTM) knowledge by investigating the cognitive and neural aspects of the potential overlap between the two systems. This question was addressed through three experimental studies employing behavioral paradigms and advanced neuroimaging techniques, including the investigation of the impact of syntactic knowledge on verbal WM performance (Study 1), an fMRI investigation of the neural substrates associated with long-term semantic knowledge and maintenance of semantic information in verbal WM (Study 2), and an fMRI investigation of the language learning-related changes in the cortices that support verbal WM (Study 3). Our findings demonstrate at least partial overlap between verbal WM and long-term linguistic knowledge, characterized by dynamic and flexible interactions. Overall, these results support hybrid, partially emergent language-based models of WM, while emphasizing that although verbal WM and LTM knowledge interact, verbal WM performance extends beyond the simple activation of linguistic knowledge. Verbal WM interacts dynamically with other cognitive processes, and LTM knowledge rather intervenes in a flexible manner in verbal WM. This thesis highlights the importance of adopting an integrative approach that encompasses all language representations, takes into account potential interactions between verbal WM and episodic memory processes, and reflects the flexible and adaptive nature of long-term linguistic knowledge activation in verbal WM.

Remerciements

De nombreuses personnes ont encouragé, facilité, coloré, voire illuminé ces quatre années de travail grâce à leur contribution et leur soutien.

Steve, merci de m'avoir permis, en première année de Master, de choisir un de tes sujets de mémoire portant sur les substrats neuronaux du contrôle langagier, une étape qui aura marqué le premier pas d'un parcours qui allait aboutir à la réalisation d'une thèse de doctorat. Je te remercie de m'avoir fait confiance en me donnant l'opportunité de postuler pour ce contrat de recherche, à peine sortie des bancs universitaires. Merci pour tes conseils avisés et ton suivi rapproché. Ton expertise aura été une source d'apprentissage inestimable au cours de ces quatre années.

Wim, ik wil je bedanken voor je advies en suggesties en voor je vriendelijkheid tijdens onze verschillende ontmoetingen. Het was een plezier om met je samen te werken.

Lucie, merci de m'avoir fait confiance en m'offrant la chance de reprendre ce projet de recherches qui te tenait à cœur. Merci de m'avoir encouragée à aller vers cette voie. Merci d'avoir partagé ton temps, jonglant entre tes propres recherches et ce projet, pour m'accompagner pendant mes premiers pas dans la découverte de ce nouvel univers.

Fabienne et **Martine,** merci à vous deux d'avoir accepté d'être membres de mon comité de thèse au cours de ces quatre ans. Fabienne, merci d'avoir été présente en cas de besoin durant ma récolte de données en IRM qui a – parfois – été ponctuée de rebondissements, notamment durant la pandémie de COVID-19. Martine, m'inscrire dans ta finalité « Neuropsychologie du langage et des apprentissages » en dernière année de Logopédie a été pour moi la confirmation que je souhaitais explorer davantage le fonctionnement cérébral. Merci pour ton accompagnement durant ces 5 + 4 années.

Aux **Prof. Thierry Nazzi** et **Prof. Gilles Vannuscorps**, merci à vous deux d'avoir accepté d'être membres de mon jury de thèse. Merci pour le temps consacré et l'attention procurée à la lecture de ce travail, et pour les échanges qui s'en suivront.

Au programme EOS-FNRS, merci pour le soutien financier apporté à ce projet de thèse. Cela m'aura donné l'opportunité de rencontrer de nombreux chercheurs, et nos échanges, qu'ils soient formels ou informels, ont été un réel enrichissement.

Aux étudiants qui m'ont accompagnée durant la récolte de données de mes études (Maximilien, Louis, Arnaud, Kevan, et aux étudiants d'Initiation à la Recherche), merci d'avoir facilité ce travail par votre investissement, d'avoir apporté vos points de vue, et suscité des échanges aussi bien scientifiques que personnels. Superviser votre travail a été un réel plaisir. Un grand merci également à **tous les participants** qui ont contribué à la réalisation des études de cette thèse pour leur temps et leur curiosité.

À mes collègues, merci pour ces moments passés à vos côtés au cours de ces quatre années, et particulièrement à mes collègues du +1, avec qui j'ai passé l'essentiel de mon temps durant ce travail de thèse : Arnaud, Arya, Charlène, Claudia, Coline, David, Hong Xiao, Lucie, Marion, Nathan, Olivier, Sophie, ainsi que Chloé, Morgane, Laura et Catherine. Et bien sûr Tania, du B32, et les logos du B38, en particulier Lauren. Votre présence a non seulement illuminé mes journées, mais a également nourri mon expérience. David, merci pour ces années de covoiturage qui m'ont procuré, certes, un soutien logistique, mais surtout une présence amicale et bienveillante chaque matin. Coline et Claudia, merci tout particulier à vous, qui avez été à mes côtés du début à la fin, aussi bien sur le plan professionnel que personnel. Vos conseils avisés et votre soutien sans faille ont été un réel trésor. Notre trio de super nanas me manquera. Avec Tania et Estelle, nos moments de joie et de peine passés toutes ensemble auront forgé des liens d'amitié solides. Je suis reconnaissante d'avoir partagé ces instants avec vous quatre.

Ces quatre années de doctorat ont également été ponctuées d'autres aventures : mon implication en tant que représentante du personnel scientifique et relais des doctorants de la faculté, et ma participation au concours « Ma Thèse en 180 Secondes ». Ces expériences m'ont permis de confirmer et/ou d'acquérir des connaissances plus transversales, de défendre des idées et valeurs qui me tenaient à cœur, et de faire des rencontres enrichissantes. Nul doute que ces expériences me seront bénéfiques à l'avenir.

Dès lors, merci à tous·tes ceux·elles qui ont rendu ces moments possibles et agréables.

À ma famille (ma maman et mon petit frère) et à **Julien**, merci de m'avoir toujours encouragée à aller plus loin dans mes études et dans la recherche insatiable de satisfaction de ma curiosité. Merci pour votre présence, votre amour, et votre soutien inconditionnel. Julien, merci d'embarquer avec moi avec enthousiasme dans toutes mes aventures passées et celles à venir, et merci pour ta présence lorsque celles-ci sont semées d'embûches. À **Ivy,** merci d'être mon rayon de soleil à quatre pattes. Ton espièglerie et ton affection ont été une leçon quotidienne de détachement et de bonheur simple.

À mes amis d'horizons divers et variés, votre humour, votre joie de vivre, votre bienveillance, ont été pour moi un réel carburant qui m'a propulsé pour me donner la motivation d'aborder chaque nouvelle semaine de travail avec enthousiasme. Mention spéciale pour Nora, Guillaume, Nadia, Jordan, mes amis inestimables. Nora, merci pour nos fous rires, pour ton réconfort, pour nos grands moments d'émotion, pour ces danses déjantées. Guillaume, merci pour ta prévenance et tes running gags qui me donnent toujours le sourire. Nadia, merci pour cette belle complicité, pour ces discussions profondes et ces moments de légèreté. Jordan, merci pour cette belle amitié qui a démarré au rythme des voitures de course durant notre adolescence. Une pensée émue également pour Marc, qui nous a quitté quelques jours avant que j'écrive ces lignes. Puisses-tu, de là où tu es, capturer des clichés aussi magnifiques que ceux que tu nous as laissés en héritage.

Enfin, la musique étant au centre de ma vie, j'aimerais remercier quatre artistes qui ont allégé mes longues journées d'analyses et de rédaction grâce à leur talent : *Hans Zimmer*, pour m'avoir donné l'impression d'être une super-héroïne et de pouvoir tout accomplir. *Konoba*, pour m'avoir transportée par ses mélodies et m'avoir inspirée par sa vision de la vie. *Petit Biscuit*, pour avoir rendu mes journées plus douces. *GÆRARD*, pour m'avoir ouvert les portes de son univers et m'avoir fait découvrir la personne au grand cœur qu'il est.

Et merci à vous, inconnu·e ou non, qui prenez le temps de lire le résultat de ces quatre années de travail. J'espère que vous le trouverez intéressant et inspirant.

Words are, in my not-so-humble opinion, our most inexhaustible source of magic. Capable of both inflicting injury, and remedying it.

J.K. Rowling

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Foreword

Verbal working memory (WM), defined as the ability to temporarily store and manipulate verbal information in memory (Baddeley, 1986), is a fundamental human capacity that we use on a daily basis. Let us take a concrete example. Many years ago, my mum taught me how to make the recipe of the famous "boulets liégeois".

"First, soften a slice of bread by soaking it in milk".

"Premièrement, ramollir une tranche de pain en l'imbibant de lait".

To follow this instruction, I had to access my preexisting phonological, lexical, semantic and syntactic knowledge in order to process the information given. I recognized the sounds of each word, identified familiar words such as "tranche" (*slice*), "imbibant" (*soaking*) or "lait" (*milk*), while accessing their meaning, and processing the morphology of the words and the structure of this complex sentence. This linguistic knowledge was acquired at some point in my childhood, when I learned, for instance, to auditorily recognize the word "tranche" by identifying and combining the phonemes /t/, /R/, /an/ and /ch/. Through repetitive exposure, I successfully stored this novel word, with meaning, in my existing vocabulary. Hence, to process and understand verbal information such as recipe instructions in WM, I relied on my long-term linguistic knowledge acquired over years of verbal learning.

This situation is just one example of the interactions between verbal WM and long-term linguistic knowledge that occur on a daily basis. However, although a substantial body of evidence demonstrates these interactions, a fundamental aspect that remains unanswered is their nature. This PhD thesis aims to investigate the extent to which verbal WM and long-term memory (LTM) overlap. We will attempt to answer three main questions. First, do all language levels (phonological, lexical, semantic, and syntactic) have an impact on verbal WM performance? Second, are the neural networks involved in verbal WM similar to the neural networks involved in language processing? Finally, are the neural substrates in verbal WM sensitive to changes in long-term linguistic knowledge? We will provide answers to these questions through three experimental studies combining behavioral and neuroimaging approaches.

The first part of this work will present the theoretical background of this thesis. In Chapter 1, we will explore the major theoretical models and key concepts of WM. Chapter 2 will present the evidence showing the impact of linguistic (phonological, lexical, semantic, syntactic) knowledge on verbal WM performance. In Chapter 3, I will present data showing how new language information is processed in verbal WM before being acquired, and the fundamental role of verbal WM in this learning process.

The experimental part of this thesis will consist of three studies. In Study 1, we investigated the impact of syntactic knowledge, a relatively little studied linguistic variable, on both item and serial order recall in verbal WM. Study 2 focuses on the neural substrates of the nature of semantic knowledge activation that defines the maintenance of semantic information in verbal WM. Finally, in Study 3, we will explore language learning-related changes in the neural substrates that support verbal WM.

The final part of this thesis will summarize and discuss the results of the three studies, highlighting their contribution to research on verbal WM and its interaction with linguistic knowledge. I will also discuss the implications for theoretical models and propose directions for future studies.

Theoretical introduction

Chapter 1

Verbal working memory, an overview

In this first chapter, I will briefly define verbal working memory (WM) and present the major concepts that emerge from several WM models. As we will see, a central issue in WM models – which is also the principal focus of this thesis – is the extent of the involvement of long-term memory (LTM) in verbal WM, with some authors positing a direct link between long-term linguistic knowledge and verbal WM, while others consider these systems to be separate entities. In this chapter, I will focus on a fundamental distinction that arises from these models: the opposition between multicomponent and emergent language-based approaches. This distinction is particularly relevant since it directly concerns the relationship between verbal WM and long-term linguistic knowledge.

Definition of verbal working memory

Verbal WM is a cognitive system responsible for the temporary retention and active manipulation of verbal information (Baddeley, 1986). It plays a fundamental role in our daily cognitive tasks, such as understanding spoken language, solving complex problems, and reasoning. A distinction has often been drawn between "working memory" and "short-term memory" (STM). Short-term memory has been characterized as a passive and temporary storage system where information is held briefly but not actively processed. In contrast, WM has been seen as an active system that not only stores information temporarily but also engages in the ongoing manipulation and processing of this information to support various cognitive tasks (e.g., Baddeley, 1986, 1992; Cowan, 1988, 1995; Engle et al., 1999; Shallice & Warrington, 1970, 1974; see also Schwering & MacDonald, 2020). However, contemporary perspectives have blurred the boundaries between these two concepts, and it is now quite common to encompass both concepts under the term "working memory" (e.g., Cowan, 2008; Cowan et al., 2005; Gray, 2007;

Majerus, 2013, 2019). Indeed, information in memory is rarely stored passively, even in short-term contexts. Instead, information is frequently transformed and actively used to serve specific cognitive goals and tasks (Buchsbaum & D'Esposito, 2019). For the purposes of this thesis, I adopt the term "working memory" to encompass both traditional short-term memory and the broader, more active conception of WM.

The following section will explore the shared fundamental processes that consistently arise in different approaches of WM models. Specifically, I will discuss the concepts of capacity and duration limitations, subvocal rehearsal, attention, and long-term knowledge.

Core concepts of verbal WM models

Capacity and duration limitations

Verbal WM is characterized by fundamental limitations in terms of capacity and retention duration. These limitations are a central aspect of WM and are common to most models that seek to explain its functioning. One of the most notable features of verbal WM is its limited capacity to retain verbal information for a relatively short period. This limited capacity is often referred to as Miller's "magic number" (1956), which suggests that verbal WM has an average capacity of about seven (plus or minus two) items. More recently, it has been suggested that this capacity was closer to four items (e.g., Cowan, 2001). However, the type of information being processed, the cognitive abilities of the individuals, and the specific task being performed can all influence WM capacity. Verbal WM is also subject to duration limitations in the retention of information, and can typically be retained for only a few seconds unless it is actively rehearsed or manipulated in some way (e.g., Cowan, 2010).

Role of subvocal rehearsal

One cognitive process that significantly enhances the limited duration of verbal WM is subvocal rehearsal. Subvocal rehearsal operates by continuously refreshing the memory trace of the information, preventing it from decay or loss over time. By mentally repeating verbal information, individuals maintain it actively in WM for extended periods. This critical process is a shared characteristic among various theoretical models of verbal WM and is widely acknowledged as indispensable for the effective retention of verbal information. In the multicomponent model proposed by Baddeley and Hitch (1974), for instance, subvocal rehearsal assumes a central role as a key component of the phonological loop. This will be explained in more detail in the next section.

Role of attentional processes

Attention and WM are closely intertwined processes. Several models consider that attention is responsible for the allocation of cognitive resources to prioritize certain items or aspects of the information, thereby influencing what becomes the current focus of attention (FoA) (e.g., Barrouillet et al., 2004; Cowan, 1988, 1995; Oberauer, 2002, 2009). For instance, the "Time-Based Resource-Sharing" (TBRS) model (Barrouillet et al., 2004) posits that WM is governed by a central executive that allocates attentional resources to maintain information temporarily, thus preventing it from degrading. The key idea of the TBRS model is that resource allocation is time-based: the more items you need to remember, the less time and attentional resources can be allocated to each item. Attentional refreshing is one of the key processes that has been proposed to support short-term maintenance, considered as a domain-general maintenance mechanism that relies on attention to keep mental representations active using attention to reactivate the contents of WM (see Camos et al., 2018, for a review). Importantly, attentional refreshing differs from subvocal rehearsal in its capacity to maintain information of different sensory modalities (e.g., verbal, visual, and spatial information) and even multimodal information, while subvocal rehearsal is exclusively dedicated to the maintenance of verbal information.

In the specific context of verbal WM, attention assumes the role of a selective mechanism, determining what verbal information is actively processed and maintained within the limited capacity of the system. In the "Embedded-Processes" model proposed by Cowan (1988, 1995), for instance, verbal WM is a limited-capacity hierarchical construct consisting of three primary components: the latent knowledge stored in LTM, the currently activated portion of the LTM system, and the subset of this activated LTM system temporarily brought into the FoA. In this perspective, attention assumes a pivotal role for two primary reasons. Firstly, it is essential for accessing and activating LTM knowledge. Secondly, it plays a crucial role in the continuous refreshing of memory items by reintroducing them into the limited-capacity FoA. More recently, the Attention-Order-WM (A-O-WM) model of Majerus (2009, 2010, 2013) placed selective attention at its core, with interactions extending to both language representations and the order of information, as we will explore in more detail later in this chapter. These elements are temporarily activated within their respective systems, and the model relies on the capacities of selective attention to sustain this activation over time.

Role of serial order processes

Temporary retention of verbal information encompasses not only the maintenance of item information (i.e., the identity of an item, such as its phonological and semantic representations), but also the retention of serial order information, i.e., the order of items or phonemes within an item. Several hypotheses have been proposed to explain the coding of serial order information. For instance, chaining models posit that serial order is defined by strong associations between adjacent items, and that it is reconstructed by using these inter-item associative chains, where preceding items serve as cues for the recall of successive items (e.g., Ebbinghaus, 1885; Murdock, 1995; Lindsey & Logan, 2021). Ordinal models, on the other hand, suggest that serial order is coded based on the relative activation of items, with initial items receiving stronger activation than subsequent items following a primacy gradient (e.g., Page & Norris, 1998). Finally, positional models suggest that order information is coded according to position, either by temporal or spatial codes (e.g., Burgess & Hitch, 1999, 2006; Brown et al., 2000; Hartley et al., 2016; Henson, 1998; Lewandowsky & Farrell, 2008).

Notably, the maintenance of serial order information has been suggested to be supported by specific, non-linguistic processes, in contrast to item information which has been considered by many WM models to be supported by the language system. This distinction between item and serial order in verbal WM is supported by a number of behavioral and neuroimaging findings.

Role of long-term linguistic knowledge

As we will see in the next section, theoretical models of WM do not all agree on the role played by long-term knowledge. Some models adopt a compartmentalized perspective, viewing WM and LTM as distinct cognitive systems with limited interaction (e.g., Baddeley, 1986; Baddeley & Hitch, 1974; Hulme et al. 1991, 1997; Lewandowsky & Farrell, 2000; Schweickert 1993). Conversely, several models emphasize the direct involvement of long-term linguistic knowledge in verbal WM (e.g., Acheson & MacDonald, 2009; Buchsbaum & D'Esposito, 2019; Cowan, 1993; Hasson et al., 2015; MacDonald, 2016; Majerus, 2009, 2013, 2019; Postle, 2006; Schwering & MacDonald, 2020). According to these models, the storage and processing of verbal information in WM heavily rely on pre-existing language representations, which are actively recruited to facilitate the temporary retention and manipulation of verbal information. In addition, regarding the item/order distinction, some WM models consider that all aspects of WM are supported by language representations, while others rather suggest that item and order information are supported by distinct systems.

To sum up, various models and concepts have been developed to explain how WM works. These models can be grouped and differentiated according to several criteria, including whether they are multicomponent or unitary models, the importance given to attentional capacities, or the degree of interaction between WM and LTM. In this thesis, I will focus on a fundamental distinction that arises from these models: the opposition between multicomponent models and emergent language-based approaches. This distinction is particularly relevant as it directly concerns the relationship between verbal WM and long-term linguistic knowledge.

Theoretical models of verbal working memory

Atkinson and Shiffrin's (1968) multi-store model can be considered as a precursor model of WM. Although it does not correspond directly to contemporary models of WM, it has greatly influenced our current understanding of memory. According to this model, memory is a three-level system including sensory memory, STM and LTM. Sensory memory acts as a temporary buffer where sensory information is briefly stored in a specific sensory form (e.g. visual, auditory). Then, this information passes into STM, considered as a unitary system of limited capacity and duration, responsible for the temporary processing and manipulation of information. Finally, if the information is sufficiently repeated and processed in STM, it is transferred to the LTM, where it can be stored on a quasi-permanent basis. Although the multi-store model does not detail the specific memory processes of STM as do modern WM models, it laid the foundations for later understanding of WM by introducing the idea that memory is not just about storing long-term information, but also about actively manipulating it to accomplish complex cognitive tasks. In addition, this model introduced fundamental notions such as rehearsal, attention, the limited capacity and duration of information in STM, and the transfer of information from STM to LTM.

Multicomponent vs. emergent approaches

Multicomponent models

Models of WM have evolved over the decades, offering different perspectives on how WM interacts with LTM. One of the most influential models of WM is the multicomponent model proposed by Baddeley and Hitch (1974). This model provided a description of the complex processes involved in WM, shedding light on how we temporarily retain and manipulate information. According to the multicomponent model, WM is not a unitary entity, but rather a system composed of multiple elements, each responsible for distinct functions. The central executive, often referred to as the "manager" of WM, is responsible for the control and coordination of two storage systems: the phonological loop and the visuospatial sketchpad (see also Baddeley, 1986). The phonological loop is responsible for the temporary storage and maintenance of verbal (phonological) information, and consists of two key elements: the phonological store, which has a limited capacity, and where phonological information is held for a short duration, and subvocal articulatory rehearsal processes that constantly refresh the phonological traces, ensuring their active presence within WM. This process effectively reintroduces the information into the phonological store, contributing to its continuous availability for cognitive tasks. In contrast, the visuospatial sketchpad is responsible for the temporary storage and manipulation of visual and spatial information, allowing individuals to maintain visual images, spatial layouts, and other non-verbal information in WM (see Figure 1.1).

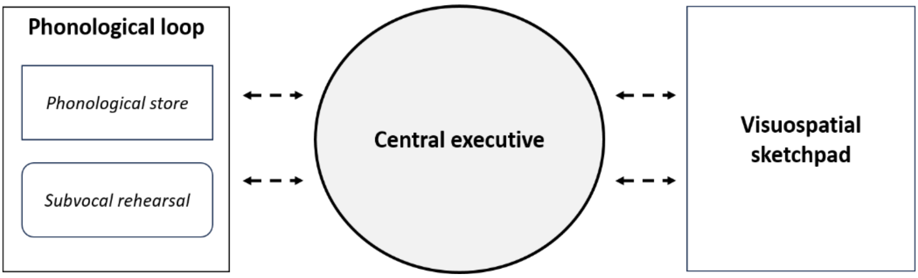

Figure 1.1. Working memory model, adapted from Baddeley and Hitch (1974)

One critical aspect of multicomponent models is their perspective on the interactions between LTM and WM, considering them as two distinct systems, each with its unique functions and limitations. Verbal WM operates largely independently of LTM and language processing mechanisms, and the interactions between WM and LTM are limited and indirect (see also Norris, 2017), with effects of long-term linguistic knowledge attributed to secondary mechanisms. In line with this perspective, redintegration-based accounts of WM (Hulme et al. 1991, 1997; Lewandowsky & Farrell, 2000; Schweickert 1993) have suggested that LTM plays a role only to reconstruct phonological degraded memory traces. According to this approach, memory traces are initially stored in a phonological format within a temporary buffer and may be subject to degradation over time or due to interference. During recall, these deteriorated memory traces undergo a clean-up process involving comparison with linguistic knowledge to facilitate their reconstruction. This perspective has been used to explain specific linguistic long-term effects in verbal WM, suggesting that the recall advantage for words over nonwords can be attributed to the clean-up process involving lexical knowledge, which enables the reconstruction of words, but not nonwords during recall.

Later, Baddeley, Gathercole, and Papagno (1998) proposed a modified version of the multicomponent model, suggesting the existence of bidirectional interactions between the phonological store in LTM and verbal WM. In this updated perspective, the phonological loop assumes a crucial role not only in the temporary storage of phonological information but also in the acquisition of the phonological form of lexical items and in syntactic learning. On the other hand, the memory traces processed in WM also involve the temporary activation of a long-term phonological system. It is not considered as an episodic memory system, but is rather viewed as a structure that reflects the residue of phonological knowledge accumulated over the long term. Baddeley (2000) further expanded the multicomponent model of WM by incorporating the "episodic buffer", which assumes a pivotal role in facilitating bidirectional information flow between WM and episodic LTM, thereby suggesting interactions between verbal WM and the semantic levels of language. Similarly, the multicomponent model proposed by Logie and colleagues (2021) posits that although WM is separate from LTM, the whole cognitive system, including LTM knowledge, contributes to WM performance. These modifications to the multicomponent models illustrate a more nuanced understanding of the dynamic interactions between verbal WM and LTM.

Emergent models

Contrary to the multicomponent models of WM, emergent models of WM consider that WM is not composed of distinct and separable components, but instead emerges from the interaction of LTM, attention, and other cognitive resources, with no strict modular division between storage and processing components. Emergent models are traditionally categorized into "fully emergent" accounts and "hybrid" or "partially emergent" accounts of WM.

In the **fully emergent approach**, WM is considered to be the activated portion of linguistic LTM (Acheson & MacDonald, 2009; Buchsbaum & D'Esposito, 2019; Cowan, 1993; Hasson et al., 2015; MacDonald, 2016; Oberauer, 2002, 2009; Postle, 2006; Schwering & MacDonald, 2020). According to this view, verbal WM is simply the ability to maintain and order linguistic information, and thus emerges directly from the actions of the language system (e.g., MacDonald, 2016; MacDonald & Christiansen, 2002). In essence, all aspects of WM are supported by language representations: the temporary representation of item information (i.e., the identity of an item such as its phonological and semantic aspects), but also of serial order information (i.e., order of the items).

The interactive activation model proposed by N. Martin and Saffran (1992), based on Dell's model (1986), postulates a dynamic process within verbal WM tasks involving a cascade of activations within the language system. When items are maintained in verbal WM, they temporarily activate different levels of long-term language representations in a sequential manner: initially, the phonological segment nodes, followed by the corresponding lexical nodes, and ultimately, the semantic content (see Figure 1.2).

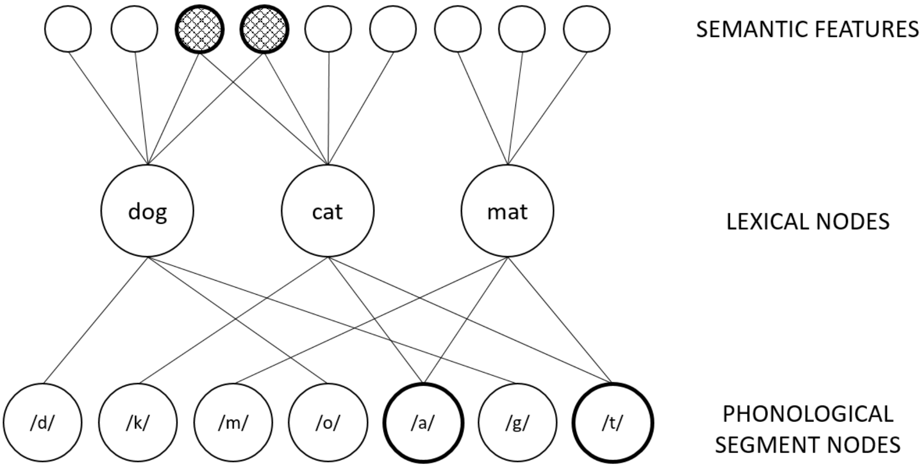

Figure 1.2. A simplified version of Dell's (1986) Interactive Activation Model of Language Processing. Notable shared components, including phonological segment nodes and semantic features, are highlighted in bold.

Crucially, the model proposes that WM recall performance depends on the amount of activation available at the moment of recall. Items that have a higher level of activation are more likely to be accurately retrieved. Furthermore, items presented at the beginning of the list receive stronger activation during encoding and thus, tend to be recalled first (primacy effect). The last items in the list will also show superior recall performance due to their persisting phonological activation at the moment of recall (recency effect). The authors even suggested that verbal WM does not exist as such but rather emerges from the temporary activation and rapid decay of this activation within the language system. This view implies a fundamental intertwining of WM and LTM and challenges traditional notions of distinct memory systems.

On the other hand, **hybrid or partially emergent accounts** consider that although WM and LTM do interact, WM performance cannot be reduced to activated linguistic knowledge. In the model proposed by R.C. Martin and colleagues (1999), language representations are activated in both the language system and in verbal WM, and long-term linguistic knowledge is connected to two distinct buffer systems reflecting phonological and semantic information. A reciprocal activation process between the language representations and the buffers enables the respective phonological and lexical-semantic representations to be maintained in verbal WM.

Hybrid models also posit the existence of additional processes supporting WM, such as attentional and serial order processes. Several authors have specifically included serial order representations alongside language representations in their models of WM (e.g., Brown et al., 2000; Burgess & Hitch, 1999, 2006; Henson, 1998; Page & Norris, 1998). For instance, Majerus (2009, 2013, 2019) posits that the maintenance of item and serial order information is supported by distinct systems working in parallel. This perspective aligns with numerous studies emphasizing the distinct nature of these processes (e.g., Attout & Majerus, 2015; Cristoforetti et al., 2022; Kowialiewski et al., 2021; Majerus et al., 2010, 2015). While the maintenance of item information reflects the temporary, direct, and automatic activation of language representations in LTM, serial order information maintenance is rather coded via multiple mechanisms simultaneously (Majerus, 2019). In line with this assumption, the integrative A-O-WM model proposed by Majerus (2009, 2010, 2013, 2018) offers a framework to encompass the processes found in the majority of WM models, which have often emphasized the importance of long-term language representations and/or the role of attentional capacity, while rarely addressing the distinction between item information and serial order. This perspective suggests that verbal WM is underpinned by three major components: the temporary activation of language representations (phonological, lexico-semantic representations) in LTM, serial order representations, and attention (see Figure 1.3). Attention includes *the scope of attention*, corresponding to the number of items that can be held in memory without strategic or controlled attention, and *control of attention*, which corresponds to the selective and strategic focus on relevant information while ignoring irrelevant information. The A-O-WM model features a bidirectional connection between the language and serial order processing systems, facilitating the association of each item activated in the language system with its corresponding serial position encoded by the serial order processing system. Attention interacts with the language system to encode and maintain item information, as well as with a separate system dedicated to serial order processing and thus, maintains the activation of both item-related information and serial order over time. Attention can also be focused on these two systems equally or differently, depending on the requirements of the verbal WM task.

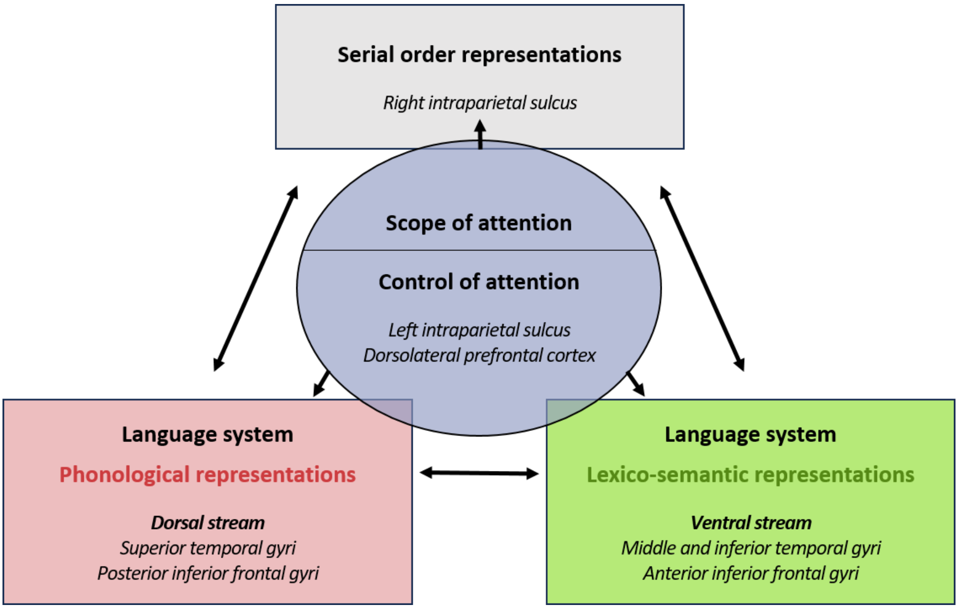

Figure 1.3. The A-O-WM model, adapted with permission from Majerus (2009, 2010, 2013, 2018)

An interesting feature of the A-O-WM model is the direct connection of its components to the corresponding neural networks underlying them. It has been suggested that language representations share neural networks with linguistic knowledge, with phonological representations underpinned by the superior temporal and posterior inferior frontal gyri (i.e., dorsal language pathway) and lexical-semantic representations supported by the middle and inferior temporal and anterior inferior frontal gyri (i.e., ventral language pathway). Representations of serial order are associated with the right intraparietal sulcus, and attention is related to the left intraparietal sulcus and dorsolateral prefrontal cortex (e.g., Majerus, 2013). We will further explore the neural networks of verbal WM in Chapter 2.

Note that the embedded-processes model of Cowan (1995) is also compatible with hybrid accounts of WM, although it is not a language-based model per se. Indeed, Cowan also considers that WM is the result of the activation of long-term representations, which are maintained in the FoA via attentional processes.

Overall, exploring the various perspectives on WM models leads us to question the role and the importance of LTM in verbal WM: does linguistic knowledge simply serve as a support during recall through the redintegration of phonological traces by comparison with phonological knowledge, or does linguistic knowledge reflect the very foundation of WM? Redintegration-based approaches have limitations in that they predominantly rely on phonological and lexical traces. However, psycholinguistic effects at the semantic level such as the imagery/concreteness effect or the semantic similarity effect, which will be described in the next chapter, remain unexplained by these models. On the other hand, fully emergent models of WM consider that all aspects, i.e., item and serial order information, are supported by language representations, while hybrid or partially emergent models of WM clearly assume interactions between language representations and serial order processes in WM, even if they are considered as separate systems. Yet, significant challenges persist, as there is still limited evidence demonstrating the impact of language representations on serial order processing, and the precise nature of the interactions between linguistic knowledge and verbal WM still needs to be further developed.

Chapter summary

In this first chapter, we explored the foundations of verbal WM. I highlighted the key concepts frequently found in the various theoretical models of verbal WM and playing a major role in its functioning: capacity and duration limitations, subvocal rehearsal, attention, serial order processing, and long-term linguistic knowledge. I have emphasized a central distinction between multicomponent models, which consider verbal WM and LTM as separate systems with limited interaction, with effects of long-term linguistic knowledge attributed to recall reconstructive processes, and "fully" or "partially" emergent models, which posit direct interactions between verbal WM and linguistic knowledge. In the following chapters, I will examine these interactions in more detail. To begin with, we will explore the impact of phonological, lexical, semantic and syntactic knowledge on verbal WM capacities.

Chapter 2

The impact of long-term memory knowledge on verbal working memory

As we have seen in Chapter 1, several theoretical models suggest that verbal WM and LTM interact, at different levels. When it comes to maintaining and manipulating information in WM, our performance can be affected by various LTM effects specific to language processing. In this chapter, I highlight the impact of long-term language representations on verbal WM capacity, emphasizing the fundamental role of phonological, lexical, semantic and syntactic knowledge, using empirical evidence from behavioral, neuropsychological and neuroimaging studies.

Psycholinguistic evidence on the impact of long-term memory knowledge on verbal working memory performance

Psycholinguistic effects can be defined as the effects produced by the interaction between cognitive processes and linguistic factors, resulting in observable impacts on cognitive performance. These effects have been constantly observed in verbal WM tasks. In this section, I review various psycholinguistic effects associated with the different levels of language representations.

Phonological effects

The most referenced psycholinguistic effect at the phonological (sublexical) level is the phonotactic frequency effect. Within a language, phonotactic rules determine which phoneme combinations are legal or frequent, and which are illegal or infrequent. Based on this principle, it has been shown that phoneme sequences of high phonotactic frequency, i.e. whose phoneme combination is frequently encountered in a language, were judged to sound more like real words and were also better recalled than phoneme sequences of low phonotactic frequency (Vitevitch et al., 2007). For instance, in French, /Ri/ is a common and frequent combination of phonemes, but /xo/ is quite rare. High phonotactic frequency phoneme sequences have also been associated with faster decision time in tasks in which participants are asked to judge whether two auditorily presented items are identical (Vitevitch & Luce, 1999).

The phonotactic frequency effect has been demonstrated in verbal WM tasks by numerous studies, with both children and adults (e.g., Gathercole et al., 1999; Majerus et al., 2004; Vitevitch & Luce, 1998; 1999; 2005). It has been observed that infants were sensitive to phonotactic rules by 9 months of age, when sensitivity to the phonological regularities of the language starts to develop (e.g., Coady & Aslin, 2004; Friederici & Wessels, 1993; Jusczyk et al., 1993; Munson et al., 2005; Zamuner et al., 2004). Using an incidental phonological learning paradigm, Majerus and colleagues (2004) exposed adults and children to an artificial phonotactic grammar manipulating phonological rules, followed by a nonword repetition task. They observed that the performance of both children and adults was better for nonwords composed of legal combinations of phonemes than for nonwords with illegal combinations of phonemes. In addition, this study further demonstrated that the phonological network could adapt quickly and relatively automatically to changes in its organization, since WM performance was impacted only by brief exposure to an artificial grammar.

Overall, the phonotactic frequency effect has been suggested to reflect the intervention of **long-term phonological knowledge on verbal WM**.

Lexical effects

Several lexical effects also play an important role in modulating verbal WM performance. A notable phenomenon in this context is the lexicality effect, which highlights the differential processing of real words compared with nonwords. Studies exploring this lexicality effect have shown that both children and adults are faster and more accurate at recognizing and recalling real words, i.e. words that are already present in our vocabulary, compared with nonwords that are unfamiliar to us (e.g., Brener, 1940; Gathercole et al., 2001; Hulme et al., 1991; Jefferies et al., 2006b; Majerus & Van der Linden, 2003). The lexicality effect remains robust when the phonotactic probability and speech rate of the items are controlled, showing that it is neither the low frequency of phoneme combinations, nor the length of articulation of the nonwords, that impact recall. Interestingly, it has also been shown that newly acquired words were better recalled than novel nonwords in immediate serial recall tasks (e.g., Savill et al., 2015; 2018), confirming the importance of lexical knowledge.

Another interesting psycholinguistic phenomenon is the lexical frequency effect, which entails that high-frequency words commonly used in a language are generally processed faster and recalled better than low-frequency words (e.g., Engle et al., 1990; Hulme et al., 1997; Poirier & Saint-Aubin, 1996; Roodenrys et al., 1994; Watkins & Watkins, 1977). Word frequency has also been shown to be positively related to free recall performance, with high-frequency words having a higher probability of being recalled than low-frequency words (Musca & Chemero, 2022).

Finally, the neighborhood density effect refers to the influence of the number of similar-sounding words (neighbors) on word recognition and production. Neighborhood density is calculated by determining the number of words created by the addition, deletion, or substitution of a single phoneme in a given word (Luce & Pisoni, 1998). Words with dense neighborhoods, i.e., with many phonological neighbors, have been shown to be better recalled than words with sparse neighborhoods, i.e., with fewer phonological neighbors (e.g., Roodenrys et al., 2002; Vitevitch & Rodriguez, 2005).

The impact of lexicality, frequency, and neighborhood density all demonstrate the influence of **long-term lexical knowledge** on verbal WM.

Semantic effects

In the study by Savill and colleagues (2018) mentioned above, newly acquired words with semantic associations were also produced more accurately than those with no meaning, showing the importance of the impact of long-term semantic knowledge on verbal WM. Indeed, a number of studies have demonstrated that verbal WM performance is supported by semantic knowledge. Better immediate serial recall performance has been observed for concrete/highly imageable words, with rich and consistent semantic features (e.g., "knife"), than for abstract or low imageability words (e.g., "liberty") (e.g., Acheson et al., 2010; Jefferies et al., 2006b; Kowialiewski & Majerus, 2018; Pexman et al., 2002; Romani et al., 2008; Walker & Hulme, 1999). Note that although the terms "concreteness" and "imageability" effects are highly correlated and often used interchangeably in the literature, they encompass slightly different concepts: the concreteness effect refers more to the extent to which a word's referent can be experienced by the senses, while the imageability effect refers more to the ease with which a word can be imagined or visualized. McDougall and Pfeifer (2012) found that participants who generated vivid, detailed mental images of concrete words performed better on word recall and recognition tasks in verbal WM.

Another semantic psycholinguistic effect is the semantic relatedness effect, which is the observation that recall performance is higher for semantically related words than for semantically unrelated words (e.g., Kowialiewski et al., 2022; Kowialiewski & Majerus, 2020; Poirier & Saint-Aubin, 1996). For instance, the sequence "dog – cat – bird" is easier to recall than "dog – chair – grape", since in the first example, items are semantically related around the category of animals. The semantic relatedness effect has been suggested to reflect inter-item associative knowledge, verbal WM performance depending on the amount of semantic features shared by the words in a sequence to be recalled (Dell et al., 1997; Kowialiewski & Majerus, 2020). It has been observed both for taxonomic relations (i.e., hierarchical classification of objects or concepts based on shared features or characteristics) and for thematic relations (i.e., relationships between objects or concepts based on their functional or situational context, such as "honk – fuel – road") between items (e.g., Tse, 2009).

Nevertheless, in contrast to the robust effects observed for phonological and lexical knowledge, the influence of semantic knowledge on verbal WM appears inconsistent. For instance, several studies have highlighted the absence of robust and consistent effects of semantic imageability effects on WM performance, pointing out that these effects are generally weaker than the effects of other linguistic variables such as the phonological and lexical status of words, or even absent when word lists are presented rapidly or continuously (e.g., Kowialiewski & Majerus, 2018, 2020; Majerus & Van der Linden, 2003). Kowialiewski & Majerus (2020) showed that the semantic relatedness of memory items protects against post-encoding WM interference effects, in contrast to the imageability/concreteness status of items. The authors suggested that when multiple words with similar semantic features are presented, they mutually reactivate each other. As a result, robust activation levels are maintained for all items during encoding, and these redundant semantic representations effectively prevent item degradation due to decay or interference. Conversely, items characterized by high imageability or concreteness will not be informative about the other items, thus preventing between-item reactivation. Similarly, research has demonstrated that access to semantic features can be influenced by specific task demands (e.g., Evans et al., 2012), suggesting that deep semantic knowledge might be activated in a task-dependent manner within verbal WM tasks.

In summary, the semantic effects discussed in this section reflect the significant impact of **long-term semantic knowledge** on verbal WM performance. However, the extent and consistency of this influence may vary based on factors such as presentation speed and task demands, indicating that not all aspects of semantic knowledge are automatically involved in verbal WM tasks.

Syntactic effects

Contrary to the phonological, lexical and semantic knowledge, syntactic knowledge, i.e. the way words can be combined within a verbal segment as a function of their grammatical function, has been a less frequently studied linguistic variable. Nonetheless, a few behavioral studies have highlighted the influence of syntax on our verbal WM performance. One of the first effects described in the literature is the sentence superiority effect (Cattell, 1886; reported in Scheerer, 1981; Massol et al., 2021; Snell & Grainger, 2017), which refers to the better recall of lists of words forming a meaningful sentence, i.e. following familiar syntactic rules, compared to lists of ungrammatical sequences of words (e.g., Brener, 1940; Jefferies, Lambon Ralph, & Baddeley, 2004). The sentence superiority effect has been observed independently of semantic consistency. It has been shown that even meaningless syllable sequences lead to better recall if presented with regular syntactic structure and morphology (e.g., Epstein, 1961). More recently, studies have shown that recall of adjective-noun pairs was better when they were presented in a canonical syntactic order (e.g., in English, adjective preceding the noun) compared to a non-canonical syntactic order (e.g., in English, adjective following the noun) (Perham et al., 2009; Schweppe et al., 2022).

An important distinction between syntactic knowledge and other language-related effects impacting verbal WM is its potential impact on serial order recall, as opposed to the phonological, lexical, and semantic effects, which primarily affect item recall (e.g., Gathercole et al., 2001; Hulme et al., 1991; 1997; Majerus & D'Argembeau, 2011; Nairne & Kelley, 2004; Poirier & Saint-Aubin, 1996; Saint-Aubin & Poirier, 1999a, b, 2000; Walker & Hulme, 1999). In line with "fully emergent" models of verbal WM, specific aspects of linguistic knowledge may impact not only the maintenance of individual items but also the maintenance of serial order (Majerus, 2019). In this context, syntactic knowledge is particularly interesting as it has the potential to impact both item and serial order recall, given the fundamental role of sequential information processing within the language system.

In summary, while phonological, lexical, and semantic knowledge have received considerable attention in the study of verbal WM, the influence of syntactic knowledge remains a relatively understudied linguistic variable. Despite its potential importance, we know little about how different aspects of syntax affect verbal WM, and whether these effects solely impact item-level or serial order information, or both. Investigating these issues could contribute to a more complete understanding of the interactions between language and WM, and could potentially provide valuable insights into current theoretical models of verbal WM.

Neuropsychological evidence on the impact of long-term memory knowledge on verbal working memory performance

In the previous part, I reviewed the numerous effects of LTM knowledge on verbal WM performance at the behavioral level. In this section, we will explore the neuropsychological evidence supporting this influence.

Studies focusing on patients with language disorders have shown strong associations between verbal WM and language deficits. Patients with semantic dementia (SD), for instance, exhibit verbal WM deficits that have been associated with impaired lexico-semantic knowledge in LTM. In immediate serial recall tasks, SD patients show a recall advantage for words that are still comprehended, as opposed to words that are no longer understood due to semantic memory loss (e.g., Jefferies et al., 2006a; Knott et al., 1997; Majerus et al., 2007; Patterson et al., 1994). In addition, they make blending errors for words involving recombinations of phoneme sequences of items from the stimulus list (e.g., "mint, rug" reproduced as "rint, mug"). It has been suggested that this pattern of deficits reflects the "semantic binding hypothesis" (Patterson et al., 1994), which posits that the deterioration of the components of semantic memory defining a word results in the loss of a crucial source of coherence in the phonological representation of the word. According to this hypothesis, phonological representations become less stable and provide poor support for recall when semantic knowledge is impaired. Similarly, Jefferies and colleagues (2004) showed immediate serial recall differences between number and non-number words in SD patients. These observations support the idea that long-term semantic knowledge plays a fundamental role in the maintenance of phonological coherence of words in verbal WM. In aphasic patients, it has also been demonstrated that phonological, lexical and semantic deficits impact the retention of verbal WM content (e.g., N. Martin & Saffran, 1990; 1997; N. Martin et al., 1996; Saffran & Martin, 1990), supporting the involvement of LTM knowledge in verbal WM.

At the same time, studies have also observed verbal WM deficits for phonological and/or semantic information with no associated language impairment (e.g., Majerus et al., 2004; R.C. Martin et al., 1994; Warrington et al., 1971; Warrington & Shallice, 1969). On the one hand, several accounts consider that verbal WM deficits stem from impairment to a specific verbal WM processing system (e.g., Hamilton & Martin, 2007; R.C. Martin, et al., 1994; 1999; Warrington & Shallice, 1969; Warrington et al., 1971). This view is driven by models of verbal WM considering that verbal WM performance is defined by the capacity of a temporary buffer (e.g., Baddeley & Hitch, 1974), which is independent of language system. Similarly, the redintegration account suggests that purely phonological memory traces are stored in a temporary buffer and that, at the moment of recall and after decay or interference, the degraded phonological memory traces are reconstructed by comparing them to lexical representations in LTM (Gathercole et al., 2001; Hulme et al., 1991; Schweickert, 1993). It has also been suggested that there could be one temporary buffer for phonological traces, and another one for semantic traces (R.C. Martin et al., 1994, 1999). However, in a review by Majerus (2009), it has been demonstrated that in the majority of aphasic patients, the specific deficit observed in verbal WM could be attributed to partial recovery from their single-word processing difficulties, while still exhibiting poor verbal WM capacities. In addition, studies have shown that LTM representations were not confined to the process of recall (e.g., Jefferies et al, 2004). Evidence showing associations between language impairment and verbal WM deficits are in line with emergent language-based accounts. It has been suggested, for instance, that verbal WM deficits emerge from structural damage to the language network that prevents the activation of language representations during verbal WM tasks, or from rapid decay of language activations (Dell, 1986; N. Martin et al., 1996).

Overall, these studies on patients with language disorders demonstrate once again the importance of the impact of LTM knowledge on verbal WM performance, although they also show that the nature of language deficits remains a matter of debate.

