Comenius University in Bratislava
Faculty of Mathematics, Physics and Informatics

# The Role of Working Memory in Controlled Semantic Cognition

Diploma Thesis

2020
Bc. Klára Horváthová

Comenius University in Bratislava
Faculty of Mathematics, Physics and Informatics

# The Role of Working Memory in Controlled Semantic Cognition

Diploma Thesis

Study Programme: Cognitive Science
Field of Study: 2503 Cognitive Science
Department: Department of Applied Informatics
Supervisor: Mgr. Martin Marko, PhD.

Bratislava, 2020
Bc. Klára Horváthová

96523523

Comenius University in Bratislava
Faculty of Mathematics, Physics and Informatics

# THESIS ASSIGNMENT

| | |
|---|---|
| **Name and Surname:** | Bc. Klára Horváthová |
| **Study programme:** | Cognitive Science (Single degree study, master II. deg., full time form) |
| **Field of Study:** | Computer Science |
| **Type of Thesis:** | Diploma Thesis |
| **Language of Thesis:** | English |
| **Secondary language:** | Slovak |

**Title:** The role of working memory in controlled semantic cognition

**Annotation:** Semantic system creates and structures knowledge that guides adaptive cognition and behavior. The ability to access and use relevant semantic information is underpinned by several neurocognitive mechanisms, which are poorly understood. This project aspires to investigate the cognitive systems and mechanisms that regulate the retrieval of information from semantic memory. Using a systematic manipulation of working memory load, we will inspect the role of working memory in automatic and controlled semantic retrieval.

**Aim:** The goal is to define fundamental determinants and correlates of lexical-semantic processing with the main focus on the role of working memory.

**Literature:** Badre, D., Poldrack, R. A., Paré-Blagoev, E. J., Insler, R. Z., & Wagner, A. D. (2005). Dissociable controlled retrieval and generalized selection mechanisms in ventrolateral prefrontal cortex. Neuron, 47(6), 907–918. https://doi.org/10.1016/j.neuron.2005.07.023
Lambon Ralph, M. A., Jefferies, E., Patterson, K., & Rogers, T. T. (2016). The neural and computational bases of semantic cognition. Nature Reviews Neuroscience, 18, 42.

**Keywords:** Semantic cognition, semantic retrieval, cognitive control, working memory

| | |
|---|---|
| **Supervisor:** | Mgr. Martin Marko, PhD. |
| **Department:** | FMFI.KAI - Department of Applied Informatics |
| **Head of department:** | prof. Ing. Igor Farkaš, Dr. |
| **Assigned:** | 14.10.2019 |
| **Approved:** | 30.01.2020 |

prof. Ing. Igor Farkaš, Dr.
Guarantor of Study Programme

.......................................................
Student

.......................................................
Supervisor

96523523

Univerzita Komenského v Bratislave
Fakulta matematiky, fyziky a informatiky

## ZADANIE ZÁVEREČNEJ PRÁCE

**Meno a priezvisko študenta:** Bc. Klára Horváthová
**Študijný program:** kognitívna veda (Jednoodborové štúdium, magisterský II. st., denná forma)
**Študijný odbor:** informatika
**Typ záverečnej práce:** diplomová
**Jazyk záverečnej práce:** anglický
**Sekundárny jazyk:** slovenský

**Názov:** The role of working memory in controlled semantic cognition
*Úloha pracovnej pamäti v kontrolovanej sémantickej kognícii*

**Anotácia:** Sémantický systém vytvára a uskladňuje poznatkové štruktúry, ktoré regulujú kognitívne funkcie a adaptívne správanie. Schopnosť vyhľadať a sprístupniť relevantné sémantické informácie je podmienená viacerými kognitívnymi mechanizmami, ktorých povaha ostáva nejasná. Tento projekt sa sústredí na preskúmanie kognitívnych systémov a mechanizmov, ktoré riadia vybavovanie informácií zo sémantickej pamäti. Pre tento účel využijeme systematickú manipuláciu záťaže pracovnej pamäti, čím určíme jej úlohu pri automatickom a kontrolovanom vybavovaní informácií zo sémantickej pamäti.

**Cieľ:** Cieľom projekt je určiť hlavné determinanty a koreláty lexikálne-sémantického spracovania informácií so zameraním na úlohu pracovnej pamäti.