Neural mechanisms underlying the impact of long-term memory knowledge on verbal working memory performance

In line with previous sections, a substantial body of neuroimaging data is available on the involvement of LTM knowledge in verbal WM. One particularly interesting account is the dual stream model of speech and language processing proposed by Hickok & Poeppel (2000, 2004, 2007; see also Saur et al., 2008; Warren, Wise & Warren, 2005; Wise, 2003). Based on the dual stream model for vision ("what" vs "where"; Ungerleider and Mishkin, 1982), this account suggests that the major network of language processing is divided into two pathways in the dominant hemisphere. On the one hand, the dorsal language pathway is associated with phonological processing: it allows for the integration of phonemes into articulatory representations and is particularly involved in sublexical speech repetition or maintenance of phonological item information (Majerus, 2013). The dorsal language pathway encompasses brain regions such as the posterior superior temporal gyrus, the inferior parietal and posterior frontal regions, and the supramarginal gyrus, via the superior longitudinal fasciculus. On the other hand, the ventral language pathway is associated with semantic processing: it is involved in integrating phonemes into conceptual/semantic representations and in the maintenance of item information. The ventral language pathway extends from the posterior superior temporal gyrus to the inferior frontal gyrus through the anterior and middle temporal cortex, via the middle longitudinal fasciculus, the inferior longitudinal fasciculus, and the inferior fronto-occipital fasciculus (e.g., Friederici, 2012; Hickok & Poeppel, 2004, 2007; Majerus, 2013).

The dual stream model offers valuable insights into the roles of dorsal and ventral language pathways in phonological and semantic processing, and demonstrates that language processing regions are recruited in verbal WM tasks such as nonword repetition. However, it does not integrate attentional and serial order processes, which, as we have seen, are essential components of verbal WM. Majerus (2013, 2019) proposed that serial order processing is supported by a right fronto-parietal network centered on the right intraparietal sulcus, while attentional control processes are suggested to be underpinned by a left fronto-parietal network centered around the left intra-parietal sulcus (see Figure 2.1). This proposal offers a comprehensive framework for integrating repetitions of multiple word or nonword sequences into the dual stream model of Hickok and Poeppel.

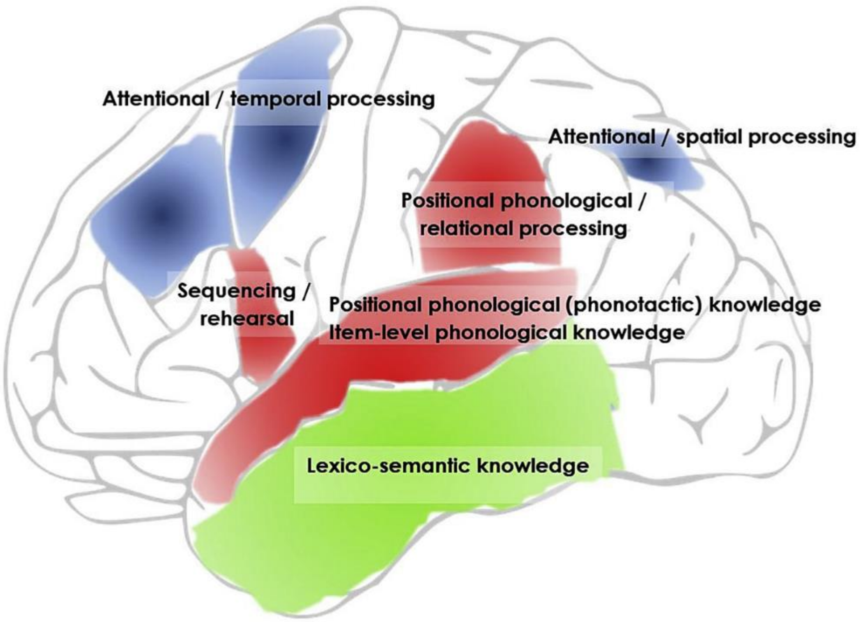

Figure 2.1. Theoretical framework of verbal WM mechanisms and their underlying neural substrates, adapted with permission from Majerus (2019)

Notably, brain regions underlying language processing have been shown to be actively recruited during all stages of verbal WM tasks in healthy adults. Phonological information maintenance in WM has been shown to result in increased brain activity in the inferior temporal-occipital junction, the supramarginal gyrus, the fusiform gyrus, the prefrontal cortex, the pre-supplementary motor area, the cerebellum and midbrain regions (e.g., Cairo et al., 2004; Crosson et al., 1999; Majerus et al., 2006, 2010; R.C. Martin et al., 2003; Salmon et al., 1996), although the most commonly reported regions for phonological processing in WM are the posterior superior temporal gyrus and the superior temporal sulcus (e.g., Bhaya-Grossman & Chang, 2022; Binder, 2000; Binder et al., 2000; Démonet et al., 1992, 1994; Graves et al, 2008; Kalm & Norris, 2014; Majerus, 2013; Majerus et al., 2002, 2003, 2004, 2005, 2006, 2010; R.C. Martin et al., 2003; Poeppel, 1996; Wise et al., 2001). On the other hand, maintaining *words* in WM has been shown to involve the left posterior middle temporal gyrus, the temporoparietal junction, the anterior inferior temporal gyrus and the angular gyrus reflecting lexico-semantic processing (e.g., Binder et al., 1997, 2009; Binney et al., 2010; Collette et al., 2001; Démonet et al., 1992, 1994; Ferreira et al., 2015; Jackson, 2021; Jackson et al., 2015; Jung et al., 2017; Howard et al., 1992; Lambon Ralph et al., 2009; Majerus et al., 2002; Perani et al., 1996; Price et al, 1996; Visser et al., 2012; Scott et al., 2000), as well as the left inferior frontal gyrus known to be involved in semantic control processes (e.g., Fiebach et al., 2007).

Several studies based on a multivariate voxel pattern analysis (MVPA) approach have also found successful decoding in language brain areas during verbal WM maintenance. For instance, Lewis-Peacock and Postle (2012) observed that the maintenance of semantic content could be discriminated from maintenance of phonological and visual content, by examining the brain regions that support the retention of phonological, semantic and non-verbal visual information. Using a fast encoding running span task, Kowialiewski and Majerus (2020) have shown that the ventral language pathway (middle and inferior temporal gyri and inferior frontal cortices) could distinguish words from nonwords during both encoding and maintenance stages, suggesting the activation of linguistic knowledge during verbal WM processing in an automatic manner. Regarding semantic knowledge more specifically, a study conducted by Yue and Martin (2021) detected significant decoding of words requiring a delayed semantic judgment in the angular gyrus, associated with semantic information integration (e.g., Farahibozorg et al., 2022), and/or with encoding knowledge about thematic associations and events (e.g., Schwartz et al., 2011). This decoding occurred during the WM maintenance stage, providing evidence that this region is involved in the maintenance of semantic information.

However, although there is considerable evidence for the involvement of language neural networks in the maintenance of verbal information in WM, the inconsistency of behavioral findings regarding semantic effects in verbal WM tasks that I have detailed in the previous section suggests that semantic knowledge may not be consistently recruited during the temporary storage of verbal information. Hence, semantic knowledge activated during a WM task may not be identical or as deep as during a language processing task. Research has shown, for instance, that while the anterior inferior temporal gyrus appears to be significantly involved in encoding abstract semantic categories, knowledge concerning specific semantic attributes that characterize category exemplars has been associated with modality-specific cortices (e.g., Chao & Martin, 1999, 2000, 2001; Culham & Valyear 2006; Gainotti et al. 1995; Gauthier et al. 1997; 2000; Goldberg et al. 2006; Kiefer et al. 2008). Hence, it is still difficult to determine the nature of semantic knowledge activation defining the maintenance of verbal information in WM.

Chapter summary

In this chapter, we examined the impact of long-term linguistic knowledge on verbal WM. Our exploration encompassed behavioral, neuropsychological and neuroimaging evidence, which collectively corroborated the influence of phonological, lexical, and semantic knowledge on verbal WM performance. Nevertheless, some questions remain, such as the specific impact of syntactic knowledge on verbal WM performance, and the nature and depth of semantic knowledge activation in verbal WM tasks. If verbal WM reflects LTM knowledge, as suggested by emergent language-based accounts, then all linguistic levels should impact verbal WM performance. Furthermore, the recruitment of similar neural networks should be observed during language processing tasks (phonological, lexical, semantic) and in verbal WM tasks involving these language representations.

As this thesis focuses on the interactions between verbal WM and long-term linguistic knowledge, another question remains to be answered: what do we know about the impact of verbal WM on language processing? This question serves as a bridge to our next chapter, in which I will detail lexical acquisition and the key role played by verbal WM in this process.

Chapter 3

From verbal working memory to long-term linguistic knowledge

In the previous chapter, I focused on data showing the impact of linguistic knowledge on verbal WM performance. In this chapter, we will see that, conversely, verbal WM capacities are an essential factor in acquiring solid long-term language representations. We will see that phonological abilities in WM play an essential role in lexical acquisition, but also that there is a bidirectional influence between vocabulary and phonological abilities in WM. I will then briefly review the main mechanisms of memory consolidation, before highlighting more specifically the existing gaps in the neuroimaging literature concerning lexical acquisition and processing in adults.

Phonological processing in lexical acquisition

As we have seen, subvocal rehearsal mechanism is an essential component of verbal WM. This mechanism not only extends the short-term retention of newly encountered phonological information, but also enhances its potential for subsequent consolidation in LTM. In this section, we will see that phonological capacities in WM, which are necessary for the proper functioning of this mechanism, play a central role in the acquisition of novel phonological forms and, by extension, in the process of vocabulary acquisition.

Role of phonological abilities

The process of lexical acquisition entails associating a new phonological word form, constructed through the arrangement and combination of its phonemes, to its corresponding semantic representation (e.g., McMurray et al., 2012; Pressley et al., 2007). Over the last decades, it has been widely demonstrated that phonological abilities in WM, involving the temporary storage of new phonological forms, are essential for lexical acquisition. Numerous studies have shown correlations between verbal WM performance and receptive vocabulary development from ages 2 to 13 (e.g., Avons et al., 1998; Bowey, 1996; Gathercole, 1995; Gathercole & Adams, 1993, 1994; Gathercole & Baddeley, 1989, 1990a, 1993; Gathercole et al., 1991, 1992, 1999; Gray et al., 2022; Majerus et al., 2006; Michas & Henry, 1994). For instance, Gathercole and Baddeley (1989) showed that nonword repetition capacities at age 4 predicted children's receptive vocabulary size one year later. Similarly, children with better nonword repetition capacities tend to show stronger vocabulary knowledge in their language compared to children with poor nonword repetition capacities (e.g., Gathercole & Adams, 1993, 1994; Gathercole & Baddeley, 1989; Gathercole et al., 1991, 1992; Michas & Henry, 1994). The impact of phonological abilities in WM has also been supported by studies with multilingual children (e.g., Engel de Abreu & Gathercole, 2012; Masoura and Gathercole; 1999, 2005; Service, 1992; Kohonen, 1995) and by evidence from children with specific language impairment (SLI) and brain-damaged patients showing deficits in nonword repetition and difficulty in acquiring the phonological forms of new words (e.g., Baddeley et al., 1988; Botting & Conti-Ramsden, 2001; Dollaghan, 1987; Gathercole & Baddeley, 1990b; Gray, 2003; Hanten & Martin, 2001; Papagno et al., 1991; Stothard et al., 1998; Weismer & Hesketh, 1996).

On the other hand, Leclercq and Majerus (2010) have shown that serial order WM capacities at the age of 4 are the strongest independent predictor of vocabulary knowledge one year later, in line with other studies showing that novel word learning critically depends on serial order processing abilities in WM (e.g., Gathercole & Baddeley, 1990; Majerus et al., 2006). Majerus and colleagues (2008) have suggested that if a relationship exists between verbal WM capacity and vocabulary acquisition, a strong relationship between new word learning and verbal WM tasks that maximize the retention of serial order information while minimizing item-specific information retention should be expected. In their study on adult participants, they observed that performance on a serial order reconstruction task was actually the strongest and most consistent predictor of new word learning performance in adults, followed by phonological knowledge for a given foreign language. In this context, Majerus and colleagues suggested a conjoined role of phonological knowledge and serial order WM capacity in lexical acquisition, with the importance of both previous exposure to foreign language phonology and serial order WM capacity.

Bidirectional influence between vocabulary and phonological abilities in WM

While several studies indicate that phonological abilities in WM are a causal factor in vocabulary acquisition, it has also been suggested that vocabulary growth itself increases verbal WM performance (e.g., Bowey, 1996, 2001; Fowler, 1991; Metsala, 1999). According to this view, as lexical knowledge develops, phonological sensitivity is stimulated, leading phonological representations to become more and more precise, which in turn improves the ability to process phonological information from new or unfamiliar words. Indeed, evidence has shown that phonological abilities in WM are crucial during the earliest stages of lexical acquisition, but they have also been suggested to have a progressively reduced impact as vocabulary knowledge develops. Gathercole and colleagues (1992) have shown, for instance, that while phonological abilities in WM at age 4 predict vocabulary knowledge at age 5, vocabulary knowledge at age 5 predicts phonological abilities in WM at age 6. In a study by Masoura and Gathercole (2005) on Greek children studying English as a second language, no association has been found between nonword repetition scores and learning of unknown English words paired with their Greek equivalents; instead, they were more closely related to the children's previously acquired English vocabulary. Cheung (1996) has observed a comparable pattern of results in a study with Chinese children learning English. Similarly, evidence from adults tends to show a shifting reliance towards LTM knowledge to facilitate the acquisition of new words, reflecting the bidirectional relationship between WM capacities and LTM knowledge (e.g., Papagno et al, 1991; Service & Craik, 1993; see also Gathercole, 2006). Hence, these results are in line with evidence for the impact of LTM knowledge on verbal WM performance described in the previous chapter.

Exploring how new linguistic information is transferred from verbal WM to a more permanent state of lexical knowledge in LTM is an important aspect for understanding the interactions between verbal WM and LTM knowledge. We have seen that phonological capacities in verbal WM, as well as serial order processing capacities, are essential for this transition from a new phonological form to the state of acquired lexical knowledge. Like all new information, these fragile, ephemeral forms must undergo a profound transformation before they can be stored in LTM. This particular process is known as "memory consolidation". In the following section, I will focus on the mechanisms of memory consolidation, a distinct and more general aspect of memory, but indirectly related to lexical acquisition.

Memory consolidation: an overview

Although memory consolidation is not one of the primary objectives of this PhD thesis, its inclusion in this chapter is relevant for providing a comprehensive understanding of how information is processed and acquired across different memory stages. In the following section, I will provide an overview of the main neurophysiological and neuroanatomical stages of memory consolidation, i.e., synaptic and system consolidation, as well as the role of sleep in this process.

Synaptic and system consolidation

Memory consolidation is a crucial process in which newly acquired information is stabilized and integrated into LTM storage (see Dudai, 1996, 2002; Dudai & Morris, 2000). It involves transforming initially fragile, short-term memories into more enduring and stable forms that can potentially last a lifetime. Memory consolidation comprises distinct stages that facilitate the transfer of information from STM/WM to LTM: synaptic and system consolidation.

Synaptic consolidation, also known as cellular consolidation, is the process by which synaptic connections between neurons involved in encoding a newly acquired memory are stabilized and strengthened. These morphological changes occur within minutes to hours after the memory encoding. Numerous studies suggest that newly encoded information is initially stored at the short-term level in both the hippocampal formation and the relevant neocortex (e.g., Dudai, 2002, 2004; Squire & Alvarez, 1995). This initial stage of consolidation, known as the hippocampus-dependent stage, can persist for up to one week after initial learning. In contrast, system consolidation is a considerably slower process, extending over weeks, months, and even years (e.g., Alberini, 2008, 2009; Dudai, 1996, 2012; McGaugh, 2000; Squire & Alvarez, 1995). It involves a gradual reorganization and the differential involvement of brain regions that support memory processing. During this process, memories initially relying on the hippocampus are slowly transferred to the neocortex, where they become permanently stored, allowing the neocortex to independently maintain the memory (e.g., Kirwan et al. 2008; Klinzing et al., 2019; Smith & Squire 2009; Squire & Alvarez, 1995; Squire et al., 2001, 2004).

Evidence on memory consolidation aligns with the Complementary Learning Systems (CLS) model of memory proposed by Davis and Gaskell (2009), built on neurocomputational accounts of lexical processing and spoken word recognition. Based on Hickok & Poeppel's (2004) dual stream model of speech and language processing, this model suggests that rapid initial word learning is supported by interactions between left temporal regions involved in the perception and comprehension of spoken words, and medial temporal systems including the hippocampal regions. On the other hand, acquiring more stable representations of new words and retaining those representations over the long term involves neocortical regions such as the middle and inferior temporal regions. The interaction between these systems facilitates the incorporation of newly acquired linguistic material into LTM networks, allowing for consolidation-related changes.

Role of sleep in memory consolidation

The integration of novel knowledge into LTM networks has been closely associated with sleep-related memory consolidation processes. During sleep, hippocampal neuronal activity patterns associated with novel representations are repeatedly reactivated, simultaneously triggering the reactivation of their neocortical projection targets. This phenomenon is known as “hippocampal replay”. These repeated reactivations result in morphological changes, including the strengthening of some synaptic connections, the weakening of others, as well as the formation of new synaptic connections with cells outside the newly encoded representation (Klinzing et al., 2019). In parallel, hippocampal replay co-activates neocortical traces and facilitates a gradual redistribution of the memory representation from the hippocampus to the neocortex (system consolidation) (see Figure 3.1).

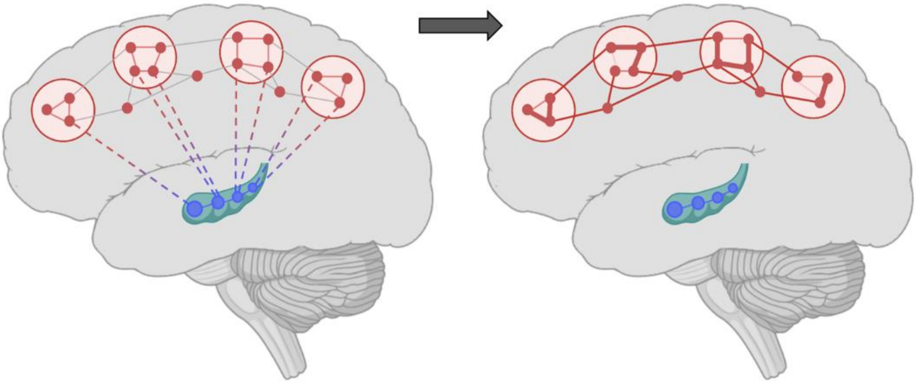

Figure 3.1. Representation of the strengthening of neocortical representations by memory reactivation, adapted from Klinzing and colleagues (2019). Blue circles represent recently encoded representation in the hippocampal system while red circles represent recently encoded representation in the neocortical system. Created with BioRender.com

In the context of lexical acquisition, studies have demonstrated improved retention of new words after a period of sleep in both children and adults, mostly linked to hippocampal replay (for a review, see Schimke et al., 2021).

Notably, research has shown that memory consolidation can also occur during periods of wakeful rest. Therefore, these “offline” states, whether during sleep or rest, seem to play a pivotal role in facilitating memory consolidation (e.g., Brokaw et al., 2016; Dewar et al., 2012; Tucker et al., 2020; Wamsley, 2019, 2022).

Overall, research conducted on the complex process of memory consolidation has improved our understanding of how the brain transforms new information into LTM knowledge. This mechanism similarly plays a crucial role in the process of transferring new lexical information from verbal WM to LTM. Still, as we will see in the final section of this theoretical introduction, neuroimaging evidence of lexical acquisition in adults is sparse, and few studies have specifically investigated the neural substrates of new lexical information processing in verbal WM.

Neuroimaging evidence of lexical acquisition in adults

While numerous studies have examined the neural substrates and neuroplasticity during language development in children, offering valuable insights into how the brain evolves and adapts during the acquisition of language capacities (e.g., Dehaene-Lambertz et al., 2002; Everts et al., 2009; Friederici et al., 2011; Karunanayaka et al., 2007; Rosselli et al., 2014; Szaflarski et al., 2006), lexical acquisition in adults has comparatively received limited attention.

On the one hand, most studies have focused on the neural substrates of second language (L2) processing in adults (e.g., Gurunandan et al., 2019; Kuhl et al., 2016; Perkins et al., 2022; Sabourin, 2009; Schimke et al., 2021). For instance, fMRI studies have observed increased brain activation within frontal and posterior parietal brain regions, and within subcortical structures such as the basal ganglia and cerebellum (e.g., Li et al., 2014; Tagarelli et al., 2019), as well as in the middle and superior temporal gyri, and the hippocampus (e.g., Bakker-Marshall et al., 2017; Davis & Gaskell, 2009) during L2 word learning. Raboyeau and colleagues (2010) have shown that the early learning stage (from day 1 to day 5) of new L2 vocabulary is characterized by significant activation in the left anterior cingulate cortex, which is involved in response competition, the right ventrolateral prefrontal cortex responsible for suppressing irrelevant stimuli and reorienting attention, the left dorsolateral prefrontal cortex involved in interference control, and the left middle frontal gyrus and Broca's area associated with phonological processing. Their findings suggest that the initial phase of L2 acquisition is characterized by attentional control processes related to the competition between L1 and L2 language representations. In the consolidation phase (after 14 days), activations have been observed in the left premotor cortex, right supplementary motor area (SMA), and medial right cerebellum, associated with articulatory planning, motor speech execution, and articulatory processing during simultaneous L1 and L2 activation.

Although research primarily focusing on L2 acquisition provides interesting insights into how neural networks adapt to a new language, there is still a notable gap in the literature in understanding the specific neural changes related to lexical acquisition. Studies that have investigated lexical acquisition in adults have mostly focused on memory consolidation processes, showing that new information can be transferred to LTM within a few days. For instance, Dobel and colleagues (2009) have shown that new word forms (lexemes) learned by association with existing objects during 20 minutes a day seemed to acquire lexical status after less than two hours of training, and that this new language information was transferred from the hippocampus to the middle temporal cortical regions after five consecutive days of training, suggesting their consolidation into LTM.

Recently, Steber and Rossi (2021) have conducted a pseudoword-picture pairings experiment using electroencephalography (EEG) and functional near-infrared spectroscopy (fNIRS). They observed a larger negativity for new compared to learned pairs in right fronto-temporo-parietal regions, which the authors associated with an old/new effect. In addition, they found that learned pseudoword-picture pairings elicited larger activations on the left frontal compared to homologous right hemispheric areas, and that the topography of these effects covered regions such as the ventro-lateral prefrontal cortex including the inferior frontal gyrus. A recent review by Tagarelli and colleagues (2019) reported significant activation in the ventral occipito-temporal areas, specifically in the inferior temporal gyrus and inferior occipital gyrus, during lexical learning, suggesting that these regions may be particularly important in the acquisition of new lexical information in adults. More Nevertheless, the neural processing of new linguistic information according to its learning status, from the novel word stage (phonological form) to the learned, consolidated word stage (lexico-semantic form) in LTM, has yet to be explored.

In this perspective, the dual stream model for auditory language processing proposed by Hickok and Poeppel (2004, 2007) along with the integrative framework of verbal WM proposed by Majerus (2019), described in the previous chapter, provide valuable insights into the identification of distinct stages in the processing and acquisition of new lexical information. Indeed, processing a novel phonological form requires subvocal repetition of the new form in WM to ensure accurate production. According to Hickok and Poeppel, and Majerus, this process primarily relies on the dorsal language pathway, connecting the superior temporal gyrus to the inferior parietal and posterior frontal regions. Subsequently, the phonological representation must be associated with its corresponding meaning, a process supported by the ventral language pathway that connects the superior temporal gyrus to the anterior and inferior medial temporal regions. The success of acquiring new verbal information, as proposed by the dual stream model, depends on the efficiency of these dorsal and ventral pathways, or in other words, on phonological, lexico-semantic – but also serial order processing (Majerus, 2019) – capacities in verbal WM.

Chapter summary

In this chapter, we explored the complex relationship between verbal WM and the acquisition of lexical knowledge. I examined the central role of phonological and serial order abilities in lexical acquisition and discussed the bidirectional influence between vocabulary and phonological abilities in WM. I provided insights into memory consolidation, an essential process that transforms newly encountered information into long-term knowledge. Neuroimaging data revealed that gaps remain in our understanding of how new lexical representations are processed, from their initial phonological form to a fully acquired word. In line with emergent language-based models of WM, neural networks involved in verbal WM processing of novel words should reflect learning-related changes.

In summary, although current psycholinguistic, neuropsychological and neuroimaging data highlight the interactions between verbal WM and long-term linguistic knowledge, many aspects remain poorly understood. This PhD thesis will attempt to provide answers to the outstanding questions raised in this introduction, by using a combination of behavioral and advanced neuroimaging techniques, including multivariate voxel pattern analyses (MVPA) and searchlight analyses, in healthy young adult participants.

Experimental part

Objectives and hypotheses

Although a substantial body of evidence demonstrates the interactions between verbal WM and LTM, a fundamental aspect that remains unanswered is the nature of these interactions. Indeed, the degree to which verbal WM reflects or differs from the language system remains unclear: to what extent do verbal WM and LTM overlap? Multicomponent models, such as Baddeley's model, postulate separate systems for WM and LTM, which interact only in a limited and indirect manner. In contrast, emergent, language-based models suggest that WM arises from LTM and relies at least partially on the same neural substrates as LTM.

The aim of this PhD thesis is to determine the nature of the dynamic interactions between verbal WM and linguistic LTM, employing a multifaceted approach encompassing behavioral paradigms and advanced neuroimaging techniques. First, by characterizing the nature of the impact of syntactic knowledge, a less studied linguistic variable, on WM. If verbal WM reflects the activation of the language system, then all language levels, including syntactic level, should have an impact on WM. Second, by investigating the extent to which neural substrates associated with verbal WM maintenance of semantic information are similar to neural substrates of semantic knowledge in LTM. Indeed, if verbal WM reflects the activation of the language system, the brain regions recruited for verbal WM tasks should be similar to those involved in language tasks. Finally, by exploring the neural substrates associated with the processing of novel verbal information in verbal WM. Indeed, if verbal WM reflects activation of the language system, then we should observe language learning-related changes in the cortices that support verbal WM. In addition, these results could lead to a better understanding of the impact of verbal WM on the long-term acquisition of new verbal information. Overall, these experiments will allow us to determine the extent of interactions between verbal WM and LTM and will provide new evidence to shape current theoretical models of verbal WM.

In **Study 1**, we investigated the impact of syntactic knowledge on both item and serial order recall in verbal WM. This linguistic variable has been relatively little studied, with most research focusing on languages characterized by deterministic syntactic rules. Surprisingly, although some theoretical models of WM include interactions with phonological and lexico-semantic representations as well as serial order processing abilities, syntactic knowledge is absent from most models of WM. However, this variable is of significant interest given that syntax is intrinsically sequential. Consequently, it could reveal effects on both item and serial order recall in WM, potentially providing support for emergent, language-based models of verbal WM. In this study, we exploited the probabilistic position of adjectives relative to nouns in French, a language in which adjectives can be placed either before or after the noun. We used an immediate serial recall task that included lists of adjective-noun pairs and noun-adjective pairs presented either in a regular or in an irregular syntactic order. In line with emergent approaches of verbal WM, lists with regular syntactic order should lead to higher recall performance than lists with irregular syntactic order, since syntactic knowledge should impact verbal WM performance in the same way as other linguistic variables, except that in this case both item recall and serial order should be affected. This study will enable us to offer an integrated perspective for verbal WM models in which the inclusion of syntactic knowledge and, by extension, its interactions with WM, are mostly absent.

Study 2 aimed to determine the nature of semantic knowledge activation that defines the maintenance of semantic information in verbal WM. Studies investigating the impact of semantic knowledge on verbal WM performance have shown inconsistent effects, showing in particular that the extent and consistency of this influence may vary according to factors such as presentation speed and task demands. Using functional magnetic resonance imaging (fMRI) and a multivariate voxel pattern analysis (MVPA) approach, we investigated the extent to which neural markers of semantic knowledge in LTM are similar to those in the maintenance stage of verbal WM. Multivariate methods are more sensitive and powerful than standard univariate methods, as they allow us to assess the informative value of functional activity rather than only identifying differences in elevated activity peaks. First, we identified the multivariate neural patterns associated with long-term semantic knowledge using an implicit semantic activation task. In this task, participants read three-word lists from four distinct semantic categories (bird, tool, color, music). We trained classifiers to distinguish voxel activity patterns associated with the four semantic categories, resulting in six pairwise classifications, allowing us to identify the neural networks associated with these distinct semantic categories. The second task aimed to determine multivariate neural patterns associated with the same four semantic categories maintained in verbal WM. Classifiers were trained to distinguish patterns of voxel activity associated with the four semantic categories over the time course (i.e., 18 seconds of event), by assessing classifier accuracies on a second-by-second basis. By conducting between-task classifications, we further assessed whether the category classifiers trained in the implicit semantic activation task were able to classify the semantic category during the maintenance stage of the verbal WM task (from seconds 8 to 13), and vice versa. Finally, a searchlight decoding approach was used to determine the local spatial distribution of the voxels that discriminate between the four semantic categories in both tasks, to assess whether the same neural networks are involved in both the activation of long-term semantic knowledge and its maintenance in verbal WM. The use of MVPA between-task classifications and the use of the searchlight MVPA technique are particularly interesting and innovative in this context, allowing us to investigate the extent of overlap between linguistic brain regions and regions involved in verbal WM, and to provide important insights into the current models of verbal WM. According to fully emergent models of verbal WM, which propose that the same representations underlie both WM and linguistic processing, we should observe significant between-task classifications during the maintenance of the semantic categories in verbal WM. In addition, we should observe an overlap in multivariate neural patterns for both tasks. Conversely, non-significant between-task classifications and distinct neural patterns would align with hybrid models of verbal WM, suggesting that language representations intervene only if useful for supporting the maintenance of specific WM content based on specific task demands.

Finally, in **Study 3**, we explored language learning-related changes in the neural substrates that support verbal WM. The neural processes associated with the acquisition of new verbal information from verbal WM to LTM remain poorly understood, as well as the neural substrates associated with the processing of this new linguistic information in verbal WM. We simulated the acquisition of novel words through a five-day experiment that combined a nonword repetition task in MRI and lexical learning sessions of word/novel word pairs – containing half of the novel words from the fMRI task – outside the MRI. We varied the ease at which the novel words could be learned by dividing learned and non-learned novel words into two phonological classes: high redundancy and high phonotactic frequency (HRPF) novel words versus low redundancy and low phonotactic frequency (LRPF) novel words. The combination of lexical learning sessions coupled with the use of MVPA and searchlight MVPA methods over a five-day period – with additional univariate analyses – represents a unique approach to our knowledge, as it allows us to determine the neural networks associated with verbal WM maintenance of new (phonological) vs. learned (lexico-semantic) verbal information. The use of the searchlight MVPA technique is particularly relevant in this context, as it allowed us to determine in which brain regions learned novel words are distinguished from non-learned novel words as lexical learning sessions progress. We hypothesized that the multivariate brain signals should reflect the progressive acquisition of new verbal information with, on the one hand, a gradual increase in the distinction between learned and non-learned novel words as the days of learning progress, and on the other hand, a gradual shift in the multivariate signals associated with the verbal WM maintenance of learned novel words specifically. In line with emergent, language-based models of WM, we expect to initially observe the decoding of learned and non-learned novel words during verbal WM maintenance within dorsal language regions associated with phonological processing, and then, as learning sessions progress, in more ventral language regions associated with lexico-semantic processing. Based on previous research that has demonstrated that new words are more easily learned when their phonological form conforms to the phonotactic rules of the native language (e.g., Ellis & Beaton, 1993; Kaushanskaya et al., 2011; Morra & Camba, 2009), we also suggest that HRPF novel words should acquire "learned" status more quickly than LRPF novel words, and that their learning-related neural substrates should change more quickly when activated in a WM context. Therefore, we should also observe faster changes in the language substrates of verbal WM for learned HRPF nonwords over the days.

Study 1

Sequential syntactic knowledge supports item but not order recall in verbal working memory

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In press, *Memory & Cognition* (2023), 1-25

Abstract. Previous studies have shown that psycholinguistic effects such as lexico-semantic knowledge effects mainly determine item recall in verbal working memory (WM). However, we may expect that syntactic knowledge, involving knowledge about word-level sequential aspects of language, should also impact serial order aspects of recall in WM. Current evidence for this assumption is scarce and inconsistent and has been conducted in language with deterministic syntactic rules. In languages such as French, word position is determined in a probabilistic manner: an adjective is placed before or after a noun, depending on its lexico-semantic properties. We exploited this specificity of the French language for examining the impact of syntactic positional knowledge on both item and serial order recall in verbal WM. We presented lists with adjective-noun pairs for immediate serial recall, the adjectives being in regular or irregular position relative to the nouns. We observed increased recall performance when adjectives occurred in regular position but this effect was observed for item recall but not order recall scores. We propose an integration of verbal WM and syntactic processing models for accounting of this finding by assuming that the impact of syntactic knowledge on serial order WM recall is indirect and mediated via syntax-dependent item retrieval processes.

Introduction

There is ample evidence for interactions between long-term memory (LTM) knowledge and verbal working memory (WM), such as the presence of different psycholinguistic effects in verbal WM tasks. Serial recall performance has been shown to be higher for nonwords with high versus low phonotactic frequency phoneme combinations, indicating that sublexical phonological knowledge supports verbal WM (Coady & Aslin, 2004; Coady, Evans & Kluender, 2010; Gathercole, Frankish, Pickering, & Peaker, 1999; Majerus et al., 2004; Zamuner et al., 2004; Munson et al., 2005). Similarly, serial recall performance is increased for words relative to nonwords (Besner & Davelaar, 1982; Brener, 1940; Hulme, Maughan, & Brown, 1991; Jefferies, Frankish, & Lambon Ralph, 2006) and for high-frequency words relative to low-frequency words, implying that verbal WM is supported by lexico-semantic knowledge (Hulme et al., 1997; Kowialiewski & Majerus, 2020; Majerus & Van der Linden, 2003; Poirier & Saint-Aubin, 1996; Watkins & Watkins, 1977). Contributions from semantic levels of knowledge have also been shown, as illustrated by the presence of word imageability, semantic relatedness or sentence superiority effects in verbal WM (Brener, 1940; Cattell, 1886; Jefferies, Lambon Ralph, & Baddeley, 2004; Poirier & Saint-Aubin, 1996; Savill et al., 2015, 2018). The present study examines the impact of syntactic knowledge on verbal WM, a less frequently studied linguistic variable but of strong interest as it may not only support WM for item information, as most of the effects listed so far do, but also WM for serial order information.

Regarding interactions between WM and long-term linguistic knowledge, a distinction of major theoretical interest is between item-level and serial-order aspects of information held in WM. While not all theoretical models make this distinction (e.g., Baddeley & Hitch, 1974; Baddeley et al., 1998; Botvinick & Plaut, 2006), many other WM models assume that item-level representations are supported by the language system (or are identical to temporary activation of long-term language representations). The representation of serial order information (i.e., the order of the items within a list of words) on the other hand is considered to be supported by specific, non-linguistic processes such as temporal, spatial or other types of contextual positional codes (e.g., Brown, Preece & Hulme, 2000; Burgess & Hitch, 1999, 2006; Hartley et al., 2016; Henson, 1998; Majerus, 2009, 2013). The item/order distinction is supported by a number of empirical findings, showing that item recall and serial order recall can be differentially impacted in WM impaired populations in the context of brain injury or neurodevelopmental disorder (Attout & Majerus, 2015; Hachmann et al., 2020; Majerus et al., 2015; Martinez Perez et al., 2012; Romani et al., 2015). Neuroimaging studies have also shown that item-level representations in verbal WM are supported by cortices in language processing areas while serial order-level representations are supported by non-linguistic cortices in intraparietal and/or inferior parietal areas (Cristoforetti et al., 2022; Kowialiewski et al., 2021; Majerus et al., 2010; Marshuetz et al., 2000; but see Papagno et al., 2018). Critically, regarding phonological, lexico-semantic and semantic psycholinguistic effects in verbal WM, phonological and lexico-semantic knowledge have been consistently shown to support item recall but not order recall (Gathercole et al., 2001; Hulme et al., 1991; 1997; Majerus & D'Argembeau, 2011; Nairne & Kelley, 2004; Poirier & Saint-Aubin, 1996; Saint-Aubin & Poirier, 1999a, b, 2000; Walker & Hulme, 1999). If there is any impact on order recall, it is usually characterized by a detrimental impact. Increased rates of order errors have been observed for semantically related words as compared to semantically unrelated words (Kowialiewski, Gorin, & Majerus, 2021; Poirier et al., 2015), as well as for word list vs. nonword list recall (e.g., Jefferies et al., 2006). This reverse impact of linguistic knowledge on serial order recall has been interpreted as reflecting between-item lexico-semantic co-activation effects interfering with the maintenance of initial word order in the memory list (Kowialiewski et al., 2021, 2022). In sum, there is ample evidence for an impact of linguistic knowledge on the retention of item rather than serial order information in verbal WM, in line with many current models of verbal WM. At the same time, these findings might appear counter-intuitive given that a core property of the language system is the processing of sequential information, such as the sequential arrangements of phonemes in a word or of words in a sentence. Hence, we may also expect that specific aspects of language knowledge impact serial order maintenance, and not only maintenance of items (Majerus, 2019). This assumption is in line with "fully emergent" models of verbal WM, which consider that the verbal WM and the language system are interconnected and interact dynamically (Acheson & MacDonald, 2009; Buchsbaum & D'Esposito, 2019; Cowan, 1993; Hasson et al., 2015; MacDonald, 2016; Postle, 2006; Schwering & MacDonald, 2020). According to this approach, language is the representational substrate for WM. Based on these models, we should expect syntactic knowledge to also support verbal WM at both item and serial order levels. Indeed, contrary to other WM models suggesting that the role of language in WM is primarily limited to item-level representations in LTM (e.g., Burgess & Hitch, 1999), linguistic models of verbal WM consider that all aspects are supported by linguistic representations, including the temporary representation of serial order information (e.g., Schwering & MacDonald, 2020). In support of this assumption, some studies have shown that the ability to reproduce verbal sequences such as arbitrary digit sequences (e.g., digit span tasks) can be predicted by the natural frequency of occurrence of digit sequences in the natural language (Jones & Macken, 2018). Similarly, better serial order reconstruction performance has been observed for word sequences presented in an order consistent with syntactic knowledge (Jones & Farrell, 2018), and better recall has been observed for grammatical versus ungrammatical sequences ("sentence superiority effect") (e.g., Cattell, 1886; Massol et al., 2021; Snell & Grainger, 2017), suggesting that memory for order can also be supported by linguistic knowledge, although it may be difficult to distinguish syntactic from semantic effects particularly for the latter studies.

Of particular theoretical interest here is the impact of syntactic knowledge on verbal WM. Syntactic knowledge concerns the way words can be combined within a verbal segment as a function of their grammatical function. For example, in many languages such as English and German, adjectives precede nouns rather than the reverse. These syntactic rules determine, by definition, sequential regularities between words. It follows that this sequential type of linguistic knowledge may support more specifically also the maintenance of serial order aspects of memoranda in verbal WM. Current evidence for the impact of syntactic knowledge on serial order recall in WM remains sparse and ambiguous. It has been shown that lists of words were overall better recalled when they formed a meaningful sentence (Brener, 1940; Jefferies, Lambon Ralph, & Baddeley, 2004), but sequences of words were also better remembered when they followed familiar syntactic rules, regardless of semantic consistency. Epstein (1961) showed that nonsense sequences of syllables led to higher recall performance if they were presented with regular English syntactical structure and morphology (e.g., "meeving gups keebed gompily") than without (e.g., "meev gup keeb gomp"). Marks and Miller (1964) found that when syntactic rules were disrupted in semantically anomalous sentences, the most disrupted sequences led to the poorest recall performance. Perham, Marsh and Jones (2009) showed better recall performance for adjective-noun pairs when presented in canonical order for English syntax, that is, when the adjective preceded the noun rather than the reverse. More recently, Schweppe, Schütte, Machleb, and Hellfritsch (2022) compared, for German language material, recall performance for canonical versus non-canonical adjective-noun pairs, by further manipulating the inflection of the adjectives, German being a highly inflected language. They observed an advantage for recall of adjective-noun lists when the pairs were presented in canonical order (adjective before noun), but only when the adjectives were also correctly inflected. This study was also one of the first making an explicit distinction between item and serial order recall measures. Interestingly, Schweppe et al. observed an advantage of canonical adjective-noun order on item recall but not on order recall measures. One other study used a serial order reconstruction task for investigating the impact of syntactic knowledge on verbal WM (Jones & Farrell, 2018). This study, for English language stimuli, showed better serial order reconstruction performance for semantically meaningless but syntactically legal vs. illegal word sequences, with reproduction errors further tending to make sequences more syntactic ("syntactic bias"). Serial order reconstruction is typically interpreted as a measure of order memory given that item information is fully available at recall and only order information has to be reconstructed. At the same time, the results of this study are difficult to interpret in terms of a specific impact of syntactic knowledge on the retention of serial order information in WM given that there was no specific measure of item WM performance. Even if recall performance in a serial order reconstruction task is only based on order judgments and items are provided at recall, participants must still remember that a given item was in the list in order to be able to retrieve its serial position. While the items are presented during encoding, participants must internally maintain the information about each item and its position in the list. This internal representation of items in their original order allows participants to accurately place them in the correct serial order during reconstruction. Therefore, although the task involves making order judgements based on the provided items, nevertheless intervenes during encoding and maintenance. If a participant does not remember anymore that a given item was in the list, even if provided at recall, it will be very difficult to retrieve its serial position. It is therefore important to measure both order and item aspects as directly as possible.

In sum, a number of studies appear to show an influence of syntactic knowledge on verbal WM performance but the locus of this effect in terms of item versus serial order aspects of WM is far from being understood. As mentioned earlier, given the sequential nature of syntactic knowledge, an impact on serial order recall performance should be expected. Most studies conducted so far on syntactic knowledge effects did not explicitly distinguish between item and order aspects of WM. Jones et al. observed an impact on a serial order reconstruction task but with no direct control of item WM aspects. The only study directly controlling for item and serial order WM aspects by Schweppe et al. observed an impact of syntactic knowledge on item recall performance only. Critically, a potential limitation of the study by Schweppe et al. is the fact that the German language, like English language, specifies adjective-noun order in a fully deterministic manner: adjectives always precede the noun. Given these very strict syntactic rules, non-canonical adjective-noun order may seem so unnatural to a German-speaking participant that it hinders efficient memorization and recall of the items, as well as the intervention of syntactic knowledge about the position of words within the list. Therefore, instead of making order errors, the participant may rather make omission item errors, as observed by the Schweppe et al. study. Note that this result should indeed be specific for adjective-noun sequences as compared to pure noun sequences. In languages such as German and French, a direct and exclusive succession of nouns will not be recognized as a syntactic structure and should therefore not activate specific syntactic knowledge about the ordering of the nouns that would interfere with or facilitate their memorization (i.e., in a given list of nouns, there are no syntactic rules that would determine that noun A should always precede noun B). On the opposite, for adjective-noun pairs, the syntactic rules specifying that an adjective always precedes a noun (in deterministic languages such as German) will become activated and will detect a major linguistic violation when a non-canonical, noun-adjective pair is presented. A related problem caused by this situation is that word order and syntactic legality are confounded: for adjective noun pairs, the legal order will always imply adjective anteposition relative to the noun, making it impossible to fully cross syntactic legality and adjective position.

The present study

Given the inconsistency and limitations of the few previous studies examining the role of syntactic knowledge effects on serial order aspects of WM, the present study re-examined the impact of adjective-noun syntactic knowledge on item and serial order recall in verbal WM for a language providing more flexibility in terms of adjective-noun order and legality. We used the French language as both adjective anteposition (i.e., adjective-noun order) and postposition (i.e., noun-adjective order) can be considered as syntactically legal. More specifically, in French, size-related adjectives, monosyllabic adjectives, and high-frequency adjectives usually precede the noun (e.g., petit chien (*small dog*), beau manteau (*beautiful coat*), dernier jour (*last day*)) while colour-related adjectives, shape-related adjectives, substance-related adjectives, polysyllabic adjectives, morphologically constructed adjectives and low frequency adjectives typically follow the noun (e.g., manteau orange (*orange coat*), chien dangereux (*dangerous dog*), homme impoli (*rude man*), travailleur besogneux (*hardworking man*)) (Abeillé & Godard, 1999; Thuilier, 2012; 2013; Thuilier et al., 2010a, b; Wilmet, 1980). At the same time, many other types of adjectives are correct in both positions. In fact, the positional pairing of adjectives and nouns is based on probabilistic regularities rather than deterministic rules in French. It follows that syntactic effects in verbal WM for French language stimuli should reflect these complex, context-dependent positional regularities.

We exploited this property of the French language to create adjective-noun lists that fully cross syntactic legality (or rather, regularity, in the present case) and adjective position relative to the noun (anteposition vs postposition), leading to four list types (regular adjective-noun anteposition, irregular adjective-noun anteposition; regular noun-adjective postposition; irregular noun-adjective postposition). Like in the study by Schweppe et al. (2022), the lists were presented for immediate serial recall, allowing for the determination of both item and order recall/error measures. Given that in the study by Schweppe et al., the expression of the syntactic effect was subject to the type of inflection (correct/incorrect) of the adjectives, we also manipulated inflection. French, like German, marks gender and plural via the inflections added to the adjective (e.g. masculine: garçon (*boy*) marrant (*funny*), feminine: fille (*girl*) marrante (*funny*); plural: garçons (*boys*) marrants (*funny*), filles (*girls*) marrantes (*funny*)). Inflection was manipulated in two different experimental groups, a first group receiving the four before-mentioned list types with correct inflection (e.g. masculine: piment (*pepper*) élégant (*elegant*); feminine: tasse (*cup*) agressive (*aggressive*)), and a second group receiving the four list types with incorrect inflection (e.g. masculine: piment (*pepper*) élégante (*elegant*), tasse (*cup*) agressif (*agressive*)). We hypothesized that syntactically regular list types should lead to higher recall performance relative to irregular list types, independently of type of adjective position, and this not only for item but also for order measures. Furthermore, we expected a syntactic regularity effect also for incorrectly inflected adjectives lists albeit smaller than for correctly inflected adjectives lists.

Methods

Participants. Sixty participants per inflection group were recruited (see Scoring and Analyses section for justification of sample size) via the University of Liège web platform, and via advertisements on social networks. Data from seven participants had to be excluded due to technical problems in data collection, four in the correct-inflection group, and three in the incorrect-inflection group. Participants were between 18 and 35 years old (M = 22.628, SD = 2.876); fifty-six participants were female. All participants were native French speakers, right-handed, and with normal hearing. They reported no history of learning, neuropsychological or neurological disorder, and no current drug use (e.g. cannabis) or alcohol abuse. The study was approved by the ethics committee of the Faculty of Medicine of the University of Liège. Participants were informed that no financial compensation was provided. All participants gave informed consent to participate in the study.

Materials. To select the adjective-noun pairings and to determine the preferred position of the adjectives relative to the noun, a group of thirteen, French-speaking young adults from the University of Liège not taking part in the main experiment was recruited prior to the study for an online syntactic preference judgment task. They were presented 120 noun-adjective/adjective-noun pairs and they had to determine whether they were in correct, correct but unusual, or incorrect syntactic order. The adjectives and nouns used were similar to the French equivalents of the stimuli used by Schweppe et al. (2022) with the addition of adjectives regularly found in anteposition, postposition, or both, according to French linguistics (Abeillé & Godard, 1999; Grevisse & Goose, 1993; Thuilier, 2013). Based on the judgments obtained from the syntactic preference judgment task, we selected the 36 anteposition/postposition adjectives that received the most consistent ratings for the 'correct order' and 'incorrect order' response categories (at least 60% agreement). These 36 adjectives where then associated with a set of 36 male and 36 female nouns.

Semantic plausibility was minimized as far as possible within pairs by avoiding direct and obvious semantic associations between the adjectives and the nouns (such as "great job"). Semantic plausibility of the adjective-noun pairs was assessed by a further independent group of 10 French-speaking, young adult participants and was rated as absent for 67.36 percent of the pairs by the majority of participants (i.e., at least 60%) and 27.78 percent of pairs were rated as semantically plausible due to the very general meaning of specific adjectives (e.g., moteur blanc (white engine); petite symétrie (small symmetry)). We ensured that this type of pairs occurred equally often in the different list conditions. Phonological similarity was further minimized within pairs by ensuring that nouns did not have the same onset as or rhyme as the adjective (e.g., discarding pairs such as "éléphant-élégant").

The final stimulus set consisted of 48 lists with three adjective-noun pairs in each list. Four list conditions were determined: regular adjective anteposition, irregular adjective anteposition, regular adjective postposition, and irregular adjective postposition (12 lists per condition). Each adjective was used once in each of the four list conditions, and was paired to either a masculine or a female noun. The same masculine/female adjective-noun pairings were used once in regular/irregular adjective anteposition list conditions and once in regular/irregular adjective postposition list conditions, thereby ensuring that the same adjectives and adjective-noun pairings were used across the four list conditions.

Two group conditions were defined: one in which the lists contained only correctly inflected adjectives, and a second one in which the lists contained only incorrectly inflected adjectives. A given list contained exclusively masculine or female adjective-noun pairs in order to avoid distinctiveness effects within the list that might arise when mixing grammatical gender type. In addition, we created two parallel versions (A and B) of the set of materials, containing the same lists but presented in a different pseudorandom order.

The auditory modality was used to focus most directly on serial order processing and associated syntactic processes. Spoken language necessarily involves sequential processing and furthermore reflects the modality in which basic syntactic structures were initially learned during the language learning process. The stimuli were recorded by a French-native female speaker adopting a neutral voice. Each item was recorded separately, and then combined to form adjective-noun/noun-adjective pairs. The full stimulus lists are presented in Appendix (**Tables A.1**, **A.2**, **A.3** and **A.4**).

Procedure. The experiment was conducted online via OpenSesame software (https://osdoc.cogsci.nl/) implemented in the Jatos web interface (https://www.jatos.org/). Instructions were given by the experimenter via a video conferencing platform. All participants were asked to turn on their cameras for the duration of the experiment to ensure that they did not take any notes. Participants were randomly assigned to one group (correct or incorrect inflection) and one version of the task (A or B). Participants were instructed to listen carefully to each of the 48 six word-lists, and to orally recall the words (adjectives and nouns) immediately in the same order. If the participants could not remember a word at a particular position of the list, they had to say “oublié” (forgotten) for that position. Before the presentation of the 48 experimental lists, the participants completed two practice trials with feedback to ensure that they had correctly understood the task instructions. To avoid any ambiguity about the specific adjective-noun pairs within each list, the interstimulus interval within each pair was smaller (350 ms) than the interstimulus interval between pairs (1000 ms). There was no time limit for the participant to respond and all responses were recorded for later transcription and scoring. The experiment lasted about 20 minutes per participant.

Scoring and analysis procedure. Three scores were calculated over all items (with no distinction of nouns or adjectives): overall accuracy (i.e. the proportion of correct items in correct position), item recall score (i.e. the proportion of correct items regardless of their position), and order recall score (i.e. the number of items recalled in correct serial position divided by the item recall score), by pooling over all trials for a given condition. We also conducted error analyses by focusing specifically on adjective inflection recall errors and adjective order recall errors. Adjective inflection errors were defined as incorrectly inflected adjectives being recalled with correct inflection (i.e., corrections) or as correctly inflected adjectives recalled with incorrect inflection (i.e., inflection errors) and adjective order recall errors were defined as an adjective in an irregular position being recalled in a regular position (i.e., regularization) or as an adjective from a regular position being recalled in an irregular position (i.e., swaps between two adjacent positions). Adjective inflection errors and adjective order recall errors scores were expressed in proportions (specific adjective error type divided by the sum of the two adjective error types). Given that adjectives and nouns are presented in pairs, an adjective order recall error should also imply the same for the corresponding noun if produced (see **Table A.7** in Appendix for the analysis of noun order recall errors). In order to avoid redundancy in the analyses, we focused only on adjectives. For the sake of completeness, we additionally conducted analyses on adjective omission errors (adjective for which the participant said “oublié” (forgotten) or adjective not recalled) and noun omission errors (nouns for which the participant said "oublié" or noun not recalled), the latter being reported in the Appendix.

The data were analysed using a Bayesian statistical framework. Bayesian statistics have the advantage, relative to frequentist statistics, of determining the strength of the evidence both against and in favour of the null hypothesis in order to identify which effect is associated with the strongest evidence (Clark et al., 2018; Kruschke, 2010; Lee & Wagenmakers, 2013; Nuijten, Wetzels, Matzke, Dolan, & Wagenmakers, 2015; Wagenmakers et al., 2018). Bayesian statistics also allow multiple statistical tests to be carried out without increasing type I error risk (Clark et al., 2018). The Bayes Factor (BF) is the likelihood ratio of a given model, the best-fitting model being the one with the highest BF. BF_{01} indicates evidence in favour of the null hypothesis, while BF_{10} indicates evidence in favour of the alternative hypothesis. Although there are no fixed thresholds for BF values, we used the following categories for describing strength of evidence: a BF of at least 1 is considered to indicate anecdotal evidence, a BF of at least 3 is considered to indicate moderate evidence, a BF of at least 10 is considered to provide strong evidence, a BF of at least 30 is considered to provide very strong evidence, and a BF of at least 100 is considered to indicate decisive evidence (Jeffreys, 1998).

Regarding statistical power, the Bayesian statistical framework is based on collecting evidence in favour or against an effect of interest and this evidence is incremental and evolves as a function of collected data (Schönbrodt & Wagenmakers, 2018). In contrast to frequentist statistical frameworks, inference taken from obtained data is also independent of the data collection plan (Berger & Wolpert, 1988; Wagenmakers et al., 2018; Dienes, 2011). It is however possible to conduct an indicative design analysis in order to determine the sensitivity of a given Bayesian statistical design: this design analysis estimates the probability of obtaining a specific BF value for a specific effect as a function of simulated sample sizes and an a priori estimation of the effect size (Schönbrodt & Wagenmakers, 2018). We used Monte Carlo simulations and the Bayesian Factor Design Analysis package (Schönbrodt, 2016) implemented in R (version 3.6.2) using the default Cauchy prior distribution parameters, also available on http://shinyapps.org/apps/

BFDA/ to assess the sensitivity of our statistical design to provide evidence for an effect of syntactic regularity/irregularity and position on overall accuracy (i.e. the proportion of correct items in correct position). This analysis showed that if the effect of interest exists, the minimal sample size needed for reaching a specific level of evidence (BF_{10}>10) in favor of the effect in 100% of simulated samples was N=40. If the effect of interest does not exist, the minimal sample size needed for reaching a specific level of evidence (BF_{01}>10) in favor of the absence of an effect in 100% of simulated samples was N=65. For this sensitivity analysis, we assumed a medium effect size of Cohen's d = 0.5 based on the study by Schweppe et al. (2022).

Results

A first 2 (Inflection: correct/incorrect) x 2 (Position: adjective ante-/postposition) x 2 (Regularity: regular/irregular position) Bayesian mixed ANOVA was performed on the overall accuracy score, using the JASP statistical package with default prior settings (JASP team, 2022, Version 0.16.3.0). The model associated with the strongest evidence included the Regularity and Inflection factors. This model was 3.13 times more likely than the model with the next-largest BF value and including Inflection only (Regularity: η^2p = 0.07; Inflection: η^2p = 0.059; evidence for the absence of a Regularity by Inflection interaction: BF_{01} = 3.135) (see **Table 1.1** and **Table 1.2**). As expected, overall accuracy was higher for lists with adjectives in regular syntactic position or when correctly inflected (see **Figure 1.1**).

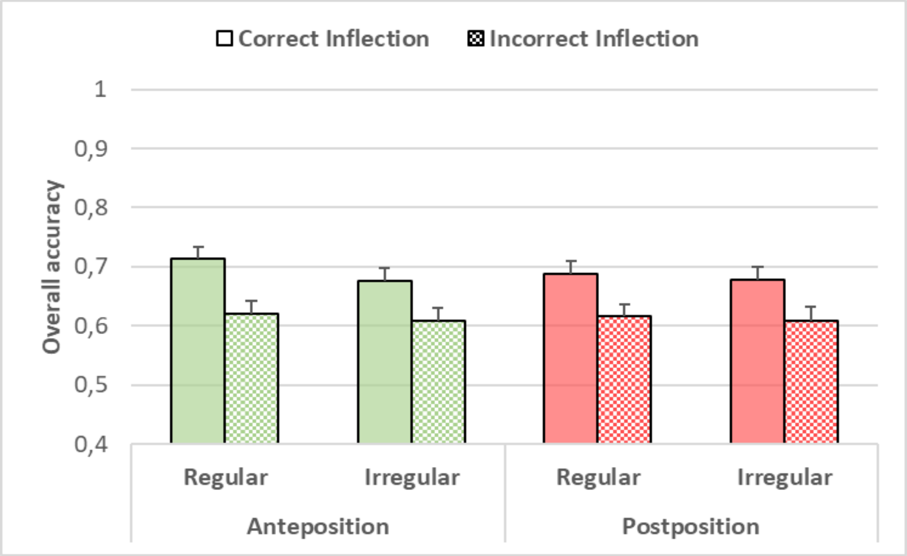

Figure 1.1. Overall accuracy in terms of Position, Regularity, and Inflection

Table 1.1. Results of the 2x2x2 Bayesian ANOVA for the overall accuracy score[1]

Model Comparison

Models	P(M)	P(M|data)	BF_M	BF_{10}	error %
Null model (incl. subject and random slopes)	0.053	0.026	0.481	1.000	
Regularity + Inflection	0.053	0.356	9.966	13.689	3.326
Inflection	0.053	0.114	2.310	4.369	12.182
Regularity + Inflection + Regularity ✻ Inflection	0.053	0.109	2.192	4.170	2.844
Regularity	0.053	0.087	1.709	3.332	72.372
Position + Regularity + Inflection	0.053	0.085	1.663	3.248	1.334
Position + Regularity + Inflection + Position ✻ Regularity	0.053	0.080	1.575	3.090	7.346
Position + Inflection	0.053	0.035	0.655	1.349	8.328
Position + Regularity + Inflection + Regularity ✻ Inflection	0.053	0.029	0.543	1.125	39.541
Position + Regularity	0.053	0.024	0.441	0.918	4.070
Position + Regularity + Inflection + Position ✻ Inflection	0.053	0.015	0.274	0.576	5.184
Position + Regularity + Inflection + Position ✻ Regularity + Regularity ✻ Inflection	0.053	0.008	0.144	0.305	3.346
Position + Regularity + Position ✻ Regularity	0.053	0.008	0.139	0.295	3.171
Position + Regularity + Inflection + Position ✻ Regularity + Position ✻ Inflection	0.053	0.006	0.114	0.242	5.100
Position	0.053	0.005	0.099	0.211	1.042
Position + Inflection + Position ✻ Inflection	0.053	0.005	0.091	0.193	6.395
Position + Regularity + Inflection + Position ✻ Inflection + Regularity ✻ Inflection	0.053	0.004	0.080	0.169	6.204
Position + Regularity + Inflection + Position ✻ Regularity + Position ✻ Inflection + Regularity ✻ Inflection	0.053	0.002	0.032	0.069	5.539
Position + Regularity + Inflection + Position ✻ Regularity + Position ✻ Inflection + Regularity ✻ Inflection + Position ✻ Regularity ✻ Inflection	0.053	0.002	0.030	0.064	48.367

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[1] $P|M$ represents the prior model probabilities, *P(M|data)* represents the posterior model probabilities, and BF_M shows the change in model odds from prior to posterior. The BF_{10} column lists the Bayes factors for each model against the null model, and the *error %* column indicates the percentage of error associated with each model comparison.

Table 1.2. Descriptive statistics of the 2x2x2 Bayesian ANOVA for the overall accuracy score

Position	Regularity	Inflection	Mean	SE	N
Ante	Regular	Correct	0.713	0.152	56
		Incorrect	0.621	0.168	57
	Irregular	Correct	0.676	0.160	56
		Incorrect	0.609	0.156	57
Post	Regular	Correct	0.688	0.156	56
		Incorrect	0.616	0.156	57
	Irregular	Correct	0.678	0.157	56
		Incorrect	0.609	0.179	57

Next, we ran the same analysis on the item recall score. Again, the strongest model included the Regularity and Inflection factors. This model was 2.45 times more likely than the following model including all three factors (Regularity, Inflection, Position) and the interaction between Regularity and Position (Regularity: $\eta^2p = 0.093$; Inflection: $\eta^2p = 0.08$; evidence for absence of interaction effect: $BF_{01} = 5.618$) (see **Table 1.3** and **Table 1.4**). As expected, item recall performance was higher for lists with adjectives in regular position or when correctly inflected (see **Figure 1.2**).

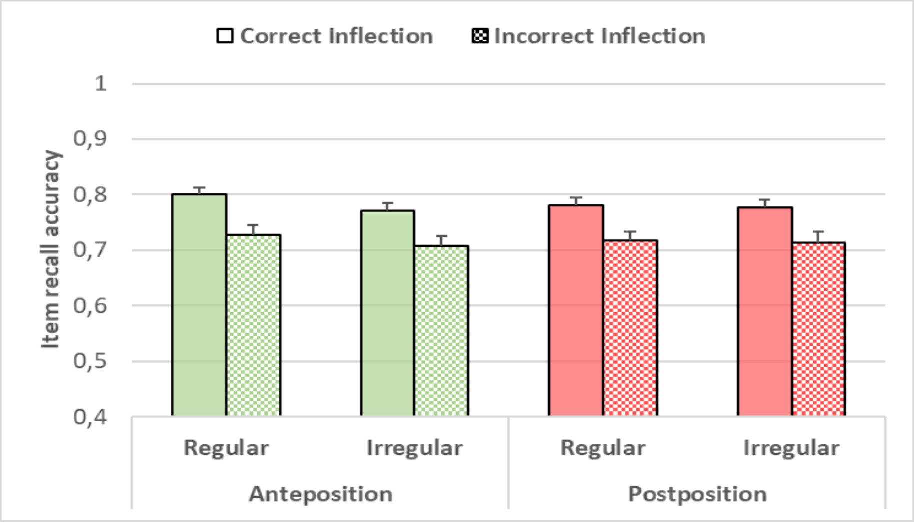

Figure 1.2. Item recall accuracy in terms of Position, Regularity, and Inflection

Table 1.3. Results of the 2x2x2 Bayesian ANOVA for the item recall score

Model Comparison

Models	P(M)	P(M|data)	BF_M	BF_{10}	error %
Null model (incl. subject and random slopes)	0.053	0.005	0.096	1.000	
Regularity + Inflection	0.053	0.416	12.801	78.262	2.662
Position + Regularity + Inflection + Position ✻ Regularity	0.053	0.169	3.667	31.874	6.526
Inflection	0.053	0.090	1.782	16.964	6.781
Position + Regularity + Inflection	0.053	0.072	1.401	13.601	2.544
Regularity + Inflection + Regularity ✻ Inflection	0.053	0.071	1.369	13.307	5.973
Position + Regularity + Inflection + Position ✻ Regularity + Position ✻ Inflection	0.053	0.035	0.657	6.636	5.890
Regularity	0.053	0.034	0.627	6.340	1.087
Position + Regularity + Inflection + Position ✻ Regularity + Regularity ✻ Inflection	0.053	0.029	0.544	5.521	4.578
Position + Regularity + Inflection + Position ✻ Inflection	0.053	0.018	0.326	3.348	17.788
Position + Regularity + Inflection + Regularity ✻ Inflection	0.053	0.016	0.288	2.966	5.220
Position + Regularity + Position ✻ Regularity	0.053	0.012	0.226	2.330	1.925
Position + Inflection	0.053	0.012	0.225	2.324	2.162
Position + Regularity	0.053	0.006	0.117	1.219	2.257
Position + Regularity + Inflection + Position ✻ Regularity + Position ✻ Inflection + Regularity ✻ Inflection	0.053	0.006	0.108	1.120	13.242
Position + Regularity + Inflection + Position ✻ Inflection + Regularity ✻ Inflection	0.053	0.003	0.055	0.574	11.420
Position + Inflection + Position ✻ Inflection	0.053	0.003	0.045	0.471	3.314
Position + Regularity + Inflection + Position ✻ Regularity + Position ✻ Inflection + Regularity ✻ Inflection + Position ✻ Regularity ✻ Inflection	0.053	0.001	0.025	0.259	8.775
Position	0.053	0.001	0.019	0.194	3.711

Table 1.4. Descriptive statistics of the 2x2x2 Bayesian ANOVA for the item recall score

Position	Regularity	Inflection	Mean	SE	N
Ante	Regular	Correct	0.800	0.099	56
		Incorrect	0.728	0.125	57
	Irregular	Correct	0.771	0.105	56
		Incorrect	0.708	0.128	57
Post	Regular	Correct	0.780	0.112	56
		Incorrect	0.718	0.115	57
	Irregular	Correct	0.776	0.114	56
		Incorrect	0.714	0.143	57

We then ran the critical analysis on the order recall score. All factors were associated with anecdotal to moderate evidence for an absence of an effect (Regularity: BF_{01} = 5.613, η^2p = 0.006; Position: BF_{01} = 7.088, η^2p = 0.002; Inflection: BF_{01} = 1.344, η^2p = 0.018) (see **Figure 1.3**, **Table 1.5** and **Table 1.6**). In contrast to the results for the overall accuracy and item recall scores, and contrary to our expectations, syntactically regular list types did not lead to higher recall performance relative to irregular list types for order recall.

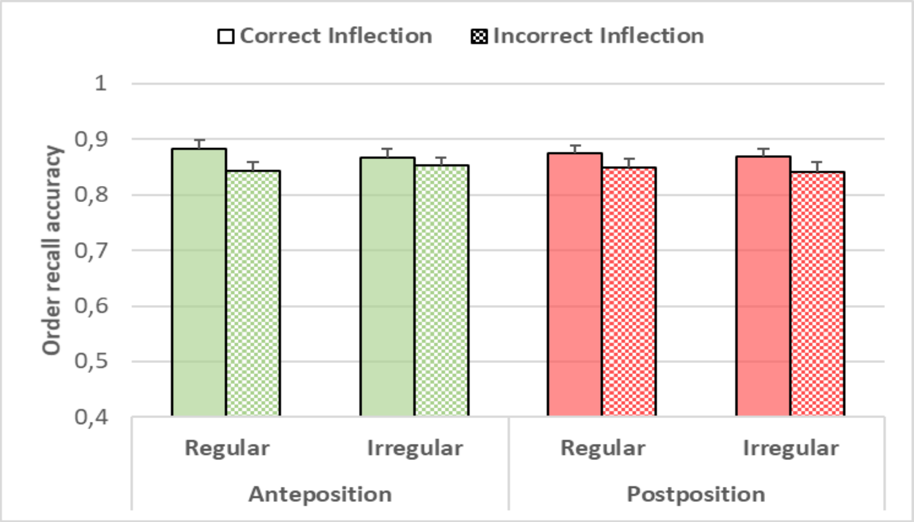

Figure 1.3. Order recall accuracy in terms of Position, Regularity, and Inflection

Table 1.5. Results of the 2x2x2 Bayesian ANOVA for the order recall score

Model Comparison

Models	**P(M)**	**P(M | data)**	**BF$_{M}$**	**BF$_{01}$**	**error %**
Null model (incl. subject and random slopes)	0.053	0.412	12.601	1.000	
Position + Regularity + Position ✻ Regularity	0.053	0.306	7.950	1.344	2.002
Inflection	0.053	0.073	1.425	5.613	2.862
Position	0.053	0.058	1.110	7.088	1.610
Regularity	0.053	0.055	1.041	7.530	2.606
Position + Regularity + Inflection + Position ✻ Regularity	0.053	0.043	0.812	9.537	2.379
Position + Inflection	0.053	0.018	0.321	23.466	9.658
Regularity + Inflection	0.053	0.012	0.216	34.792	12.259
Position + Regularity + Inflection + Position ✻ Regularity + Position ✻ Inflection	0.053	0.008	0.140	53.215	3.193
Position + Regularity + Inflection + Position ✻ Regularity + Regularity ✻ Inflection	0.053	0.007	0.135	55.434	2.510
Position + Regularity	0.053	0.002	0.041	180.724	2.875
Position + Inflection + Position ✻ Inflection	0.053	0.002	0.031	238.713	6.700
Regularity + Inflection + Regularity ✻ Inflection	0.053	0.002	0.030	250.669	18.561
Position + Regularity + Inflection	0.053	0.001	0.021	351.919	4.559
Position + Regularity + Inflection + Position ✻ Regularity + Position ✻ Inflection + Regularity ✻ Inflection	0.053	4.759^{e-4}	0.009	865.320	12.756
Position + Regularity + Inflection + Position ✻ Regularity + Position ✻ Inflection + Regularity ✻ Inflection + Position ✻ Regularity ✻ Inflection	0.053	3.497^{e-4}	0.006	1177.368	4.370
Position + Regularity + Inflection + Regularity ✻ Inflection	0.053	2.380^{e-4}	0.004	1729.904	7.017
Position + Regularity + Inflection + Position ✻ Inflection	0.053	6.832^{e-5}	0.001	6026.958	10.083
Position + Regularity + Inflection + Position ✻ Inflection + Regularity ✻ Inflection	0.053	5.098^{e-5}	9.177^{e-4}	8076.757	37.939

Table 1.6. Descriptive statistics of the 2x2x2 Bayesian ANOVA for the order recall score

Position	Regularity	Inflection	Mean	SE	N
Ante	Regular	Correct	0.883	0.110	56
		Incorrect	0.843	0.116	57
	Irregular	Correct	0.867	0.115	56
		Incorrect	0.853	0.099	57
Post	Regular	Correct	0.875	0.100	56
		Incorrect	0.849	0.120	57
	Irregular	Correct	0.868	0.112	56
		Incorrect	0.842	0.121	57

Error analysis

To examine the impact of Regularity and Inflection on item and order recall performance in a more fine grained manner, we determined adjective inflection recall errors and adjective order recall errors. For inflection, errors could be an incorrectly inflected adjective becoming correctly inflected (i.e., corrections) or a correctly inflected adjective becoming an incorrectly inflected adjective (i.e., inflection errors). For order, errors could be irregular positioned adjectives being produced in a regular position (i.e., regularization) or regular positioned adjectives being produced in an irregular position (i.e., swaps between two adjacent positions). We may expect that incorrectly inflected adjectives lead to errors that involve recall of the correct inflection. Likewise, for adjectives in an irregular, non-preferred position relative to a noun, they may be erroneously recalled in their preferred serial position relative to a noun. For the sake of completeness, we also determined adjective omission errors and noun omission errors (see Appendix for the latter). As a reminder, adjective inflection recall errors, adjective order recall and omission errors scores were expressed in proportions. Adjective inflection recall errors and adjective omission errors were divided by the sum of relevant item errors (i.e. the sum of total adjective inflection recall errors and total adjective omission errors). Adjective order recall errors were divided by the sum of order errors (i.e. the sum of the total adjective order recall errors and the sum of the total item recall score minus the overall accuracy score). Given that an adjective order recall error should also imply the same for the corresponding noun if produced, we focused only on adjectives in order to avoid redundancy in the analyses. For information purposes, the same analysis on nouns, also taking into account nouns recalled individually but in irregular position, led to similar results (see Appendix).

Regarding adjective inflection recall errors, a 2 x 2 x 2 Bayesian three-way ANOVA showed that the data were best explained by a model including Inflection, Error Type, the interaction between Regularity and Position, as well as the interaction between Inflection Error Type and Position (Inflection Error Type: η^2_p = 0.248; Regularity*Position: η^2_p = 0.068; Inflection Error Type*Position: η^2_p = 0.087) (see **Table 1.7** and **Table 1.8**). This analysis suggests that adjective inflection recall errors involved "corrections" more often than "inflection errors". This situation tended to be more frequent when the adjective was also in postposition, while fewer corrections were observed when the adjective was in anteposition. Given that in French, adjectives occur more frequently in postposition than anteposition (e.g., Benzitoun, 2014; Henkel, 2016; Thuilier et al., 2010a, b), and given that correct adjective inflection is determined by the associated noun, we may indeed expect more adjective inflection corrections to occur when the adjective follows a noun. Finally, the interaction between Regularity and Position suggests that more inflection recall errors overall are produced when adjectives are in regular postposition and in irregular anteposition. As can be seen in **Figure 1.4** , the observation of an increased proportion of adjective inflection recall errors when in regular postposition was mainly due to an increase of the proportion of "corrections", i.e., the pattern of results we already discussed. On the other hand, the relative increase of adjective inflection recall errors in irregular anteposition concerned both types of errors and was less expected. However, since French adjectives occur more frequently in postposition than anteposition, an adjective (expected to occur in postposition) appearing in an irregular anteposition could be particularly disruptive regarding the processing of the adjectives as a syntactically coherent item, leading to particularly poor encoding of the associated inflection. It should be noted that adjective inflection recall errors accounted for only a small proportion of the relevant item errors (mean proportion = 0.119, SE = 0.012), with adjective omission errors being predominant (mean proportion = 0.784, SE = 0.022).

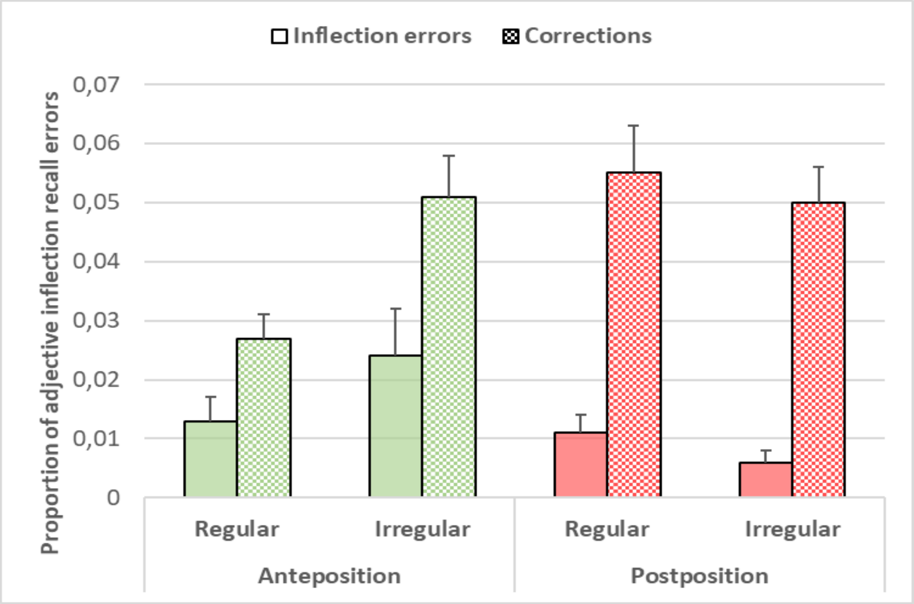

Figure 1.4. Proportion of adjective inflection recall errors, in terms of Position, Regularity, and Inflection

Table 1.7. Results of the 2x2x2 Bayesian ANOVA for adjective inflection recall errors

Model Comparison

Models	P(M)	P(M | data)	BF_M	BF_{10}	error %
Null model (incl. Position, Regularity, subject, and random slopes)[2]	0.091	7.362^{e-9}	7.362^{e-8}	1.000	
Inflection Error Type + Inflection Error Type ✻ Position + Position ✻ Regularity	0.091	0.672	20.486	9.127^{e+7}	5.186
Inflection Error Type + Inflection Error Type ✻ Position + Inflection Error Type ✻ Regularity + Position ✻ Regularity	0.091	0.145	1.696	1.970^{e+7}	3.809
Inflection Error Type + Position ✻ Regularity	0.091	0.088	0.968	1.199^{e+7}	3.778
Inflection Error Type + Inflection Error Type ✻ Position + Inflection Error Type ✻ Regularity + Position ✻ Regularity + Inflection Error Type ✻ Position ✻ Regularity	0.091	0.042	0.438	5.698^{e+6}	4.442
Inflection Error Type + Inflection Error Type ✻ Position	0.091	0.024	0.241	3.193^{e+6}	3.638
Inflection Error Type + Inflection Error Type ✻ Regularity + Position ✻ Regularity	0.091	0.019	0.199	2.648^{e+6}	5.320
Inflection Error Type + Inflection Error Type ✻ Position + Inflection Error Type ✻ Regularity	0.091	0.005	0.055	746115.825	4.841
Inflection Error Type	0.091	0.003	0.033	447193.202	3.052
Inflection Error Type + Inflection Error Type ✻ Regularity	0.091	9.860^{e-4}	0.010	133924.942	16.915
Position ✻ Regularity	0.091	1.827^{e-7}	1.827^{e-6}	24.820	3.669

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[2] The main effects of Regularity and Position were not robust ($\eta^2_p = 0.027$ and $\eta^2_p = 0.003$, respectively), and hence, these factors were added to the null model for correct interpretation of the model including the interactions.

Table 1.8. Descriptive statistics of the 2x2x2 Bayesian ANOVA for adjective inflection recall errors

Position	Regularity	Inflection	Error type	Mean	SE	N
Ante	Regular	Correct	Inflection errors	0.013	0.034	56
		Incorrect	Corrections	0.027	0.033	57
	Irregular	Correct	Inflection errors	0.024	0.061	56
		Incorrect	Corrections	0.051	0.055	57
Post	Regular	Correct	Inflection errors	0.011	0.022	56
		Incorrect	Corrections	0.055	0.059	57
	Irregular	Correct	Inflection errors	0.006	0.016	56
		Incorrect	Corrections	0.050	0.048	57

Next, regarding adjective omission errors, the data were best explained by a model including Regularity and Inflection factors, as well as the interaction between Regularity and Inflection. This model was however only 2.85 times more likely than the model including Regularity and Inflection factors only, and hence the interaction needs to be interpreted with caution (Regularity: η^2_p = 0.092; Inflection: η^2_p = 0. 484; Regularity*Inflection: η^2_p = 0.071) (see **Table 1.9** and **Table 1.10**). As expected, more adjective omission errors were observed when the adjective was in an irregular syntactic position but also when correctly inflected (see **Figure 1.5**). Correct inflection is likely to reinforce the expectation of the participant that the adjective and the noun are linked, and this expectation is then contradicted when the noun and adjective are presented in irregular syntactic order, leading to an increase of omission errors. The same principle could also tentatively explain the increase of omission errors overall when adjectives are correctly vs. incorrectly inflected by assuming that the expected association is contradicted by the mainly implausible semantic links between the adjectives and the nouns.

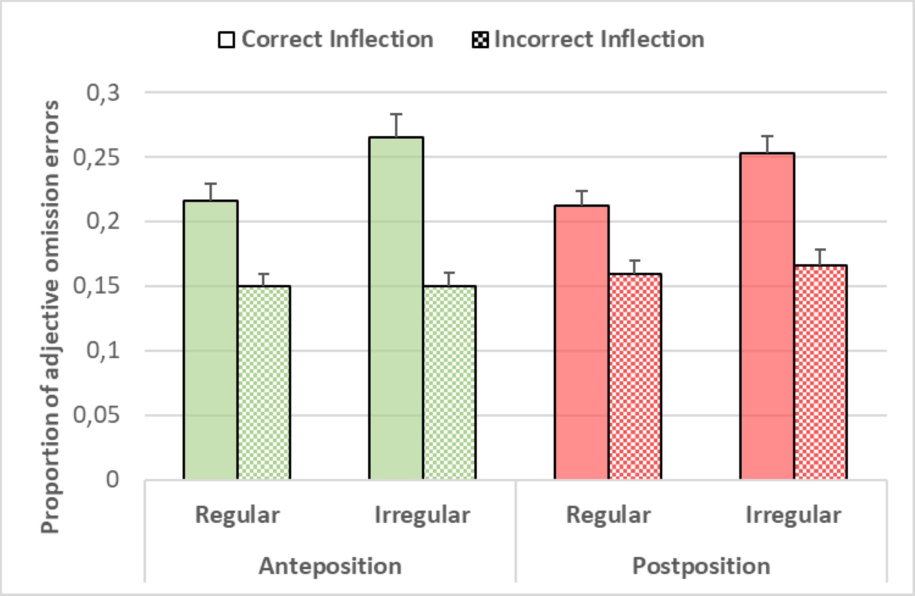

Figure 1.5. Proportion of adjective omission errors, in terms of Position, Regularity, and Inflection

Table 1.9. Results of the 2x2x2 Bayesian ANOVA for adjective omission errors

Model Comparison

Models	P(M)	P(M | data)	BF$_{M}$	BF$_{10}$	error %
Null model (incl. subject and random slopes)	0.053	1.085^{e-14}	1.953^{e-13}	1.000	
Regularity + Inflection + Regularity ✻ Inflection	0.053	0.576	24.500	5.312^{e+13}	2.655
Regularity + Inflection	0.053	0.202	4.569	1.865^{e+13}	2.928
Position + Regularity + Inflection + Regularity ✻ Inflection	0.053	0.086	1.696	7.937^{e+12}	2.705
Inflection	0.053	0.038	0.706	3.477^{e+12}	1.460
Position + Regularity + Inflection	0.053	0.028	0.526	2.618^{e+12}	3.519
Position + Regularity + Inflection + Position ✻ Inflection + Regularity ✻ Inflection	0.053	0.028	0.510	2.539^{e+12}	5.494
Position + Regularity + Inflection + Position ✻ Regularity + Regularity ✻ Inflection	0.053	0.014	0.249	1.257^{e+12}	7.532
Position + Regularity + Inflection + Position ✻ Inflection	0.053	0.010	0.175	8.861^{e+11}	9.638
Position + Inflection	0.053	0.006	0.101	5.152^{e+11}	2.310
Position + Regularity + Inflection + Position ✻ Regularity	0.053	0.005	0.082	4.193^{e+11}	10.392
Position + Regularity + Inflection + Position ✻ Regularity + Position ✻ Inflection + Regularity ✻ Inflection	0.053	0.004	0.076	3.861^{e+11}	11.600
Position + Inflection + Position ✻ Inflection	0.053	0.002	0.029	1.497^{e+11}	2.643
Position + Regularity + Inflection + Position ✻ Regularity + Position ✻ Inflection	0.053	0.001	0.022	1.112^{e+11}	2.829
Position + Regularity + Inflection + Position ✻ Regularity + Position ✻ Inflection + Regularity ✻ Inflection + Position ✻ Regularity ✻ Inflection	0.053	8.610^{e-4}	0.016	7.934^{e+10}	7.385
Regularity	0.053	4.272^{e-14}	7.690^{e-13}	3.937	1.715
Position + Regularity	0.053	6.325^{e-15}	1.138^{e-13}	0.583	4.083
Position	0.053	1.539^{e-15}	2.771^{e-14}	0.142	3.302
Position + Regularity + Position ✻ Regularity	0.053	8.498^{e-16}	1.530^{e-14}	0.078	2.307

Table 1.10. Descriptive statistics of the 2x2x2 Bayesian ANOVA for adjective omission errors

Position	Regularity	Inflection	Mean	SE	N
Ante	Regular	Correct	0.216	0.094	56
		Incorrect	0.150	0.068	57
	Irregular	Correct	0.265	0.134	56
		Incorrect	0.150	0.075	57
Post	Regular	Correct	0.212	0.093	56
		Incorrect	0.159	0.083	57
	Irregular	Correct	0.253	0.095	56
		Incorrect	0.166	0.092	57

Finally, regarding adjective order recall errors, all factors were again associated with moderate evidence for an *absence* of an effect, in line with the main analyses on order recall performance (Regularity: BF_{01} = 7.92, η^2_p = 0.0002; Position: BF_{01} = 6.971, η^2_p = 0.0002; Inflection: BF_{01} = 3.936, η^2_p = 0.023) (see **Figure 1.6, Table 1.11** and **Table 1.12**). Once again, contrary to our expectations, adjectives in an irregular position were not recalled more frequently in a regular position than were adjectives in a regular position recalled more frequently in an irregular position. It should be noted that a further analysis showed that most of the adjective order recall errors involved permutations between two adjacent positions (87.7%), while a minority of errors involved swaps between two adjectives (e.g. swaps between adjective on position 1 and adjective on position 3) (11.26%).

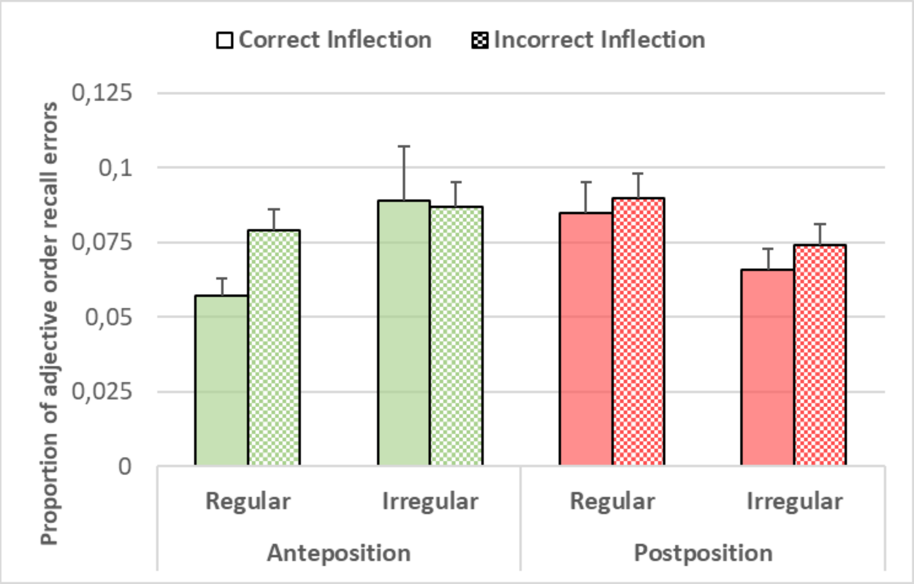

Figure 1.6. Proportion of adjective order recall errors, in terms of Position, Regularity, and Inflection

Table 1.11. Results of the 2x2x2 Bayesian ANOVA for adjective order recall errors

Model Comparison

Models	**P(M)**	**P(M|data)**	**BF_M**	**BF_{01}**	**error %**
Null model (incl. subject and random slopes)	0.053	0.461	15.408	1.000	
Position + Regularity + Position ✻ Regularity	0.053	0.180	3.950	2.563	5.103
Inflection	0.053	0.117	2.389	3.936	1.184
Position	0.053	0.066	1.275	6.971	4.770
Regularity	0.053	0.058	1.113	7.920	1.285
Position + Regularity + Inflection + Position ✻ Regularity	0.053	0.044	0.819	10.596	4.008
Position + Inflection	0.053	0.016	0.295	28.587	2.040
Regularity + Inflection	0.053	0.015	0.266	31.715	1.482
Position + Regularity + Inflection + Position ✻ Regularity + Position ✻ Inflection	0.053	0.013	0.245	34.339	40.318
Position + Regularity	0.053	0.009	0.171	48.926	3.156
Position + Regularity + Inflection + Position ✻ Regularity + Regularity ✻ Inflection	0.053	0.008	0.143	58.707	1.838
Position + Inflection + Position ✻ Inflection	0.053	0.004	0.070	118.934	5.394
Regularity + Inflection + Regularity ✻ Inflection	0.053	0.003	0.051	164.010	5.065
Position + Regularity + Inflection	0.053	0.002	0.035	238.249	2.085
Position + Regularity + Inflection + Position ✻ Regularity + Position ✻ Inflection + Regularity ✻ Inflection	0.053	0.002	0.035	240.972	9.427
Position + Regularity + Inflection + Position ✻ Regularity + Position ✻ Inflection + Regularity ✻ Inflection + Position ✻ Regularity ✻ Inflection	0.053	7.694^{e-4}	0.014	599.419	17.231
Position + Regularity + Inflection + Position ✻ Inflection	0.053	4.405^{e-4}	0.008	1047.069	3.716
Position + Regularity + Inflection + Regularity ✻ Inflection	0.053	3.620^{e-4}	0.007	1274.222	3.723
Position + Regularity + Inflection + Position ✻ Inflection + Regularity ✻ Inflection	0.053	2.433^{e-4}	0.004	1895.844	66.106

Table 1.12. Descriptive statistics of the 2x2x2 Bayesian ANOVA for adjective order recall errors

Position	Regularity	Inflection	Mean	SE	N
Ante	Regular	Correct	0.057	0.044	56
		Incorrect	0.079	0.055	57
	Irregular	Correct	0.085	0.077	56
		Incorrect	0.090	0.058	57
Post	Regular	Correct	0.089	0.134	56
		Incorrect	0.087	0.057	57
	Irregular	Correct	0.066	0.051	56
		Incorrect	0.074	0.052	57

Partial pairs recall

Further analyses were conducted on recall of partial pairs by reporting the mean number of pairs for which the first item was recalled but not the second and vice versa. The Position factor was not included in this analysis for reducing model complexity given the addition of the Item factor, with Item 1 representing pairs with only the first item recalled, and Item 2 representing pairs with only the second item recalled. A 2 x 2 x 2 Bayesian three-way ANOVA showed that the data were best explained by a model including the interaction between Regularity and Item (Regularity*Item: $\eta^2_p = 0.391$) (see **Table 1.13**). While more second items were indeed recalled for pairs in regular position, likely reflecting a baseline recency effect for the second item of the final pairs, the opposite was observed for pairs in irregular position, with more first items recalled for pairs in irregular position (see **Figure 1.7**). The importance of this result will be discussed in the Discussion section. For information purposes, the same analysis was performed on adjectives and nouns separately (see Appendix).

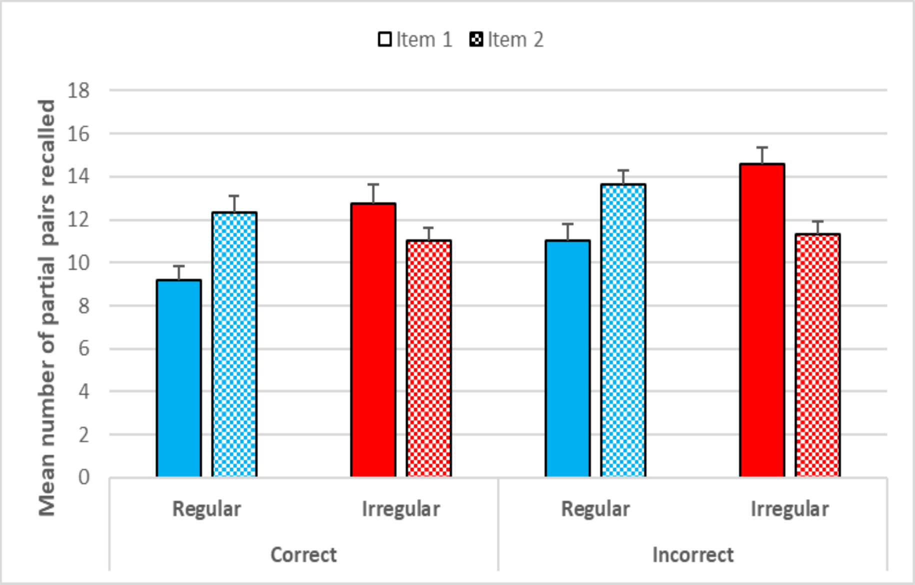

Figure 1.7. Mean number of partial pairs, in terms of Regularity, Item, and Inflection

Table 1.13. Results of the 2x2x2 Bayesian ANOVA for partial pairs recall

Models	P(M)	P(M | data)	BF$_M$	BF$_{10}$	error %
Null model (incl. Item, Regularity, Inflection, subject, and random slopes)[3]	0.111	6.060e^{-17}	4.848^{e-16}	1.000	
Item ✻ Regularity	0.111	0.567	10.459	9.350^{e+15}	3.549
Item ✻ Regularity + Item ✻ Inflection	0.111	0.236	2.476	3.900^{e+15}	3.519
Item ✻ Regularity + Regularity ✻ Inflection	0.111	0.126	1.154	2.080^{e+15}	7.672
Item ✻ Regularity + Item ✻ Inflection + Regularity ✻ Inflection	0.111	0.057	0.482	9.386^{e+14}	8.699
Item ✻ Regularity + Item ✻ Inflection + Regularity ✻ Inflection + Item ✻ Regularity ✻ Inflection	0.111	0.014	0.115	2.330^{e+14}	5.584
Item ✻ Inflection	0.111	2.434^{e-17}	1.947^{e-16}	0.402	4.160
Regularity ✻ Inflection	0.111	1.223^{e-17}	9.784^{e-17}	0.202	4.651
Item ✻ Inflection + Regularity ✻ Inflection	0.111	4.706^{e-18}	3.765^{e-17}	0.078	6.494

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[3] The main effects of Regularity, Item and Inflection were not robust ($\eta^2_p = 0.09$; $\eta^2_p = 0.002$; $\eta^2_p = 0.022$, respectively), and hence, these factors were added to the null model for correct interpretation of the model including the interactions.

Discussion

The results of the present study are striking as they reproduce the null findings of the Schweppe et al. (2022) study regarding the impact of adjective-noun syntactic knowledge specifically on serial order aspects of verbal WM, while, critically, using a language that allows for both adjective anteposition and postposition. Schweppe et al. (2022) used German language stimuli only allowing for adjective anteposition, resulting in illegal adjective postposition stimuli sounding extremely unfamiliar and preventing efficient encoding and retrieval in verbal WM. The present study shows that a null effect of adjective-noun syntactic knowledge on serial order WM is not specific to the German language and also characterizes syntactically much more flexible languages such as French. On the other hand, our results showed a robust impact of adjective-noun associative knowledge on item recall, as also observed by Schweppe et al. (2022).

From a broad theoretical perspective, these results appear to add further evidence for the role of linguistic knowledge in verbal WM. In line with a number of language-based accounts of verbal WM (Jones et al., 2006; Martin & Saffran, 1992; R.C. Martin et al., 1994; Majerus, 2009, 2013; Acheson & MacDonald, 2009; Poirier et al., 2015), the present results support the idea that verbal WM performance is determined to a large extent by access to long-term linguistic structures that correspond to the stimuli to be memorized. While many studies have shown that phonological, lexical and semantic levels of long-term linguistic knowledge support verbal WM, fewer studies have specifically studied the impact of syntactic knowledge. The present study adds new evidence to the limited number of studies that have specifically investigated the impact of syntactic linguistic knowledge on verbal WM by showing that syntactic knowledge about adjective-noun associations supports at least item aspects of verbal WM.

Linguistic knowledge effects in verbal WM are interpreted as reflecting the intervention of language representations that support and reconstruct decaying WM traces (e.g., Schweickert, 1993; Hulme et al., 1991) and/or that directly provide the representational basis for information held in WM (Kowialiewski et al., 2020, 2021; Martin & Saffran, 1992; Majerus, 2009;

Acheson & MacDonald, 2009). This support is considered to act at the level of the phonological, lexical and semantic features of individual memoranda (Martin & Saffran, 1992; Majerus, 2009), and the fact that most linguistic effects exert an impact on item recall in WM tasks is in line with this assumption. However, as already discussed earlier, fully emergent linguistic accounts of WM (e.g., Schwering & MacDonald, 2020) consider that any type of knowledge that defines language processing should also define WM processing, given that language is the representational substrate for WM. Following these accounts, we should also expect that knowledge about linguistic sequential structures should support sequence-level aspects of verbal WM, and more specifically the maintenance of serial order information in WM. It is therefore interesting to observe that sequential knowledge about adjective-noun order, although having a strong impact at the item level, does not appear to support the maintenance of order information.