**Literatúra:** Badre, D., Poldrack, R. A., Paré-Blagoev, E. J., Insler, R. Z., & Wagner, A. D. (2005). Dissociable controlled retrieval and generalized selection mechanisms in ventrolateral prefrontal cortex. Neuron, 47(6), 907–918. https://doi.org/10.1016/j.neuron.2005.07.023
Lambon Ralph, M. A., Jefferies, E., Patterson, K., & Rogers, T. T. (2016). The neural and computational bases of semantic cognition. Nature Reviews Neuroscience, 18, 42.

**Kľúčové slová:** Sémantická kognícia, sémantické vybavovanie, kognitívna kontrola, pracovná pamäť

**Vedúci:** Mgr. Martin Marko, PhD.
**Katedra:** FMFI.KAI - Katedra aplikovanej informatiky
**Vedúci katedry:** prof. Ing. Igor Farkaš, Dr.

**Dátum zadania:** 14.10.2019

**Dátum schválenia:** 30.01.2020

prof. Ing. Igor Farkaš, Dr.
garant študijného programu

.................................................. ..................................................

študent vedúci práce

I hereby declare that the presented master's thesis is original and the result of my own investigations. Formulations and ideas taken from other sources are cited as such.

. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .

Acknowledgments: I would like to thank my supervisor Mgr. Martin Marko, PhD. , whose guidance, patience with my questions and valuable commentaries helped with this research and the thesis. Also, I am very thankful to my colleague Danijela, with whom I conducted our experiments.

# Abstract

The semantic system creates and structures knowledge that is crucial for cognition and context-relevant behavior. In order to access and use relevant semantic information, our executive system employs various neurocognitive mechanisms. Previous research has proposed several accounts to explain control over semantic processes, but this issue still remains poorly understood. The aim of this thesis was to investigate the cognitive systems and mechanisms responsible for semantic memory retrieval. To assess complex lexical-semantic functioning we used a novel methodology designed by Marko et al. (2019b), which enables the assessment of automatic and controlled lexical-semantic retrieval. We conducted an experiment with 44 healthy young adults to study the role of working memory (WM) in automatic (associative) and controlled (dissociative) semantic retrieval. For these purposes, we used a dual-task paradigm to systematically manipulate the WM load. Participants completed the lexical-semantic task in two conditions (associative, dissociative) under different WM load (no-load, low load, high load). For control measures, they completed also WM tasks, to assess individual WM capacity. Our results showed longer response latency under WM load in both retrieval conditions, thus WM load impaired both forms of retrieval in a similar fashion. This suggests that WM interacts with the semantic system in a generic way, likely biasing activation spreading and/or semantic search towards appropriate retrieval candidates. Further research is needed to account for this effect in lexical-semantic tasks using the dual-task paradigm.

Keywords: Semantic cognition, semantic retrieval, cognitive control, working memory

# Abstrakt

Sémantický systém vytvára a usporadúva poznatky, ktoré sú kľúčové pre naše poznávanine a relevantné správanie v danom kontexte. Aby sme získali prístup k týmto poznatkovým štruktúram a mohli ich používať, náš exekutvny systém využíva rôzne neurokognitívne mechanizmy. Predchádzajúci výskum navrhol viaceré prístupy, ktoré vystvetľujú riadenie sémantických procesov, avšak tento problém ostáva stále nedostatočne pochopený. Cieľom tejto práce bolo preskúmať kognitívne systémy a mechanizmy, ktoré sú zodpovedné za vybavovanie zo sémantickej pamäte. Aby sme posúdili komplexné lexikálno-sémantické fungovanie poznávania, použili sme novú metodológiu navrhnutú Markom a kol. (2019b), ktorá umožňuje hodnotenie automatického a riadeného lexikálno-sémantického vybavovania. Uskutočnili sme experiment so 44 zdravými mladými dospelými ľuďmi, u ktorých sme sledovali úlohu pracovnej pamäte (PP) v automatickom (asociatívnom) a riadenom (disociatívnom) sémantickom vybavovaní. Na tieto účely sme použili paradigmu dvojitej úlohy, aby sme mohli systematicky manipulovať so záťažou PP. Účastníci mali splniť lexikálno-sémantickú úlohu v dvoch podmienkach (asociatívna a disociatívna), a pri rôznom zaťažení PP (bez zaťaženia, nízke zaťaženie, vysoké zaťaženie). Ako kontrolné merania sme mali úlohy na PP, ktorými sme merali kapacitu PP jednodlivcov. Naše výsledky ukázali dlhšiu latenciu odpovedí pri záťaži PP v oboch podmienkach, takže zaťaženie PP narušilo obe formy vybavovania podobným spôsobom. To naznačuje, že PP všeobecne interaguje so sémantickým systémom, pravdepodobne ovplyvňuje šírenie aktivácie a/alebo sémantické vyhľadávanie smerom k vhodnému kandidátovi na sémantické vybavenie. Na zohľadnenie tohto javu v lexikálno-sémantických úlohách pomocou paradigmy dvojitej úlohy je potrebný ďalší výskum.