How can we then explain this apparent paradoxical finding of sequential linguistic knowledge supporting item-level but not sequence-level aspects of WM? We argue that our results support an *indirect* effect of syntactic knowledge on serial order WM, by assuming dependency rather than independency of item and serial order levels of representation in WM, and by assuming that retrieval of item information is conditioned by sequential regularities, in line with recurrent network models of verbal WM that assume unified item-order representations (Botvinick & Plaut, 2006), full linguistic models of verbal WM (Schwering & MacDonald, 2020) as well as psycholinguistic models of syntactic processing. At the same time, our findings allow to exclude a *direct* effect of syntactic adjective-noun order on serial order WM and an associated full independency of item and serial order recall (as assumed for example by contextual, positional models of serial order WM; Burgess & Hitch, 1999, 2006) by showing that sequential knowledge does not directly lead to an increase in serial order recall performance or serial order errors, independently of its effect in item-level encoding and retrieval. In other words, the results of the present study suggest that illegal adjective-noun orderings prevent the retrieval of associated item information rather than directly leading to order errors. This could be explained by a chaining-type representation of item and serial order representation: an adjective (noun) stored in WM cues the associated noun (adjective), but only if the chain corresponds to its corresponding long-term sequential representation (i.e., if the specific adjective (noun) precedes the specific noun (adjective) in natural language chains). If the same adjective-noun pair is presented in reversed, irregular order, the noun (adjective), presented first, will not cue the following adjective (noun) as this adjective (noun) is usually not produced after the noun (adjective). Hence, irregular order of adjective-noun pairs will prevent efficient encoding, maintenance and retrieval of item information. This interpretation is in line with chaining models of serial order recall (at least with those assuming unidirectional chaining such as Ebbinghaus, 1885; Lindsey & Logan, 2021): when a string of words to be recalled does not correspond to the usual succession of the words, successive items cannot be retrieved as inter-item associative chains are disrupted. A similar interpretation of our findings can be made based on the additional error analyses we carried out. We observed an increase of item omission errors when adjectives (and also post-positioned nouns) occur in irregular positions and, most critically, an increase of partial pairs with the first adjective (noun) recalled but not the second noun (adjective) for irregularly ordered adjective-noun pairs. In case of irregularity of adjective-noun order, the first item of a given pair may be retrieved but it will not provide a cue for the following word, leading to an increased proportion of partial pairs with only the first item recalled. Notably, similar results are observed from the separate analyses of partial pairs involving either nouns or adjectives, supporting the existence of a general chaining mechanism and of a disruptive effect of irregular syntactic position on cuing. In sum, any deviation from expected syntactic position should disrupt cuing. The results of Jones and Farrell (2018) using a serial order reconstruction task could be explained in a similar manner: the advantage observed in serial order reconstruction for syntactically legal word sequences could actually stem from a better ability to maintain items and to cue successive items during retrieval based on a better match between the syntactic nature of items and their associated position in the syntactic frame.

A similar explanation of the results can be derived from psycholinguistic models of syntactic processing (Garrett, 1988; Levelt, 1999). In these models, syntactic order is encoded via a syntactic frame structure, which defines the position in which each constituent of a sentence should be located, depending on its syntactic and lexical nature. Once the syntactic frame has been defined, the syntactic slots are filled with the phonological (item) content of the selected words. For the memory lists used in the present study, the syntactic frame to be constructed would be Adj N + Adj N + Adj N or N Adj + N Adj + N Adj, depending on the type of WM list. More specifically, when a list has to be recalled, either the Adj N + Adj N + Adj N or the N Adj + N Adj + N Adj frame created during memory list encoding will be activated, and the syntactic slots have to be completed with their respective phonological content. The slots will not be filled if the adjective (noun) to be placed in a specific slot does not correspond to the types of adjectives (nouns) that are usually allocated to the ante/post position of this slot, relative to the noun (adjective). Adjective inflection recall errors on the other hand can freely occur as type of inflections is determined by the noun to which adjectives are associated rather than by syntactic position. Note however that this psycholinguistic account alone cannot explain our results. While it is compatible with the increased omission errors for irregular adjective-noun order lists, it would not predict an increase of partial pairs with the first but not the second item recalled. It would instead predict an increase of recall omission of both first and second items. Our results rather support an account where item and serial order are linked via inter-item associative sequential knowledge, in addition to syntactic parsing and frame prediction processes (see **Figure 1.8**).

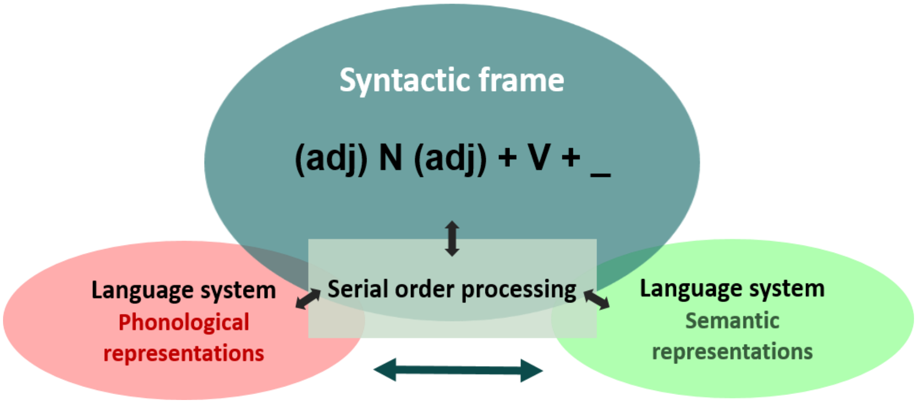

Figure 1.8. Macroscopic proposal for an integrated WM and language processing architecture that includes syntactic levels of processing, in which item and serial order are linked via inter-item associative sequential knowledge

A potential limitation of the present study is that the specific outcome of results might have been facilitated by the redundant and predictable nature of the WM list. However, as already stated above, while this situation may have led to increased omission errors for irregular lists due to the predictability of the resulting syntactic-frame, this situation alone cannot explain the increased partial pairs with only the first item recalled. In any case, it remains to be shown whether increased serial order errors could be observed in WM lists where adjective-noun order is less predictable, by presenting lists mixing adjective-noun and noun-adjective pairs and without any interval separating the pairs, by inserting a delay between the lists and recall to reduce the impact of phonological sequential representation, or by instructing participants to use a free recall strategy. Also, a stronger and more direct effect on serial order may be observed when manipulating noun-verb order (boy eats bread vs. boy bread eats) rather than noun-adjective order given that verbs are an obligatory constituent of natural sentences unlike adjectives. The results of increased serial order WM for syntactically legal sequences in the study by Jones and Farrell (2018) could indeed be driven by the inclusion of verbs in their memory lists.

Finally, Schweppe et al. observed an impact of syntactic order regularity on item WM recall only when the adjectives were correctly inflected. Interestingly, a similar interaction between regularity and inflection emerged in the context of our analysis of adjective omission errors, with a higher proportion of omission errors when adjectives were both in an irregular syntactic position and correctly inflected. Correct inflection may indeed reinforce the expectation that the adjective and noun are related, and presenting them in an irregular syntactic order may lead to increased omission errors. However, this interaction was not robust and needs to be interpreted with caution. In addition, syntactic order and inflection exerted two independent effects in most analyses, suggesting that, for the French language stimuli used in this study, they stemmed from different sources. Schweppe et al. considered that there is an overlap between syntactic constraints on word order and morphosyntactic constraints such as adjective inflection. This may indeed be the case for languages with highly deterministic morpho-syntactic structures: as soon as one constraint is violated, WM recall performance sharply drops as the entire sequence is perceived as highly ungrammatical and may not receive further (syntactic) linguistic support anymore. For languages with probabilistic morpho-syntactic structures such as French, morphological (inflections) and syntactic constraints appear to interact in a more flexible manner and the irregularity of one of the constraints does not automatically invalidate the other constraint. This is also supported by the complex interactions with syntactic order that were observed for inflection recall errors in this study. However, it should be noted that the sample size had been determined for the main effect of regularity (order), not the interaction between order and inflection. Despite a rather large sample size (N=113), our interpretation therefore still needs to be considered with caution.

In this study, inflection of the adjective reflects morpho-phonological knowledge associated to items and not positional (syntactic) knowledge about items in the list. One may wonder why the impact of adjective inflection was much more important than the impact of adjective order. Inflectional effects are probably stronger because they are deterministic: every adjective needs to be correctly inflected and there is only one possible correct inflection. Adjective-noun order effects on the other hand, as already mentioned, are, in the French language, probabilistic: an adjective can be found in both ante-position and post-position, and these flexible rules may also explain the lesser impact of adjective-noun order.

To conclude, the present study provides evidence for the impact of syntactic order knowledge on verbal WM performance and calls for a deep integration of language processing and WM architectures, by including syntactic levels of processing in addition to the phonological, lexical and semantic processing levels considered by most WM architectures. Although additional clarification is needed regarding the interactions between syntactic sequential knowledge structures and order recall in WM, the present results provide further evidence for an indirect effect of syntactic knowledge on serial order WM by predicting successive item cues based on inter-item associative and sequential knowledge.

Appendix

Table A.1. Materials used in Group 1 (Correct inflection), version A. IRREG/REG = irregular or regular position; ANTE/POST = anteposition or postposition of the adjective

List	Condition	Gender	Item 1	Item 2	Item 3	Item 4	Item 5	Item 6
1	IRREG + ANTE	masc	familier	muguet	naïf	soda	sec	coussin
2	REG + ANTE	fem	importante	bière	nouvelle	paupière	joyeuse	casserole
3	REG + POST	fem	vipère	brillante	myrtille	jalouse	vanille	glissante
4	IRREG + POST	fem	serrure	élégante	texture	grande	résine	seconde
5	IRREG + ANTE	fem	sèche	écharpe	bruyante	lavande	familière	amande
6	REG + ANTE	masc	gros	pseudonyme	petit	laiton	vieux	pentagone
7	REG + POST	masc	moteur	blanc	soda	naïf	orteil	agressif
8	IRREG + POST	masc	titane	grand	carnaval	léger	béret	joyeux
9	IRREG + ANTE	masc	discret	poivron	gluant	poignet	gourmand	balcon
10	IRREG + POST	masc	pentagone	vieux	nombril	puissant	laiton	petit
11	IRREG + ANTE	fem	maladroite	poitrine	creuse	chorale	brumeuse	gazelle
12	IRREG + ANTE	fem	agressive	tasse	discrète	fourchette	brillante	vipère
13	IRREG + POST	fem	agence	légère	vésicule	dernière	virgule	belle
14	REG + ANTE	masc	puissant	nombril	bref	whisky	élégant	piment
15	REG + POST	masc	tiroir	compétent	coussin	sec	poignet	gluant
16	REG + ANTE	masc	premier	terroir	léger	carnaval	précieux	fleuve
17	REG + POST	masc	jasmin	méfiant	poivron	discret	champagne	glissant
18	REG + ANTE	masc	grand	titane	dernier	thorax	important	béton
19	IRREG + POST	fem	nectarine	brève	salamandre	première	bouilloire	longue
20	REG + POST	fem	batterie	blanche	cannelle	compétente	patate	naïve
21	REG + ANTE	masc	long	acier	nouveau	trapèze	mauvais	vestibule
22	IRREG + ANTE	masc	brillant	palmier	ringard	saumon	méfiant	jasmin
23	REG + POST	fem	oreille	gourmande	écharpe	sèche	poitrine	maladroite

24	IRREG + POST	fem	vessie	précieuse	symétrie	petite	pommette	vieille
25	REG + POST	masc	terroir	premier	piment	élégant	whisky	bref
26	IRREG + ANTE	masc	blanc	moteur	agressif	orteil	bruyant	bonnet
27	IRREG + POST	fem	casserole	joyeuse	urgence	mauvaise	banane	puissante
28	REG + POST	fem	chorale	creuse	amande	familière	limace	ringarde
29	REG + ANTE	fem	grande	texture	élégante	serrure	puissante	banane
30	IRREG + POST	masc	vecteur	beau	pseudonyme	gros	béton	important
31	REG + POST	fem	lavande	bruyante	tasse	agressive	gazelle	brumeuse
32	REG + ANTE	fem	mauvaise	urgence	vieille	pommette	première	salamandre
33	IRREG + ANTE	fem	naïve	patate	blanche	batterie	compétente	cannelle
34	REG + POST	masc	pull	jaloux	balcon	gourmand	muguet	familier
35	REG + ANTE	masc	joyeux	béret	beau	vecteur	second	silicone
36	IRREG + POST	masc	fleuve	précieux	thorax	dernier	vestibule	mauvais
37	IRREG + POST	masc	silicone	second	acier	long	trapèze	nouveau
38	REG + POST	masc	menton	brumeux	bonnet	bruyant	saumon	ringard
39	REG + ANTE	fem	grosse	religion	dernière	vésicule	belle	virgule
40	IRREG + ANTE	fem	jalouse	myrtille	gourmande	oreille	glissante	vanille
41	IRREG + POST	masc	palmier	brillant	miroir	maladroit	tissu	creux
42	IRREG + ANTE	fem	gluante	fourmi	ringarde	limace	méfiante	tisane
43	IRREG + POST	fem	bière	importante	paupière	nouvelle	religion	grosse
44	REG + ANTE	fem	petite	symétrie	longue	bouilloire	précieuse	vessie
45	IRREG + ANTE	masc	compétent	tiroir	jaloux	pull	brumeux	menton
46	REG + ANTE	fem	seconde	résine	légère	agence	brève	nectarine
47	REG + POST	fem	tisane	méfiante	fourchette	discrète	fourmi	gluante
48	IRREG + ANTE	masc	glissant	champagne	creux	tissu	maladroit	miroir

Table A.2. Materials used in Group 1 (Correct inflection), version B. IRREG/REG = irregular or regular position; ANTE/POST = anteposition or postposition of the adjective

List	Condition	Gender	Item 1	Item 2	Item 3	Item 4	Item 5	Item 6
1	IRREG + POST	masc	terroir	premier	piment	élégant	whisky	bref
2	IRREG + ANTE	fem	agressive	tasse	discrète	fourchette	brillante	vipère
3	REG + ANTE	masc	gros	pseudonyme	petit	laiton	vieux	pentagone
4	REG + POST	masc	menton	brumeux	bonnet	bruyant	saumon	ringard
5	IRREG + POST	masc	titane	grand	carnaval	léger	béret	joyeux
6	IRREG + POST	masc	fleuve	précieux	thorax	dernier	vestibule	mauvais
7	IRREG + ANTE	fem	jalouse	myrtille	gourmande	oreille	glissante	vanille
8	REG + POST	masc	palmier	brillant	miroir	maladroit	tissu	creux
9	REG + ANTE	masc	puissant	nombril	bref	whisky	élégant	piment
10	REG + POST	fem	tisane	méfiante	fourchette	discrète	fourmi	gluante
11	REG + ANTE	fem	mauvaise	urgence	vieille	pommette	première	salamandre
12	IRREG + ANTE	masc	familier	muguet	naïf	soda	sec	coussin
13	REG + POST	fem	chorale	creuse	amande	familière	limace	ringarde
14	REG + ANTE	masc	long	acier	nouveau	trapèze	mauvais	vestibule
15	REG + ANTE	fem	grosse	religion	dernière	vésicule	belle	virgule
16	REG + POST	masc	moteur	blanc	soda	naïf	orteil	agressif
17	REG + ANTE	fem	grande	texture	élégante	serrure	puissante	banane
18	REG + POST	masc	pull	jaloux	balcon	gourmand	muguet	familier
19	REG + ANTE	fem	petite	symétrie	longue	bouilloire	précieuse	vessie
20	REG + POST	fem	oreille	gourmande	écharpe	sèche	poitrine	maladroite
21	REG + ANTE	masc	joyeux	béret	beau	vecteur	second	silicone
22	REG + POST	fem	lavande	bruyante	tasse	agressive	gazelle	brumeuse
23	REG + POST	masc	jasmin	méfiant	poivron	discret	champagne	glissant
24	REG + ANTE	masc	premier	terroir	léger	carnaval	précieux	fleuve
25	IRREG + ANTE	masc	compétent	tiroir	jaloux	pull	brumeux	menton

26	IRREG + POST	masc	vecteur	beau	pseudonyme	gros	béton	important
27	IRREG + POST	fem	casserole	joyeuse	urgence	mauvaise	banane	puissante
28	IRREG + ANTE	masc	blanc	moteur	agressif	orteil	bruyant	bonnet
29	IRREG + ANTE	fem	maladroite	poitrine	creuse	chorale	brumeuse	gazelle
30	IRREG + POST	fem	nectarine	brève	salamandre	première	bouilloire	longue
31	IRREG + POST	fem	serrure	élégante	texture	grande	résine	seconde
32	REG + POST	fem	batterie	blanche	cannelle	compétente	patate	naïve
33	REG + ANTE	fem	importante	bière	nouvelle	paupière	joyeuse	casserole
34	IRREG + POST	masc	pentagone	vieux	nombril	puissant	laiton	petit
35	IRREG + ANTE	masc	glissant	champagne	creux	tissu	maladroit	miroir
36	IRREG + ANTE	fem	gluante	fourmi	ringarde	limace	méfiante	tisane
37	IRREG + POST	fem	agence	légère	vésicule	dernière	virgule	belle
38	IRREG + ANTE	fem	naïve	patate	blanche	batterie	compétente	cannelle
39	IRREG + POST	masc	silicone	second	acier	long	trapèze	nouveau
40	IRREG + ANTE	fem	sèche	écharpe	bruyante	lavande	familière	amande
41	IRREG + ANTE	masc	brillant	palmier	ringard	saumon	méfiant	jasmin
42	REG + ANTE	masc	grand	titane	dernier	thorax	important	béton
43	IRREG + POST	fem	vessie	précieuse	symétrie	petite	pommette	vieille
44	IRREG + ANTE	masc	discret	poivron	gluant	poignet	gourmand	balcon
45	REG + POST	fem	vipère	brillante	myrtille	jalouse	vanille	glissante
46	IRREG + POST	fem	bière	importante	paupière	nouvelle	religion	grosse
47	REG + POST	masc	tiroir	compétent	coussin	sec	poignet	gluant
48	REG + ANTE	fem	seconde	résine	légère	agence	brève	nectarine

Table A.3. Materials used in Group 2 (Incorrect inflection), version A. IRREG/REG = irregular or regular position; ANTE/POST = anteposition or postposition of the adjective

List	Condition	Gender	Item 1	Item 2	Item 3	Item 4	Item 5	Item 6
1	IRREG + ANTE	masc	sec	écharpe	familier	amande	glissant	vanille
2	REG + POST	fem	chorale	creux	cannelle	compétent	patate	naïf
3	REG + ANTE	fem	première	terroir	légère	carnaval	précieuse	fleuve
4	IRREG + ANTE	masc	gluant	fourmi	discret	fourchette	méfiant	tisane
5	IRREG + POST	masc	silicone	seconde	acier	longue	béret	joyeuse
6	REG + POST	masc	palmier	brillante	miroir	maladroite	tissu	creuse
7	REG + ANTE	masc	gros	religion	long	bouilloire	premier	salamandre
8	IRREG + ANTE	fem	familière	muguet	naïve	soda	jalouse	pull
9	IRREG + POST	masc	piment	élégante	vecteur	belle	trapèze	nouvelle
10	REG + POST	masc	saumon	ringarde	balcon	gourmande	menton	brumeuse
11	IRREG + ANTE	masc	maladroit	poitrine	blanc	batterie	brumeux	gazelle
12	REG + POST	masc	pull	jalouse	soda	naïve	muguet	familière
13	IRREG + POST	fem	serrure	élégant	texture	grand	résine	second
14	REG + ANTE	masc	petit	symétrie	vieux	pommette	précieux	vessie
15	IRREG + ANTE	fem	glissante	champagne	gluante	poignet	méfiante	jasmin
16	IRREG + POST	fem	nectarine	bref	salamandre	premier	virgule	beau
17	IRREG + POST	masc	fleuve	précieuse	thorax	dernière	vestibule	mauvaise
18	IRREG + ANTE	masc	naïf	patate	compétent	cannelle	creux	chorale
19	IRREG + ANTE	masc	jaloux	myrtille	gourmand	oreille	bruyant	lavande
20	REG + ANTE	fem	longue	acier	grosse	pseudonyme	élégante	piment
21	REG + POST	fem	tisane	méfiant	fourchette	discret	fourmi	gluant
22	IRREG + POST	masc	terroir	première	whisky	brève	béton	importante
23	IRREG + ANTE	fem	brillante	palmier	ringarde	saumon	gourmande	balcon
24	REG + ANTE	fem	importante	béton	petite	laiton	belle	vecteur
25	REG + POST	fem	vipère	brillant	myrtille	jaloux	vanille	glissant

26	REG + POST	masc	orteil	agressive	bonnet	bruyante	moteur	blanche
27	REG + ANTE	fem	joyeuse	béret	mauvaise	vestibule	grande	titane
28	REG + POST	masc	tiroir	compétente	coussin	sèche	poignet	gluante
29	IRREG + ANTE	masc	agressif	tasse	ringard	limace	brillant	vipère
30	IRREG + POST	fem	bière	important	paupière	nouveau	religion	gros
31	IRREG + ANTE	fem	discrète	poivron	creuse	tissu	compétente	tiroir
32	IRREG + POST	fem	vessie	précieux	symétrie	petit	bouilloire	long
33	REG + ANTE	masc	important	bière	joyeux	casserole	dernier	vésicule
34	REG + POST	fem	lavande	bruyant	tasse	agressif	gazelle	brumeux
35	REG + ANTE	masc	mauvais	urgence	léger	agence	beau	virgule
36	IRREG + POST	masc	pentagone	vieille	nombril	puissante	pseudonyme	grosse
37	REG + POST	fem	batterie	blanc	limace	ringard	amande	familier
38	REG + ANTE	masc	nouveau	paupière	élégant	serrure	grand	texture
39	REG + POST	fem	oreille	gourmand	écharpe	sec	poitrine	maladroit
40	REG + ANTE	fem	vieille	pentagone	dernière	thorax	nouvelle	trapèze
41	REG + ANTE	fem	puissante	nombril	brève	whisky	seconde	silicone
42	IRREG + POST	masc	titane	grande	carnaval	légère	laiton	petite
43	REG + POST	masc	jasmin	méfiante	poivron	discrète	champagne	glissante
44	IRREG + ANTE	fem	blanche	moteur	agressive	orteil	bruyante	bonnet
45	IRREG + POST	fem	agence	léger	vésicule	dernier	pommette	vieux
46	IRREG + ANTE	fem	maladroite	miroir	sèche	coussin	brumeuse	menton
47	IRREG + POST	fem	casserole	joyeux	urgence	mauvais	banane	puissant
48	REG + ANTE	masc	second	résine	puissant	banane	bref	nectarine

Table A.4. Materials used in Group 2 (Incorrect inflection), version B. IRREG/REG = irregular or regular position; ANTE/POST = anteposition or postposition of the adjective

List	Condition	Gender	Item 1	Item 2	Item 3	Item 4	Item 5	Item 6
1	REG + POST	fem	lavande	bruyant	tasse	agressif	gazelle	brumeux
2	IRREG + POST	masc	pentagone	vieille	nombril	puissante	pseudonyme	grosse
3	REG + ANTE	masc	mauvais	urgence	léger	agence	beau	virgule
4	REG + POST	fem	oreille	gourmand	écharpe	sec	poitrine	maladroit
5	REG + ANTE	masc	nouveau	paupière	élégant	serrure	grand	texture
6	IRREG + ANTE	masc	naïf	patate	compétent	cannelle	creux	chorale
7	IRREG + POST	fem	agence	léger	vésicule	dernier	pommette	vieux
8	REG + ANTE	masc	second	résine	puissant	banane	bref	nectarine
9	REG + POST	masc	orteil	agressive	bonnet	bruyante	moteur	blanche
10	REG + POST	masc	saumon	ringarde	balcon	gourmande	menton	brumeuse
11	REG + ANTE	fem	longue	acier	grosse	pseudonyme	élégante	piment
12	IRREG + ANTE	masc	sec	écharpe	familier	amande	glissant	vanille
13	REG + POST	fem	chorale	creux	cannelle	compétent	patate	naïf
14	IRREG + POST	fem	casserole	joyeux	urgence	mauvais	banane	puissant
15	IRREG + ANTE	masc	maladroit	poitrine	blanc	batterie	brumeux	gazelle
16	IRREG + POST	masc	piment	élégante	vecteur	belle	trapèze	nouvelle
17	IRREG + POST	masc	titane	grande	carnaval	légère	laiton	petite
18	IRREG + ANTE	fem	brillante	palmier	ringarde	saumon	gourmande	balcon
19	REG + ANTE	fem	puissante	nombril	brève	whisky	seconde	silicone
20	REG + POST	fem	tisane	méfiant	fourchette	discret	fourmi	gluant
21	IRREG + ANTE	fem	maladroite	miroir	sèche	coussin	brumeuse	menton
22	IRREG + POST	masc	fleuve	précieuse	thorax	dernière	vestibule	mauvaise
23	REG + POST	fem	batterie	blanc	limace	ringard	amande	familier
24	IRREG + ANTE	masc	jaloux	myrtille	gourmand	oreille	bruyant	lavande
25	IRREG + POST	fem	nectarine	bref	salamandre	premier	virgule	beau

26	IRREG + ANTE	masc	gluant	fourmi	discret	fourchette	méfiant	tisane	
27	REG + POST	masc	palmier	brillante	miroir	maladroite	tissu	creuse	
28	REG + ANTE	fem	joyeuse	béret	mauvaise	vestibule	grande	titane	
29	IRREG + POST	fem	vessie	précieux	symétrie	petit	bouilloire	long	
30	REG + POST	masc	pull	jalouse	soda	naïve	muguet	familière	
31	REG + ANTE	fem	vieille	pentagone	dernière	thorax	nouvelle	trapèze	
32	IRREG + ANTE	fem	glissante	champagne	gluante	poignet	méfiante	jasmin	
33	IRREG + POST	fem	serrure	élégant	texture	grand	résine	second	
34	REG + ANTE	fem	importante	béton	petite	laiton	belle	vecteur	
35	IRREG + ANTE	fem	blanche	moteur	agressive	orteil	bruyante	bonnet	
36	IRREG + POST	masc	terroir	première	whisky	brève	béton	importante	
37	REG + POST	masc	jasmin	méfiante	poivron	discrète	champagne	glissante	
38	REG + ANTE	masc	important	bière	joyeux	casserole	dernier	vésicule	
39	IRREG + ANTE	fem	familière	muguet	naïve	soda	jalouse	pull	
40	REG + POST	masc	tiroir	compétente	coussin	sèche	poignet	gluante	
41	REG + ANTE	masc	gros	religion	long	bouilloire	premier	salamandre	
42	REG + ANTE	masc	petit	symétrie	vieux	pommette	précieux	vessie	
43	REG + POST	fem	vipère	brillant	myrtille	jaloux	vanille	glissant	
44	IRREG + POST	masc	silicone	seconde	acier	longue	béret	joyeuse	
45	IRREG + ANTE	fem	discrète	poivron	creuse	tissu	compétente	tiroir	
46	IRREG + POST	fem	bière	important	paupière	nouveau	religion	gros	
47	REG + ANTE	fem	première	terroir	légère	carnaval	précieuse	fleuve	
48	IRREG + ANTE	masc	agressif	tasse	ringard	limace	brillant	vipère	

Complementary analysis: noun omission errors

Regarding noun omission errors, the most parsimonious model with the strongest evidence included the Inflection factor, and the interaction between Position and Regularity (Inflection: η^2_p = 0.043; Position*Regularity: η^2_p = 0.067) (see **Table A.5** and **Table A.6**). Like for adjective omission errors, noun omission errors were more frequent in the correct adjective inflection condition. The position-by-regularity interaction furthermore showed that noun omission errors were more frequent when occurring in irregular post-position like for associated adjectives in irregular anteposition, but also when occurring in regular anteposition (see **Figure 1.9**). The latter finding may again be the result of the semantically mainly implausible noun-adjective associations, the noun occurring in the expected position relative to the adjective; this syntactic association will then be contradicted by the semantic incongruency between the two elements, increasing the probability of the nouns not being efficiently maintained and recalled.

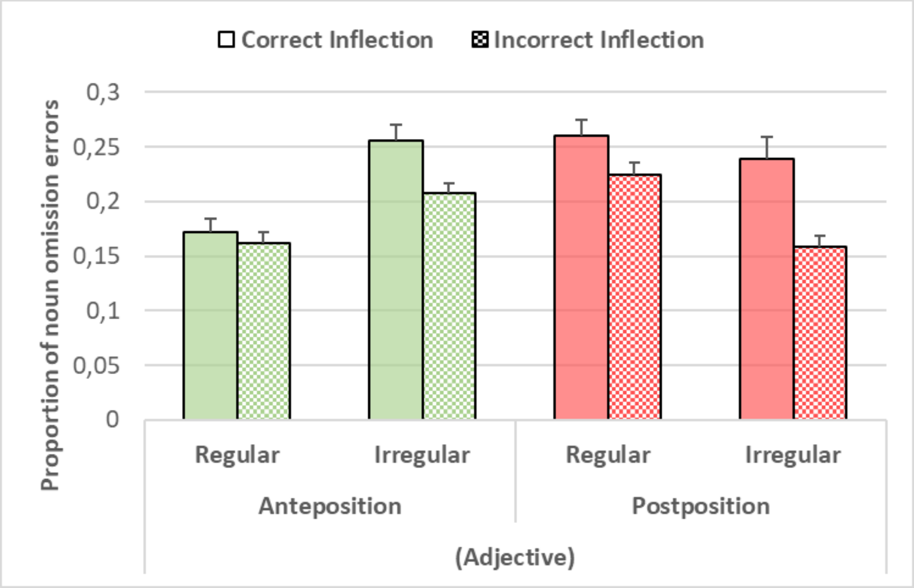

Figure 1.9. Proportion of noun omission errors, in terms of Position, Regularity, and Inflection

Table A.5. Results of the 2x2x2 Bayesian ANOVA for noun omission errors

Model Comparison

Models	P(M)	P(M|data)	BF_M	BF_{10}	error %
Null model (incl. Position, Regularity, subject, and random slopes)[4]	0.091	8.056^{e-13}	8.056^{e-12}	1.000	
Inflection + Inflection ✻ Regularity + Position ✻ Regularity	0.091	0.410	6.951	5.090^{e+11}	5.693
Inflection + Position ✻ Regularity	0.091	0.279	3.873	3.466^{e+11}	3.965
Inflection + Inflection ✻ Position + Inflection ✻ Regularity + Position ✻ Regularity	0.091	0.161	1.915	1.995^{e+11}	4.072
Inflection + Inflection ✻ Position + Position ✻ Regularity	0.091	0.118	1.339	1.466^{e+11}	3.945
Inflection + Inflection ✻ Position + Inflection ✻ Regularity + Position ✻ Regularity + Inflection ✻ Position ✻ Regularity	0.091	0.032	0.329	3.948^{e+10}	4.215
Position ✻ Regularity	0.091	7.153^{e-5}	7.153^{e-4}	8.878^{e+7}	2.676
Inflection + Inflection ✻ Regularity	0.091	1.199^{e-9}	1.199^{e-8}	1488.444	2.898
Inflection	0.091	1.105^{e-9}	1.105^{e-8}	1371.233	4.403
Inflection + Inflection ✻ Position + Inflection ✻ Regularity	0.091	7.046^{e-10}	7.046^{e-9}	874.608	28.393
Inflection + Inflection ✻ Position	0.091	3.903^{e-10}	3.903^{e-9}	484.486	3.952

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[4] The main effect of Regularity was not robust ($\eta^2_p = 0.011$), and hence, this factor was added to the null model for correct interpretation of the model including the interactions.

Table A.6. Descriptive statistics of the 2x2x2 Bayesian ANOVA for noun omission errors

Position	Regularity	Inflection	Mean	SE	N
Ante	Regular	Correct	0.172	0.012	56
		Incorrect	0.162	0.010	57
	Irregular	Correct	0.256	0.014	56
		Incorrect	0.208	0.009	57
Post	Regular	Correct	0.260	0.015	56
		Incorrect	0.225	0.011	57
	Irregular	Correct	0.239	0.020	56
		Incorrect	0.159	0.010	57

Complementary analysis: separate partial pairs recall analysis for adjectives and nouns

Additional analyses were conducted on recall of partial pairs, by focussing specifically on either adjectives or nouns as item reference. For the analysis on adjectives as item reference, the conditions were defined as follows: Item 1 in regular position (regular anteposition), Item 1 in irregular position (irregular anteposition), Item 2 in regular position (regular postposition), and Item 2 in irregular position (irregular postposition). A 2 x 2 x 2 Bayesian three-way ANOVA showed that the data were best explained by a model including the interaction between Regularity and Item (Regularity*Item: $\eta^2_p = 0.239$) (see **Table A.7**). In line with the results of partial pairs analysis, more second items were recalled for pairs in regular position, while the opposite was observed for pairs in irregular position, with more first items recalled for pairs in irregular position (see **Figure 1.10**).

Regarding partial pairs analysis on nouns as item reference, the conditions were defined as Item 1 in regular position (regular postposition), Item 1 in irregular position (irregular postposition), Item 2 in regular position (regular anteposition), and Item 2 in irregular position (irregular anteposition). The model with strongest evidence included Regularity, and, critically, the interaction between Item and Regularity factors (Regularity: $\eta^2_p = 0.126$; Item*Regularity: $\eta^2_p = 0.301$) (see **Table A.8**). Once again, more second items were recalled for pairs in regular position, while the opposite was observed for pairs in irregular position, with more first items recalled for pairs in irregular position (see **Figure 1.11**).

Table A.7. Results of the 2x2x2 Bayesian ANOVA for partial pairs recall of adjectives

Model Comparison

Models	P(M)	P(M|data)	BF_M	BF_{10}	error %
Null model (incl. Item, Regularity, Inflection, subject, and random slopes)[5]	0.111	2.544e^{-8}	2.035e^{-7}	1.000	
Item ✻ Regularity	0.111	0.453	6.635	1.782e^{+7}	3.122
Item ✻ Regularity + Item ✻ Inflection	0.111	0.350	4.314	1.377e^{+7}	4.610
Item ✻ Regularity + Item ✻ Inflection + Regularity ✻ Inflection	0.111	0.099	0.877	3.885e^{+6}	42.878
Item ✻ Regularity + Regularity ✻ Inflection	0.111	0.087	0.759	3.407e^{+6}	9.081
Item ✻ Regularity + Item ✻ Inflection + Regularity ✻ Inflection + Item ✻ Regularity ✻ Inflection	0.111	0.011	0.087	423023.348	3.984
Item ✻ Inflection	0.111	1.761e^{-8}	1.409e^{-7}	0.692	4.040
Regularity ✻ Inflection	0.111	4.568e^{-9}	3.654e^{-8}	0.180	5.841
Item ✻ Inflection + Regularity ✻ Inflection	0.111	2.898e^{-9}	2.318e^{-8}	0.114	4.562

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[5] The main effects of Regularity, Item and Inflection were not robust ($\eta^2_p = 0.001$; $\eta^2_p = 0.005$; $\eta^2_p = 0.014$, respectively), and hence, these factors were added to the null model for correct interpretation of the model including the interactions.

Table A.8. Results of the 2x2x2 Bayesian ANOVA for partial pairs recall of nouns

Model Comparison

Models	P(M)	P(M | data)	BF$_M$	BF$_{10}$	error %
Null model (incl. Item, Inflection, subject, and random slopes)[6]	0.091	2.310^{e-13}	2.310^{e-12}	1.000	
Regularity + Regularity ✻ Item	0.091	0.664	19.777	2.875^{e+12}	8.251
Regularity + Regularity ✻ Item + Regularity ✻ Inflection	0.091	0.155	1.837	6.717^{e+11}	9.978
Regularity + Regularity ✻ Item + Item ✻ Inflection	0.091	0.123	1.401	5.319^{e+11}	8.915
Regularity + Regularity ✻ Item + Regularity ✻ Inflection + Item ✻ Inflection	0.091	0.045	0.476	1.966^{e+11}	34.329
Regularity + Regularity ✻ Item + Regularity ✻ Inflection + Item ✻ Inflection + Regularity ✻ Item ✻ Inflection	0.091	0.012	0.125	5.337^{e+10}	13.269
Regularity	0.091	4.637^{e-12}	4.637^{e-11}	20.069	8.328
Regularity + Regularity ✻ Inflection	0.091	9.231^{e-13}	9.231^{e-12}	3.995	8.384
Regularity + Item ✻ Inflection	0.091	8.211^{e-13}	8.211^{e-12}	3.554	8.348
Regularity + Regularity ✻ Inflection + Item ✻ Inflection	0.091	1.702^{e-13}	1.702^{e-12}	0.737	8.541
Item ✻ Inflection	0.091	3.899^{e-14}	3.899^{e-13}	0.169	8.318

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[6] The main effects of Item and Inflection were not robust ($\eta^2_p = 0.024$; $\eta^2_p = 0.024$, respectively), and hence, these factors were added to the null model for correct interpretation of the model including the interactions.

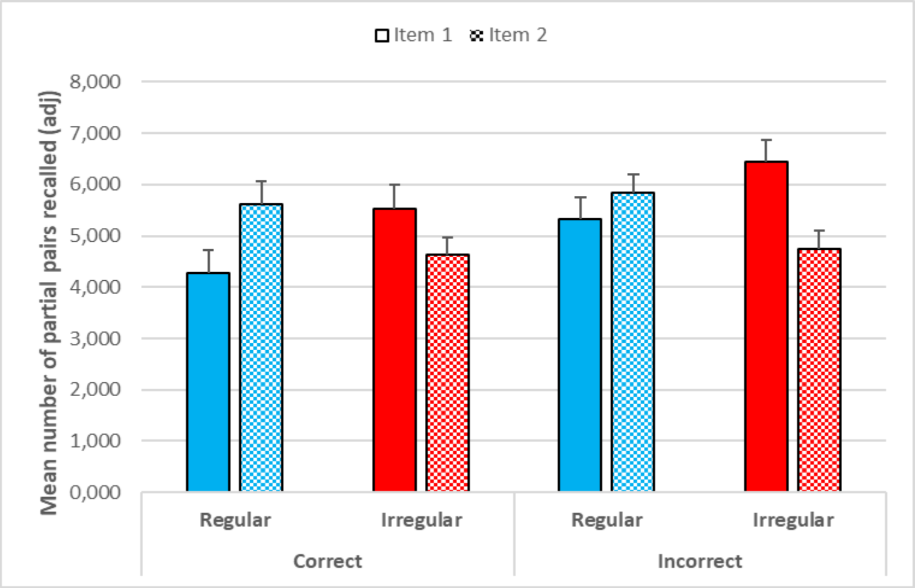

Figure 1.10. Mean number of partial pairs (adjectives only), in terms of Regularity, Item, and Inflection

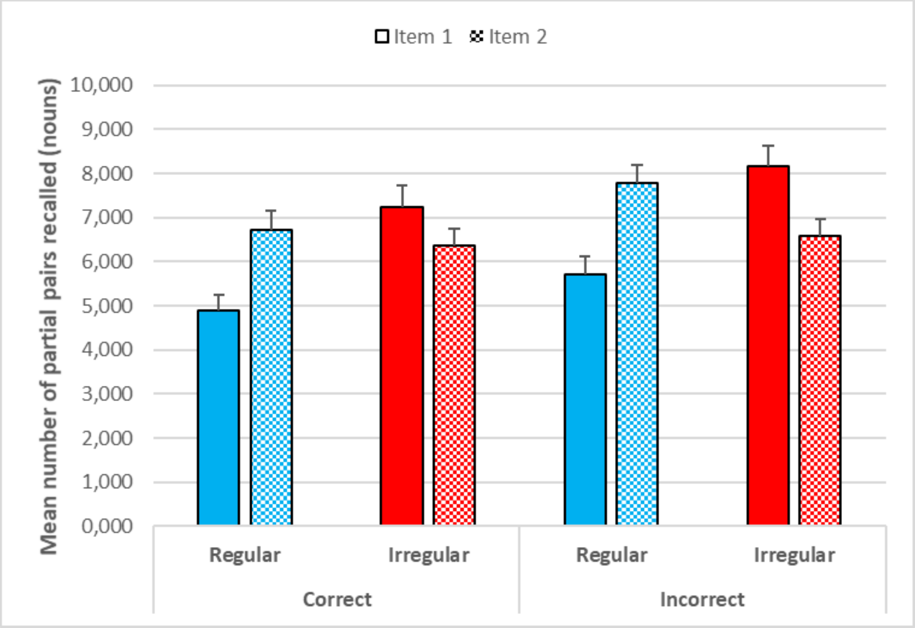

Figure 1.11. Mean number of partial pairs (nouns only), in terms of Regularity, Item, and Inflection

Study 2

From long-term to short-term: Distinct neural networks underlying semantic knowledge and its recruitment in working memory

Pauline Querella, Lucie Attout, Wim Fias, and Steve Majerus

Under review

Abstract. Although numerous studies suggest that working memory (WM) and semantic long-term knowledge interact, the nature and underlying neural mechanisms of this intervention remain poorly understood. Using functional magnetic resonance imaging (fMRI), this study investigated the extent to which neural markers of semantic knowledge in long-term memory (LTM) are activated during the WM maintenance stage in 32 young adults. First, the multivariate neural patterns associated with four semantic categories were determined via an implicit semantic activation task. Next, the participants maintained words – the names of the four semantic categories implicitly activated in the first task – in a verbal WM task. Multi-voxel pattern analyses showed reliable neural decoding of the four semantic categories in the implicit semantic activation and the verbal WM tasks. Critically, however, no between-task classification of semantic categories was observed. Searchlight analyses showed that for the WM task, semantic category information could be decoded in anterior temporal areas associated with abstract semantic category knowledge. In the implicit semantic activation task, semantic category information was decoded in superior temporal, occipital and frontal cortices associated with domain-specific semantic feature representations. These results indicate that item-level semantic activation during verbal WM involves shallow rather than deep semantic information.

Introduction

Many theoretical models consider that working memory (WM) and long-term memory (LTM) interact (e.g., Baddeley, 2012; Barrouillet & Camos, 2012; Cowan, 1995; Majerus, 2013; McElree, 1998; Oberauer, 2002). One approach, known as "fully emergent" models of verbal WM, consider that the verbal WM and the language system are at least partially overlapping systems (e.g., Acheson & MacDonald, 2009; Buchsbaum & D'Esposito, 2019; Cowan, 1993; Hasson et al., 2015; MacDonald, 2016; Postle, 2006; Schwering & MacDonald, 2020). According to these models, language is the representational substrate for WM, and performance in verbal WM should be determined by all types of language representations associated with phonological, lexical, and semantic knowledge. On the other hand, hybrid or partially emergent accounts consider that although WM and LTM interact, language representations intervene only if useful for supporting the maintenance of specific WM content based on specific task demands (e.g., Cowan, 1995; Majerus, 2009, 2013, 2019). This controversy is illustrated by the inconsistent effects of semantic knowledge on verbal WM. At the neuroimaging level, a similar controversy exists, with some studies suggesting that the neural substrates of temporary memory representations are defined by linguistic cortices (e.g., Kowialiewski et al., 2020; Majerus et al., 2010; Postle, 2006) while other studies suggest that memoranda are represented in fronto-parietal cortices specific to WM and/or attentional control and unrelated to the language network (e.g., Yue & Martin, 2021). This study examined this fundamental question about the linguistic nature of WM in an unprecedented direct manner, by determining the extent to which the neural representations of semantic memoranda in WM are equivalent to those ensuring the long-term representation of semantic information.

At the behavioural level, a number of studies have shown, on the one hand, that verbal WM performance is supported by semantic knowledge, in support of fully emergent accounts of verbal WM. For example, immediate serial recall performance has been observed to be higher for concrete/highly imageable words than for abstract or low imageability words (e.g., Walker & Hulme, 1999), and is also higher for semantically related words than for semantically unrelated words (e.g., Poirier & Saint-Aubin, 1996). McDougall and Pfeifer (2012) found that individuals with better mental imagery skills, characterized by their ability to generate vivid and detailed mental images of concrete words, performed better in word recall and recognition tasks in verbal WM. It has been suggested that concrete and highly imageable words are characterized by a higher amount of sensory and perceptual semantic features, leading to more robust and easy-to-visualize representations (e.g., Jones, 1985; Plaut & Shallice, 1993). On the other hand, other studies have highlighted the lack of robust and consistent effects of semantic imageability effects on WM performance: if present, these effects are generally weaker than the effects of other linguistic variables such as the phonological and lexical status of the words (e.g., Kowialiewski & Majerus, 2018, 2020; Majerus & Van der Linden, 2003). Kowialiewski and Majerus (2018) showed that word imageability effects could be absent in immediate serial recall tasks, particularly when the word lists are presented in a fast or continuous manner. Kowialiewski and Majerus (2020) showed that while semantic relatedness of memory items protected against post-encoding WM interference effects, this was much less the case for the semantic imageability status of memory items, suggesting that not all aspects of semantic knowledge automatically intervene in verbal WM tasks.

At the level of neuroimaging studies, a number of studies have investigated the effects of LTM on verbal WM (see Deldar et al., 2021, for a review). Regarding semantic knowledge more specifically, a meta-analysis of Binder and colleagues (2009) revealed that semantic memory mainly activated the left posterior inferior parietal lobe, middle temporal gyrus, fusiform and parahippocampal gyri, dorsomedial prefrontal cortex, inferior frontal gyrus, ventromedial prefrontal cortex, and posterior cingulate gyrus. Early univariate neuroimaging have also demonstrated that brain regions involved in semantic processing can show increased activity peaks during verbal WM maintenance. In a study by Fiebach and colleagues (2006), participants performed a delayed cued recall task involving words and pseudowords. The findings showed increased activity in the inferotemporal cortex during the maintenance of words vs. pseudowords in WM under high memory load conditions. This selective modulation of the inferotemporal cortex, part of the ventral ‘semantic’ language pathway, was further characterized by enhanced connectivity with the left prefrontal cortex, known to be involved in (semantic) control processes (e.g., Jackson, 2021; Jefferies, 2013; Lambon Ralph et al., 2017; Noonan et al., 2013). Additionally, Fiebach and colleagues (2007) demonstrated increased activity in other parts of the ventral language pathway (the left middle and inferior posterior temporal gyri), when participants maintained conceptual combinations (e.g., dog house, red apple) in WM. An earlier study by Collette and colleagues (2001) using PET neuroimaging had already shown similar results, with increased involvement of the left middle temporal gyrus and temporo-parietal cortex during WM maintenance of words compared to nonwords. Overall, these findings from univariate studies highlight the co-activation of neural regions associated with lexico-semantic processes and semantic control during short-term maintenance of items with a lexico-semantic content.

While these different studies show the co-activation of semantic processing regions in verbal WM tasks, they do not yet indicate that these regions actively contribute to the representation and maintenance of information in WM. More recent studies using multivariate methods indicate that language processing regions can represent memoranda in WM tasks, although perhaps not in an exclusive manner. Kowialiewski and colleagues (2020) showed that multivariate neural patterns in the ventral language processing pathway (middle and inferior temporal gyri and inferior frontal cortices) represent memoranda based on their lexico-semantic status (i.e., word vs nonword) during both encoding and maintenance stages. Similarly, Lewis-Peacock (2012) examined the brain regions supporting the retention of phonological, semantic and non-verbal visual information and observed that maintenance of semantic content (i.e., words requiring a subsequent synonym judgment) could be discriminated from maintenance of phonological content (i.e., pseudowords requiring a subsequent rhyme judgement) and visual content (i.e., line segments requiring a subsequent orientation judgement). Yue and Martin (2021) investigated the decoding of semantic information in a semantic judgment task using representational similarity analysis. Their study revealed significant decoding of words requiring a delayed semantic judgment in the angular gyrus (AG) during the WM maintenance stage providing support for the involvement of this region in the maintenance of semantic information. The AG region is considered to allow for the integration of semantic information, to serve as a bridge between semantic and other cognitive systems (e.g., Farahibozorg et al., 2022), and/or to encode knowledge about thematic associations and events (e.g., Schwartz et al., 2011). Finally, Lewis-Peacock and colleagues (2015) investigated the neural basis of strategic prioritization of mental codes (i.e., the format in which information is represented in the brain) in WM. Their study, involving delayed judgment and recognition tasks, revealed that when participants were informed about the specific stimulus dimension (visual, phonological/verbal, or semantic) to be tested, brain activity patterns were oriented towards the stimulus dimension relevant to the probe. In contrast, decoding accuracy for irrelevant dimensions, including semantic codes, dropped to chance levels. These findings suggest that the intervention of semantic codes may be an optional strategy, at least in the context of strategic WM tasks. However, this study does not inform us about the non-strategic, spontaneous use of semantic codes in WM tasks as the specific task instructions may have led to active disengagement of semantic level of processing when known to be irrelevant.

These different studies show that regions associated with semantic knowledge or processing are involved in verbal WM tasks, and can to some extent decode the type of information being maintained in WM. However, this does not necessarily mean that the semantic knowledge that is being activated during a WM task is the same or as deep as during a language processing task. The earlier mentioned behavioural studies, revealing inconsistent semantic effects in verbal WM tasks, suggest that semantic knowledge may not be recruited in a systematic and full manner during the short-term maintenance of verbal information. The study by Lewis-Peacock and colleagues (2012, 2015) also suggests that semantic codes may be recruited in a strategic manner in a WM task. Semantic knowledge is traditionally separated in higher-level, abstract information (superordinate categories such as ‘animal’, ‘colour’) and lower-level feature-specific information, the latter level representing the specific exemplars and their associated features (i.e., visual, auditory, affective, tactile, motor features, that define specific exemplars of a semantic category). One key region implicated in abstract semantic category representation appears to be the anterior temporal lobe (ATL), which has been consistently associated with the identification and categorization of objects, concepts, and word meanings (e.g., Lambon Ralph, 2014; Lambon Ralph et al., 2010; Lambon Ralph & Patterson, 2008; Patterson et al., 2007; Pobric et al., 2007; Rogers et al., 2004). The ATL has been suggested to form an amodal semantic representational system that shows increased activity when processing basic semantic concepts (e.g., "bird") and broader domain-level distinctions (e.g., "animal" vs. "food") (e.g., Malone et al., 2016; Patterson et al., 2007; Pobric et al., 2010; Rogers et al., 2004; Visser et al., 2010; 2011). The ATL has also been associated more specifically with taxonomic levels of representation – i.e., the hierarchical organization of concepts according to similarity relations based on shared properties (e.g., bee – butterfly) – in contrast to the AG that would be associated with thematic levels of representations – i.e., the organization of concepts according to contiguity relations based on co-occurrence in events or scenarios (e.g., bee – honey) (e.g., Geng & Schnur, 2016; Mirman & Graziano, 2012; Schwartz et al., 2011; Zhang et al., 2023; see also Xu et al., 2018, for showing that the ATL may be sensitive to both taxonomic and thematic levels of representation). In sum, the ATL appears to play a crucial role in the representation of abstract semantic categories, mainly (but not exclusively) at the taxonomic level. On the other hand, semantic knowledge about specific semantic features that define exemplars of a category have been associated with modality-specific cortices. Inferotemporal neural regions have been associated with the representation of visual and object-related features (e.g., Gauthier et al., 1997, 2000), while parietal cortices have been associated with the representation of action-related or functional attributes of objects (e.g., Chao & Martin, 2000; Culham & Valyear, 2006; Gainotti et al., 1995; Goldberg et al., 2006; Martin & Chao, 2001). Furthermore, the generation of a specific colour word has been associated with activity in temporo-occipital cortices (bilateral fusiform gyrus) close to areas associated with colour perception (e.g., Chao & Martin, 1999; Martin & Chao, 2001; Martin et al., 1995) while the generation of words representing acoustic conceptual features has been shown to involve the superior temporal gyrus supporting auditory processing (e.g., Kiefer et al., 2008). It has also been suggested that features shared by members of a category tend to cluster together in similar brain regions (e.g., Simmons & Barsalou, 2003). In the same vein, recent dual coding theories have proposed that meaning is represented in the brain by a dual code, which comprises language-derived representations located in the dorsal ATL and sensory-derived representations within perceptual and motor regions (e.g., Bi, 2021; Vignali et al., 2023). Vignali and colleagues further demonstrated that, in the case of semantic concreteness, activation of language-derived representations precedes the activation of sensory-derived representations. Overall, these findings suggest that the representation of semantic knowledge involves both higher-level, abstract category information supported by amodal semantic regions such as the ATL and feature-specific semantic knowledge supported by modality-specific regions (but see Popham et al., 2021, for showing that modality specific regions may contain both modality specific feature information and corresponding verbal descriptors of represented features).

This study aimed at determining the nature of semantic knowledge activation that defines the spontaneous, non-strategic maintenance of verbal information in WM. According to the fully emergent models of WM, semantic activation in WM and language tasks should fully overlap given that the same representations support WM and linguistic processing. According to hybrid models of WM, supported by behavioural results of inconsistent semantic effects in verbal WM tasks, full activation of deep, feature-specific semantic knowledge may not be a defining aspect of the neural and cognitive architecture of verbal WM. We examined this question by directly comparing neural substrates supporting semantic knowledge activation in a language processing task and in a verbal WM task for different semantic categories. In a first semantic localizer task, we determined the multivariate neural substrates associated with deep, feature specific semantic information via an implicit semantic activation task, as has been done in several previous studies on semantic processing (Baumgaertner et al., 2002; Huang et al., 2012 ; Jedidi et al., 2021; Rissman et al., 2003; Ruff et al., 2008). In this task, participants had to read triplets of words without any additional processing on the stimuli in order to probe spontaneous, non-strategic activation of semantic information associated with the words. This paradigm probing non-intentional semantic processing was chosen in order to match it as closely as possible with the situation of words in the verbal WM task where verbal information is presented for maintenance and recall without any intentional processing of semantic information. Indeed, this study examined the role of semantics as a fundamental, non-strategic determinant of verbal maintenance, even when semantic information does not need to be explicitly processed. The word triplets of the implicit semantic activation task were different exemplars from either the bird, tool, colour or (type of) music categories. The multivariate neural patterns elicited by this task were considered to reflect the deep semantic features characterizing the different categories, hence primarily reflecting bottom-up activation of semantic category information (e.g., Chao & Martin, 1999; Devereux et al., 2013; Gainotti et al., 1995; Goldberg et al., 2006; Kiefer et al., 2008; Martin et al., 1995; Martin & Chao, 2001; Simmons et al., 2005; 2007; see also Warrington & McCarthy, 1983, 1987; Warrington & Shallice, 1984). Next, a verbal WM task was presented in which the verbal labels of the categories pre-activated in the first, linguistic task were used as memory items. Participants had to maintain lists of four category names and were then cued to continue maintaining one of the four memory items. We determined the multivariate neural substrates associated with the maintenance of the specific category name and their similarity with the neural patterns associated with the same semantic category in the implicit semantic activation task. A positive between-task classification of the semantic categories would indicate that the maintenance of the category label in the WM tasks elicits the same deep semantic features as the linguistic task. An unbiased searchlight strategy was furthermore used to determine the neural substrates that allow for semantic category decoding in the WM and linguistic tasks. Critically, by using category labels in the WM tasks and item triplets for activating the categories in the linguistic task, we ensured that any between-task classification does not stem from the use of the same physical labels/words but reflects the intervention of the underlying semantic representations.

Methods

Participants. Thirty-eight monolingual native French-speaking participants were recruited via the University of Liège web platform and advertisements on social networks (see section *Bayesian statistical procedures* for justification of sample size). Data from six participants had to be excluded due to premature stopping of the scanner. The final sample was composed of thirty-two datasets (18 males; mean age = 23.937, age range = 19-30). All participants were right-handed, and with normal hearing. They reported no history of learning, neuropsychological or neurological disorder, and no current drug use (e.g. cannabis) or alcohol abuse. The study has been approved by the ethics committee of the Faculty of Medicine of the University of Liège. A financial compensation of 15 euros was provided to all participants for their involvement in the experiment. In line with the Declaration of Helsinki (1964), all participants gave written informed consent before their inclusion in the study.

Materials

Implicit semantic activation task. We selected verbal labels representing exemplars of the semantic categories bird, tool, colour and music as these are the categories most frequently studied in the neuroimaging literature (e.g., Banks & Connell, 2022; Battig & Montague, 1969; Capitani et al., 2003; Larochelle et al., 2000; McEvoy & Nelson, 1982; Rosch, 1975; Uyeda & Mandler, 1980; Van Overschelde et al., 2004). We selected six frequent nouns representing prototypical exemplars of each of the four categories and ensured that they were not polysemic (e.g., "orange" colour, "metal" music, etc.). The six nouns were combined equally so that the same triplets did not appear on each trial. Thirty-six triplets per semantic category (6 nouns x 6 combinations) were constructed. Hence, all the triplets presented during the task were different.

Verbal WM task. In the verbal WM task, the verbal category labels of the four semantic categories used in the implicit semantic activation task were presented in trials of four items. The four category words were bisyllabic stimuli (i.e., oiseau, outil, couleur, and musique) (see **Table B.1** in Appendix for full stimulus lists, including psycholinguistic data).

Procedure

Implicit semantic activation task. Participants were instructed to read aloud triplets of words as they appeared simultaneously on the screen (Arial font, font size = 40, white font on black screen). The instruction to read the words aloud was chosen to reflect natural language processing conditions and enabled us to verify that participants were actively performing the task. In addition, this design enabled spontaneous semantic activation to be detected in a task that is as similar as possible in terms of presentation and processing conditions to the verbal WM task. Head movements of all participants were examined and algorithms for motion adjustment were applied when necessary (see section *Image Processing*). Each triplet contained three words of the same semantic category. Participants were given a maximum of six seconds to read each set of three words and pressed on a button when they had finished reading; the button press response initiated the next trial (see **Figure 2.1a**). There was a total of 144 trials.

Verbal WM task. Participants were presented with four words (the four category names implicitly activated in the previous task) appearing successively on the screen at the rate of one word every 1000 ms (Arial font, font size = 40, white font on black screen). Immediately after, a digit from 1 to 4 appeared, prompting participants to repeat and maintain the word corresponding to the position indicated by the digit. In order to ensure that participants maintained the exact word and started maintaining at the same time, they had to repeat the cued word aloud right after presentation of the cue and pressed a response button when finished (time limit of 4000 ms). This allowed us to control for differences in item retrieval times, as start-of-list and end-of-list items will be faster to retrieve than mid-of-list items (Glanzer & Cunitz, 1966; Postman & Phillips, 1965). They maintained the word during a further six seconds and then recalled it again (time limit of 5000 ms) (see **Figure 2.1b**). The trials were presented in pseudo-random order, ensuring that a same word/semantic category was not cued on two consecutive trials. Furthermore, each word and position were tested equally often. There were

92 trials. All responses were recorded for later transcription and scoring. Each word recalled after the cue and at recall was scored as correct (1) or incorrect (0).

The entire experiment lasted approximately 1h10 per participant (25-30 minutes for the first task, 35-40 minutes for the second task). The two tasks were separated by a break during which a T1-weighted image was acquired. Prior to installation in the scanner, the participants completed three practice trials per task with feedback. The practice trials could be repeated if necessary.

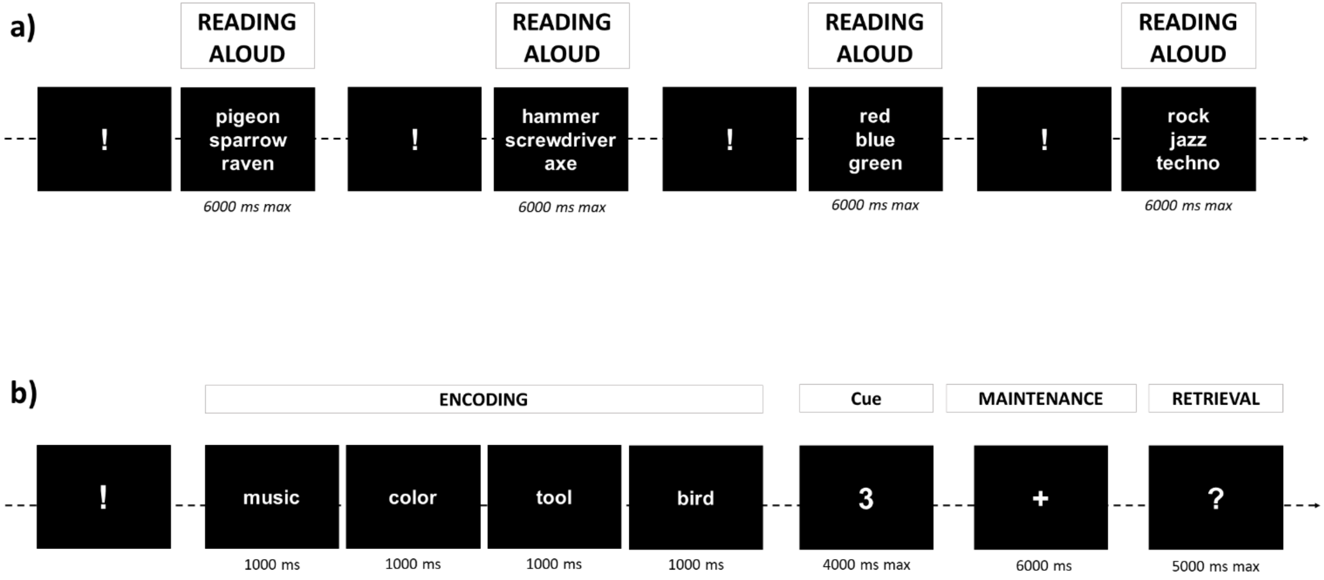

Figure 2.1. Design of the implicit semantic activation task **(a)** and the verbal WM task **(b)**. The tasks were performed in French language. The full stimulus lists with English translation are presented in Appendix (**Table B.1**).

Bayesian statistical procedures

All analyses, except for cluster-based searchlight analyses (see below), were analysed using a Bayesian statistical framework. Bayesian statistics have the advantage, relative to frequentist statistics, of determining the strength of the evidence both against and in favour of the null hypothesis in order to identify which effect is associated with the strongest evidence (Clark et al., 2018; Kruschke, 2010; Lee & Wagenmakers, 2013; Nuijten et al., 2015; Wagenmakers et al., 2018). Bayesian statistics also allow multiple statistical tests to be carried out without increasing type I error risk (Clark et al., 2018). The Bayes Factor (BF) is the likelihood ratio of a given model, the best-fitting model being the one with the highest BF. BF01 indicates evidence in favour of the null hypothesis, while BF10 indicates evidence in favour of the alternative hypothesis. Although there are no fixed thresholds for BF values, we used the following categories for describing strength of evidence: a BF of at least 1 is considered to indicate anecdotal evidence, a BF of at least 3 is considered to indicate moderate evidence, a BF of at least 10 is considered to provide strong evidence, a BF of at least 30 is considered to provide very strong evidence, and a BF of at least 100 is considered to indicate decisive evidence (Jeffreys, 1998).

Regarding statistical power, the Bayesian statistical framework is based on collecting evidence in favour or against an effect of interest and this evidence is incremental and evolves as a function of collected data (Schönbrodt & Wagenmakers, 2018). In contrast to frequentist statistical frameworks, inference taken from obtained data is also independent of the data collection plan (Berger & Wolpert, 1988; Dienes, 2011; Wagenmakers et al., 2018). It is however possible to conduct an indicative design analysis in order to determine the sensitivity of a given Bayesian statistical design : this design analysis estimates the probability of obtaining a specific BF value for a specific effect as a function of simulated sample sizes and an a priori estimation of the effect size (Schönbrodt & Wagenmakers, 2018). We used Monte Carlo simulations and the Bayesian Factor Design Analysis package (Schönbrodt, 2016) implemented in R (version 3.6.2) using the default Cauchy prior distribution parameters, also available on http://shinyapps.org/apps/BFDA/ to assess the sensitivity of our statistical design to provide evidence for above-chance level classification in the MVPA analyses. This design sensitivity analysis showed that if the effect of interest exists, the minimal sample size needed for reaching a specific level of evidence (BF10>3) in favour of the effect in 100% of simulated samples was N=29. If the effect of interest does not exist, the minimal sample size needed for reaching a specific level of evidence (BF01>3) in favour of the absence of an effect in 100% of simulated samples was N=29. For this sensitivity analysis, we assumed a medium effect size of Cohen's d = 0.5 based on previous studies that have used similar multivariate classification methodologies (see Cristoforetti et al., 2022).

MRI Acquisition

The experiment was carried out on a whole-body 3T scanner (MAGNETOM Prisma; Siemens Medical Solutions, Erlangen, Germany) operated with a 20-channel receiver head coil. Multislice T2*-weighted functional images were acquired with the multiband gradient-echo echo-planar imaging sequence (CMRR, University of Minnesota) using axial slice orientation and covering the whole brain (36 slices, multiband factor = 2, FoV = 216 × 216 mm^2, voxel size 3 × 3 × 3 mm^3, 25% interslice gap, matrix size 64 × 64 × 32, TR = 1170 ms, TE = 30 ms, FA = 90°, bandwidth = 2572 Hz/pixel). The five initial volumes were discarded to avoid T1 saturation effects. A gradient-recalled sequence was applied to acquire two complex images with different echo times (TE = 10.00 and 12.46 ms, respectively) and generate field maps for distortion correction of the echo-planar images (EPIs) (TR = 634 ms, FoV = 192 × 192 mm2, 64 × 64 matrix, 40 transverse slices [3 mm thickness, 25% interslice gap], flip angle = 90°, bandwidth = 260 Hz/pixel). For anatomical reference, a high-resolution T1-weighted image was acquired for each subject (T1-weighted 3D magnetization prepared rapid gradient echo sequence, TR = 1900 ms, TE = 2.19 ms, inversion time (TI) = 900 ms, FoV = 256 × 240 mm2, matrix size = 256 × 240 × 224, voxel size = 1 × 1 × 1 mm3, bandwidth = 250 Hz/pixel). Head movement was minimized by restraining the participant's head using a vacuum cushion. The stimuli were displayed on a screen positioned at the rear of the scanner, which the participant could comfortably see via a head coil mounted mirror. For the implicit semantic activation task, between 1222 and 1531 functional volumes were acquired (M

= 1327.63, SD = 68.65) while for the verbal WM task, between 1774 and 2109 functional volumes were acquired (M = 1924.33, SD = 90.00).

fMRI analyses

Image processing. For both tasks, data were preprocessed and analyzed using SPM12 software (version 12.3; Wellcome Trust Centre for Neuroimaging, (http://www.fil.ion.ucl.ac.uk/spm) implemented in MATLAB (MathWorks, Inc., Sherborn, MA). EPI time series were corrected for motion and distortion with "Realign and Unwarp" (Andersson et al., 2001) using the generated field map together with the FieldMap toolbox (Hutton et al., 2002) provided in SPM12. A mean realigned functional image was then calculated by averaging all the realigned and unwrapped functional scans and the structural T1-image was coregistered to this mean functional image (using a rigid body transformation optimized to maximize the normalized mutual information between the two images). The mapping from subject to Montreal Neurological Institute space was estimated from the structural image with the "unified segmentation" approach (Ashburner & Friston, 2005). The warping parameters were then separately applied to the functional and structural images to produce normalized images of resolution 2×2×2 mm^3 and 1×1×1 mm^3, respectively. Finally, the warped functional images were spatially smoothed with a Gaussian kernel of 5 mm full-width at half-maximum. ArtRepair was used to remove residual motion from the functional images prior to normalization (Mazaika et al., 2009). Volumes with rapid scan-to-scan movements greater than 1.5 mm were repaired by interpolation of the two nearest non-repaired scans. Each trial with more than 15% of the total number of volumes replaced was removed from the analyses (Attout et al., 2019). The mean number of repaired scans was 2.86 % (SD = 0.945%).

Univariate analysis. For each participant, brain responses were estimated at each voxel, using a general linear model with epoch regressors and event-related regressors. For the implicit semantic activation task, the design matrix contained one regressor for each linear contrast defined ("oiseau" (*bird*), "outil" (*tool*), "couleur" (*colour*), "musique" (*music*)) that ranged from the onset of the probe display to the participant's button press indicating that they had finished reading. For the verbal WM task, the trials were segmented in 18

1-second time steps and modelled separately for allowing time-step specific analyses and a differentiation of encoding, maintenance and recall stages (each event was modelled of a 0-duration event). Each model also included the realignment parameters to account for any residual movement-related effect. A high-pass filter was implemented using a cut-off period of 128 s to remove the low-frequency drifts from the time series. Serial autocorrelations were estimated via a restricted maximum likelihood algorithm with an autoregressive model of order 1 (plus white noise). Note that the univariate analyses were used only to obtain the beta images needed as input for the multivariate searchlight analyses. No further results are reported for the univariate analyses.

Multivariate Analysis. Multivariate analyses of the 5-mm smoothed functional images were conducted using PRoNTo, a pattern recognition toolbox for neuroimaging (www.mlnl.cs.ucl.ac.uk/pronto; Schrouff et al., 2013), to determine the neural patterns associated with the four semantic categories in both tasks. For the implicit semantic activation task, we trained classifiers to distinguish voxel activity patterns associated with the four semantic categories (*bird*, *tool*, *colour*, *music*), resulting in six pairwise classifications. Pairwise classifications were preferred over a multinomial four-way classification to allow precise monitoring of classification accuracy separately for each semantic category relative to each other category; for example, the bird category may show stronger separability from the tool category than from the colour category. For the verbal WM task, we trained classifiers to distinguish patterns of voxel activity associated with the four semantic categories (six pairwise classifications) over the time course (i.e., 18 seconds of event), by assessing classifier accuracies on a second-by-second basis. For both tasks, a binary support vector machine (Burges, 1998) was used. We further performed critical between-task classifications assessing whether the category classifiers trained in the implicit semantic activation task were able to classify the semantic category during the maintenance stage of the verbal WM task (from seconds 8 to 13), and vice versa. All models included timing parameters for HRF delay (5 s) and HRF overlap (5 s), ensuring that stimuli from different categories falling within the same 5 s were excluded (Schrouff et al., 2013). For within-task classification of semantic categories, a leave-one-block-out (LOBO) cross-validation procedure was used. For between-task classifications of semantic categories, a leave-one-run-out (LORO) cross-validation procedure was used, resulting in training the classifier on one task and testing the classifier on the other task. At the group level, classifier performance was tested by comparing the group level distribution of classification accuracies to a chance-level distribution using Bayesian one sample t-tests, performed with the JASP statistical package with default prior settings (JASP team, 2022, Version 0.17.2.1).

Searchlight Analysis. A searchlight decoding approach was used to determine the local spatial distribution of the voxels that discriminate between the four semantic categories in both tasks (Kriegeskorte et al., 2006) using the beta images. Univariate voxel activity levels associated with each event of interest were first estimated at the individual level by using the beta images for each event, resulting in a total of 144 beta images per participant for the implicit semantic activation task, and 92 beta images per participant for each of the six seconds of the maintenance stage in the verbal WM task. Searchlight spheres of 10 mm were iteratively applied on the whole-brain multivariate feature map built from the extracted beta images, and the classification accuracy of each voxel cluster was determined, using ad hoc code built for the Pronto toolbox and available at https://github.com/CyclotronResearchCentre/PRoNTo_SearchLight. We obtain one classification accuracy map per contrast resulting from the two-by-two classifications. These maps were then centered on zero and averaged across semantic categories conditions. These zero-centered and averaged accuracy maps were then compared to a chance-level classification distribution (e.g., Correia et al., 2014; Hebart & Baker, 2018) using one-sample t-tests conducted with SPM12. The maps were normalised to MNI space and the group results assessed by looking for voxels with significant above-chance classification using a one-sample t-test at the whole-brain level ($p<0.001$ uncorrected, $k \geq 10$). We used here a cluster-based frequentist approach instead of the voxel-based Bayesian approach implemented in SPM12 (Han & Park, 2018) given that the searchlight strategy, involving spheres of voxels, is itself cluster-based (Haynes, 2015; Haynes & Rees, 2006; Hebart et al., 2015).

Furthermore, given that previous studies also used frequentist approaches, this allowed for better comparability of results.

Results

Behavioural results

As expected, performance in the WM task was at ceiling (accuracy: 0.96 ± 0.03 (SD)).

Neuroimaging results – Multivariate Analyses

Implicit semantic activation task. A first Bayesian one sample t-test was performed to determine whether the classification rates of the six MVPA models were above chance level (0.5), using the JASP statistical package with default prior settings (JASP team, 2022, Version 0.17.2.1). We found decisive evidence in favour of category decoding against chance level decoding, for all models, with very large effect sizes (bird vs. tool (BF_{10} = 8.112e+7; d = 1.616), bird vs. colour (BF_{10} = 6.617e+8; d = 1.776), bird vs. music (BF_{10} = 2.001e+13; d = 2.696), tool vs. colour (BF_{10} = 4.916e+11; d = 2.337), tool vs. music (BF_{10} = 3.956e+15; d = 3.281), colour vs. music (BF_{10} = 2.715e+8; d = 1.707)) (see **Table B.2**). As shown in **Figure 2.2**, we were able to distinguish the neural patterns associated with the four semantic categories in the implicit semantic category activation task.

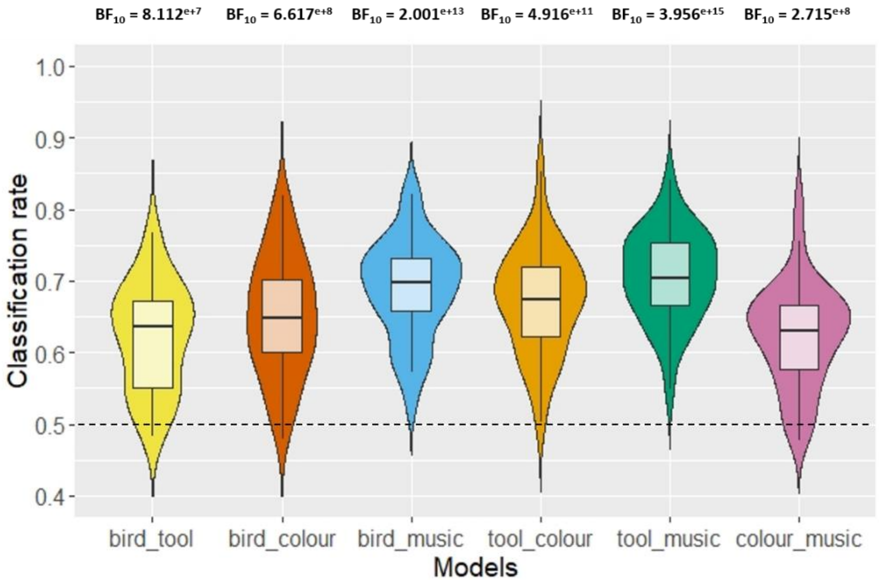

Figure 2.2. Classification rate of the six MPVA models comparing the four categories in the implicit semantic activation task.

Verbal WM task. For the verbal WM task, we examined classification accuracies as a function of the time course of the WM task, by using 1-second time windows. As expected, Bayesian one sample t-tests showed strong to decisive evidence in favour of category decoding against chance level decoding at the eighth second of the time course of the task, after the appearance of the cue indicating the position of word to be maintained, for four of the six classifications (bird vs. tool (BF$_{10}$ = 25719.097; *d* = 1.053), bird vs. music (BF$_{10}$ = 24.327; *d* = 0.568), tool vs. colour (BF$_{10}$ = 243.701; *d* = 0.737), colour vs. music (BF$_{10}$ = 917.777; *d* = 0.829)) (see **Figure 2.3**; see also **Table B.3** and **Table B.4** for full statistical results). This analysis also showed anecdotal to moderate evidence in favour of category decoding against chance level decoding at the moment of final recall stage for two out of the six classifications (tool vs. colour (BF$_{10}$ = 1.697; *d* = 0.330), colour vs. music (BF$_{10}$ = 3.327; *d* = 0.398)). Note that given that our decoding analyses targeted the specific semantic category name that was cued on each trial at T=6 sec, no decoding of semantic category information was expected during encoding given that the four semantic category names were coactivated at different serial positions on each trial.

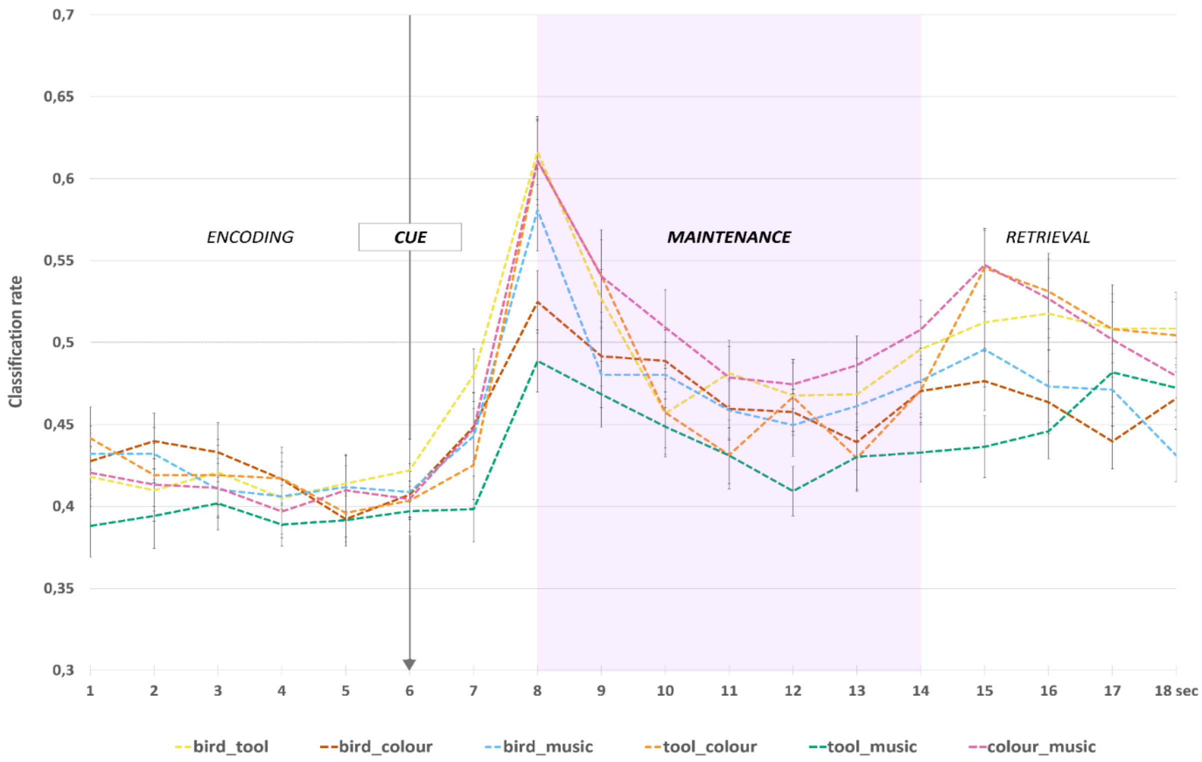

Figure 2.3. Classification rate of the six MVPA models comparing the four semantic categories, at each of the 18 seconds of the verbal WM task.

Between-task classifications. Next, we ran the critical between-task classifications of semantic category by training semantic category classification in one of the tasks, and by testing the classifier on the other task. This analysis was limited to the beginning of the maintenance stage where reliable semantic category classification was observed for the verbal WM task. When predicting from the implicit semantic activation task to the WM task, Bayesian one sample t-tests showed moderate evidence against a between-task classification for most category pairs: bird vs. tool (BF_{01} = 6.788; *d* = -0.062), bird vs. colour (BF_{01} = 7.383; *d* = -0.086), bird vs. music (BF_{01} = 7.181; *d* = -0.078), tool vs. colour (BF_{01} = 3.582; *d* = 0.081), and colour vs. music (BF_{01} = 4.507; *d* = 0.036) (see **Figure 2.4a**; see also **Table B.5** for full statistical results). Only the tool vs. music pair was associated with moderate evidence in favour of a between-task classification (BF_{10} = 4.241; *d* = 0.421). When running the analyzes from the WM task to the implicit semantic activation task, anecdotal to strong evidence was found again against a between-task classification for the majority of pairs: bird vs. tool (BF_{01} = 10.071; *d* = -0.188), bird vs. colour (BF_{01} = 8.068; *d* = -0.112), bird vs. music (BF_{01} = 3.944; *d* = 0.063), and tool vs. music (BF_{01} = 6.203; *d* = -0.038), and colour vs. music (BF_{01} = 2.275; *d* = 0.240) (see **Figure 2.4b**; see also **Table B.6** for full statistical results). Anecdotal evidence in favour of a between-task classification was only observed for tool vs. colour (BF_{10} = 1.555; *d* = 0.321). In sum, classification rates did not exceed chance level for the vast majority of between-task classifications, suggesting that the multivariate brain signals associated with the maintenance of semantic category names in the WM task and those associated with the implicit semantic activation of categories differ.

Notably, we conducted the same analysis using an onset with a duration of 0, which led to substantially similar results.

Figure 2.4. Classification rate of the six MVPA models comparing the four semantic categories, at each of the 18 seconds, for the between-task classification. Semantic category classifiers of the implicit semantic activation task classifying the semantic categories of the verbal WM task (LTM_WM) **(a)**. Semantic category classifiers of the verbal WM task classifying the semantic categories of the implicit semantic activation task (WM_LTM) **(b)**.

Neuroimaging results – Searchlight Analyses

Finally, we performed a whole-brain searchlight analysis on the within-task MVPA classification in order to determine more precisely which neural regions contributed to classification of the four semantic categories in each task. As shown in **Figure 2.5**, in the implicit semantic activation task, decoding of the four categories was observed in areas mainly associated, as expected, with deep, feature specific semantic knowledge. The *bird vs. tool* classification involved multivariate patterns mainly in the precentral and the postcentral gyri bilaterally, the left superior temporal gyrus, the right lingual gyrus and cuneus, associated with motor, auditory and visual-related semantic features. The *bird vs. colour* classification involved the left superior temporal, precentral and postcentral gyri, the bilateral lingual gyrus and the calcarine sulcus, in line again with the recruitment of auditory, motor and visual semantic features. Similarly, the *bird vs. music* classification relied on the left superior and middle temporal, inferior and middle frontal, and postcentral gyri, the precentral gyrus bilaterally, and the right lingual gyrus and cerebellum, associated again with visual, motor and auditory semantic features. For the *tool vs. colour* classification, decoding was observed in the left middle temporal, lingual and fusiform gyri, the superior temporal, precentral and postcentral gyri and the cuneus bilaterally, and the right inferior occipital gyrus, associated with motor, visual and auditory semantic features. The classification of *tool vs. music* relied on the left pre and postcentral, and lingual gyri, the inferior occipital gyrus bilaterally, and the right cuneus, suggesting again involvement of visual and motor features. Finally, for *colour vs. music* classification, decoding was observed in the left precentral and middle temporal gyri, and the superior temporal gyrus bilaterally, associated with motor and auditory semantic features (see **Table B.7** and **Figure 2.5**).

In striking contrast, when decoding the category labels during the verbal WM maintenance stage, the regions that contributed the most to the classifications were mainly clustered in the bilateral ATL. Indeed, for *bird vs. tool* classification, the most contributing regions included the bilateral ATL, extending to the parahippocampal gyri, midbrain structures and the cerebellum bilaterally. Regarding the *bird vs. music* classification, the most contributing regions were again the bilateral ATL extending to the parahippocampal gyri and the left subcallosal gyrus. The regions that contributed the most to the *tool vs. colour* classification the ATL bilaterally, extending to the parahippocampal gyri and the left fusiform gyrus. Finally, for the *colour vs. music* classification, the most contributing regions were located in the ATL bilaterally, extending to the bilateral parahippocampal, middle and inferior frontal gyri, the cerebellum and globus pallidus bilaterally, and the right fusiform gyrus and hypothalamus (see **Table B.8** and **Figure 2.5**). In line with the whole-brain classifications for the WM task, no voxels survived for *bird vs. colour* classification and *tool vs. music* searchlight classification analyses. Given the role of the ATL in higher-level, abstract semantic category knowledge, these results suggest that the maintenance of semantic category labels in WM does not lead to widespread activation of semantic, feature specific knowledge but remains restricted to an abstract level of semantic processing, which is the most immediate level of semantic processing when processing an individual semantic category label.

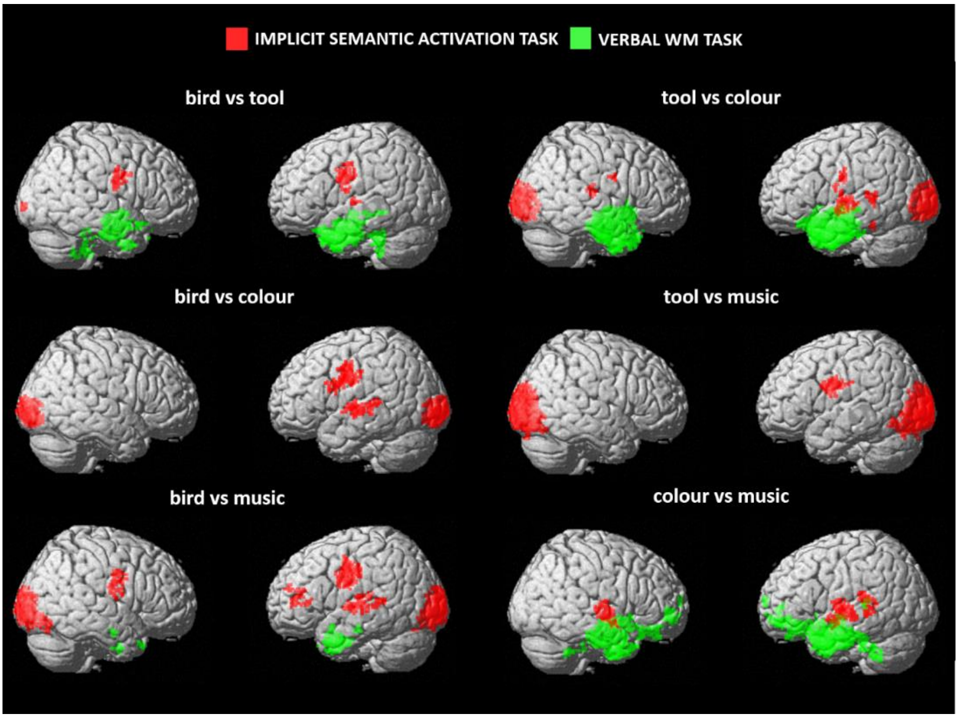

Figure 2.5. Searchlight MPVA results at the whole-brain level, at the group-level: regions contributing the most to classifications of the six models of the implicit semantic activation task (in red) and the verbal WM task, at the first second of the maintenance stage (in green). Regions are displayed at an uncorrected voxel-level threshold of p<.001 with a minimum cluster size of 10 voxels.

Discussion

The present study investigated the nature of semantic knowledge activation defining the maintenance of verbal information in WM. While observing reliable within-task decoding of semantic category information during an implicit semantic activation task and during the maintenance of verbal information in WM (for four out of six classifications in the latter case), between-task classifications of semantic category information were associated with evidence for their absence. Critically, searchlight analyses showed that for the implicit semantic activation task, categorical semantic information was decoded in superior temporal, temporo-occipital and fronto-parietal regions associated with semantic feature specific knowledge, while category decoding in the verbal WM task was observed mainly in ATL regions associated with abstract semantic category knowledge.

A critical finding of this study is that decoding of words referring to specific semantic categories in verbal WM involves a restricted set of regions of the ATL, in contrast to the implicit semantic activation task in which decoding of the same semantic category information is observed in a widespread set of temporo-occipital and fronto-parietal cortices. Many studies have consistently associated ATL regions with the representation and retrieval of abstract conceptual knowledge, supporting the notion that the ATL plays a critical role in processing higher-level, abstract aspects of semantic information (e.g., Lambon Ralph, 2014; Lambon Ralph et al., 2010; Lambon Ralph & Patterson, 2008; Patterson et al., 2007; Pobric et al., 2007; Rogers et al., 2004). In contrast, information relating to specific semantic features (i.e., visual, auditory, sensory-motor related features) that define exemplars within a category have been associated with modality-specific cortices (e.g., Chao & Martin, 1999, 2000; Culham & Valyear, 2006; Gainotti et al., 1995; Gauthier et al., 1997; 2000; Goldberg et al., 2006; Kiefer et al., 2008; Martin & Chao, 2001; Martin et al., 1995). This is an important finding, showing that simple maintenance of words in verbal WM does not necessarily lead to full activation of the semantic content that defines the words. Indeed, our results suggest that semantic content is only activated at the most immediate, surface level during simple short-term maintenance, in line with the overall weak and inconsistent word imageability effects in immediate serial recall-type WM tasks (Kowialiewski & Majerus, 2018, 2020; Majerus & Van der Linden, 2003). It could be argued that semantic long-term information intervenes only at a later, retrieval stage to reconstruct decayed memory representations (the redintegration account; Walker & Hulme, 1999). Our results do not support this theoretical view either as decoding of semantic category information at the final retrieval stage was even lower than during the initial maintenance stage. We need however to remain cautious here given that WM load was low (see also below) as a single item had to be maintained after appearance of the maintenance cue, reducing the likelihood of major memory decay at the moment of retrieval. Overall, our results could support hybrid models of WM-language interactions, considering that language knowledge, including semantic knowledge, intervenes in a flexible manner, depending on their utility and necessity for accomplishing the WM task (e.g., Baddeley et al., 2000; Majerus et al., 2013, 2019; Martin et al., 1994). More generally, previous research suggests that the processes defining WM performance depend on specific task demands and goals (e.g., Badre & Wagner, 2007; Barrouillet et al., 2011; Braver, 2012; Duncan, 2010; Koechlin & Summerfield, 2007). More recently, Kowialiewski and colleagues (2023) have shown that semantic knowledge is used in verbal WM tasks only if it allows to make the memoranda more distinctive and/or to group them in a smaller number of semantically-related units, for example by presenting lists of words with words stemming from three distinct semantic categories; when the memoranda all stemmed from the same semantic category or were all from different semantic categories, no differential performance was observed. Critically, however, the present study shows that even if deep semantic knowledge is not spontaneously recruited during the active maintenance of verbal information in WM, the regions that allowed decoding of the memoranda were still regions involved in semantic processing, although in more abstract levels of semantic knowledge. Hence, the findings of this study highlight the spontaneous, non-strategic involvement of at least some aspects of semantic knowledge in short-term maintenance of verbal information, even when semantic information does not need to be explicitly processed. We may assume that the retention of the most immediate, abstract categorical semantic knowledge associated with semantic category words is sufficient for simple maintenance in verbal WM, and that activation of deeper, feature specific knowledge is not necessary and useful, at least for the specific task and WM load used in this study.

Regarding the implicit semantic activation task, the regions allowing for decoding of semantic category information included the expected temporo-occipital and fronto-parietal cortices associated with feature-specific semantic information (i.e., visual, auditory, sensory-motor related features) (e.g., Chao & Martin, 1999, 2000; Culham & Valyear, 2006; Gainotti et al., 1995; Gauthier et al., 1997; 2000; Goldberg et al., 2006; Kiefer et al., 2008; Martin & Chao, 2001; Martin et al., 1995). One may consider it surprising that there was no major contribution of ATL areas to semantic category decoding in the implicit semantic activation task, suggesting that this task did not lead to activation of higher-level, abstract category information. It should be noted that other studies using the same type of implicit semantic processing tasks for category exemplars as in the present study also did not observe involvement of ATL (e.g., Baumgaertner et al, 2002; Huang et al., 2012; Rissman et al., 2003; Ruff et al., 2008). For example, Jedidi and colleagues (2021) used an fMRI adaptation paradigm in which participants performed a visual search task while being exposed to an auditory stream composed of alternating series of exemplars from a specific semantic category (*tools*, *clothes*, *colours*, and *animals*). They observed semantic category adaptation effects in feature-specific and amodal semantic representation areas (temporo-parietal and temporo-occipital cortices, inferior frontal gyrus), notably excluding the ATL areas. In other words, presentation of exemplars of specific semantic categories, while involving activation of category-specific feature information, does not necessarily lead to the activation of higher-level abstract category representations, when the task does not require explicit processing and comparison of semantic information. It could be argued that this interpretation is in line with behavioral studies on the production effect (Caplan, 2023), suggesting less extensive semantic activation when words are processed at the formal level such as during reading-aloud tasks. At the same time, it has been shown that semantic levels of processing are activated in an automatic manner very early during word reading (e.g., Barrós-Loscertales et al., 2012; Borghesani et al., 2019). Most importantly, we should note here that the implicit semantic processing task we used was specifically chosen to match the formal requirements of the verbal WM task, and that we were interested in the spontaneous semantic activation elicited in these contexts. Both tasks did lead to recruitment of semantic processing areas and allowed decoding of semantic content in these areas, but, critically, the nature of semantic processing areas involved differed between both tasks despite the similar formal requirements.

A possible limitation of the present study that needs to be discussed is the relatively low WM load. Although four words had to be encoded and one of the words had to be prioritized after initial encoding for further maintenance, maintenance load was low once the target word had been selected. This may also explain why classification accuracy of semantic category information very quickly dropped to chance level after initial maintenance and did not fully recover at the final recall stage (e.g., Boksem et al., 2005; Käthner et al., 2014; Kohlmorgen et al., 2007; Pergher et al., 2019). This situation is also similar to other stimulus-specific MVPA decoding studies of WM (e.g., LaRocque et al., 2013; Lewis-Peacock et al., 2015; 2018). Recent studies have furthermore shown that the persistence of neural memory representations may not be necessary for efficient memory maintenance and retrieval, and that synaptic plasticity processes may allow recovering a memory item (e.g., Rose et al., 2016). On the other hand, studies using a higher verbal WM load have generally shown decoding of memory information over larger portions of the maintenance stage including in the ATL, however at the cost of restricting decoding to type of memory information (small versus large list sets; words vs. nonword lists) as opposed to individual memoranda (Kowialiewski et al., 2020).

To conclude, this study suggests that spontaneous semantic activation in verbal WM tasks is mainly restricted to the intervention of relatively abstract and shallow semantic knowledge located in the ATL and does not reflect full activation of the deeper semantic features that characterize the memoranda. These results support partial emergent linguistic accounts of verbal WM, considering that WM is supported by linguistic knowledge structures but does not purely mirror these structures

Appendix

Table B.1. Stimuli from verbal WM and implicit semantic activation tasks, along with lexical frequency and number of syllables [7]

Semantic Category	Lexical Frequency (*freqlivres*) (counts per million)	Number of syllables	Semantic Concept	Lexical Frequency (*freqlivres*) (counts per million)	Mean number of syllables
Oiseau (bird)	47.97	2	*Pigeon*	7.97	1.83
			Aigle (eagle)	7.91	
			Moineau (sparrow)	4.32	
			Corbeau (raven)	3.92	
			Faucon (falcon)	2.36	
			Hibou (owl)	2.36	
Outil (tool)	10.14	2	*Marteau* (hammer)	13.31	1.83
			Hache (axe)	11.76	
			Scie (saw)	8.11	
			Tournevis (screwdriver)	3.24	
			Truelle (trowel)	2.3	
			Perceuse (drill)	0.2	
Couleur (color)	118.65	2	*Bleu* (blue)	100.41	1
			Jaune (yellow)	75.81	
			Rose (pink)	66.62	
			Rouge (red)	62.77	
			Vert (green)	59.12	
			Mauve (purple)	10.68	
Musique (music)	109.8	2	*Rock*	19.53	1.33
			Jazz	8.11	
			Pop	0.61	
			Disco	0.34	
			Rap	0.07	
			Techno	0	

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[7] Lexique 3.83 database (New 2006).

Table B.2. Results of the Bayesian one sample t-test for the implicit semantic activation task (evidence for the alternative hypothesis).