Kľúčové slová: Sémantická kognícia, sémantické vybavovanie, kognitívna kontrola, pracovná pamäť

# Contents

Introduction 1

1 Semantic cognition 3
1.1 Semantic retrieval . . . 4
1.1.1 Automatic semantic retrieval . . . 4
1.1.2 Controlled semantic retrieval . . . 5
1.2 Neural bases of semantic cognition . . . 6
1.2.1 Controlled semantic cognition (CSC) framework . . . 8

2 Working memory 11
2.1 Phonological loop . . . 12
2.2 Visuo-spatial sketchpad . . . 12
2.3 Episodic buffer . . . 12
2.4 Cognitive models of working memory . . . 13
2.5 Neural mechanisms of working memory . . . 13
2.5.1 Persistent neural activity . . . 14
2.5.2 Hierarchical representations in prefrontal cortex . . . 14
2.5.3 Top-down signaling . . . 14
2.5.4 Long-range connectivity . . . 15
2.5.5 Brainstem neuromodulators . . . 15
2.6 The role of WM in semantic processing . . . 16

3 Research problem 19
3.1 General objective . . . 19
3.2 Methodological approach . . . 19
3.3 Hypotheses . . . 19

4 Method 21
4.1 Participants . . . 21
4.2 Procedure . . . 21
4.2.1 Associative chain test . . . 22

4.2.2 Dual-task paradigm . . . . . . . . . . . . . . . . . . . . . . . . . 23
4.2.3 Working memory measures . . . . . . . . . . . . . . . . . . . . . . 25
4.3 Data analysis . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 26

5 Results 29
5.1 Main experiment . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 29
5.2 Working memory correlation results . . . . . . . . . . . . . . . . . . . 30

6 Discussion 35
6.1 The contribution of working memory in semantic retrieval . . . . . . . . 36
6.2 The effect of Working memory capacity in semantic cognition . . . . . 38
6.3 Limitations . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 39

Conclusion 41

# List of Figures


1.1 A depiction of components in the Controlled semantic cognition framework 10

4.1 The associative chain test in associative and dissociative condition . . . 23
4.2 Associative chain test with concurrent working memory task . . . . . . 24
4.3 The working memory capacity measures . . . . . . . . . . . . . . . . . 25

5.1 Mean RT ( $1SE$) of the ACT measures . . . . . . . . . . . . . . . . . 30
5.2 Working memory correlation plots I. . . . . . . . . . . . . . . . . . . . . 32
5.3 Working memory correlation plots II. . . . . . . . . . . . . . . . . . . . . 33

# List of Tables

5.1 Main effects of ACT . . . . . . . . . . . . . . . . . . . . . . . . . . . . 29
5.2 Pearson Correlations . . . . . . . . . . . . . . . . . . . . . . . . . . . . 31

# Introduction

Semantic cognition is increasingly becoming a vital factor in a context relevant behavior. Last decades of research suggested that semantic cognition relies on the interaction between two cognitive and neural systems including left lateral prefrontal cortex and left anterior temporal regions (Ralph et al., 2017; Whitney et al., 2011). The system for representation of conceptual knowledge supports bottom-up automatic processes of semantic retrieval. The system for semantic control exerts executive semantic processing to regulate the propagation of semantic activation in a top-down manner. This control system is crucial for task-relevant semantic retrieval and takes part in high-level executive processes like semantic memory search or inhibition. Ralph et al. (2017) proposed a controlled semantic cognition (CSC) framework which links these two systems and their interaction. They also suggest that the general-domain executive brain network is engaged when the control system is occupied by the highly demanding task. Nevertheless, the neuro-cognitive mechanisms for the employment of such executive functions in semantic retrieval remain poorly understood.