	BF_{10}	error %
bird_tool	8.112^{e+7}	NaN[a]
bird_colour	6.617^{e+8}	NaN[a]
bird_music	2.001^{e+13}	NaN[a]
tool_colour	4.916^{e+11}	NaN[a]
tool_music	3.956^{e+15}	NaN[a]
colour_music	2.715^{e+8}	NaN[a]

[a] t-value is large. A Savage-Dickey approximation was used to compute the Bayes factor but no error estimate can be given.

Table B.3. Results of the Bayesian one sample t-test for the verbal WM task (evidence for the alternative hypothesis).

	bird_tool		**bird_music**		**tool_colour**		**colour_music**	
	BF_{10}	**error %**	**BF_{10}**	**error %**	**BF_{10}**	**error %**	**BF_{10}**	**error %**
SEC1	0.043	~ $1.608^{e -5}$	0.045	~ 0.007	0.052	~ 3.879^{e-4}	0.040	~ 3.975^{e-4}
SEC2	0.041	~ 3.958^{e-4}	0.043	~ 1.007^{e-4}	0.043	~ 1.620^{e-4}	0.021	NaN[a]
SEC3	0.045	~ 0.008	0.019	NaN[a]	0.043	~ 4.169^{e-5}	0.041	~ 4.108^{e-4}
SEC4	0.043	~ 4.145^{e-5}	0.022	NaN[a]	0.043	~ 3.994^{e-5}	0.017	NaN[a]
SEC5	0.022	NaN[a]	0.043	~ 5.898^{e-5}	0.015	NaN[a]	0.018	NaN[a]
SEC6	0.045	~ 0.005	0.020	NaN[a]	0.022	NaN[a]	0.011	NaN[a]
SEC7	0.093	~ 7.576^{e-4}	0.050	~ 0.199	0.048	~ 0.050	0.061	~ 0.008
SEC8	**25719.097**	**NaN[a]**	**24.327**	**~ 8.433^{e-4}**	**243.701**	**~ 3.318^{e-5}**	**917.777**	**~ 1.704^{e-6}**
SEC9	0.913	~ 4.582^{e-5}	0.102	~ 0.001	0.891	~ 4.725^{e-5}	1.645	~ 3.164^{e-5}
SEC10	0.068	~ 0.072	0.102	~ 0.001	0.080	~ 1.809^{e-4}	0.262	~ 8.977^{e-6}
SEC11	0.107	~ 0.002	0.063	~ 0.016	0.051	~ 4.303^{e-4}	0.096	~ 8.973^{e-4}
SEC12	0.084	~ 3.177^{e-4}	0.058	~ 9.934^{e-4}	0.081	~ 2.081^{e-4}	0.076	~ 1.057^{e-4}
SEC13	0.085	~ 3.574^{e-4}	0.072	~ 0.143	0.047	~ 0.042	0.114	~ 0.002
SEC14	0.162	~ 0.003	0.093	~ 7.663^{e-4}	0.086	~ 4.212^{e-4}	0.272	~ 8.527^{e-6}
SEC15	0.376	~ 1.871^{e-6}	0.165	~ 0.004	**1.697**	~ 3.658^{e-5}	**3.327**	~ 1.264^{e-4}
SEC16	0.390	~ 3.324^{e-6}	0.093	~ 7.643^{e-4}	0.778	~ 5.169^{e-5}	0.566	~ 0.029
SEC17	0.264	~ 8.901^{e-6}	0.088	~ 0.089	0.241	~ 9.240^{e-6}	0.200	~ 0.029
SEC18	0.261	~ 9.038^{e-6}	0.043	~ 1.506^{e-7}	0.220	~ 0.053	0.104	~ 0.001

[a] t-value is large. A Savage-Dickey approximation was used to compute the Bayes factor but no error estimate can be given.

Table B.4. Results of the Bayesian one sample t-test for the verbal WM task (evidence for the null hypothesis).

	bird_colour		**tool_music**	
	BF_{01}	**error %**	**BF_{01}**	**error %**
SEC1	23.094	~ 2.718^{e-4}	53.826	NaN[a]
SEC2	20.406	~ 0.110	48.493	NaN[a]
SEC3	21.144	~ 0.039	55.784	NaN[a]
SEC4	47.197	NaN[a]	85.076	NaN[a]
SEC5	76.719	NaN[a]	67.728	NaN[a]
SEC6	61.559	NaN[a]	67.143	NaN[a]
SEC7	16.527	~ 0.006	46.372	NaN[a]
SEC8	**1.382**	**~ 5.130^{e-5}**	**7.861**	**~ 0.085**
SEC9	7.331	~ 7.620^{e-4}	12.623	~ 1.714^{e-4}
SEC10	7.891	~ 0.057	18.859	~ 3.122^{e-4}
SEC11	15.574	~ 0.024	22.608	~ 0.002
SEC12	18.483	~ 1.584^{e-4}	56.272	NaN[a]
SEC13	20.499	~ 0.098	20.179	~ 0.147
SEC14	14.021	~ 0.125	21.028	~ 0.046
SEC15	11.260	~ 5.274^{e-4}	19.683	~ 4.301^{e-4}
SEC16	13.993	~ 0.128	19.200	~ 3.961^{e-4}
SEC17	20.643	~ 0.081	9.144	~ 0.002
SEC18	13.386	~ 8.092^{e-5}	12.386	~ 2.131^{e-4}

[a] t-value is large. A Savage-Dickey approximation was used to compute the Bayes factor but no error estimate can be given.

Table B.5. Results of the Bayesian one sample t-test for the between-task classification (LTM_WM)[8]

	LTM_WM									
	bird_tool		**bird_colour**		**bird_music**		**tool_colour**		**colour_music**	
	BF$_{01}$	**error %**	**BF$_{01}$**	**error %**	**BF$_{01}$**	**error %**	**BF$_{01}$**	**error %**	**BF$_{01}$**	**error %**
SEC1	5.111	~ 0.025	20.172	~ 0.149	7.174	~ 4.869^{e-4}	12.064	~ 2.817^{e-4}	2.938	~ 2.240^{e-6}
SEC2	0.916	~ 3.226^{e-5}	11.717	~ 3.733^{e-4}	2.695	~ 1.609^{e-6}	3.783	~ 8.905^{e-6}	3.485	~ 7.403^{e-6}
SEC3	2.384	~ 7.639^{e-6}	5.093	~ 0.026	2.578	~ 3.025^{e-6}	1.381	~ 5.130^{e-5}	9.571	~ 0.001
SEC4	11.371	~ 4.870^{e-4}	12.179	~ 2.548^{e-4}	5.933	~ 0.005	8.754	~ 0.002	8.049	~ 0.020
SEC5	5.295	~ 0.019	12.702	~ 1.593^{e-4}	6.161	~ 0.003	6.414	~ 0.001	2.934	~ 2.201^{e-6}
SEC6	9.116	~ 0.002	7.406	~ 8.863^{e-4}	2.989	~ 2.739^{e-6}	11.335	~ 0.098	5.900	~ 0.006
SEC7	13.056	~ 1.135^{e-4}	13.633	~ 6.236^{e-5}	9.100	~ 0.002	0.406	~ 1.187^{e-4}	6.010	~ 0.005
SEC8	**6.788**	**~ 3.876^{e-5}**	**7.383**	**~ 8.489^{e-4}**	**7.181**	**~ 4.994^{e-4}**	**3.582**	**~ 8.029^{e-6}**	**4.507**	**~ 0.056**
SEC9	4.416	~ 0.062	9.186	~ 0.002	8.405	~ 0.002	1.726	~ 0.017	3.642	~ 8.351^{e-6}
SEC10	3.015	~ 3.011^{e-6}	5.085	~ 0.026	5.667	~ 0.010	1.482	~ 4.921^{e-5}	3.280	~ 5.714^{e-6}
SEC11	10.695	~ 7.738^{e-4}	8.697	~ 0.002	6.177	~ 0.003	2.264	~ 1.175^{e-5}	6.809	~ 1.670^{e-5}
SEC12	11.102	~ 5.899^{e-4}	17.492	~ 6.963^{e-4}	5.123	~ 0.025	3.443	~ 7.099^{e-6}	7.014	~ 2.102^{e-4}
SEC13	11.058	~ 6.081^{e-4}	12.361	~ 2.178^{e-4}	4.202	~ 9.169^{e-6}	7.957	~ 0.012	3.871	~ 9.121^{e-6}
SEC14	12.097	~ 2.737^{e-4}	6.553	~ 6.160^{e-4}	7.833	~ 0.001	7.663	~ 0.001	5.295	~ 0.019
SEC15	9.138	~ 0.002	11.141	~ 5.741^{e-4}	4.438	~ 0.060	4.806	~ 0.038	7.483	~ 0.001
SEC16	0.775	~ 2.050^{e-5}	0.215	~ 6.795^{e-5}	2.204	~ 1.415^{e-5}	3.937	~ 9.227^{e-6}	3.490	~ 7.439^{e-6}
SEC17	7.180	~ 4.977^{e-4}	8.569	~ 0.002	9.437	~ 0.001	5.098	~ 0.025	4.674	~ 0.045
SEC18	9.774	~ 0.001	5.581	~ 0.011	6.377	~ 0.001	5.743	~ 0.008	10.724	~ 7.596^{e-4}

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[8] Semantic category classifiers of the implicit semantic activation task classifying the semantic categories of the verbal WM task (LTM_WM), for each second of the verbal WM task.

Table B.6. Results of the Bayesian one sample t-test for the between-task classification (WM_LTM)[9]

WM_LTM										
	bird_tool		**bird_colour**		**bird_music**		**tool_music**		**colour_music**	
	BF$_{01}$	**error %**	**BF$_{01}$**	**error %**	**BF$_{01}$**	**error %**	**BF$_{01}$**	**error %**	**BF$_{01}$**	**error %**
SEC1	7.983	~ 0.002	17.836	~ 1.470^{e-4}	13.586	~ 6.543^{e-5}	6.014	~ 0.005	2.777	~ 1.274^{e-6}
SEC2	6.937	~ 9.555^{e-5}	19.611	~ 4.302^{e-4}	8.186	~ 0.002	2.620	~ 2.363^{e-6}	6.355	~ 0.002
SEC3	5.778	~ 0.008	9.581	~ 0.001	14.964	~ 0.049	5.705	~ 0.009	5.138	~ 0.024
SEC4	5.826	~ 0.007	18.420	~ 1.288^{e-4}	15.782	~ 0.019	9.684	~ 0.001	6.077	~ 0.004
SEC5	6.982	~ 1.598^{e-4}	12.940	~ 1.269^{e-4}	7.944	~ 0.019	9.618	~ 0.001	6.077	~ 0.004
SEC6	14.812	~ 0.058	13.802	~ 0.152	4.937	~ 0.032	4.613	~ 0.049	0.403	~ 1.210^{e-4}
SEC7	14.626	~ 0.070	13.082	~ 1.106^{e-4}	11.586	~ 4.136^{e-4}	2.485	~ 4.906^{e-6}	11.512	~ 4.379^{e-4}
SEC8	**10.071**	**~ 0.001**	**8.068**	**~ 0.031**	**3.944**	**~ 9.234^{e-6}**	**6.203**	**~ 0.003**	**2.775**	**~ 1.276^{e-6}**
SEC9	16.771	~ 0.004	14.538	~ 0.077	2.692	~ 1.626^{e-6}	7.614	~ 0.001	0.830	~ 2.469^{e-5}
SEC10	9.148	~ 0.002	7.709	~ 0.001	4.324	~ 0.068	7.141	~ 4.291^{e-4}	1.973	~ 2.513^{e-5}
SEC11	15.094	~ 0.043	6.102	~ 0.004	3.432	~ 7.013^{e-6}	6.964	~ 1.326^{e-4}	11.592	~ 4.115^{e-4}
SEC12	19.039	~ 3.629^{e-4}	10.254	~ 0.001	8.835	~ 0.002	5.446	~ 0.015	9.210	~ 0.002
SEC13	10.242	~ 0.001	8.825	~ 0.002	5.809	~ 0.007	1.773	~ 0.031	7.629	~ 0.001
SEC14	7.037	~ 2.485^{e-4}	12.809	~ 1.441^{e-4}	4.228	~ 9.140^{e-6}	2.408	~ 6.911^{e-6}	7.338	~ 7.748^{e-4}
SEC15	3.322	~ 6.100^{e-6}	4.079	~ 9.279^{e-6}	1.719	~ 0.015	0.663	~ 2.180^{e-5}	9.716	~ 0.001
SEC16	7.745	~ 0.001	7.093	~ 3.441^{e-4}	4.759	~ 0.041	1.792	~ 0.037	1.837	~ 3.244^{e-5}
SEC17	14.590	~ 0.073	5.441	~ 0.015	1.759	~ 0.027	1.833	~ 3.267^{e-5}	1.746	~ 0.023
SEC18	16.605	~ 0.005	6.264	~ 0.002	8.515	~ 0.002	6.216	~ 0.003	5.000	~ 0.029

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[9] Semantic category classifiers of the verbal WM task classifying the semantic categories of the implicit semantic activation task (WM_LTM), for each second of the verbal WM task.

Table B.7. Clusters showing above-chance level classification for the four semantic categories in the implicit semantic activation task.[10]

Anatomical regions	No. voxels	Left/Right	x	y	z	*SPM Z*-value for peak-level	*T* value
bird vs. tool							
Precentral gyrus	88	L	-54	-4	28	5.71	7.68
	15	L	-56	-4	40	5.11	6.48
	30	R	52	0	32	4.56	5.49
	14	R	50	-10	26	4.90	6.09
Postcentral gyrus	11	L	-64	-2	16	4.03	4.67
	30	R	56	-10	24	3.89	4.45
Superior temporal gyrus, *middle*	14	L	-56	-10	6	4.18	4.89
Cuneus	17	R	18	-96	-2	4.12	4.8
Lingual gyrus	17	R	6	-100	0	3.68	4.17
bird vs. colour							
Precentral gyrus	192	L	-50	0	36	5.91	8.15
Postcentral gyrus	192	L	-56	-10	30	5.62	7.50
Superior temporal gyrus, *middle*	134	L	-56	-18	2	6.28	9.03
Superior temporal gyrus, *posterior*	134	L	-56	-28	2	5.34	6.92
Lingual gyrus	507	L	-12	-98	-6	5.70	7.66
	507	R	8	-96	6	5.76	7.81
Calcarine sulcus	507		0	-90	0	5.89	8.08

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[10] All regions are significant at $p < .05$, with cluster-level family wise error (FWE) corrections for whole-brain volume.

bird vs. music							
Middle frontal gyrus, *anterior*	14	L	-42	46	20	4.47	5.35
Inferior frontal gyrus, *pars triangularis*	49	L	-50	34	6	4.69	5.71
Precentral gyrus	214	L	-58	-10	38	5.70	7.66
	25	R	58	-2	26	4.66	5.67
	24	R	60	-4	38	4.69	5.72
	19	R	50	-10	26	4.74	5.80
Postcentral gyrus	15	L	-68	-10	24	4.44	5.30
Superior temporal gyrus, *Heschl gyrus*	10	L	-44	-26	12	4.01	4.63
Superior temporal gyrus, *middle*	16	L	-52	-20	6	6.12	8.63
	12	L	-56	-18	4	5.74	7.76
Superior temporal gyrus, *posterior*	59	L	-54	-16	2	5.04	6.34
	13	L	-54	-34	2	5.01	6.28
Middle temporal gyrus, *posterior*	14	L	-62	-38	6	4.53	5.45
Lingual gyrus	891	L	-12	-98	-6	5.50	7.24
	891	R	12	-94	-6	6.04	8.44
Cerebellum	46	R	14	-74	-18	4.28	5.06
tool vs. colour							
Precentral gyrus	28	L	-60	-10	30	5.14	6.53
	12	R	56	-2	26	3.95	4.55
Postcentral gyrus	10	L	-52	-4	14	4.28	5.06
	10	R	60	-24	14	4.68	5.71
Superior temporal gyrus, *posterior*	66	L	-54	-20	4	5.97	8.28
	17	L	-56	-8	-6	4.93	6.13
	12	L	-66	-14	6	4.70	5.74
	10	L	-66	-14	0	5.00	6.27
Superior temporal gyrus, *Heschl gyrus*	11	R	56	-22	10	4.31	5.10

Middle temporal gyrus, *posterior*	32	L	-62	-40	2	4.47	5.35
Cuneus	34	L	-18	-100	4	5.03	6.33
	11	L	-10	-94	20	4.19	4.91
	624	R	8	-96	6	6.06	8.50
Inferior occipital gyrus	624	R	12	-96	-2	5.91	8.13
Lingual gyrus	624	L	-2	-92	2	5.79	7.88
Fusiform gyrus	10	L	-48	-42	-24	4.27	5.03
tool vs. music							
Precentral gyrus	123	L	-54	-6	32	5.92	8.15
Postcentral gyrus	123	L	-56	-16	28	4.92	6.12
Inferior occipital gyrus	1905	L	-10	-98	2	6.12	8.63
		R	8	-92	0	5.95	8.24
Lingual gyrus	1905	L	-2	-92	0	6.35	9.22
Cuneus	1905	R	2	-98	6	6.25	8.97
colour vs. music							
Precentral gyrus	10	L	-60	-6	8	4.76	5.84
Superior temporal gyrus, *Heschl gyrus*	168	L	-64	-18	6	5.56	7.37
	105	R	64	-10	10	4.56	5.50
Superior temporal gyrus, *posterior*	168	L	-56	-14	0	7.08	11.35
	56	L	-62	-32	14	5.01	6.28
	105	R	58	-8	2	5.24	6.72
Middle temporal gyrus, *posterior*	168	L	-60	-6	-6	5.54	7.32
	16	L	-64	-36	0	4.55	5.49
	10	L	-60	-40	4	4.13	4.81
	105	R	62	-8	-8	4.90	6.08

Table B.8. Clusters showing above-chance level classification for the four semantic categories in the verbal WM task.[11]

Anatomical regions	No. voxels	Left/Right	x	y	z	*SPM Z*-value for peak-level	*T* value
bird vs. tool							
Superior temporal gyrus, *anterior*	610	L	-24	10	-26	6.69	10.15
	40	R	32	8	-36	5.27	6.78
Middle temporal gyrus, *anterior*	40	R	32	2	-42	5.84	7.97
Inferior temporal gyrus, *anterior*	610	L	-38	-4	-38	6.10	8.59
	11	L	-48	-8	-26	4.88	6.05
	40	R	32	-6	-38	4.67	5.69
Parahippocampal gyrus	13	L	-20	-40	-8	3.87	4.43
	11	L	-22	-32	-8	3.94	4.53
	256	R	20	-12	-26	5.13	6.51
	18	R	40	-22	-28	4.79	5.89
Hippocampus	17	L	-26	-20	-16	4.69	5.72
Amygdala	17	L	-26	-12	-18	4.93	6.14
	11	L	-26	-12	-14	4.88	6.06
Subcallosal gyrus	19	R	24	18	-18	4.40	5.25
	12	R	24	6	-22	4.25	5.00
Subthalamic nucleus	18	L	-10	-10	-4	4.22	4.95
Midbrain, *red nucleus*	11	L	-2	-14	-10	3.88	4.45
Midbrain, *substantia negria*	10	R	6	-12	-14	4.26	5.01
Cerebellum	48	L	-22	-38	-36	4.82	5.94

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[11] All regions are significant at $p < .05$, with cluster-level family wise error (FWE) corrections for whole-brain volume. No voxels survived for the bird vs. colour and the tool vs. music classifications.

	11	L	-20	-34	-50	4.86	6.02
	10	L	-16	-38	-40	4.96	6.20
	24	R	18	-38	-36	4.46	5.34
	13	R	16	-48	-44	4.29	5.07
bird vs. colour				*no voxel survived*			
bird vs. music							
Superior temporal gyrus, *anterior*	12	R	34	20	-36	4.66	5.66
Inferior temporal gyrus, *anterior*	13	R	36	0	-38	4.68	5.71
Parahippocampal gyrus	159	L	-26	8	-28	5.38	7.00
	11	L	-22	-18	-22	4.82	5.95
	10	R	18	-8	-22	4.93	6.14
Subcallosal gyrus	12	L	-20	6	-20	5.23	6.70
tool vs. colour							
Superior temporal gyrus, *anterior*	2543	L	-36	16	-34	6.66	10.06
Middle temporal gyrus, *anterior*	2543	L	-46	-4	-38	6.41	9.38
Inferior temporal gyrus, *anterior*	2543	L	-32	10	-32	6.68	10.12
Inferior temporal gyrus, *middle*	2543	L	-50	-2	-42	6.34	9.18
		R	32	-2	-46	6.74	10.31
Paraphippocampal gyrus	2543	L	-20	0	-22	6.37	9.27
		R	14	-10	-24	6.74	10.23
Fusiform gyrus	2543	L	-40	-8	-28	6.47	9.54
tool vs. music				*no voxel survived*			
colour vs. music							
Middle frontal gyrus, *anterior*	21	L	-22	54	2	4.83	5.96

	34	R	36	56	-6	4.19	4.91
Medial frontal gyrus	12	L	-4	64	-2	4.52	5.44
Inferior frontal gyrus, *pars orbitalis*	34	L	-42	54	-8	4.80	5.90
	19	L	-18	38	-18	4.61	5.58
	35	R	20	30	-16	4.83	5.97
Superior temporal gyrus, *anterior*	30	L	-50	12	-20	5.94	8.20
	20	R	44	12	-38	6.04	8.44
Superior temporal gyrus, *middle*	12	L	-58	-10	-4	4.68	5.71
	13	R	30	10	-26	5.02	6.30
Superior temporal gyrus, *posterior*	10	L	-56	-32	8	3.72	4.22
Middle temporal gyrus, *middle*	725	L	-38	-4	-30	7.26	11.96
Inferior temporal gyrus, *middle*	19	L	-60	-12	-26	4.65	5.64
	17	L	-52	-18	-32	5.31	6.87
	15	R	48	-12	-28	5.27	6.78
Inferior temporal gyrus, *posterior*	33	L	-40	-24	-26	4.89	6.07
	31	R	48	-20	-30	5.26	6.77
Parahippocampal gyrus	45	L	-32	-28	-30	4.82	5.94
	152	R	38	-22	-26	5.47	7.19
	20	R	26	6	-24	5.23	6.70
Fusiform gyrus	18	R	40	-8	-26	5.44	7.11
Hypothalamus	10	R	2	-6	-12	4.62	5.60
Nucleus accumbens	28	L	-6	10	-12	4.47	5.35
Globus pallidus, lentiform nucleus	154	R	14	2	-8	5.43	7.09
Cerebellum	30	L	-42	-44	-46	5.39	7.02
	20	L	-18	-38	-38	4.88	6.05
	21	R	34	-44	-38	4.69	5.72

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Study 3

The multiple neural states of linguistic information in verbal working memory: Evidence from a lexical learning study

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In preparation

Abstract. There is increasing evidence for the involvement of language-related neural cortices in the maintenance of information in verbal working memory (WM). The present study goes one step further by documenting language learning-related changes in the cortices that support verbal WM. Participants learned new lexical labels over four learning sessions and their neural activity was repeatedly measured via fMRI while they had to maintain the learned and non-learned novel words. Increased univariate activity was progressively observed for learned novel words in fronto-parietal cortices associated with episodic memory retrieval as well as in temporo-parietal cortices part of the dorsal language pathway. At the multivariate level, the WM-related neural patterns progressively discriminated between learned and non-learned novel words, with discriminatory neural patterns observed in inferior frontal, supramarginal and superior temporal cortices associated with phonological processing and posterior middle temporal cortices associated with lexico-semantic processing. These results highlight the dynamic, learning-induced changes of the representational neural substrates of verbal WM as well as the mainly linguistic nature of these substrates.

Introduction

An increasing number of studies suggest that verbal WM is supported not only by domain-general fronto-parietal cortices, but also by language-related cortices, indicating that existing phonological and lexico-semantic knowledge actively supports maintenance in verbal WM (e.g., Kalm & Norris 2014; Kowialiewski et al., 2019; Lewis-Peacock & Postle, 2012; Majerus et al., 2010; Postle, 2006). The present study goes one step further by documenting language learning-related changes in the cortices that support verbal WM, through a five-day lexical learning and functional magnetic resonance imaging (fMRI) study.

Various neuroimaging studies have demonstrated that fronto-parietal networks are involved during the retention of both visual and verbal information in WM. The left intraparietal sulcus and dorsolateral prefrontal cortex have been shown to be activated independently of the type of information to be maintained (e.g., Chein et al., 2011; Cowan et al., 2011; Nystrom et al. 2000; Majerus et al., 2010, 2012, 2016), indicating that these regions subserve a domain-general attentional control and focalization function in WM tasks. At the same time, a growing body of evidence also highlights the recruitment of neural regions supporting language processing during verbal WM tasks, suggesting that the neural substrates of temporary memory representations are defined by linguistic cortices (e.g., Kowialiewski et al., 2019; Majerus et al., 2010; Postle, 2006; see Deldar et al., 2021, for a review). Specifically, the posterior superior temporal gyrus, the superior temporal sulcus, and the supramarginal gyrus, either in the left hemisphere or bilaterally, have been found to be involved in phonological (sub-lexical) processing (e.g., Bhaya-Grossman & Chang, 2022; Binder, 2000; Binder et al., 2000; Buchsbaum et al. 2005; Démonet et al., 1992, 1994; Graves et al, 2008; Kalm & Norris, 2014; Majerus et al., 2002; 2005; 2010; Majerus, 2019; Poeppel, 1996; Ravizza et al. 2011; Strand et al., 2008). Studies have also highlighted the recruitment of left posterior middle temporal gyrus, the temporoparietal junction, the anterior inferior temporal gyrus and the angular gyrus in lexico-semantic processing (e.g., Binder et al., 1997, 2009; Binney et al., 2010; Collette et al., 2001; Démonet et al., 1992, 1994; Ferreira et al., 2015; Jackson, 2021;

Jackson et al., 2015; Jung et al., 2017; Howard et al., 1992; Lambon Ralph et al., 2009; Majerus et al., 2002; Price et al, 1996; Visser et al., 2012; Scott et al., 2000), as well as the left inferior frontal gyrus known to be involved in semantic control processes (e.g., Fiebach et al., 2007). More integrative perspectives have suggested that the auditory language network is divided into two pathways in the dominant hemisphere (Hickok & Poeppel, 2004, 2007). On the one hand, the dorsal language pathway connects the superior temporal gyrus associated with speech perception to the inferior parietal and posterior frontal regions via the arcuate and superior longitudinal fasciculus, allowing for the integration of phonemes into articulatory representations. On the other hand, the ventral language pathway connects the superior temporal gyrus to the anterior and inferior medial temporal regions and is involved in integrating phonemes into conceptual/semantic representations. Similarly, Majerus (2019) suggested that the superior temporal gyrus supports temporary retention of item and list-level serial order information for nonword sequences, while middle and inferior temporal gyri are associated with temporary maintenance of lexico-semantic information.

Findings on the involvement of linguistic cortices during verbal WM retention are further supported by behavioral and neuropsychological evidence showing, on the one hand, the impact of psycholinguistic variables on verbal WM performance, (e.g., phonotactic frequency, lexicality, frequency, imageability and semantic relatedness effects; Gathercole et al., 1999; Hulme et al., 1991, 1997; Jefferies et al., 2006; Majerus et al., 2004; Poirier & Saint-Aubin, 1996; Walker & Hulme, 1999; Watkins & Watkins, 1977) and the other hand, robust associations between verbal WM and language deficits in patients with language disorders, such as in aphasia (e.g., N. Martin & Saffran, 1990; 1997; N. Martin et al., 1996; Saffran & Martin, 1990), or in semantic dementia (e.g., Jefferies et al., 2006; Knott et al., 1997; Majerus et al., 2007; Patterson et al., 1994). At the theoretical level, the impact of linguistic knowledge on verbal WM performance and the recruitment of linguistic cortices during verbal WM tasks corroborate emergent, language-based models of verbal WM, which propose that language is the representational substrate for WM. This perspective suggests that verbal WM constitutes the activated portion of linguistic LTM, and that there exists at least partial overlap between verbal WM and the language system (e.g., Acheson & MacDonald, 2009; Buchsbaum & D'Esposito, 2019; Cowan, 1993, 1995; Hasson et al., 2015; MacDonald, 2016; Majerus, 2009, 2013, 2019; Postle, 2006; Schwering & MacDonald, 2020).

Although numerous evidence highlights the involvement of linguistic knowledge during verbal WM tasks, there remains an ongoing debate regarding the neural basis for verbal WM retention. For instance, Kowialiewski and colleagues (2019) found that WM maintenance of items was decoded in specific regions within the dorsal and ventral language pathways supporting phonological and semantic processing. Evidence has also shown that neural patterns in the superior temporal gyrus can differentiate between different types of nonwords during encoding and recall in WM (e.g., Kalm & Norris 2014), and that neural patterns in linguistic cortices can distinguish between WM maintenance of word and nonword stimuli (e.g., Lewis-Peacock & Postle, 2012). Other studies, however, have observed neural decoding of speech vs. non-speech stimuli maintained in verbal WM, but not within phonological processing regions (e.g., Yue & Martin, 2019; see also Yue & Martin, 2022), while others have observed neural decoding of items in domain-general fronto-parietal cortices related to WM and/or attentional control, but not within linguistic processing regions (e.g., Yue & Martin, 2021). In summary, while several studies using a multivariate decoding approach provide evidence for the recruitment of linguistic cortices during verbal WM tasks, there have also been several recent studies showing that non-linguistic (fronto-parietal) cortices are involved during retention of verbal information in WM.

An alternative approach to investigate the involvement of linguistic neural substrates in verbal WM is to examine the neural changes associated with language learning, i.e., the specific impact of language learning on the activation of linguistic knowledge in verbal WM. Extensive research exists on brain activity related to second language (L2) learning in adults (e.g., Gurunandan et al., 2019; Kuhl et al., 2016; Perkins et al., 2022; Raboyeau et al., 2010; Sabourin, 2009; Schimke et al., 2021). Several fMRI studies have observed, for instance, increased brain activation within frontal and posterior parietal brain regions, and within subcortical structures like the basal ganglia and cerebellum (e.g., Li et al., 2014; Tagarelli et al., 2019), as well as in the middle and superior temporal gyri, and the hippocampus (e.g., Bakker-Marshall et al., 2018; Davis & Gaskell., 2009) during L2 word learning. Breitenstein and colleagues (2005) have shown that repeated presentations of picture-word pairings led to decreasing activation in the left hippocampus and fusiform gyrus, and to increasing activation in the left parietal lobe. Mestres-Missé and colleagues (2008) observed the involvement of the left anterior inferior frontal gyrus, the middle temporal gyrus, the parahippocampal gyrus, and several subcortical structures when participants were presented triplets of sentences during which the meaning of a novel word became increasingly clear through both contextual semantic and syntactic information. It has also been shown that newly acquired language information transfers from the hippocampus to the middle temporal cortical regions after five consecutive days of training on a word–picture matching task conducted in a magnetoencephalography scanner, suggesting a process of consolidation into LTM (Dobel et al., 2009, 2010). However, there is still a notable gap in the literature in understanding the specific neural changes related to lexical acquisition.

The present study

The aim of this study was to investigate how the linguistic cortices assumed to support the maintenance of information in verbal WM change as a function of learning-related changes in language representations. We simulated the acquisition of new words over a five-day period via a word-novel word paired associate learning task. We repeatedly scanned (before the first, after the second and after the fourth learning session) the brain of the participants while they performed a nonword delayed repetition task, with the nonwords being the novel words learned in the learning sessions or novel words only presented during the nonword delayed repetition task in the fMRI scanner. This approach allowed us to trace the changes related to lexical learning and their impact on the neural representation of the novel words in WM. In line with the dual stream model for auditory language processing (Hickok & Poeppel, 2004, 2007) and the linguistic/hybrid models of WM (e.g., Majerus, 2019), we hypothesized progressive differentiation of the neural patterns supporting learned vs. non-learned novel words in WM, with no differentiation before the first learning session, differentiation restricted to phonological processing areas in superior temporal gyri after the first learning sessions due to progressive phonological familiarization with the novel word forms, and differentiation involving also lexico-semantic processing in middle/inferior temporal areas due to the consolidated learning of specific lexico-semantic associations after the final learning session. Furthermore, we varied the ease at which the novel words could be learned, by using novel word forms of either high phonological redundancy and phonotactic frequency (HRPF) or low phonological redundancy and phonotactic frequency (LRPF). Previous research has demonstrated that new foreign language words are more easily learned when their phonological form conforms to the phonotactic rules of the native language (e.g., Ellis & Beaton, 1993; Kaushanskaya et al., 2011; Morra & Camba, 2009). HRPF novel words should therefore acquire a "learned" status more quickly than LRPF novel words, and their learning-related neural substrates should change more quickly when activated in a WM context.

Methods

Participants

Forty-two monolingual native French-speaking participants were recruited via the University of Liège web platform and advertisements on social networks. Data from ten participants had to be excluded due to technical problems (e.g., premature stopping of the scanner) during one of the three MRI sessions. The final sample was composed of thirty-two complete datasets (9 males; mean age = 22.906, SD = 3.291, age range = 18-34). Sample size justification is provided in the *Bayesian statistical procedures* section. All participants were native French speakers, right-handed, and with normal hearing. They reported no history of learning, neuropsychological or neurological disorder, and no current drug use or alcohol abuse. The study was approved by the ethics committee of the Faculty of Medicine of the University of Liège. A financial compensation of 15 euros per MRI session and lexical learning sessions was provided to all participants for their involvement in the experiment. In line with the Declaration of Helsinki (1964), all participants gave written informed consent before their inclusion in the study.

Materials

Delayed nonword repetition task. 28 nonwords were constructed, consisting of 14 trisyllabic nonwords with high redundancy phoneme combinations and high phonotactic frequency (HRPF), and 14 trisyllabic nonwords with low redundancy phoneme combinations and low phonotactic frequency (LRPF). Redundancy was manipulated by using the same vowel for each syllable composing a nonword (e.g., lapara). Phonotactic frequency was manipulated by selecting the most frequent and least frequent consonant-vowel biphones of the French language using the Diphones database (version 1.00) (New & Spinelli, 2013). We combined these biphones to create trisyllabic nonwords, half of these nonwords having syllables including the same vowel phonemes (high redundancy), and the other half having syllables including different vowel phonemes (low redundancy) (see **Table 3.1** for full stimulus lists). In addition, the nonwords could not be direct phonological neighbors of existing words ("voisphon" in *Lexique 3.83* database; New et al., 2001). Participants were instructed to listen carefully to each nonword and to maintain it in WM for 6 seconds, before repeating the nonword. An attention mark appeared on the screen, followed by a blank screen with the auditory presentation of the nonword (encoding stage). Then, a screen with a cross indicated that participants had to maintain the nonword in verbal WM for 6 seconds (maintenance stage), followed by a question mark indicating that participants had to recall the nonword orally (with a time limit of 6000 ms) (retrieval stage). To increase the neural sampling quality, each nonword occurred three times over the entire task, resulting in a total of 84 trials (7 trials per nonword condition). Three versions of the task (one list per MRI session) were created, with each version presenting the nonwords in a different order, the presentation order of the task versions being pseudorandomized across participants. All responses were recorded for transcription and scoring verification, in addition to real-time scoring. Each correctly recalled nonword was scored as 1, while each non-recalled or incorrectly recalled nonword was scored as 0. Four scores were calculated: the score of correctly recalled learned HRPF novel words, the score of correctly recalled learned LRPF novel words, the score of correctly recalled non-learned HRPF novel words, and the score of correctly recalled non-learned LRPF novel words (each of these scores out of 7). Head movements of all participants were examined and algorithms for motion adjustment were applied when necessary (see section *Image Processing*). Before the session, participants systematically completed three practice trials with feedback to ensure that they had correctly understood the task instructions.

Lexical learning sessions. Half of the HRPF novel words and half of the LRPF novel words from the delayed nonword repetition task were selected for association with existing words. The words were the seven most prototypical exemplars of the semantic categories "bird" and "tool" based on the *BASETY* database (Léger et al., 2008) (see **Table 3.1** for full stimulus lists, including psycholinguistic data). The novel word learning task thus mimicked the learning of novel names for well-known exemplars of 'bird' and 'tool' categories, with the additional constraint for fine-grained learning of lexical and semantic associations due to the semantic closeness of half of the word targets. The stimuli were recorded by a French-native female speaker adopting a neutral voice. Each learning session was divided into two phases. In the familiarization phase, participants were asked to listen carefully to 14 word/novel word associations one by one, to repeat them directly (with corrective feedback) and try to memorize as many as possible. First, an attention mark appeared on the screen, directly followed by the auditory presentation of the word/novel word association. Then, a question mark indicated that participants had to repeat the association orally. The familiarization phase was directly followed by the test phase in which participants were asked to listen to the words of the 14 associations one by one and then recalled the associated novel words with corrective feedback. There was no time limit for the participant to respond. The associations were presented in a random order for the familiarization phase and in a pseudo-random order for the test phase (four possible orders randomized between participants). Two versions of the task were constructed, so that half the novel words learned by half the participants were the non-learned novel words for the other half of the participants. Each correctly recalled learned novel word was scored as 1, while each non-recalled or incorrectly recalled learned novel word was scored as 0. Three scores were calculated: a total score of correctly recalled learned novel words (out of 14), as well as scores for the number of correctly recalled learned HRPF novel words, and the number of correctly recalled learned LRPF novel words (each of these scores out of 7). The task was set up using OpenSesame software (https://osdoc.cogsci.nl/; Mathôt et al., 2012) implemented in the Jatos web interface (https://www.jatos.org/; Lange et al., 2015).

Table 3.1. Stimuli used in the lexical learning task, and associated psycholinguistic characteristics for the word stimuli.

Word	Semantic category	NOC (number of occurrences of the exemplar)[12]	Lexical Frequency (*freqlfilms2*) (counts per million)[13]	Novel word to be learned (stimulus set 1)	Novel word to be learned (stimulus set 2)
Pigeon (pigeon)	Bird	85	8.56	*lapara*	*marala*
Perruche (budgie)	Bird	23	0.47	*golanbe*	*chanbake*
Moineau (sparrow)	Bird	64	2.92	*soukoutou*	*toupoukou*
Corbeau (raven)	Bird	55	3.57	*redeve*	*mepere*
Vautour (vulture)	Bird	22	2.41	*kechagan*	*rochougan*
Hibou (owl)	Bird	24	4.08	*langouba*	*lopega*
Mésange (tit)	Bird	16	0.19	*komodo*	*possomo*
Marteau (hammer)	Tool	92	11.84	*danmanvan*	*panlanman*
Râteau (rake)	Tool	22	0.77	*bakelan*	*goupochan*
Brouette (wheelbarrow)	Tool	4	1.1	*dovoko*	*mopovo*
Ciseaux (scissors)	Tool	22	7.86	*vatapa*	*pakama*
Tenailles (pincers)	Tool	8	1.34	*mougabo*	*guemoubo*
Équerre (square)	Tool	6	0.19	*vanbero*	*tabanpo*
Ponceuse (sander)	Tool	33	0.31	*todachou*	*bechangou*

Note. HRPF novel words are underlined.

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[12] *BASETY database* (Léger et al., 2008)

[13] *Lexique 3.83* database (New et al., 2001)

Leeds Sleep Evaluation Questionnaire. This adaptation of the Leeds Sleep Evaluation Questionnaire (LSEQ) (Parrott & Hindmarch, 1978) subjectively assessed the participants’ sleep quality and quantity using nine visual analogue scales represented by a 100-mm horizontal line with two extremes defined at the ends of the line (e.g., *tired* = score of 0, *alert* = score of 10). For participant convenience, we placed ten markers (one per centimeter) on the line with corresponding numbers from 0 to 10. The questionnaire consisted of four sections (*Getting to Sleep*, *Quality of Sleep*, *Awakening from Sleep* and *Behaviour following Wakefulness*). We added short-answer questions on the number of hours of sleep, the number of waking episodes, the time before falling asleep and the duration of waking episodes during the night. This questionnaire was administered on each experimental day to control for confounding variables related to sleep and fatigue. Participants were instructed to encircle the corresponding number to indicate their self-assessment for each question within the four sections (*Getting to Sleep*, *Quality of Sleep*, *Awakening from Sleep* and *Behaviour following Wakefulness*) and to answer objectively to the short-answer questions (number of hours of sleep, number of waking episodes, time before falling asleep and duration of waking episodes during the night). A score out of 10 was calculated for each analogue scale, and the scores from the scales were summed for each domain (*Getting to Sleep*: score out of 30, *Quality of Sleep*: score out of 20, *Awakening from Sleep*: score out of 20, *Behaviour following Wakefulness*: score out of 20).

Reaction time task (adapted from Grandjean and Collette, 2011). The reaction time task was administered on each experimental day in order to establish a level of performance at the time of the test and to detect any fatigue effect depending on the experimental day. The test consisted of deciding as quickly as possible whether two alphabetical letters appearing on the screen were identical or different. The 26 letters of the alphabet were repeated three times with either an identical letter or a different letter. Participants were instructed to decide as quickly as possible whether two alphabetical letters appearing on a computer screen were identical (by pressing the right arrow) or different (by pressing the left arrow). The task consisted of 78 trials presented in a random order. Stimuli were presented in capital letters, in white on a black screen (sans serif font, font size = 70px). Each pair was presented for a maximum of

4000 ms. An accuracy score was calculated, with each correct response scored as 1 and each incorrect response or omission scored as 0. Additionally, a reaction time was calculated in milliseconds for each trial. All scores were averaged. The task was set up using OpenSesame software implemented in the Jatos web interface.

General procedure

The experiment took place at the Cyclotron Research Centre of the University of Liège on days 1, 3 and 5, and by videoconference on days 2 and 4. On days 1 and 3, participants filled in the paper version of the LSEQ, followed by the reaction time task, the in-scanner delayed nonword repetition task, and then the corresponding lexical learning session outside the scanner. On days 2 and 4, participants completed a computerized version of the LSEQ, followed by the reaction time task and the lexical learning session; all the instructions were given live by the experimenter via a video conferencing platform. On day 5, participants filled in the paper version of the LSEQ, followed by the reaction time task, the in-scanner delayed nonword repetition task, and then, instead of the lexical learning session, participants received feedback on the aims of the study (see **Figure 3.1**).

The entire experiment lasted approximately one hour per participant on days 1 and 3, 20 minutes on days 2 and 4, and 40 minutes on day 5 (approximately 5 minutes for the LSEQ, 3 minutes for the reaction time task, 20-25 minutes for the delayed nonword repetition task, and 10 minutes for the lexical learning session). For a given participant, each session was scheduled at approximately the same time of the day to avoid any time-of-day bias.

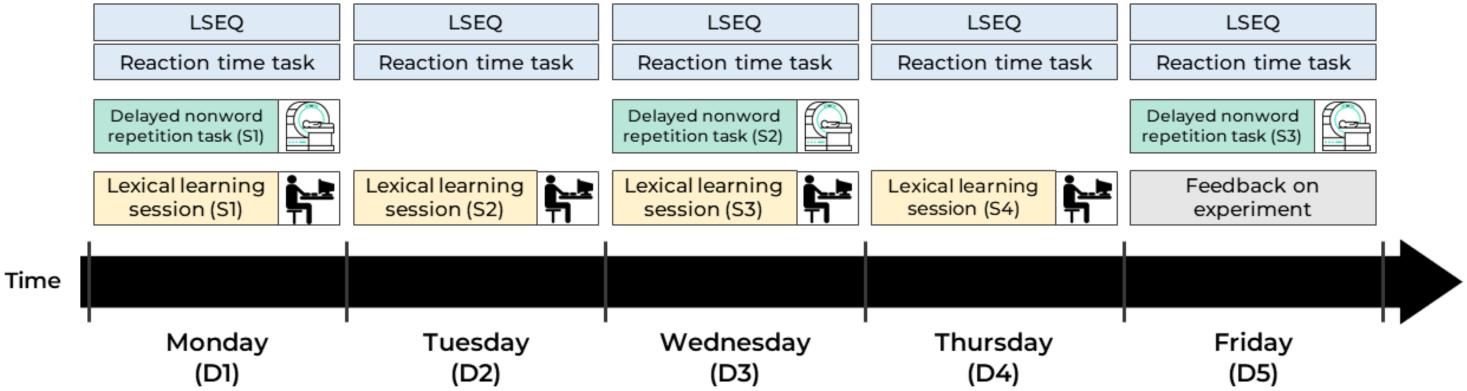

Figure 3.1. Overall procedure of the experiment.

Bayesian statistical procedures

All analyses, except for cluster-based searchlight analyses (see below), were conducted using a Bayesian statistical framework. Bayesian statistics have the advantage, relative to frequentist statistics, of determining the strength of the evidence both against and in favor of the null hypothesis in order to identify which effect is associated with the strongest evidence (Clark et al., 2018; Kruschke, 2010; Lee & Wagenmakers, 2013; Nuijten et al., 2015; Wagenmakers et al., 2018). Bayesian statistics also allow multiple statistical tests to be carried out without increasing type I error risk (Clark et al., 2018). The Bayes Factor (BF) is the likelihood ratio of a given model, the best-fitting model being the one with the highest BF. BF_{01} indicates evidence in favor of the null hypothesis, while BF_{10} indicates evidence in favor of the alternative hypothesis. Although there are no fixed thresholds for BF values, we used the following common categories for describing strength of evidence: a BF of at least 1 is considered to indicate anecdotal evidence, a BF of at least 3 is considered to indicate moderate evidence, a BF of at least 10 is considered to provide strong evidence, a BF of at least 30 is considered to provide very strong evidence, and a BF of at least 100 is considered to indicate decisive evidence (Jeffreys, 1998). Regarding statistical power, in favor in contrast to frequentist statistical frameworks, inference taken from obtained data is independent of the data collection plan (Berger & Wolpert, 1988; Wagenmakers et al., 2018; Dienes, 2011). It is however possible to conduct an indicative analysis in order to determine the sensitivity of a given Bayesian statistical design : this analysis estimates the probability of obtaining a specific BF value for a specific effect as a function of simulated sample sizes and an *a priori* estimation of the effect size (Schönbrodt & Wagenmakers, 2018). We used Monte Carlo simulations and the Bayesian Factor Design Analysis package (Schönbrodt, 2016) implemented in R (version 3.6.2) using the default Cauchy prior distribution parameters, also available on http://shinyapps.org/apps/BFDA/ to assess the sensitivity of our statistical design to provide evidence for above-chance level classification in the MVPA analyses. This design sensitivity analysis showed that if the effect of interest exists, the minimal sample size needed for reaching a specific level of evidence ($BF_{10}>3$) in favor of the effect in 100% of simulated samples was N=29. If the effect of interest does not exist, the minimal sample size needed for reaching a specific level of evidence ($BF_{01}>3$) in favor of the absence of an effect in 100% of simulated samples was N=29. For this sensitivity analysis, we assumed a medium effect size of Cohen's d = 0.5 based on previous studies that have used similar multivariate classification methodologies (see Kowialiewski et al., 2020).

MRI Acquisition

The experiment was carried out on a whole-body 3T scanner (MAGNETOM Prisma; Siemens Medical Solutions, Erlangen, Germany) operated with a 20-channel receiver head coil. Multislice T2*-weighted functional images were acquired with the multiband gradient-echo echo-planar imaging sequence (CMRR, University of Minnesota) using axial slice orientation and covering the whole brain (36 slices, multiband factor = 2, FoV = 216 × 216 mm^2, voxel size 3 × 3 × 3 mm^3, 25% interslice gap, matrix size 64 × 64 × 32, TR = 1170 ms, TE = 30 ms, FA = 90°, bandwidth = 2572 Hz/pixel). The five initial volumes were discarded to avoid T1 saturation effects. A gradient-recalled sequence was applied to acquire two complex images with different echo times (TE = 10.00 and 12.46 ms, respectively) and generate field maps for distortion correction of the echo-planar images (EPIs) (TR = 634 ms, FoV = 192 × 192 mm2, 64 × 64 matrix, 40 transverse slices [3 mm thickness, 25% interslice gap], flip angle = 90°, bandwidth = 260 Hz/pixel). For anatomical reference, a high-resolution T1-weighted image was acquired for each subject (T1-weighted 3D magnetization prepared rapid gradient echo sequence, TR = 1900 ms, TE = 2.19 ms, inversion time (TI) = 900 ms, FoV = 256 × 240 mm2, matrix size = 256 × 240 × 224, voxel size = 1 × 1 × 1 mm3, bandwidth = 250 Hz/pixel). Head movement was minimized by restraining the participant's head using a cushion. The stimuli were displayed on a screen positioned at the rear of the scanner, which the participant could comfortably see via a head coil mounted mirror. Between 1344 and 1571 functional volumes were acquired (M = 1412.052, SD = 37.804) for each session.

fMRI analyses

Image processing. Data were preprocessed and analyzed using SPM12 software (version 12.3; Wellcome Trust Centre for Neuroimaging, www.fil.ion.ucl.ac.uk/spm) implemented in MATLAB (MathWorks, Inc., Sherborn, MA). EPI time series were corrected for motion and distortion with "Realign and Unwarp" (Andersson et al., 2001) using the generated field map together with the FieldMap toolbox (Hutton et al., 2002) provided in SPM12. A mean realigned functional image was then calculated by averaging all the realigned and unwarped functional scans and the structural T1-image was coregistered to this mean functional image (using a rigid body transformation optimized to maximize the normalized mutual information between the two images). The mapping from subject to Montreal Neurological Institute space was estimated from the structural image with the "unified segmentation" approach (Ashburner & Friston, 2005). The warping parameters were then separately applied to the functional and structural images to produce normalized images of resolution 2×2×2 mm^3 and 1×1×1 mm^3, respectively. Finally, the warped functional images were spatially smoothed with a Gaussian kernel of 5 mm full-width at half-maximum. ArtRepair was used to remove residual motion from the functional images (Mazaika et al., 2009). Volumes with rapid scan-to-scan movements greater than 1.5 mm were repaired by interpolation of the two nearest non-repaired scans. No trial showed more than 2.14% of the total number of volumes replaced. The mean number of repaired scans was 0.977 % (SD = 0.499%).

Univariate analysis. Univariate analyses assessed brain activity levels associated with stimulus conditions within each stage of the delayed nonword repetition task (encoding, maintenance, recall). For each participant, brain responses were estimated at each voxel, using a general linear model with epoch regressors and event-related regressors. For the encoding stage, the regressors ranged from the onset of the probe display to the end of the stimulus broadcast. For the maintenance stage, the regressors ranged from the onset of the cross display and extended for 6000 milliseconds, stopping just before the retrieval stage. For the retrieval stage, the regressors ranged from the onset of the question mark display until the participant pressed the button on the remote control to move on to the next trial, or until 5000 milliseconds after the question mark display if no button had been pushed. The design matrix included four regressors that modeled the encoding stage, the maintenance stage and the retrieval stage: one regressor for the learned HRPF novel words, one for the non-learned HRPF novel words, one regressor for the learned LRPF novel words and one for the non-learned LRPF novel words. Each model included the realignment parameters to account for any residual movement-related effect. A highpass filter was implemented using a cut-off period of 128 s to remove the low-frequency drifts from the time series. Serial autocorrelations were estimated with a restricted maximum likelihood algorithm with an autoregressive model of order 1 (plus white noise). At the second level, we conducted repeated measures ANOVA 2 (learn vs. no learn) x 2 (HRPF vs. LRPF) for each MRI session to identify the brain regions involved in the processing of learned versus non-learned novel words and HRPF versus LRPF novel words during encoding, maintenance and retrieval in WM, for each MRI session. Linear contrasts were defined for assessing differential main effects over the three MRI sessions, for each WM stage. The resulting sets of voxel values constituted maps of t statistics [SPM{T}]. The contrasts of interest were first computed for each participant and were entered in second-level analyses. One-sample t-tests assessed the significance of the effects. Statistical inferences were performed at the cluster or voxel-level at $p < .05$ corrected for multiple comparisons (FWE corrections) across the entire brain volume. We used here a frequentist approach in order to allow better comparability with previous univariate studies which mainly used standard frequentist approaches.

Multivariate Analysis. Multivariate analyses were conducted using PRoNTo, a pattern recognition toolbox for neuroimaging (www.mlnl.cs.ucl.ac.uk/pronto; J. Schrouff et al. 2013) to determine the neural patterns associated with the four contrasts. We trained classifiers to distinguish voxel activity patterns associated with the learned vs. non-learned novel words (overall and by Novel word class) in the preprocessed and 5-mm smoothed functional images for each WM stage separately, using a binary support vector machine (Burges 1998). All models included timing parameters for HRF delay (5 s) and HRF overlap (5 s), ensuring that stimuli from different categories falling within the same 5 s were excluded (Schrouff et al. 2013). For within-task classification of semantic categories, a leave-one-block-out (LOBO) cross-validation procedure was used. At the group level, classifier performance was tested by comparing the group-level distribution of classification accuracies to a chance-level distribution using Bayesian one-sample t-tests, performed with the JASP statistical package with default prior settings (JASP team, 2023, Version 0.17.3). In addition, statistical classifier performance was assessed at the individual level using Bayesian binominal tests, which determined above chance-level individual classification accuracy thresholds with $BF_{10} > 3$. Data visualizations for the multivariate analyses were performed in R Studio (2023.09.1) with R (4.03.0).

Searchlight Analysis. Finally, a searchlight decoding approach was used to determine the local spatial distribution of the voxels that discriminate between the learned vs. non-learned novel words during encoding, maintenance and retrieval in WM (Kriegeskorte et al., 2006). Univariate voxel activity levels associated with each event of interest were first estimated at the individual level by using the beta images for each event, resulting in a total of 84 beta images per participant for the learned novel words and non-learned novel words (42 beta images per condition). Searchlight spheres of 10 mm were iteratively applied on the whole-brain multivariate feature map built from the extracted beta images, and the classification accuracy of each voxel cluster was determined, using ad hoc code built for the Pronto toolbox and available at https://github.com/CyclotronResearchCentre/PRoNTo_SearchLight.

We obtain one classification accuracy map per contrast resulting from the two-by-two classifications. These maps were then centered on zero and averaged across semantic categories conditions. These zero-centered and averaged accuracy maps were then compared to a chance-level classification distribution (e.g., Correia et al., 2014; Hebart & Baker, 2018) using one-sample t-tests conducted with SPM12. The maps were normalized to MNI space and the group results were assessed by looking for voxels with significant above-chance classification using a one-sample t-test at the whole-brain level ($p_{FWE\_corrected} < .05$, with a cluster-forming threshold of $p_{uncorrected} < 0.001$ at the voxel level; Eklund, Nichols, & Knutsson, 2016). We used here a cluster-based frequentist approach instead of the voxel-based Bayesian approach implemented in SPM12 (Han & Park, 2018) given that the searchlight strategy, involving spheres of voxels, is itself cluster-based (Haynes, 2015; Haynes &

Rees, 2006; Hebart et al., 2015). Furthermore, given that previous studies also used frequentist approaches, this allowed for better comparability of results.

Results

Behavioral results

Lexical learning sessions. A first 4 (Session: 1 vs. 2 vs. 3 vs. 4) x 2 (Novel word class: HRPF vs LRPF) Bayesian mixed ANOVA was performed on the novel word recall score in the lexical learning sessions using the JASP statistical package with default prior settings (JASP team, 2023, Version 0.17.3). The model associated with the strongest evidence included the Session and the Novel word class factors (Session: $\eta^2_p = 0.761$, Novel word class: $\eta^2_p = 0.651$) (see **Table 3.2** and **Table 3.3**). As expected, the mean number of novel words correctly recalled increased significantly with each day of learning, and the mean number of associations recalled was higher for HRPF novel words (see **Figure 3.2**).

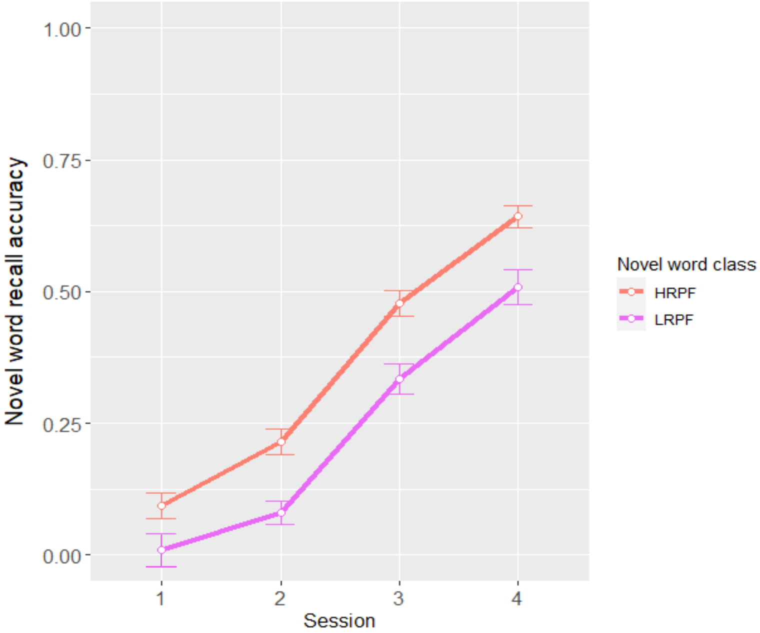

Figure 3.2. Novel word recall accuracy in terms of Session and Novel word class for the lexical learning sessions.

Table 3.2. Results of the 4x2 Bayesian mixed ANOVA for novel word recall accuracy[14]

Model Comparison

Models	**P(M)**	**P(M|data)**	**BF_M**	**BF_{10}**	**error %**
Null model (incl. subject and random slopes)	0.200	3.361^{e-32}	1.344^{e-31}	1.000	
Session + Novel word class	0.200	0.860	24.663	2.560^{e+31}	1.475
Session + Novel word class + Session ✻ Novel word class	0.200	0.140	0.649	4.152^{e+30}	2.554
Session	0.200	1.868^{e-6}	7.471^{e-6}	5.557^{e+25}	1.376
Novel word class	0.200	1.626^{e-26}	6.504^{e-26}	483793.708	1.732

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[14] $P|M$ represents the prior model probabilities, $P(M|data)$ represents the posterior model probabilities, and BF_M shows the change in model odds from prior to posterior. The BF_{10} column lists the Bayes factors for each model against the null model, and the *error %* column indicates the percentage of error associated with each model comparison.

Table 3.3. Descriptive statistics of the 4x2 Bayesian mixed ANOVA for novel word recall accuracy

Session	Novel word class	Mean	SE
1	HRPF	0.094	0.016
	LRPF	0.009	0.006
2	HRPF	0.214	0.035
	LRPF	0.080	0.020
3	HRPF	0.478	0.047
	LRPF	0.335	0.052
4	HRPF	0.643	0.043
	LRPF	0.509	0.056

In-scanner delayed nonword repetition task. Next, we performed a 3 (Session: 1 vs. 2 vs. 3 vs. 4) x 2 (Novel word class: HRPF vs LRPF) x 2 (Learning status: learned vs. non-learned) Bayesian mixed ANOVA on recall accuracy in the delayed nonword repetition task during the MRI sessions. The strongest model included the three main factors, the interaction between Session and Novel word class, and the interaction between Session and Learning status (Session: $\eta^2_p = 0.580$; Novel word class: $\eta^2_p = 0.499$; Learning status: $\eta^2_p = 0.503$; Session*Novel word class: $\eta^2_p = 0.309$; Session*Learning Status: $\eta^2_p = 0.272$) (see **Table 3.4** and **Table 3.5**). Nonword delayed repetition accuracy improved for each successive session, this improvement being particularly pronounced for the learned novel words, as expected. There was no difference between learned vs. non-learned novel words during the first MRI session, i.e. before the first learning session, but this difference started to appear during the second MRI session, i.e., after the second learning session. Nonword delayed repetition was also better for HRPF vs. LRPF novel words, this advantage becoming smaller over successive sessions (see **Figure 3.3**).

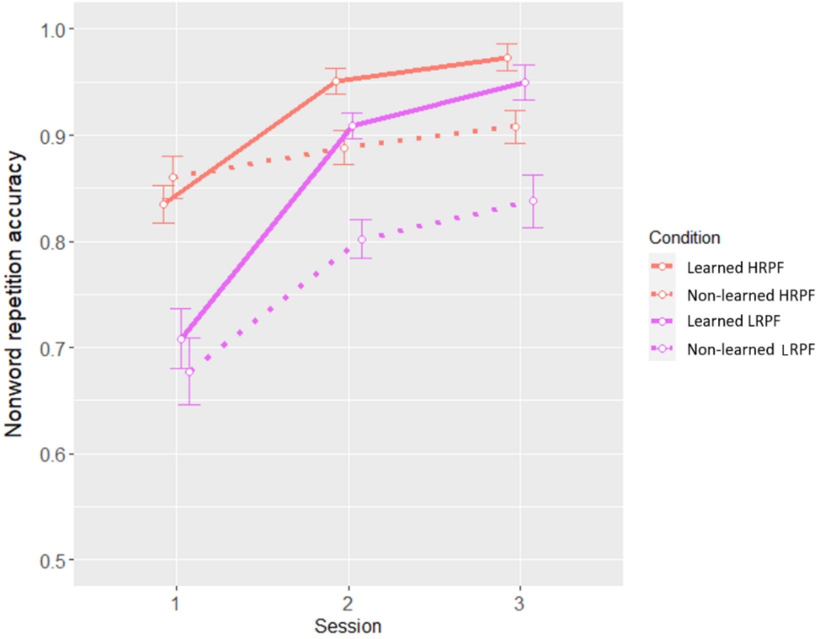

Figure 3.3. Nonword repetition accuracy in terms of Session and Condition (Learning status and Novel word class) for the delayed nonword repetition task in MRI.

Table 3.4. Results of the 3x2x2 Bayesian mixed ANOVA for the nonword repetition accuracy (MRI task)

Model Comparison

Models	**P(M)**	**P(M|data)**	**BF_M**	**BF_{10}**	**error %**
Null model (incl. subject and random slopes)	0.053	1.277^{e-22}	2.298^{e-21}	1.000	
Session + Nonword class + Learning status + Session ✻ Nonword class + Session ✻ Learning status	0.053	0.547	21.697	4.282^{e+21}	10.913
Session + Nonword class + Learning status + Session ✻ Nonword class + Session ✻ Learning status + Nonword class ✻ Learning status	0.053	0.403	12.168	3.160^{e+21}	4.271
Session + Nonword class + Learning status + Session ✻ Nonword class + Session ✻ Learning status + Nonword class ✻ Learning status + Session ✻ Nonword class ✻ Learning status	0.053	0.043	0.803	3.346^{e+20}	4.445
Session + Nonword class + Learning status + Session ✻ Nonword class	0.053	0.004	0.066	2.882^{e+19}	4.578
Session + Nonword class + Learning status + Session ✻ Nonword class + Nonword class ✻ Learning status	0.053	0.003	0.051	2.234^{e+19}	4.274
Session + Nonword class + Learning status + Session ✻ Learning status	0.053	4.459^{e-4}	0.008	3.493^{e+18}	4.928
Session + Nonword class + Learning status + Session ✻ Learning status + Nonword class ✻ Learning status	0.053	4.023^{e-4}	0.007	3.151^{e+18}	8.801
Session + Nonword class + Learning status	0.053	3.680^{e-6}	6.623^{e-5}	2.882^{e+16}	3.499
Session + Nonword class + Learning status + Nonword class ✻ Learning status	0.053	2.901^{e-6}	5.222^{e-5}	2.273^{e+16}	3.883
Session + Nonword class + Session ✻ Nonword class	0.053	2.149^{e-6}	3.869^{e-5}	1.684^{e+16}	4.981
Session + Learning status + Session ✻ Learning status	0.053	1.006^{e-7}	1.811^{e-6}	7.883^{e+14}	2.955
Session + Nonword class	0.053	2.373^{e-9}	4.272^{e-8}	1.859^{e+13}	3.112
Session + Learning status	0.053	9.028^{e-10}	1.625^{e-8}	7.072^{e+12}	3.461
Session	0.053	6.236^{e-13}	1.123^{e-11}	4.885^{e+9}	5.895
Nonword class + Learning status	0.053	7.761^{e-16}	1.397^{e-14}	6.080^{e+6}	3.274
Nonword class + Learning status + Nonword class ✻ Learning status	0.053	6.544^{e-16}	1.178^{e-14}	5.127^{e+6}	4.584
Nonword class	0.053	5.305^{e-19}	9.549^{e-18}	4155.716	3.493
Learning status	0.053	1.904^{e-19}	3.428^{e-18}	1491.691	4.957

Table 3.5. Descriptive statistics of the 3x2x2 Bayesian mixed ANOVA for the nonword repetition accuracy (MRI task)

Session	Novel word class	Learning Status	Mean	SE
1	HRPF	Learned	0.835	0.019
		Non-learned	0.860	0.022
	LRPF	Learned	0.708	0.036
		Non-learned	0.677	0.038
2	HRPF	Learned	0.951	0.013
		Non-learned	0.888	0.018
	LRPF	Learned	0.909	0.017
		Non-learned	0.802	0.027
3	HRPF	Learned	0.973	0.010
		Non-learned	0.908	0.018
	LRPF	Learned	0.949	0.015
		Non-learned	0.838	0.031

Control variables. In order to control for confounding variables potentially impacting performance in the learning and fMRI sessions, we conducted a Bayesian One-way Repeated Measures ANOVA on each of the *LSEQ* scores with Session (Session 1 vs. Session 2 vs. Session 3) as a within-participant factor. The analysis revealed only anecdotal evidence for an effect of Session on GTS score ($BF_{10} = 1.108$, $\eta^2_p = 0.081$), and anecdotal to moderate evidence for the *absence* of an effect of day on the three other scores (*QOS*: $BF_{01} = 2.246$, $\eta^2_p = 0.054$, *AFS*: $BF_{01} = 9.861$, $\eta^2_p = 0.003$, *BFW*: $BF_{01} = 3.308$, $\eta^2_p = 0.044$). These results suggest that the quality and quantity of sleep and wakefulness reported by participants remained stable throughout the experiment (see **Figure 3.4**).

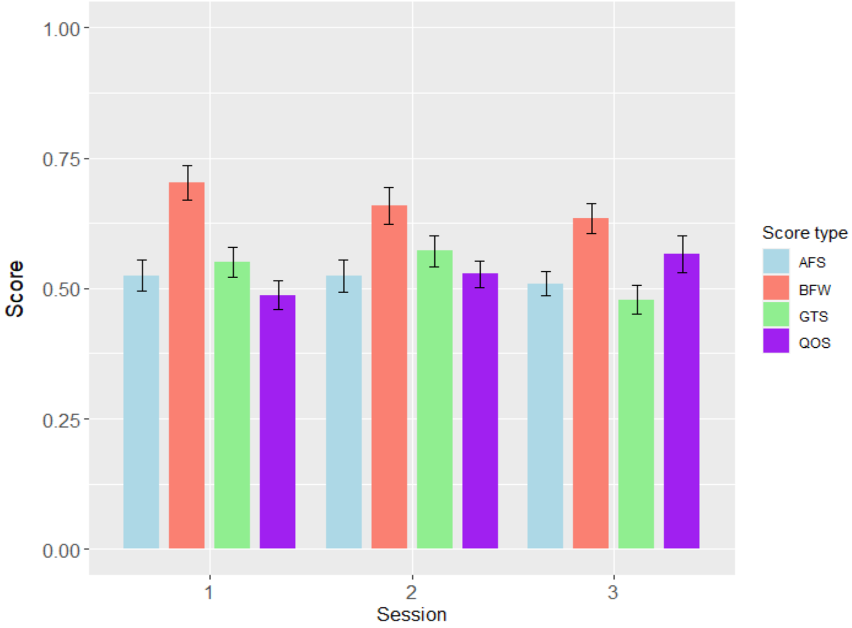

Figure 3.4. Results of the Leeds Sleep Evaluation Questionnaire, in terms of MRI session and type of score.

The same analysis was performed on performance on the *Reaction time task* aimed at assessing cognitive responsiveness over the days. The analysis revealed decisive evidence for a *negative* effect of day on reaction time (BF_{10} =

4.403^{e+6}, $\eta^2_p = 0.467$), indicating that the participants' responsiveness did improve rather than decline over the experiment (see **Figure 3.5**).

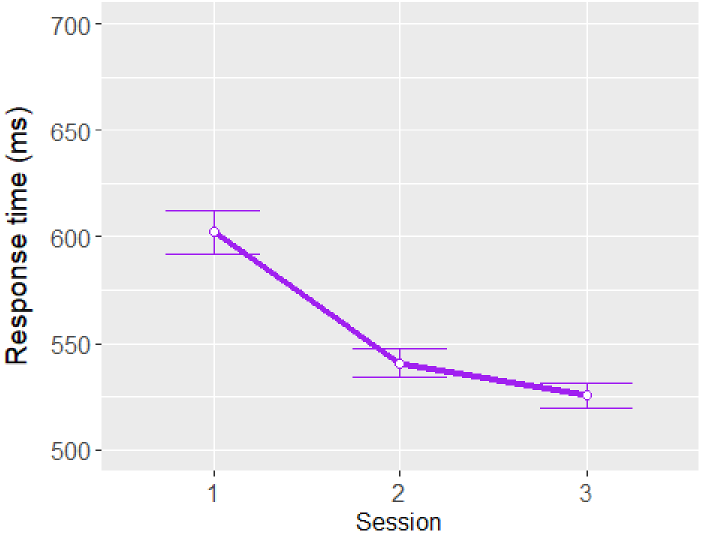

Figure 3.5. Response time (ms) for the Reaction time task in terms of MRI session.

Neuroimaging results – Univariate Analyses

Encoding. The repeated measures 2 (learning status) x 2 (novel word class) ANOVA revealed a positive main effect of learning status only, and this during the second and the third MRI sessions. In the second MRI session, a main effect of learning status was observed in the left middle and medial frontal, posterior superior temporal, bilateral angular and anterior cingulate gyri as well as the precuneus. In the third MRI session, a similar fronto-parietal network was observed with in addition the involvement of the left supramarginal gyrus and the right posterior superior temporal gyrus (see **Figure 3.6** and **Table 3.6**). For both sessions, one-sample t-tests showed that these effects reflected mainly increased activity for learned novel words. These fronto-parietal brain regions, centered on the angular gyrus, have been shown to be involved in successful episodic memory retrieval, acting to support consciously accessible representations of prior experiences (e.g., Rugg & Vilberg, 2013); a subpart of the regions showing elevated activity was also part of the dorsal language network (posterior superior temporal gyri and supramarginal gyrus).

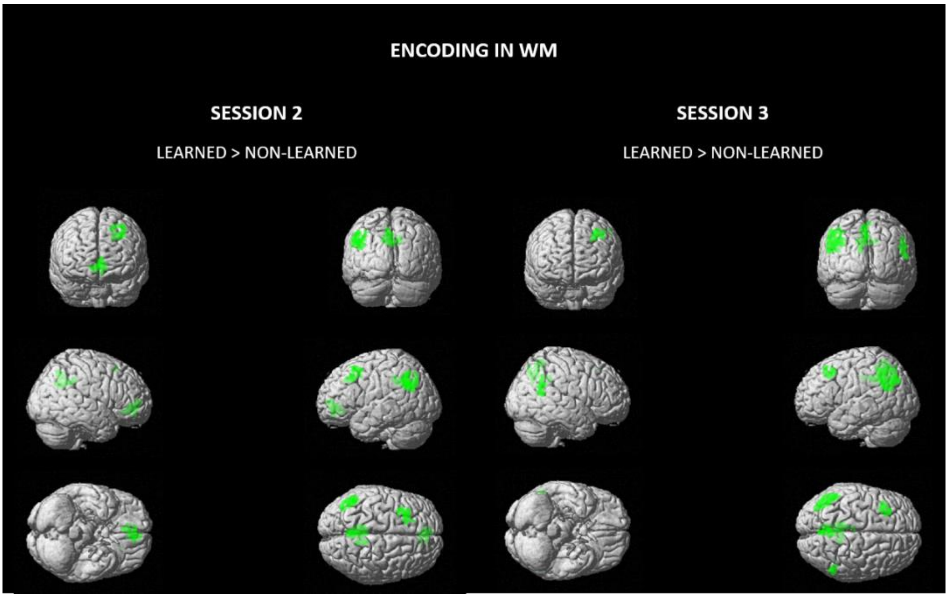

Figure 3.6. Univariate activity peaks for learned vs. non-learned novel words for the encoding stage of the second and third MRI sessions. Regions are displayed at $p < .05$ cluster-level corrected for family wise error (FWE) for whole-brain volume.

Maintenance. We observed a positive main effect of learning status only during the third MRI session, and this is in a similar although more restricted network including the left supramarginal gyrus, inferior parietal lobule, angular gyrus and precuneus, and reflecting regions of episodic memory and dorsal language networks (see **Figure 3.7** and **Table 3.6**). Once again, one-sample t-tests revealed that these effects reflected mainly increased activity for learned novel words.

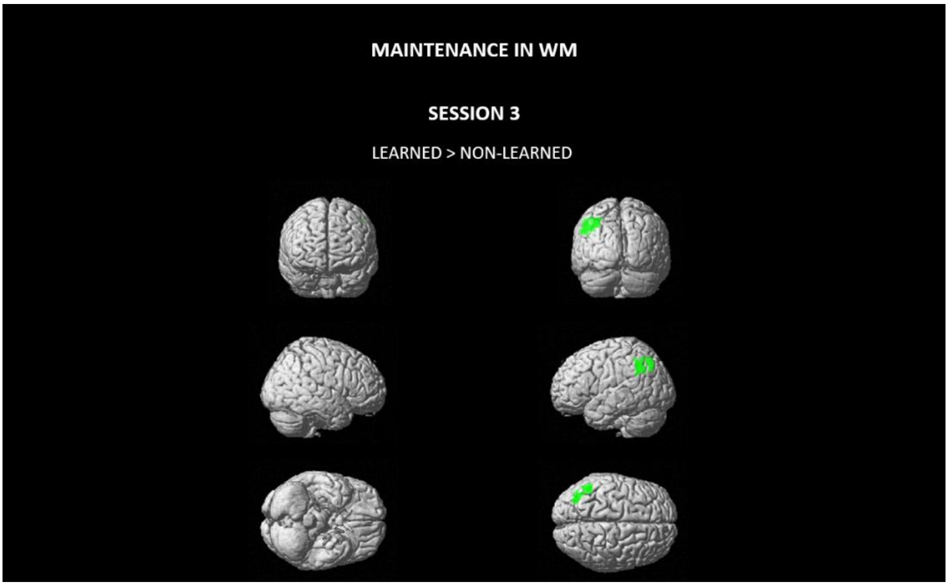

Figure 3.7. Univariate activity peaks for learned vs. non-learned novel words for the maintenance stage of the third MRI session. Regions are displayed at $p < .05$ cluster-level corrected for family wise error (FWE) for whole-brain volume.

Retrieval. No main effect or interaction was observed during retrieval in any of the sessions.

Table 3.6. Univariate main effects and between novel words comparisons for encoding and maintenance stages of the delayed nonword repetition task.

Anatomical regions	Direction of the effect	No. voxels	Left/ Right	x	y	z	*SPM Z*-value for peak-level	*F* value
Main effect of Learning status (encoding - S2)	**Learned > non-learned**							
Middle frontal gyrus		74	L	-30	20	42	4.58	24.58
Medial frontal gyrus		148	L	-2	52	6	3.69	15.89
Cingulate gyrus, *anterior*			L	-4	46	-2	3.92	17.95
Superior temporal gyrus, *posterior*		240	L	-46	-56	34	3.77	16.63
Angular gyrus			L	-40	-74	38	3.80	16.88
Inferior parietal lobule			L	-48	-56	44	4.53	24.01
Precuneus		343	L	-10	-48	36	4.11	19.70
			L	-4	-58	46	3.99	18.58
Main effect of Learning status (encoding – S3)	**Learned > non-learned**							
Superior frontal gyrus		151	L	-32	28	50	3.76	16.49
Middle frontal gyrus			L	-28	24	42	4.36	22.18
Superior temporal gyrus, *posterior*		105	R	50	-54	24	3.63	15.42
Supramarginal gyrus		392	L	-52	-54	34	3.98	18.51
Angular gyrus			L	-44	-70	36	4.69	25.76
Inferior parietal lobule			L	-48	-56	48	4.54	24.11
Cingulate gyrus, *posterior*		407	L	-10	-40	36	5.00	29.51
Precuneus			L	-4	-60	48	3.93	18.00
				0	-68	42	3.85	17.34
Main effect of Learning status (maintenance – S3)	**Learned > non-learned**							
Supramarginal gyrus		114	L	-54	-54	34	4.27	21.30
Inferior parietal lobule			L	-50	-54	46	3.88	17.59

Angular gyrus	85	L	-40	-66	50	3.67	15.79
Precuneus		L	-34	-72	48	4.34	21.97

Note. All regions are significant at $p < .05$ cluster-level corrected for family wise error (FWE) for whole-brain volume.

Neuroimaging results – Multivariate Analyses

Next, we assessed the multivariate neural patterns underlying learned vs. non-learned novel words, as a function of learning session and novel word class, for each WM stage, by running 3 (Session: 1 vs. 2 vs. 3 vs. 4) x 2 (Novel word class: HRPF vs LRPF) Bayesian mixed ANOVAs on learned vs. non-learned classification rates, and by further determining above-chance level status of these classification rates.

Encoding. The strongest model included the Session factor only (Session: $\eta^2_p = 0.188$) (see **Table 3.7**). As expected, the neural distinction between learned vs. non-learned novel words increased significantly over the three MRI sessions for the encoding stage. Bayesian One Sample T-Tests showed decisive evidence in favor of above-chance level decoding of learned vs. non-learned status for each MRI Session with progressively increasing effect sizes (Session 1[15]: $BF_{10} = 5.444^{e+7}$, $d = 1.586$; Session 2: $BF_{10} = 2.915^{e+9}$, $d = 1.894$; Session 3: $BF_{10} = 6.062^{e+9}$, $d = 1.954$). This was also confirmed by individual Bayesian binomial tests indicating that an increasing number of participants showed neural discrimination of learned vs. non-learned novel words as the sessions progressed (31.25%, 68.75%, and 71.88% of participants for Session 1, Session 2 and Session 3, respectively) (see **Figure 3.8**).

Maintenance. Similar results were observed for the ANOVA on classification accuracies for the maintenance stage, with the strongest model including the Session factor only (Session: $\eta^2_p = 0.411$) (see **Table 3.8**). As expected, the neural distinction between learned vs. non-learned novel words increased significantly over the three sessions for the maintenance stage. This is also in line with the Bayesian One Sample T-Tests showing decisive evidence in favor of above-chance level decoding only for Session 3 (Session 1: $BF_{10} = 0.019$, $d = -1.026$; Session 2: $BF_{10} = 0.969$, $d = 0.267$; Session 3: $BF_{10} =$

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[15] Above-chance level classification of learning status on Session 1 was not expected as this was a pre-learning session. This situation is most likely explained by subtle differences in phonetic aspects of the stimulus sets used for the learned and non-learned novel word sets. While the learned vs. non-learned stimulus sets were controlled for length, syllabic structure, redundancy and phonotactic frequency, a closer examination showed that the two sets showed minor differences in terms of point of articulation for the consonants of the first, second, and last syllables (see **Table C.1** in Appendix for details).

102.503, *d* = 0.675). Individual Bayesian binomial tests confirmed these results by showing that 21.88% of participants showed above-chance level decoding in Session 3, but only 3.13%, in Session 2 and none in Session 1 (see **Figure 3.8**).

Retrieval. For the retrieval stage, the strongest ANOVA model also included the Session factor only although it was associated with anecdotal evidence (Session: $BF_{10} = 1.065$, $\eta^2_p = 0.107$)[16] (see **Table 3.9**). Session-specific, Bayesian One Sample T-Tests showed decisive evidence in favor of above-chance level decoding of learned vs. non-learned novel word status with a two-fold increase between Session 1 and 3 in terms of effect size (Session 1: $BF_{10} = 919.897$, $d = 0.829$; Session 2: $BF_{10} = 396161.304$, $d = 1.237$; Session 3: $BF_{10} = 1.173^{e+9}$, $d = 1.821$). This was confirmed by individual Bayesian binomial tests indicating that 59.38% and 56.25% of participants showed above-chance level classification in Sessions 3 and 2, respectively, but only 18.75% in Session 1[17] (see **Figure 3.8**).

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[16] Note that frequentist statistical analyses reveal a significant effect of Session with a p-value of 0.03.

[17] Above-chance level classification of learning status in Session 1 is again likely due to the subtle phonetic differences in the stimulus material used for the learned vs. non-learned stimulus sets.

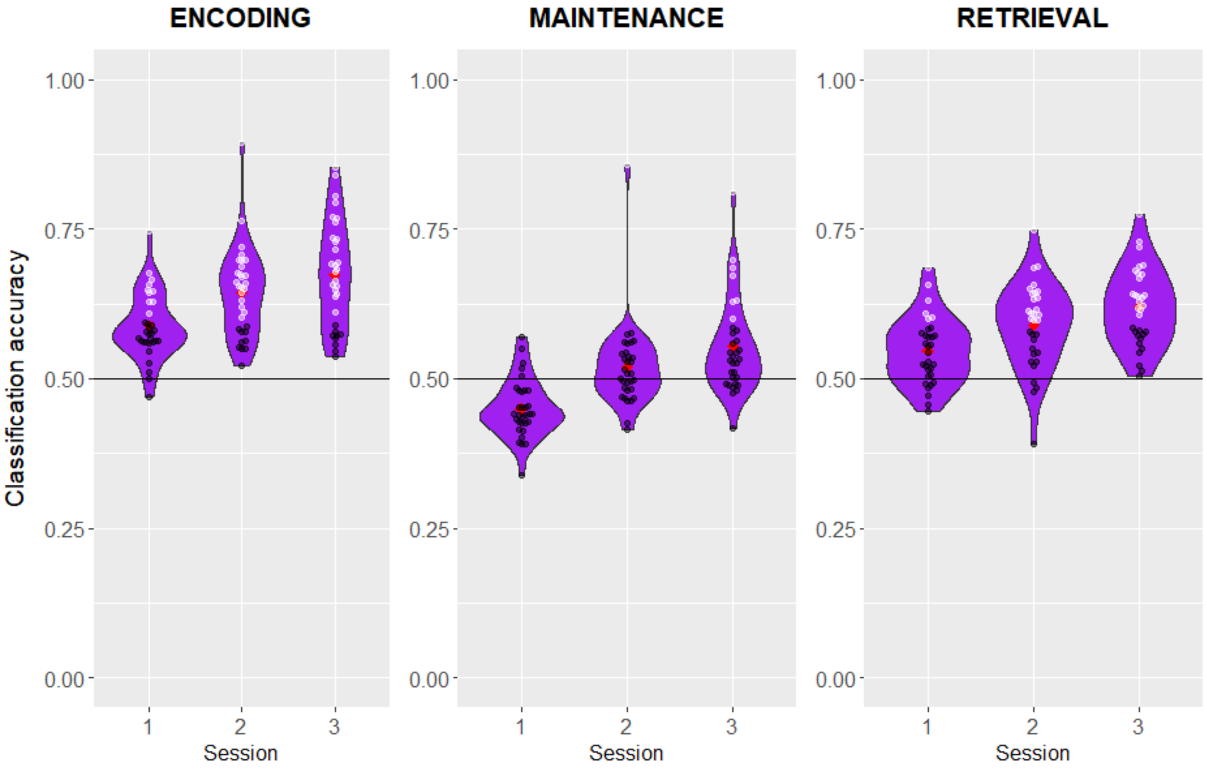

Figure 3.8. Classification accuracy for learned vs. non-learned novel words in terms of WM stage and Session, for the delayed nonword repetition task. White dots represent individual-level classifications exceeding the binomial threshold for above-chance level classification accuracy (accuracy > .595 with $BF_{10} > 3$). Red dots represent the means.

Table 3.7. Results of the 3x2 Bayesian mixed ANOVA for the MVPA classification accuracies of the delayed nonword repetition task (encoding stage)

Model Comparison

Models	P(M)	P(M|data)	BF_M	BF_{10}	error %
Null model (incl. subject and random slopes)	0.200	0.033	0.136	1.000	
Session	0.200	0.686	8.753	20.859	1.347
Session + Novel word class	0.200	0.212	1.073	6.428	1.709
Session + Novel word class + Session ✻ Novel word class	0.200	0.059	0.252	1.798	2.245
Novel word class	0.200	0.010	0.041	0.306	1.271

Table 3.8. Results of the 3x2 Bayesian mixed ANOVA for the MVPA classification accuracies of the delayed nonword repetition task (maintenance stage).

Model Comparison

Models	**P(M)**	**P(M|data)**	**BF_M**	**BF_{10}**	**error %**
Null model (incl. subject and random slopes)	0.200	4.941^{e-6}	1.976^{e-5}	1.000	
Session	0.200	0.740	11.381	149761.285	1.531
Session + Novel word class	0.200	0.224	1.154	45319.597	1.311
Session + Novel word class + Session ✻ Novel word class	0.200	0.036	0.150	7313.225	2.006
Novel word class	0.200	1.657^{e-6}	6.630^{e-6}	0.335	7.484

Table 3.9. Results of the 3x2 Bayesian mixed ANOVA for the MVPA classification accuracies of the delayed nonword repetition task (retrieval stage)

Model Comparison

Models	P(M)	P(M|data)	BF_M	BF_{10}	error %
Null model (incl. subject and random slopes)	0.200	0.375	2.402	1.000	
Session	0.200	0.400	2.662	1.065	2.633
Session + Novel word class	0.200	0.088	0.388	0.236	2.122
Novel word class	0.200	0.082	0.357	0.219	1.303
Session + Novel word class + Session ✻ Novel word class	0.200	0.055	0.232	0.146	1.819

Neuroimaging results – Searchlight Analyses

Finally, we performed a whole-brain searchlight analysis to determine the specific regions that allow for decoding of learned vs. non-learned novel words in the delayed nonword repetition task, as a function of the progression of the learning sessions. Given that the previous analyses did not reveal any specific impact of the HRPF/LRPF novel word class on the learned vs. non-learned classification accuracies and their progression over the learning sessions, we combined the two novel word classes for the searchlight analyses.

Encoding. As shown in **Figure 3.9**, significant clusters supporting the decoding of *learned vs. non-learned* novel words were identified from Session 2. These clusters involved the left superior temporal and inferior frontal gyri, which are part of the dorsal, phonological language network. Left middle frontal, pre and postcentral gyri clusters were also identified. In Session 3, decoding was observed in a more extended part of the dorsal language network (left superior temporal gyrus, supramarginal gyrus) as well as in the middle temporal gyrus part of the ventral, lexico-semantic language network. In addition, decoding was also observed in the angular gyrus as well as in the inferior parietal, middle frontal cingulate and cuneus areas reflecting regions part of the episodic memory that also showed elevated activity in the univariate analyses (see **Table 3.10**).

Maintenance. As for the encoding phase, no clusters allowing for decoding of learned/non-learned novel word status were identified in Session 1. In Session 2, clusters part of the dorsal language network (left superior temporal gyrus and posterior inferior frontal gyrus), but also clusters part of the ventral language network (middle part of the inferior temporal gyrus) allowed for decoding of novel word status. In Session 3, a more extended set of regions of the dorsal and ventral language network supported decoding. Furthermore, decoding was also observed in a more extended and bilateral set of areas in fronto-parietal cortices that had also showed increased univariate activity (see **Figure 3.9** and **Table 3.10**).

Retrieval. Finally, significant clusters allowing for decoding of learned/non-learned novel word status were identified only in Session 3, involving the right middle frontal gyrus (see **Figure 3.9** and **Table 3.10**).

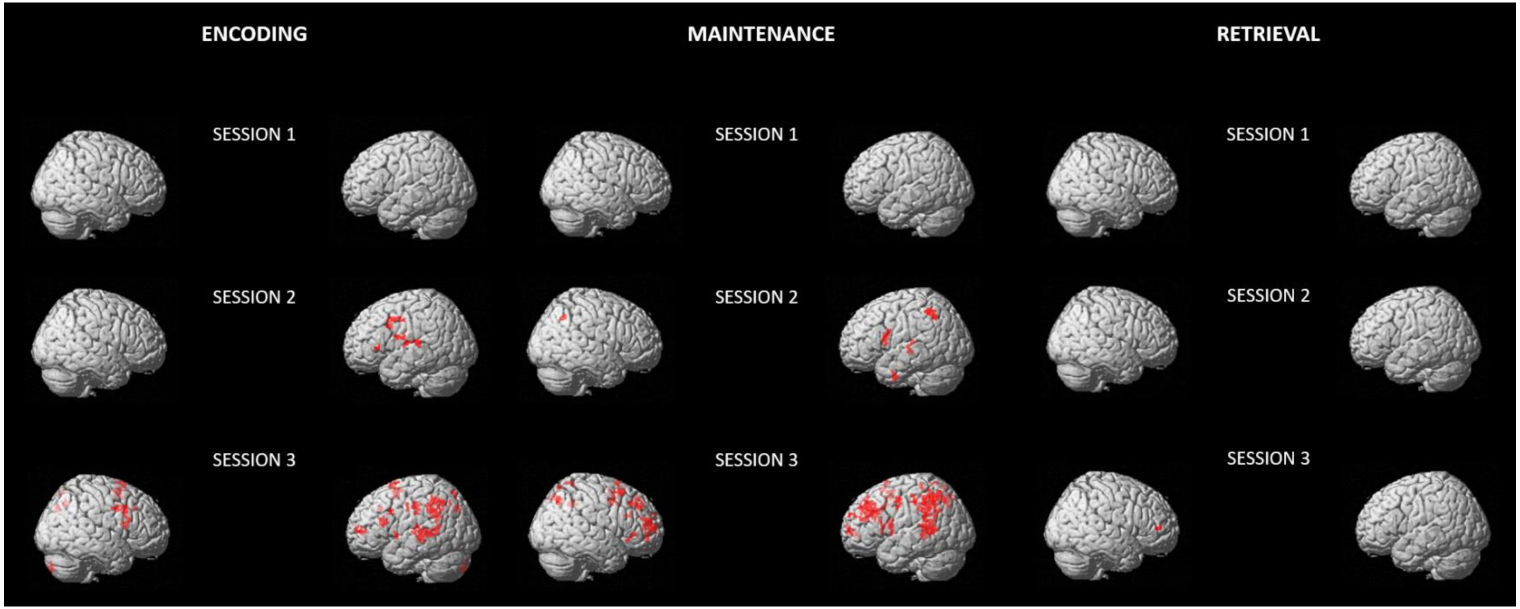

Figure 3.9. Searchlight MVPA results at the whole-brain level, at the group-level: regions contributing the most to classifications of the learned vs. non-learned novel words overall, for each session of delayed nonword repetition task, during the encoding and maintenance stages. Regions are displayed at $p < .05$ cluster-level corrected for family wise error (FWE) for whole-brain volume.

Table 3.10. Clusters showing above-chance level classification for the learned vs. non-learned novel words for each session of the delayed nonword repetition task.

Anatomical regions	No. voxels	Left/Right	x	y	z	*SPM Z*-value for peak-level	*T* value
Encoding (Session 1)				*no voxel survived*			
Encoding (Session 2)							
Middle frontal gyrus	12	L	-44	12	32	4.39	5.23
Inferior frontal gyrus	13	L	-50	0	18	5.00	6.27
	11	L	-58	28	4	4.69	5.71
Precentral gyrus	17	L	-44	4	44	3.50	3.91
	12	L	-46	-4	42	4.01	4.64
Postcentral gyrus		L	-52	-8	16	4.08	4.75
Superior temporal gyrus, *middle*	15	L	-60	-30	12	4.83	5.96
Encoding (Session 3)							
Middle frontal gyrus	34	L	-38	52	6	4.18	4.89
	19	L	-46	22	22	4.29	5.06
	16	R	52	10	40	4.37	5.19
Medial frontal gyrus	39	L	-10	12	66	4.34	5.15
	32	R	4	2	60	4.26	5.01
Inferior frontal gyrus, *pars opercularis*	13	R	54	14	14	4.54	5.47
Inferior frontal gyrus	11	R	58	18	20	3.93	4.53
Precentral gyrus	10	L	-52	-10	36	4.43	5.29
	16	R	54	4	36	4.23	4.97
Postcentral gyrus	24	L	-60	-20	38	5.28	6.80
Superior temporal gyrus, *middle*	25	L	-68	-28	2	4.77	5.85
	12	L	-56	-22	8	4.39	5.22
Superior temporal gyrus, *posterior*	14	L	-44	-52	26	4.01	4.64
	11	L	-56	-52	10	4.85	5.99

Middle temporal gyrus, *middle*	23	L	-68	-32	2	4.48	5.37
	22	L	-54	-46	44	3.88	4.45
Middle temporal gyrus, *posterior*	17	L	-58	-50	8	4.21	4.94
	13	L	-60	-38	2	3.90	4.47
Supramarginal gyrus	63	L	-48	-42	38	5.20	6.64
	11	L	-42	-50	50	3.90	4.47
Cingulate gyrus	10	L	-2	24	36	3.90	4.47
Inferior parietal lobule	63	L	-50	-36	36	4.99	6.25
	24	L	-62	-20	30	5.42	7.07
	14	L	-34	-46	46	4.25	5.00
Precuneus	11	L	-26	-74	56	3.78	4.30
		R	2	-66	48	4.13	4.81
Cuneus	20	L	-12	-78	34	4.74	5.81
Cerebellum	17	R	12	-84	-40	4.37	5.19
Maintenance (Session 1)				*no voxel survived*			
Maintenance (Session 2)							
Inferior frontal gyrus, *pars opercularis*	31	L	-58	12	16	4.54	5.46
Superior temporal gyrus, *middle*	16	L	-56	-24	8	4.86	6.02
Middle temporal gyrus, *inferior*	19	L	-52	-2	-36	4.62	5.60
Angular gyrus	12	R	40	-58	44	4.04	4.69
Supramarginal gyrus	34	L	-54	-56	46	4.48	5.37
Maintenance (Session 3)							
Superior frontal gyrus	28	L	-26	58	2	4.98	6.23
	76	R	34	60	8	5.01	6.29
	25	R	12	14	72	4.83	5.95
Middle frontal gyrus	180	L	-40	26	30	5.47	7.19
	13	L	-54	-8	42	4.87	6.03
		L	-26	44	36	4.01	4.64

	76	R	36	50	18	4.63	5.61
	21	R	28	38	36	4.37	5.19
	14	R	44	28	42	4.10	4.77
Medial frontal gyrus	21	L	-8	8	56	3.86	4.42
	10	L	-6	62	8	3.73	4.23
Inferior frontal gyrus, *pars orbitalis*	15	R	48	26	-6	4.59	5.56
Precentral gyrus	180	L	-32	28	34	4.67	5.69
	24	L	-52	6	8	4.65	5.65
	17	L	-56	-2	44	4.87	6.03
	10	R	50	2	44	4.37	5.20
Postcentral gyrus	22	L	-64	-26	42	4.39	5.23
Superior temporal gyrus, *posterior*	69	L	-62	-38	12	4.69	5.71
	11	L	-36	56	30	4.24	4.99
Middle temporal gyrus, *posterior*	69	L	-50	-48	4	5.74	7.76
Supramarginal gyrus	198	L	-48	-38	40	4.69	5.72
	18	L	-56	-54	32	4.45	5.32
Cingulate gyrus	13	L	-6	12	42	4.79	5.90
Cingulate gyrus, *anterior*	14		0	6	46	4.34	5.14
Superior parietal lobule	198	L	-42	-60	58	4.65	5.65
	10	R	10	-66	62	4.72	5.76
Inferior parietal lobule	198	L	-50	-48	46	5.49	7.22
	10	L	-32	-36	62	4.70	5.74
Precuneus	16	L	-22	-72	38	4.28	5.05
		L	-2	-74	54	4.27	5.03
	23	R	36	-66	44	4.26	5.02
	20	R	6	-44	40	4.39	5.23
Insula	19	L	-40	8	16	3.76	4.27

Retrieval (Session 1)				*no voxel survived*			
Retrieval (Session 2)				*no voxel survived*			
Retrieval (Session 3)							
Middle frontal gyrus	9	R	38	46	8	3.78	4.30

Note. All regions are significant at $p < .05$ cluster-level corrected for family-wise error (FWE) for whole-brain volume.