The aim of this study is to examine the contribution of a domain-general executive system in automatic and controlled semantic retrieval. For these purposes, we utilize a dual-task paradigm to effectively manipulate the working memory load. That involves executive processing while focusing on performance in the lexical-semantic task.

This research is a part of a larger project investigating the automatic and controlled cognitive processes underlying the semantic retrieval. The general goal of the project is to determine the main correlates of processes involved in semantic retrieval. Our focus is the relationship between semantic retrieval and performance in accompanying tasks assessing core executive functions.

For the purposes of the project Marko et al. (2019b) developed a new methodology for complex assessment of lexical-semantic functioning. The associative chain test (ACT) enables the assessment of automatic and controlled lexical-semantic retrieval. In this thesis we investigate the interaction between these two systems with the use of a concurrent task loading working memory. For the purposes of this research we only use a manipulation of cognitive load with an accompanying working memory task without transcranial electrical stimulation of the prefrontal cortex.

The first and second chapter provide a brief overview of the literature on the semantic system, automatic and controlled semantic retrieval and working memory as a part of general-domain executive functions. The third chapter presents our research question and hypothesis. In the following chapter we describe a novel methodology for addressing this problem together with described participants, procedure and each task. The next chapter reports results from the experiment which leads to a discussion about their possible implications. Some conclusions and possible limitations are drawn in the final chapter.

# Chapter 1

# Semantic cognition

Semantic memory is the core of our human behavior. The way it encodes and retains information about the world is critical to our cognition. In various contexts or environments we are able to access information about objects or events and represent concepts. We can form context-relevant answers or responses to various sensory-motor inputs. In addition, semantic memory stores knowledge of words and their meanings, and can represent concepts in the form of natural language. It also stores the knowledge about the world in the form of facts, concepts and information about objects (Tulving et al., 1972). Together with episodic memory, it is part of the declarative long-term memory. In contrast to episodic memory, semantic knowledge is abstracted from experience, generalized and then extracted from any reference to previous experience, whereas episodic memory supports the conscious remembering of our everyday life experiences (Binder and Desai, 2011).

The research on semantic memory was pioneered by Tulving et al. (1972). The nature of stored information in semantic memory is influenced by episodic memory, because we had to learn everything at some point in our lives, but this information of how the learning occurred is usually not remembered for a long time. However, we do not acquire knowledge only actively, but we also do it in a passive manner and thus this information must be encoded and stored in semantic memory, too. All information which enters the episodic memory is from perceptual inputs and similarly such perceived environment is an input to the semantic memory, too. Various studies focused on patients with brain lesions show that they are unable to form new episodic memories, their ability to form new semantic memories is not affected. It is suggested that these two memory systems closely interact with each other but at the same time are separate memory storages.

The retrieval from each memory system is entered to episodic memory, strengthening the representation of these contents. The process of semantic retrieval is described in the next section.

## 1.1 Semantic retrieval

One of the crucial functions of semantic memory is semantic retrieval. In order to use and manipulate semantic knowledge in a given context, we need to retrieve this information from our semantic structure. There is a considerable amount of literature dealing with retrieval from semantic memory. Already in 1973 Kesner proposed two distinct processes of long-term memory retrieval. Later in 1975 Posner et al. (1975) identified the so-called automatic spreading-activation process and the limited-capacity attentional mechanism involved in such retrieval.

Nowadays the spreading activation process would describe bottom-up automatic retrieval from semantic memory and the limited capacity attentional mechanism would stand for top-down control mechanisms of semantic memory. This was demonstrated using the paradigm of semantic priming (Neely, 1977; Hill et al., 2002). Until today these two processes are considered to be crucial in semantic retrieval and in recent years there has been considerable interest in describing semantic cognition as an emerging feature from the interaction of these two processes. Automatic semantic retrieval is considered to be very fast and it depends on the strength of associations between the retrieval cues and relevant knowledge. Controlled semantic retrieval, on the other hand, is slower, and usually depletes some executive resources. Sometimes it is also called an inhibitory process because the automatically cued knowledge must be suppressed in order to retrieve more effortful, goal-oriented knowledge from the semantic memory storage.

### 1.1.1 Automatic semantic retrieval

Automatic semantic retrieval is supported by spreading activation within semantic structures that encode knowledge. When a cue is presented, its representation in the long-term memory is activated together with other associated representations or because these two representations overlap in some features. The concurrent activated associations depend on the strength of previous association activation. It is called the central prediction of the spreading-activation model (Baror and Bar, 2016). Automatic retrieval is not consciously controlled, thus the activation occurs very rapidly and is context-independent. The retrieval requires minimal attention and is compulsory. The retrieved association does not need to be relevant to the cue or task (Badre and Wagner, 2002), the retrieval is based on the strength of the association. According to Badre and Wagner (2007) the mechanism underlying activation of associated concepts works in a bottom-up fashion. Inputs are processed cues from the environment and these activate associated representations in the temporal cortex independent of the control mechanism in the prefrontal cortex.

In a study by Baror and Bar (2016), they examined automatic associations under high-load and low-load working memory conditions. The task was to report rapidly the first association that came to mind as the participants viewed each of a series of target words. The cognitive load was manipulated by a concurrent working memory task as cognitive load and working memory are taken as an equivalent (Baror and Bar, 2016). For the working memory task they used the Digit-span task (Wechsler, 1949). They manipulated the load under low (4 digits) and high (7 digits) load conditions. In one of the experiments, they compared remembering 4 or 7 digits and suggest that associative activation relies on available resources. In the low-load condition they proposed, that the brain was in an exploratory state and that the immediate associations were inhibited in favour of more original or remote associations.In contrast to the low-load condition, the high-load condition lowered the resources, which suggests that the brain was more in the exploitative state. Considering this, they indicated that the load changes the threshold for conscious access and not the strength of activation, which means that in the high-load condition the associations were more automatic than in low-load. It also shows that the spreading activation of associations depends on executive resources.

### 1.1.2 Controlled semantic retrieval

Controlled semantic retrieval in comparison to automatic semantic retrieval is engaged when the task demands are not sufficiently met by activation of automatic associative representations (Badre and Wagner, 2002). As we mentioned in the paragraph above, the automatic retrieval is not always context dependent, so when there is the need for goal-oriented or task-relevant representation to be activated, the control mechanism is engaged to bias the retrieval of certain conceptual representations to satisfy the demand of the task. Controlled semantic retrieval is a more conscious mechanism thus it is slower and more demanding. It can incline to the retrieval of a more task-relevant representations or information when competing with stronger automatic activation of task-irrelevant representations and can inhibit the retrieval of such unrelated, dominant representation (Badre and Wagner, 2002). This mechanism searches memory strategically and can direct attention to the related retrieved information. The processes behind controlled semantic retrieval are referred to as (semantic) control mechanisms, which are supported by the prefrontal cortex and are crucial for the effective manipulation of relevant semantic knowledge. The cognitive determinants of controlled semantic retrieval have mostly been studied using dual-task interference studies and using an individual differences approach (Herdman, 1992; Becker and Killion, 1977).

### Cognitive control mechanisms

Badre et al. (2005) studied cognitive control mechanisms and proposed the contribution of the ventrolateral prefrontal cortex (VLPFC) to the cognitive control of semantic memory. They considered two functionally and neuroanatomically distinct mechanisms underlying the controlled semantic retrieval (1) *the generalized selection mechanism* and (2)*the controlled retrieval process*.

The generalized selection mechanism or post-retrieval selection engages when a competition of various retrieved representations occurs and helps to choose the task-relevant information. This mechanism activates regardless of automatic or controlled activation. The domain of such selectivity is putatively domain-general, i.e., it is involved when multiple representations are activated whether from the semantic, phonological or perceptual domain. The control demand will increase when the level of competition between relevant and irrelevant retrieved knowledge is high.

The controlled retrieval process works in a top-down manner by activating task-related representations. When automatic retrieval with bottom-up cues is not sufficient to retrieve relevant knowledge, the demands on controlled retrieval increase. When automatic and controlled processes retrieve multiple representations, the post-retrieval selection is needed to resolve the competition. In the controlled retrieval of conceptual knowledge, distinct left VLPFC mechanisms activate and influence activation in conceptual stores which are in the lateral temporal cortex. The controlled processes are demanding when the automatic bottom-up processes are not effective in retrieving goal-relevant knowledge from memory. The domain of controlled mechanisms is only semantic.