Discussion

The present study examined the dynamic nature of the neural substrates defining verbal WM, by studying univariate and multivariate neural changes associated with WM for verbal stimuli before and after undergoing a lexical learning process. At the univariate level, we observed, over the different learning sessions, progressively increasing activity for the encoding and maintenance of learned novel words in fronto-parietal cortices as well in temporo-parietal cortices part of the dorsal language pathway. Multivariate analyses showed that these regions, with additional contribution of regions of the ventral language pathway, reflected changes in the WM representations for learned vs. non-learned novel words, with increasing differentiation of the associated representations over the different learning sessions.

At the univariate level, our results reveal increasingly learning-related activity during a verbal WM task in at least two different types of neural substrates. On the one hand, we observed progressively increased activity for novel words in a set of fronto-parietal regions centered on the angular gyrus. This network has been consistently shown to be recruited during episodic memory recollection/retrieval (e.g., Berryhill et al., 2007; Davidson et al., 2008; Flanagin et al., 2023; Kim, 2010; Rugg & Vilberg, 2013). Although this network is very close to the fronto-parietal network involved in attentional control aspects of WM (e.g., Majerus et al., 2012, 2016), the fact that this network involved the angular gyrus and shows increased activity for learned over non-learned novel words, i.e. those becoming progressively easier to process and maintain, argues for an intervention of episodic memory rather than attentional control processes. Indeed, in the latter case, increased activity would be expected for the non-learned, most difficult-to-process novel words. Furthermore, increased activity in this fronto-parietal network for learned material is also consistent with other learning studies, showing that lexical learning does not only involve purely linguistic learning processes but also episodic learning and retrieval processes (Li et al., 2014; Tagarelli et al., 2019). Critically, the present study shows that these episodic memory processes also contribute to the short-term maintenance in verbal WM, in line with recent behavioral studies increasingly showing episodic memory contributions to

WM (Bartsch & Oberauer, 2023). On the other hand, we observed progressive univariate activity level differences in left posterior superior temporal and supramarginal areas part of the linguistic network, and more precisely of the dorsal language network. Prior research has shown that these regions are mainly associated with phonological processing (e.g., Bhaya-Grossman & Chang, 2022; Binder, 2000; Binder et al., 2000; Buchsbaum et al. 2005; Démonet et al., 1992, 1994; Graves et al, 2008; Kalm & Norris, 2014; Majerus et al., 2002; 2005; Poeppel, 1996; Ravizza et al. 2011; Strand et al., 2008), and define the dorsal stream for auditory language processing (i.e., dorsal language pathway) allowing for the integration of phonemes into articulatory representations (e.g., Hickok & Poeppel, 2004, 2007). In the present study, the word learning paradigm included both lexical and sublexical aspects of phonological learning, and the progressively increasing contribution of the dorsal language pathway for learned novel words reflects probably the learning of the sublexical mapping between the input and output representation for the novel words. Critically, increased activity for learned novel words was observed in these regions as from the second MRI session (i.e., after the second learning session) during both encoding and maintenance of these stimuli in verbal WM, demonstrating that regions associated with these sublexical phonological learning processes also progressively contribute to their maintenance in verbal WM.

Importantly, multivariate analysis provided further evidence for this progressively increasing intervention of language processing cortices in the encoding and maintenance of the learned novel words, by showing that neural patterns in the dorsal language network progressively allowed to differentiate learned from non-learned novel words during their encoding and maintenance in verbal WM. These multivariate results show that these linguistic cortices not only present elevated activity, but actually represent the learned novel words during their encoding and maintenance in verbal WM. Furthermore, the multivariate patterns in linguistic areas allowing for decoding of learned vs non-learned novel words were more widespread as the activity peaks observed in the univariate analyses, by showing a broader implication of the dorsal language network, with extensive parts of the supramarginal gyrus and larger parts of the superior temporal gyrus, but also progressive decoding in posterior mid-temporal cortices. These latter cortices are part of the ventral language network associated with lexico-semantic processes, and could reflect in the present case a progressive lexicalization of the phonological form associated with the learned novel words (e.g., Binder et al., 1997, 2009; Binney et al., 2010; Collette et al., 2001; Démonet et al., 1992, 1994; Ferreira et al., 2015; Howard et al., 1992; Hickok & Poeppel, 2004, 2007; Jackson, 2021; Jackson et al., 2015; Jung et al., 2017; Lambon Ralph et al., 2009; Majerus, 2019; Perani et al., 1996; Price et al, 1996; Visser et al., 2012; Scott et al., 2000). Critically, again, the present study shows that these changes in the nature of language representations have a direct impact on the neural substrates that support verbal WM. Finally, decoding was also observed in parts of the episodic memory fronto-parietal cortices identified in the univariate analyses, although decoding of learned vs. non-learned novel word status was not very robust in the angular gyrus, the most central part of this network.

Notably, the results for retrieval differed from the robust findings observed for the encoding and maintenance stages in WM. Univariate analyses revealed no significant effect, and although decoding was observed in the right middle frontal gyrus in Session 3 for learned vs. non-learned novel words, the extent of this decoding was limited. Similarly, although learned novel words distinguished significantly from non-learned novel words in each session, this differentiation appears to be stable over time and is not associated with significant changes in brain activity or recruitment of specific regions (e.g., Eger et al., 2009; Etzel et al., 2013). It is essential to note that with the specific design used, the actual retrieval occurs prior to the maintenance stage, and the final retrieval stage instead involves primarily articulation processes. Subtle differences in phonetic aspects of the stimulus sets must also be taken into account in explaining this pattern of results.

At a broader level, the dynamic and flexible nature of the neural substrates supporting verbal WM challenges the notion of a singular, fixed buffer system for verbal WM (Baddeley & Hitch, 1974). Our results are in line with a series of previous studies showing that neural substrates associated with phonological or lexico-semantic processing are recruited during verbal

WM maintenance of words vs. nonwords and define their representational substrates in a WM context (e.g., Lewis-Peacock & Postle, 2012; Kalm & Norris, 2014; Kowialiewski et al., 2020). The observation of the recruitment of linguistic cortices in verbal WM, and critically, their flexible updating following language learning processes, support WM models that consider that the language representations provide at least part of the representational basis for short-term maintenance of verbal information, such as hybrid models of WM-language processing (Burgess & Hitch, 1999, Cowan, 1995; Majerus, 2009, 2013, 2019; R.C. Martin et al., 1994; Postle, 2006) or fully emergent linguistic models of WM (e.g., Acheson & MacDonald, 2009; Schwering & MacDonald, 2020; N. Martin & Saffran, 1992). A phonological buffer account would have difficulties in accounting for our results as we should observe increased activity in buffer areas for the most difficult-to-maintain verbal material such as the non-learned novel words (Buchsbaum & D'Esposito, 2008). The supramarginal gyrus has been proposed to exert the role of a phonological buffer (e..g., Yue & Martin, 2021). In the present study, we observed increased activity in this area, precisely for the learned novel words, in opposite with the predictions of a phonological buffer account.

One limitation of this study that needs to be acknowledged is the absence of an effect of novel word class (HRPF/LRPF). Although we observed a robust advantage for HRPF over LRPF novel words at the behavioral level, with better recall of the HRPF novel words both during the delayed nonword repetition task and during the lexical learning sessions, no effect of novel word class was observed in either the univariate or multivariate analyses. This does not mean that HRPF and LRPF would not be decodable based on multivariate pattern analysis (this aspect was not the focus of the present study). Our results however show that the multivariate decoding of learned vs. non-learned novel words and the associated behavioral effect on novel word learning and delayed repetition did not interact with the phonological structure of the novel words, contrary to our predictions. It is possible that the redundant phonological status of the novel words provided memory cues helping processing and maintenance of highly redundant novel words, and that this benefit remained even after the lexical learning process. Future studies using novel words differing only at the level of sublexical phonotactic frequency but having all the same non-redundant structure may be better suited for examining the interaction between lexical learning and sublexical phonotactic structure of the to-be-learned novel words.

To conclude, the present study highlights the dynamic changes in neural substrates of verbal WM induced by lexical learning. These results provide further evidence for the linguistic nature of verbal WM substrates, but also emphasize the interdependence between verbal WM and episodic memory.

Appendix

Table C.1. Differences in terms of point of articulation for the first, second and last consonant of the learned and non-learned novel words sets.

POINT OF ARTICULATION	PERCENTAGE					
	SET 1			SET 2		
	Consonant 1	Consonant 2	Consonant 3	Consonant 1	Consonant 2	Consonant 3
labial	14.29%	28.57%	28.57%	50.00%	57.14%	35.71%
labiodental	14.29%	7.14%	14.29%	0.00%	0.00%	7.14%
dental	35.71%	28.57%	21.43%	21.43%	14.29%	7.14%
palatal	0.00%	7.14%	7.14%	7.14%	14.29%	7.14%
velar	21.43%	28.57%	14.29%	14.29%	7.14%	35.71%
dorsovelar	7.14%	0.00%	14.29%	7.14%	7.14%	7.14%

Note. SET 1 refers to the learned novel words and SET 2 refers to the non-learned novel words and vice versa, depending on the version of the task.

General discussion

Discussion

This PhD thesis examined the nature of the interactions between verbal WM and LTM knowledge by investigating the cognitive and neural aspects of the potential overlap between the two systems. In this Discussion section, I will start with a synthesis of the main results of the three experimental studies conducted in this PhD thesis. Then, I will discuss the implications of our findings. Finally, I will close this section by discussing the limitations and perspectives for future research on the interactions between verbal WM and LTM.

Overview of the results

In **Study 1**, we investigated the impact of syntactic knowledge on both item and serial order recall in verbal WM. Despite the potential impact of syntactic knowledge on these aspects, this linguistic variable has been little studied and is absent from most verbal WM models, contrary to phonological and lexico-semantic knowledge. We exploited the probabilistic position of adjectives relative to nouns in the French language, in which adjectives can be placed either before or after the noun, in an immediate serial recall task that included lists of adjective-noun pairs and noun-adjective pairs presented either in a regular or in an irregular syntactic order. Overall, we observed a robust impact of adjective-noun associative knowledge on item recall, while no significant effect was observed on order recall in WM. The increase in item omission errors as well as in partial pairs with the first item (adjective/noun) recalled but not the second (noun/adjective), for irregularly ordered adjective-noun pairs, suggests that irregular syntactic order of adjective-noun pairs prevents efficient encoding, maintenance and retrieval of item information. In addition, these results exclude a full independency of item and serial order recall by showing that sequential knowledge does not directly lead to an increase in serial order recall performance or serial order errors. Instead, we suggest an indirect effect of syntactic knowledge on serial order WM, mediated via syntax-dependent item retrieval processes. These findings are crucial for the present thesis, as they show that syntactic knowledge about adjective-noun associations supports at least item aspects of verbal WM.

In **Study 2**, we examined the nature of semantic knowledge activation that defines the maintenance of semantic information in verbal WM. We assessed the extent to which neural markers of semantic knowledge in LTM were similar to those in the maintenance stage of verbal WM by using an implicit semantic activation task and a verbal WM task in MRI. In the implicit semantic activation task, participants were instructed to read three-word lists from four distinct semantic categories (bird, tool, color, music). In the verbal WM task, the participants had to maintain the same four semantic categories in verbal WM. Critically, although MVPA showed reliable neural decoding of the four semantic categories in the implicit semantic activation and the verbal WM tasks, no between-task classification of semantic categories was observed. Furthermore, searchlight analyses revealed that semantic category information for the implicit semantic activation and verbal WM tasks were decoded in distinct brain regions. In the implicit semantic activation task, results showed neural decoding in superior temporal, occipital and frontal cortices associated with domain-specific semantic feature representations, while in the verbal WM task, semantic category information was decoded in anterior temporal regions associated with abstract semantic category knowledge. These findings suggest that, in verbal WM tasks, spontaneous semantic activation is mainly restricted to the intervention of relatively abstract and shallow semantic knowledge located in the anterior temporal lobe and does not reflect the full activation of the deeper semantic features that define the items to memorize. Overall, the results of Study 2 show that although WM is supported by linguistic knowledge structures, it does not purely mirror these structures.

In **Study 3**, we explored the dynamic nature of the neural substrates defining verbal WM by investigating language learning-related changes in the neural substrates that support verbal WM. We simulated the acquisition of novel words through a five-day experiment that combined a nonword repetition task in MRI and lexical learning sessions of word/novel word pairs. Over the different lexical learning sessions, we observed progressively increasing univariate activity for the encoding and maintenance of learned novel words in fronto-parietal cortices associated with episodic memory retrieval as well as in temporo-parietal cortices part of the dorsal language pathway. At the multivariate level, the WM-related neural patterns progressively discriminated between learned and non-learned novel words, and critically, searchlight analyses revealed discriminatory neural patterns in inferior frontal, supramarginal and superior temporal cortices associated with phonological processing, and posterior middle temporal cortices associated with lexico-semantic processing. Overall, the results of Study 3 reflect dynamic, learning-induced changes in the representational neural substrates of verbal WM representations.

Implications for the interactions between verbal WM and LTM knowledge

The central question addressed in the present PhD thesis was to determine the extent to which verbal WM and LTM overlap. To explore this aspect, the studies conducted aimed to answer three main sub-questions. First, do all the aspects of language levels impact WM? Second, are the neural networks involved in verbal WM similar to the neural networks involved in language processing? Finally, are the neural substrates in verbal WM sensitive to changes in long-term linguistic knowledge? In this section, I will examine the novel evidence brought by the three studies of this PhD thesis for dynamic interactions between verbal WM and LTM knowledge.

Role of LTM knowledge in verbal WM

Do all aspects of language levels impact WM?

In Chapter 2 of the Theoretical introduction, we saw that numerous evidence showed the impact of long-term linguistic knowledge on verbal WM performance, especially phonological and lexico-semantic knowledge. If verbal WM reflects LTM knowledge, as suggested by emergent language-based accounts, then all linguistic levels, including the little studied syntactic level, should impact verbal WM performance.

Study 1 was designed to investigate the specific impact of syntactic knowledge on verbal WM. We observed strong effects of syntactic knowledge on verbal WM, by showing that irregular syntactic order of adjective-noun/noun-adjective pairs prevented efficient encoding, maintenance and retrieval of item information, leading to decreased item recall performance. At the same time, no impact of irregular syntactic order was found on serial order recall performance in verbal WM.

On the one hand, it could be argued that these results add further evidence for distinction between item and serial order processes, with item information supported by language representations, and serial order information supported by specific, non-linguistic processes such as temporal, spatial, or other types of contextual positional codes (Brown et al., 2000; Burgess & Hitch, 1999, 2006; Hartley et al., 2016; Henson, 1998; Majerus, 2009, 2013). Numerous studies have indeed shown that item and serial order recall can be differentially impacted in WM and are supported by distinct brain regions. On the other hand, we argued that the absence of an effect of irregular syntactic order on serial order performance does not necessarily mean that syntactic knowledge has no impact on serial order, but could instead reflect an indirect effect of item on order recall. Indeed, given that syntactic knowledge is by essence sequential, we could expect that both item and serial order would be impacted by irregular syntactic order. We suggested that retrieval of item information is conditioned by sequential regularities, so that when a string of words (adjective-noun/noun-adjective) does not correspond to the usual succession of the words, i.e., to its corresponding sequential representation in LTM, inter-item associative chains are disrupted and successive items cannot be retrieved, leading to omission errors. Indeed, one of the most critical results of this study is the impact of irregular syntactic order on partial pairs recall. We showed that irregularly-ordered adjective-noun pairs lead to an increase of partial pairs with the first item recalled but not the second, whether the item is an adjective or a noun. In line with chaining models (e.g., Ebbinghaus, 1885; Lindsey & Logan, 2021), these results suggest that in a pair of items linked together by syntactic rules, the first item of the pair should provide a cue for the following one, but that irregular syntactic order will disrupt cuing. As a result, the first item may be retrieved, but the second will be omitted.

In sum, the results of Study 1 show that syntactic knowledge, like the other linguistic variables, has a strong impact on item recall in WM. In addition, we cannot rule out the possibility that syntactic knowledge also impacts serial order processing in WM, at least indirectly. Hence, these findings suggest that all levels of long-term linguistic knowledge have an effect on WM performance.

Are the neural networks involved in verbal WM similar to the neural networks involved in language processing?

Numerous neuroimaging data has shown the recruitment of brain regions underlying language processing during verbal WM maintenance.

In Study 3, we demonstrated that learned novel words were represented by brain regions involved in phonological and lexico-semantic processing, during encoding and maintenance in WM, as evidenced by both univariate and multivariate analyses showing the recruitment of the dorsal and the ventral language networks (Hickok & Poeppel, 2004; 2007). However, the inconsistency of behavioral findings regarding semantic effects in verbal WM also suggests that semantic knowledge may not be consistently recruited during the temporary storage of verbal information. If verbal WM reflects LTM knowledge, then we should observe the recruitment of similar neural networks during language processing tasks (including semantic processing tasks) and in verbal WM tasks involving these language representations.

Study 2 aimed to determine the nature of semantic knowledge activation defining the maintenance of verbal information in WM, by examining whether the same neural networks are involved in a language (semantic) processing task and a verbal WM task. We observed distinct brain regions involved in the implicit activation of semantic categories in LTM and their maintenance in WM, with the recruitment of superior temporal, occipital and frontal cortices vs. anterior temporal regions, respectively. It could be argued that the absence of overlap between these brain regions reflects the absence of activation of long-term semantic knowledge during verbal WM maintenance, and that semantic knowledge may not be recruited in a systematic and full manner during the short-term maintenance of verbal information, contrary to phonological and lexical knowledge. However, this aspect must be nuanced. Although the neural networks were not similar during the semantic processing and the verbal WM tasks, we did observe the recruitment of neural networks involved in semantic knowledge processing during maintenance of semantic categories in WM. Indeed, anterior temporal regions have been consistently associated with semantic identification and categorization, and with an amodal semantic representational system. We argued that maintenance of words in verbal WM does not necessarily lead to full activation of the semantic content of these words in LTM, which aligns, for instance, with the overall weak and inconsistent word imageability effects in immediate serial recall-type WM tasks (Kowialiewski & Majerus, 2018, 2020; Majerus & Van der Linden, 2003). Instead, it seems that semantic content is only activated at the most immediate, surface level during simple short-term maintenance and that semantic knowledge intervenes in a flexible manner, depending on its utility and necessity for accomplishing the WM task. Hence, although Study 2 did not show full overlap between neural networks associated with long-term semantic knowledge and verbal WM, the results still suggest that semantic knowledge is involved during verbal WM maintenance of semantic information, and this even with a single word maintained in verbal WM. However, retention in verbal WM does not simply mirror the activation of long-term semantic knowledge; rather, the extent, deepness of this activation may depend on the demands and the goals of the WM task.

Overall, these results support the idea that verbal WM at least partially reflects activation of the linguistic system, providing further evidence for the linguistic nature of the neural substrates of verbal WM. Nevertheless, activation of the linguistic system in verbal WM remains flexible and adaptive to the specific demands and context of the task.

Are the neural substrates in verbal WM sensitive to changes in long-term linguistic knowledge?

Finally, if verbal WM reflects LTM knowledge, then neural networks involved in verbal WM processing of novel words should reflect dynamic learning-related changes in long-term linguistic knowledge.

In Study 3, we did observe that neural substrates recruited during the encoding and maintenance of novel words in WM change according to the progressive acquisition of these novel words. The experimental design of Study 3 simulated the natural process of language learning, examining how the neural networks adapt to the introduction of novel words over a five-day period. The observed changes in neural activity across sessions provided valuable insights into the dynamic nature of the representational substrates in verbal WM. Univariate results showed increased activity in linguistic brain regions for learned novel words from the second session of the nonword repetition task. Multivariate analyses further highlighted the evolving nature of verbal WM representations, with learned and non-learned novel words becoming increasingly differentiated in brain region parts of the dorsal and ventral language pathways. The dynamic, learning-related neural changes in the encoding and maintenance of learned novel words in brain regions associated with language processing reflect the linguistic nature of verbal WM representations.

Notably, we also observed the involvement of fronto-parietal cortices during the encoding and maintenance of learned novel words. Although fronto-parietal networks have been associated with domain-general WM and/or attentional processes (e.g., Majerus et al., 2012, 2016; Yue & Martin, 2021), the fronto-parietal brain regions observed in this study from the second session for the nonword repetition task, centered on the angular gyrus, have been shown to be involved in successful episodic memory retrieval (e.g., Berryhill et al., 2007; Davidson et al., 2008; Flanagin et al., 2023; Kim, 2010; Rugg & Vilberg, 2013). Indeed, if the involvement of fronto-parietal regions reflected more attentional control aspects of WM, we should also have observed increased activity for non-learned novel words, which are most difficult to process. In this context, fronto-parietal brain regions may rather act to support consciously accessible representations of prior experiences, i.e., in this case, the experience of word/novel-word pairs learning. Hence, in addition to the intervention of linguistic knowledge in verbal WM, Study 3 suggests that episodic memory retrieval processes can also be recruited in verbal WM, at least in the context of lexical learning. This could indicate that verbal WM benefits from previous experiences to support processing.

In sum, the three studies conducted in this PhD thesis provide robust evidence supporting the notion of at least partial overlap between verbal WM and long-term linguistic knowledge, while emphasizing the dynamic, flexible and adaptive nature of the interactions between verbal WM and LTM knowledge. In the next section, I will discuss the implications of these findings in the broader context of verbal WM capacities and their role in the acquisition and consolidation of long-term language representations.

Role of verbal WM in the acquisition and consolidation of novel verbal information in LTM

In Chapter 3 of the Theoretical Introduction, I highlighted the pivotal role of phonological and serial order processing abilities, as well as memory consolidation processes, in the acquisition of robust long-term language representations. Although the studies of this PhD thesis were not explicitly designed to address these aspects, in this section, I discuss the bidirectional influence between verbal WM and LTM knowledge, and how verbal WM capacities contribute to the acquisition and consolidation of long-term language representations.

The bidirectional relationship between verbal WM and LTM

As we have seen, phonological abilities in WM are particularly important in the early stages of acquiring a language. They also remain available to support word acquisition across the lifespan for the efficient acquisition of novel verbal information (Gathercole, 2006). As learning novel words consists of learning both a sequence of phonemes and their correct order, phonological and serial order processes are still fundamental for lexical acquisition in adults. At the same time, adults also rely on their LTM knowledge when learning novel word forms. Previous research on language acquisition has indeed shown a shifting reliance from phonological abilities towards LTM knowledge to facilitate the acquisition of new words (e.g., Papagno et al, 1991; Service & Craik, 1993; see also Gathercole, 2006). Phonological abilities develop through exposure and acquisition of new phonological forms. Conversely, the more new forms are learned over the years, the more phonological abilities are extended and refined. Hence, while linguistic abilities in WM impact lexical acquisition, linguistic knowledge reciprocally influences verbal WM performance.

In this context, psycholinguistic effects in verbal WM might also impact the acquisition of novel verbal information, by facilitating or interfering with the temporary retention of novel word forms. The neighborhood density and phonotactic frequency effects, for instance, might play a decisive role in the ease and efficiency with which novel verbal forms are maintained in WM, and then integrated as LTM knowledge. Novel words with high neighborhood density may be easier to learn than those with low neighborhood density (e.g., Vitevich & Storkel, 2013), and novel words with high phonotactic frequency may be easier to learn than those with low phonotactic frequency (e.g., Ellis & Beaton, 1993; Kaushanskaya et al., 2011; Morra & Camba, 2009). With regard to this last aspect, in Study 3, we observed that the learning curve was relatively similar between the learned HRPF and LRPF novel words in the lexical learning sessions, although the learned HRPF novel words were better recalled overall. In the delayed nonword repetition task, repetition was better for learned HRPF vs. LRPF novel words, but while this advantage was significant in the first session, it became smaller over successive sessions. In addition, at the neural level, no effect of novel word class was observed in either the univariate or multivariate analyses, suggesting that there was no interaction between the phonological structure and the ease or speed of learning these novel words.

Previous studies did observe the impact of psycholinguistic effects on lexical learning (e.g., Ellis & Beaton, 1993; Kaushanskaya et al., 2011; Morra & Camba, 2009). Bartolotti and Marian (2016) have shown that neighborhood density and phonotactic probability impact memory for novel words in adults. Storkel and colleagues (2006) suggested that phonotactic frequency might aid in triggering new learning, whereas neighborhood density may influence the integration of new lexical representations with existing representations. In this study, we combined two types of psycholinguistic variables: phonological redundancy and phonotactic frequency. However, the potentially strong effect of redundancy on repetition and recall of novel words (words with the same vowel in each syllable being easier to recall overall) may have masked possible interactions between phonotactic frequency and the learning status of novel words. In this context, using only non-redundant novel words with high or low phonotactic frequency might be more relevant for the potential observation of the interaction between phonological structure and the learning status of novel words.

Hence, although it is difficult to interpret whether phonotactic frequency actually had an impact on the ease of learning novel words in Study 3, it is essential to recognize and take into account the bidirectional relationship between verbal WM capacities and LTM knowledge, either in verbal WM tasks or in language learning.

Memory consolidation

Study 3 was specifically designed to simulate the acquisition of novel words. Novel phonological forms were associated with existing words and these associations were trained during brief yet repetitive learning sessions. Learning-related changes during the delayed nonword repetition task occurred after only two lexical learning sessions of less than ten minutes each, showing the impressive potential for dynamic adaptation of the cognitive system.

A number of studies on memory consolidation suggest that newly encoded information is initially stored in the short term in both the hippocampal formation and the corresponding neocortex (e.g. Dudai, 2002, 2004; Squire & Alvarez, 1995), and that word learning is initially supported by interactions between left temporal regions involved in the perception and comprehension of spoken words, and medial temporal systems including the hippocampal regions (e.g., Davis & Gaskell, 2009; Gupta & Tisdale, 2009;

Ripollés et al., 2017; Ullman, 2005, 2016). However, we did not observe the recruitment of hippocampal regions in either univariate or multivariate analyses. Instead, we observed progressively increasing contribution of the dorsal language pathway for learned novel words, after the second learning session, and then, progressive decoding in posterior mid-temporal cortices, parts of the ventral language pathway, of learned vs. non-learned novel words.

Given that numerous studies did show the involvement of the medial temporal lobe and particularly hippocampal regions in adult lexical learning, the recruitment of dorsal and ventral language pathways with the absence of involvement of hippocampal regions in Study 3 seems somewhat surprising at first. However, it is important to note that the brain regions observed primarily reflect the processes involved during a nonword repetition task. If we had conducted a lexical learning task in MRI, it would probably have been possible to observe the involvement of hippocampal regions during initial learning, reflecting the formation of novel memory traces. As our task does not specifically involve significant new learning, but rather the repetition of phonological stimuli, it is logical that the brain regions involved reflect language and verbal WM aspects. In addition, several studies also showed that aspects of lexical learning can rely on language pathways and neocortical brain regions even without hippocampal involvement (e.g., Merhav et al., 2015; Sharon et al., 2011; Tagarelli et al., 2019). In this context, the results that we obtained in Study 3, not aligning with traditional memory consolidation theories, rather reflect the partial overlap between verbal WM and long-term linguistic knowledge during nonword repetition *before and after* lexical learning. The neural changes that we observed during encoding and maintenance of learned and non-learned novel words in verbal WM reflected, first, learning of the sublexical mapping between the input and output representation for the novel words, and then, the progressive lexicalization of the phonological form associated with the learned novel words, with the integration of this novel information into the existing lexico-semantic network (Hickok & Poeppel, 2004; 2006), with the additional involvement of fronto-parietal networks supporting episodic learning and retrieval processes (e.g., Bartsch & Oberauer, 2023).

In sum, the results of the current PhD thesis suggest that dynamic interactions exist between verbal WM and LTM knowledge. First, all linguistic levels appear to have an impact on verbal working memory performance. Secondly, the nature and extent of activation of linguistic, or at least semantic, knowledge can be flexible and may depend on the goals and demands of the task. Furthermore, the involvement of linguistic knowledge may be associated with learning-related changes and episodic memory processes. Finally, the bidirectional influence between language capacities, such as phonological capacities, and verbal WM must be considered in these interactions. In the next section, I will describe the theoretical implications of the results of this PhD thesis in the light of WM models.

Theoretical implications

Overall assessment of multicomponent accounts

According to multicomponent accounts of verbal WM, the interactions between WM and LTM are limited and indirect, with verbal WM operating largely independently of LTM and language processing mechanisms (Baddeley, 1986; Baddeley & Hitch, 1974; Norris, 2017). Verbal WM performance is defined by the capacity of a temporary buffer. In line with this view, effects of long-term linguistic knowledge have been attributed to secondary, redintegration-based mechanisms, with degraded phonological traces stored in a WM buffer undergoing a post-encoding clean-up process involving comparison with linguistic knowledge to facilitate their reconstruction (Hulme et al. 1991, 1997; Lewandowsky & Farrell, 2000; Schweickert 1993). Several aspects of the results of this PhD thesis do not align with these accounts.

First, the impact of all linguistic levels, including syntactic knowledge, on verbal WM performance, is not compatible with a potential independence between verbal WM and LTM. In addition, the progressive recruitment of linguistic neural networks during encoding and maintenance of learned vs. non-learned novel words in Study 3 rather shows that verbal WM and long-term linguistic knowledge interact dynamically. At the behavioral level, it could be argued that the recall advantage for learned novel words over non-learned novel words in the delayed nonword repetition task reflects reconstruction processes occurring during recall, but our results show that long-term linguistic knowledge is already recruited from encoding. Notably, although significant decoding between learned and non-learned novel words was observed for the three sessions of the delayed nonword repetition task during recall, no main effect of learning status was observed, and except the right middle frontal gyrus in the third session, no significant clusters allowed for decoding learned and non-learned novel words during recall.

In Study 2, we observed that the maintenance of words in verbal WM does not necessarily lead to full activation of the semantic content that defines the words. In line with redintegration-based accounts, it could be argued that long-term semantic knowledge only intervenes later, via reconstruction mechanisms occurring during retrieval. Our results do not support this view, since they showed that decoding of semantic category information at the retrieval stage was even lower than during the initial maintenance stage. At the same time, the low WM load reduces the likelihood of memory decay at the moment of retrieval, and we cannot completely reject this hypothesis.

Finally, the existence of a single, fixed phonological buffer system is not compatible with the results observed in Study 3. We showed an advantage for learned novel words as compared to non-learned novel words, as well as increasing decoding between the novel words in the dorsal and ventral language pathways, from the second delayed nonword repetition task in MRI. To support the phonological buffer account, the results should have shown increased activity in buffer areas such as the supramarginal gyrus for the most difficult-to-maintain verbal material such as the non-learned novel words, but instead, we observed increased activity specifically for the learned novel words.

In sum, the majority of the results obtained from the three studies of this PhD thesis are not consistent with multicomponent accounts of verbal WM. In the following section, I will discuss the evidence supporting or in contradiction with fully and partially emergent, language-based accounts of verbal WM.

Overall assessment of emergent accounts

As described in Chapter 1, fully emergent accounts of verbal WM consider that WM is the activated portion of long-term linguistic knowledge, with both the temporary representation of item information and serial order information supported by language representations (e.g., Acheson & MacDonald, 2009; MacDonald, 2016; MacDonald & Christiansen, 2002; N. Martin & Saffran, 1992; Schwering & MacDonald, 2020). On the other hand, hybrid or partially emergent accounts suggest that although WM and LTM interact, WM performance cannot be reduced to activated linguistic knowledge. In this context, serial order and attentional control processes are distinct from linguistic knowledge activation in verbal WM (e.g., Cowan, 1995; Majerus, 2009, 2013, 2019; R.C. Martin et al., 1994, 1999). Our results more strongly align with the latter account, showing that verbal WM and long-term linguistic knowledge at least partially overlap, and that LTM knowledge may rather intervene in a flexible manner in verbal WM.

In Study 1, we showed that syntactic knowledge about adjective-noun associations supports at least item aspects of verbal WM, in line with the view that verbal WM performance is determined to a large extent by access to long-term linguistic structures that correspond to the stimuli to be memorized. In addition, we observed that sequential knowledge about adjective-noun order, although having a strong impact at the item level, does not appear to support the maintenance of order information. These findings are not consistent with fully emergent linguistic accounts of WM that consider that any type of knowledge that defines language processing should also define WM processing. These results rather support hybrid, partially emergent accounts of verbal WM considering that serial order processing is distinct from linguistic knowledge activation. At the same time, we cannot completely rule out a potential effect of syntactic knowledge on serial order processing. Instead, illegal adjective-noun orderings may prevent the retrieval of associated item information rather than directly leading to order errors, with successive items not being retrieved as inter-item associative chains are disrupted (e.g., Ebbinghaus, 1885; Lindsey & Logan, 2021). The predictable nature of the syntactic frame may also have prevented order recall errors from occurring (e.g., Garrett, 1988; Levelt, 1999). Nevertheless, the results of Study

1 suggest that all levels of linguistic knowledge, including syntactic knowledge, have an impact on verbal WM performance.

R.C. Martin and colleagues (1994, 1999) suggested that long-term linguistic knowledge is connected to two distinct buffer systems reflecting phonological and semantic information, based on research demonstrating that phonological and semantic deficits in verbal WM were associated with different patterns of impairment in language comprehension and production. While the phonological buffer has been suggested to be located in the posterior superior temporal/supramarginal gyrus, the semantic buffer is rather associated with middle and inferior temporal gyri involved in representing semantic information. As discussed, in Study 3, we observed increased activity in the supramarginal gyrus specifically for the learned novel words, which is not in line with the existence of a phonological buffer. In addition, we observed in Study 2 that maintenance of words in verbal WM does not necessarily lead to full activation of the semantic content of these words in LTM, by showing distinct neural networks recruited in a language-processing task and in a verbal WM task involving semantic categories. On the one hand, the recruitment of anterior temporal regions related to abstract semantic processing still suggests that semantic knowledge is activated in verbal WM maintenance, albeit at a more superficial level. On the other hand, it also suggests that retention in verbal WM does not simply mirror the activation of long-term semantic knowledge, but rather, that the extent and deepness of semantic knowledge activation depend on its utility and necessity for accomplishing the WM task. These findings are in line with partially emergent accounts and research suggesting that the processes defining WM performance depend on specific task demands and goals (e.g., Badre & Wagner, 2007; Barrouillet et al., 2011).

Finally, in Study 3, the progressive recruitment of linguistic neural networks during encoding and maintenance of learned vs non-learned novel words, and their flexible updating following language learning, support emergent, language-based accounts of verbal WM considering that the language representations provide at least part of the representational basis for short-term maintenance of verbal information. In addition, the recruitment of additional fronto-parietal brain regions involved in successful episodic memory retrieval also suggests that the short-term retention of learned novel words not only involves purely linguistic learning processes but also episodic learning and retrieval processes.

Overall, the results of the present PhD thesis support hybrid, partially emergent accounts of verbal WM, while adding novel insights to these models. We showed that there is at least partial overlap between verbal WM and long-term linguistic knowledge, and that LTM knowledge intervenes in a flexible manner in verbal WM. In the next section, I provide suggestions for adapting hybrid, partially emergent models to take account of these novel aspects.

Proposals for an integrative hybrid account

In light of the evidence presented in the previous sections, it would be interesting to have a comprehensive theoretical framework capable of encompassing the dynamic, flexible and adaptive nature of the interactions between verbal WM and long-term linguistic knowledge. While hybrid models, which take into account language representations in LTM (Cowan, 1995; Majerus, 2009, 2013, 2019), serial order processing, as well as attentional and control processes, align closely with our empirical data, certain elements appear to need adaptation. This section aims to propose suggestions for an integrative hybrid approach of verbal WM by synthesizing key elements of existing models and adapting them to account for the findings from the studies of this PhD thesis.

As a starting point for the development of an integrative hybrid model, it is worth noting a recent proposal by Rose (2020), who introduced a dynamic processing model of WM. According to this perspective, WM is conceptualized as a dynamic collection of processes intimately linked to perception, attention, semantic and episodic memory, and prospective action - all working in harmony to facilitate goal-relevant behaviors. Rose insists that the nature of these representations and processes evolves over time and in different contexts. While this conceptualization provides a valuable foundation, it must be adapted to account for the nuanced interactions between verbal WM and long-term linguistic knowledge, as revealed by the studies presented in this thesis.

The first fundamental addition to existing models of verbal WM is the incorporation of syntactic knowledge. Emergent models have primarily focused on phonological and lexico-semantic representations, without explicitly incorporating the complex role that sequential syntactic knowledge plays in the processing of verbal information. By integrating syntactic representations into the conceptualization of verbal WM, we should more accurately reflect the multifaceted nature of long-term language representations. However, one question remains unanswered: do these syntactic representations only have an impact on item information, or do they also influence serial order processing in verbal WM? Given its intrinsically sequential nature, syntactic knowledge may not only impact item recall, as evidenced in Study 1, but may also play a crucial role in the maintenance and retrieval of sequential information.

Second, models should capture the flexible and adaptive nature of at least some language representations, such as semantic knowledge. The recruitment of neural networks involved in abstract semantic processing during a verbal WM task, as observed in Study 2, highlights the need to go beyond static views of direct activation of deep linguistic knowledge. The depth and extent of semantic activation, for instance, may depend on the demands and goals of the task, as well as being influenced by attentional and control processes (Cowan, 1995; Oberauer, 2002). Furthermore, it would be interesting for verbal WM models to reflect variations linked to different stages of learning or processing, as demonstrated in Study 3. The evolution of neural patterns observed during the acquisition of novel words underlines the importance of incorporating a temporal dimension into this theoretical framework. Models must not only take into account the maintenance of steady-state information, but also the dynamic changes that can occur during learning. This temporal adaptability is a crucial aspect of verbal WM, as it enables the model to flexibly capture the cognitive processes involved in the initial encoding, maintenance and retrieval of verbal information over time. This emphasis on flexibility and adaptation would ensure that this theoretical account aligns with the interactions between verbal WM and long-term linguistic knowledge revealed in this thesis.

Finally, in addition to long-term linguistic knowledge, verbal WM models need to establish a connection with episodic memory processes, as discussed in Study 3. The observed involvement of fronto-parietal brain regions associated with successful episodic memory retrieval suggests that verbal WM also interacts with these LTM processes. Recognition of this link is essential for a comprehensive understanding of the functioning of verbal WM, particularly in tasks involving the acquisition and retention of novel verbal information.

In sum, dynamic interactions are clearly present between verbal WM and linguistic LTM knowledge. These systems are not separate, but rather in constant interaction. Hence, it is important to emphasize not only the bidirectional links between all verbal WM components, but also to capture the flexible and adaptive nature of linguistic activations.

Limitations and perspectives

The studies conducted in the present PhD thesis provide valuable insights into the dynamic and flexible nature of the interactions between verbal WM and long-term linguistic knowledge. However, no research is perfect, and it is crucial to address the limitations and remaining open questions raised by our studies. Propositions for future research will also be presented in this section.

One of the limitations of the present studies is the relatively limited consideration of inter-individual variability among participants. Individual differences, such as age, educational background, linguistic proficiency, as well as cognitive factors such as executive functions, may also impact verbal WM performance. First, the studies did not include comprehensive pre-experimental assessments of participants' cognitive and linguistic abilities, which could have provided valuable insights into potential variations within the samples. Another notable limitation is the exclusive focus on a homogeneous group of healthy young adults with a high level of education. While this demographic choice offers certain advantages in terms of experimental control, it raises questions about the generalizability of results to the broader population. On the one hand, relying on a sample of young adults may not fully reflect the variations present in children or the elderly. Similarly, verbal WM and its interactions with linguistic long-term knowledge may exhibit distinct patterns in patients with neuropsychological or linguistic deficits, such as in aphasia. Expanding the sample of participants to a more diverse range of ages and neuropsychological profiles would provide a better understanding of how the interactions between verbal WM and LTM knowledge vary across the lifespan and in diverse populations. This consideration becomes particularly relevant when extrapolating the implications of the results to educational or clinical contexts beyond the demographic scope of the current participants.

In Chapter 3 of the theoretical introduction, I mentioned that numerous studies have shown correlations between children's receptive vocabulary and verbal WM performance (e.g., Avons et al., 1998; Bowey, 1996; Gathercole, 1995; Gathercole & Adams, 1993, 1994; Gathercole & Baddeley, 1989, 1990a, 1993; Gathercole et al., 1991, 1992, 1999; Gray et al., 2022; Leclercq & Majerus, 2010; Majerus et al., 2006; Michas & Henry, 1994). Extensive research has indeed focused on the impact of language development on verbal WM performance. At the neural level, numerous studies have explored the maturation of neural substrates associated with WM (e.g., Finn et al., 2010; Kharitonova et al., 2015), but few of them have specifically investigated the evolving neural substrates associated with the impact of language development on verbal WM performance (see for example Attout et al., 2019). Longitudinal neuroimaging studies may be useful to explore the developmental trajectory of neural activation patterns during language acquisition and its interaction with verbal WM processes. It would provide a more nuanced understanding of how the neural networks supporting verbal WM undergo dynamic changes in response to the development of language capacities.

Similarly, studies have demonstrated that older adults show clear deficits in WM, characterized by poorer recall performance and slower response times compared to younger adults (e.g., Bopp & Verhaeghen, 2005; Verhaeghen et al., 2019; Nittrouer et al., 2016). General factors of cognitive aging have been proposed to affect WM functioning, such as decline of processing resources, decrease of processing speed or inefficient inhibition (see Park & Festini, 2017 for a review) but poorer efficiency of attentional refreshing and phonological awareness have also been suggested as contributors to decreased serial order recall accuracy in aging (e.g., Jarjat et al., 2019; Nittrouer et al., 2016). In addition, WM capacity has been suggested to account for much of the variance in preserved language comprehension in older adults (e.g., Carpenter et al, 1994; DeCaro et al., 2016; Nittrouer et al., 2016). However, further research is needed to define age-related changes in the neural substrates associated with verbal WM. Additionally, while linguistic knowledge may remain intact or even improve with age, deficits in language production, word-finding failures, increased slips of the tongue, and increased pauses in speech have been observed (e.g., Rossi & Diaz, 2016). Hence, exploring whether age-related changes in the neural substrates of verbal WM can be associated with linguistic knowledge deficits would be an interesting perspective of investigation.

At the neuropsychological level, robust associations have been shown between verbal WM and language deficits in patients with language disorders, such as in aphasia (e.g., N. Martin & Saffran, 1990; 1997; N. Martin et al., 1996; Saffran & Martin, 1990). In this context, research has shown promising outcomes regarding the impact of interventions targeting verbal WM on language processing in aphasia, which impairs access to and retrieval of language representations (e.g., Nikravesh et al., 2021). Indeed, if verbal WM involves the temporary activation and maintenance of linguistic knowledge, interventions that train these processes can potentially improve language processing. Numerous studies have explored the neural plasticity associated with aphasia treatments (see Schevenels et al., 2020 for a review), but there remains a need for further research specifically focusing on the neural changes in linguistic brain regions related to verbal WM training – for instance, in the dorsal and ventral language pathways. At the same time, verbal WM does not only involve linguistic knowledge but also serial order, attentional and control, and potentially episodic memory retrieval processes, which partly explains the heterogeneity of verbal WM impairment observed in aphasia. In this context, it seems essential to characterize more precisely the nature of the WM components altered and trained during rehabilitation. By investigating the specific neural substrates and cognitive processes impacted in verbal WM in patients with aphasia, interventions may be more precisely adapted to target the underlying mechanisms responsible for linguistic deficits, potentially allowing for more targeted and effective rehabilitation strategies.

Other perspectives could rely on the neuroimaging techniques used. Several complementary techniques would be interesting for investigating the dynamic, flexible interactions between verbal WM and long-term linguistic knowledge. The complementary use of connectivity analyses, EEG to capture real-time neural dynamics, and magnetoencephalography (MEG) for high temporal resolution, could offer a more nuanced understanding of the dynamic interactions between verbal WM and long-term linguistic knowledge. As verbal WM is associated with extended and potentially adaptive neural networks, formed by interconnected cortical and subcortical areas, investigating the changes in connectivity patterns should be considered. Connectivity analyses may provide valuable insights into the specific distribution of neural activity over the networks involved in verbal WM, and may reveal how brain regions change dynamically in verbal WM as a function of task demands and cognitive load. In addition, the use of EEG may be particularly relevant in verbal WM studies as it could allow for the examination of rapid neural oscillations and event-related potentials associated with different verbal WM stages. Similarly, MEG may provide additional temporal precision, capturing the millisecond-level dynamics of cognitive processes. Integrating these complementary neuroimaging techniques alongside fMRI could provide a more comprehensive and multi-faceted understanding of the neural substrates supporting the dynamic interactions between verbal WM and long-term linguistic knowledge.

Remaining questions

While our studies have provided valuable novel evidence, several aspects specific to our studies warrant further investigation. The first one is the potential impact of syntactic knowledge on serial order processing in verbal WM. As previously discussed, the redundant and predictable nature of the WM lists in Study 1 could partially explain the absence of an effect of irregularly ordered sequences on serial order recall. To address this, further research could mix adjective-noun and noun-adjective pairs to prevent predictability of the sequence, and without any interval between the pairs. Additionally, exploring the same effects on noun-verb sequences in regular and irregular order could provide further insights into the impact of syntactic knowledge on verbal WM, given that verbs are an obligatory constituent of natural sentences, unlike adjectives.

Another aspect is the interaction between lexical learning and the sublexical phonotactic structure of learned novel words in Study 3. The redundant phonological status of the novel words may have provided memory cues helping the processing and maintenance of highly redundant novel words. To better understand this interaction, future studies could use novel words having all the same non-redundant structure, varying only in sublexical phonotactic frequency.

Finally, an interesting line of investigation would be to assess the stability of the learning-related neural changes observed in Study 3, observed after four lexical learning sessions, over an extended period of time. Investigating the persistence or evolution of these neural changes after several weeks or months could provide valuable information about the long-term effects of lexical learning on the neural substrates associated with verbal WM.

Conclusion

This PhD thesis investigated the nature of the interactions between verbal working memory and long-term memory knowledge by investigating the cognitive and neural aspects of the potential overlap between the two systems. Our findings revealed at least a partial overlap between verbal WM and long-term linguistic knowledge, characterized by dynamic and flexible interactions. First, we showed that all linguistic levels, including syntactic knowledge, have a strong impact on item recall in WM. In addition, we cannot rule out the possibility that syntactic knowledge also impacts serial order processing in WM given the possibility of disrupted inter-item associative chains associated with irregular sequential order preventing the retrieval of successive items. Second, we showed that the activation of semantic knowledge in verbal WM is flexible. Although brain regions involved in semantic processing are recruited during maintenance of semantic information in verbal WM, retention in verbal WM does not simply mirror the activation of long-term semantic knowledge. Instead, the extent of this activation may depend on the demands and the goals of the WM task. Finally, we demonstrated that neural substrates in verbal WM are sensitive to changes in long-term linguistic knowledge, with the involvement of linguistic neural substrates being dynamic and adaptive to learning, and the additional implication of episodic memory processes. Overall, this PhD thesis supports hybrid, partially emergent language-based models of WM, while highlighting the need for a more integrative approach that takes account of all language representations, recognizes possible interactions with episodic memory processes, and reflects the flexible and adaptive nature of interactions between verbal WM and LTM knowledge.

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