These two cognitive control mechanisms are centred in different parts of PFC, the post-retrieval selection is situated in the mid-VLPFC and the controlled retrieval process is placed in the anterior VLPFC. The distinction between these mechanisms follows from the nature of representations manipulated by each of these mechanisms. The controlled retrieval process may directly influence long-term semantic representations stored in lateral temporal regions, while the post-retrieval selection is resolving the competition between multiple retrieved representations sustained in working memory (Badre et al., 2005).

## 1.2 Neural bases of semantic cognition

Various approaches have been suggested to describe the structure of the semantic system (Jefferies et al., 2020). It has been indicated that this system consists of various subsystems and interacts with not only semantic specific networks but also general-domain executive networks. In the classical approach, the semantic system was described as a hierarchical structure with concepts in the nodes and its parameters in the leaves, interconnected with other concepts and based on their proximity of concepts. This view served mostly for computational models of the semantic system and it failed to provide an extensive description of the underlying mechanisms sub-serving the semantic system.

In a more recent review Fedorenko and Thompson-Schill (2014) propose a quite different structure of the language network. Firstly, they investigated when a network is considered to be domain specific and when it can be described as multiple demand or general-domain network. They argue that by having one node functionally specialized, the network is qualified as domain specific but at the same time having one general-domain node is not sufficient to call a network domain-general, because it is known that various domain-general processes as attention or working memory are involved in all mental processes. To address this, they propose a different strategy, that the specific co-activation between various nodes to be is the key to defining whether a network is domain-specific or not.

A number of studies have found that the language network includes both functionally specialized brain regions and brain regions which are considered to be part of the general domain network. The functionally specialized regions co-activate and interact with each other consistently throughout time. Whether the general domain regions are recruited, depends on the task demands and current goals.

The past decade of neuroimaging studies and studies with patients has shown that the semantic system is regulated by top-down and bottom-up processes. Previous lesion studies provided evidence that language processing in the brain is sub-served by representational and executive processes. These studies have shown an importance of the left inferior prefrontal cortex (LIPC) in high-level executive processes as semantic search, strategic access, inhibition and selection (Badre et al., 2005; Thompson-Schill et al., 1997), whereas the representation processes are tought to be part of temporal or parietal lobes mostly in angular gyrus (AG) and anterior temporal lobes (ATL) (Ralph et al., 2017) .

More recent evidence (Schwartz et al., 2011) shows that semantic processing is supported by two separate semantic stores – hubs. One of them is situated in the ATL and represents knowledge of taxonomic categories[1]. The second hub is located in AG or posterior middle temporal gyrus (pMTG) and represents knowledge of thematic associations.

In contrast to the dual hub theory, Whitney et al. (2011) suggest, that conceptual knowledge is in a single semantic hub located in ATL. The semantic cognition thus emerges from the interaction between the semantic hub and the semantic control.

[1]categories organised according to similarities between groups in hierarchical order

### 1.2.1 Controlled semantic cognition (CSC) framework

The CSC framework describes the semantic hub as a system of representation (Ralph et al., 2017). This system is responsible for forming knowledge of concepts and creating relationships between higher order sensory, motor, linguistic and affective sources. It consists of one trans-modal hub (hub which receives information from sources of various modalities – e.g. visual, auditory) which interacts and mediates information from various modality-specific sources. This system is further described as the Hub and spoke theory. It explains how concepts are created and learned in the semantic memory from multi-modal verbal and non-verbal experiences. They suggest that these concepts and sources of information are then encoded in modality-specific cortices from which one central hub receives multi-modal information and can construct a representation. This single trans-modal hub is located bilaterally in the anterior temporal lobes (ATLs). The importance of ATLs in semantic processing was suggested also from cognitive neuroscience and computational models. In neuroscience they found that when there was damage in the brain in higher order association cortices – which are trans-modal cortices in the hub and spoke theory, then it could produce trans-modal semantic impairments. Note also that patients with semantic dementia usually have brain lesions in ATLs, so it may suggest that ATLs are important for all conceptual domains and it shows impairments across all modalities. In computational models they found they could model such a hub and spoke system with neural networks, which adopts such hubs for all concepts and modalities (Rogers and McClelland, 2004).

The system for control is responsible for goal-oriented behavior and controls and manipulates the activation within the system of representation. Ralph et al. (2017) propose the brain regions involved in semantic control. The control of activation within the representational system is suggested to be in the VLPFC. This system of control should produce representations which are goal or task-oriented, and thus if needed it should be able to focus attention on non-dominant features or inhibit active associations of given concepts which are not suited for the task. This network of control is proposed to be distinct from the representational system but closely interacts with it. When a situation is well-known, very little control is needed to shape the behavior or manipulate the activated representations. On the other hand, ambiguous context, or inhibition of pre-learned concepts and/or similar inputs needs more executive control to constrain actions and behavior.

It is suggested that this network also supports working memory and executive representations which encode information about the current behavior. The semantic control was also proved by patients with semantic amnesia (SA), which fail on high executively demanding tasks, tasks with ambiguous information and inhibition of strong associations. A meta-analysis of functional MRI (fMRI) showed that the prefrontal cortex is involved in semantic control, especially pars triangularis in the inferior frontal gyrus. The analysis also found involvement of pMTG and intraparietal sulcus. This was tested with transcranial magnetic stimulation (TMS) and the activation peaks overlapped with the patients with SA. They found that the dorsal and posterior aspects of the inferior frontal sulcus (IFS) were more active during tasks with multiple domain executive demands. Ventral and anterior aspects of IFS correlated with executive demands of controlled memory retrieval.

This finding is consistent with Badre and Wagner's (2007) proposition of specialization of two parts of VLPFC, where post-retrieval the selection is situated in Mid-VLPFC (pars triangularis). Post retrieval selection needs to employ multiple domain information to generate context relevant representation, and a controlled retrieval process is placed in the anterior VLPFC (pars orbitalis).

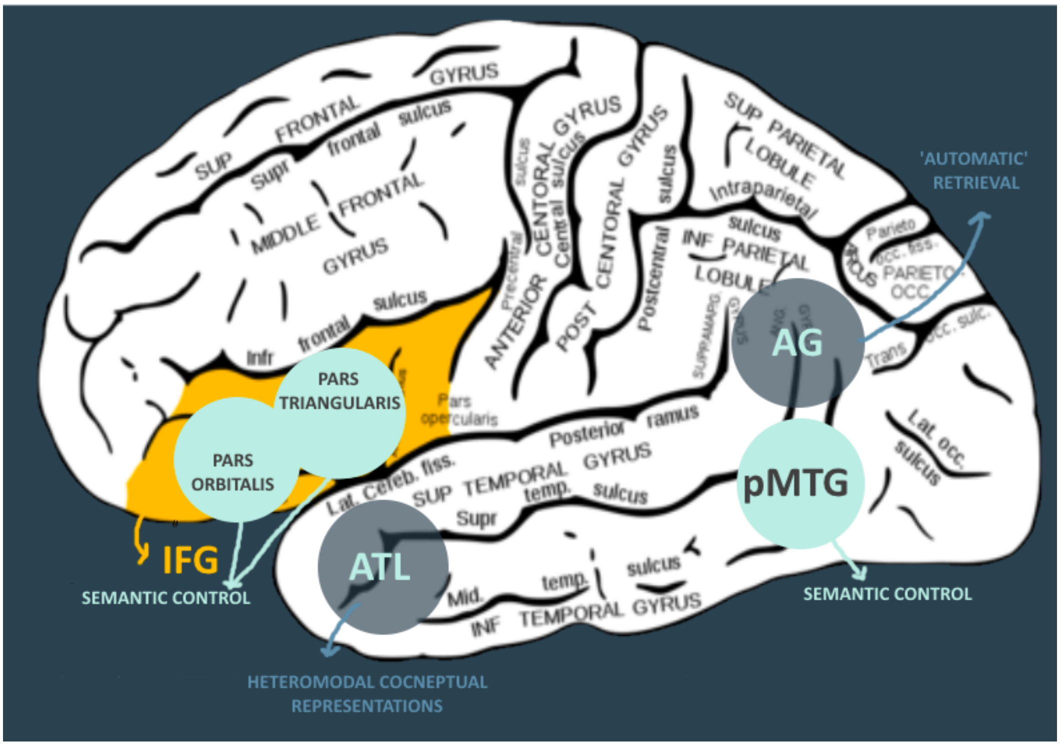


Figure 1.1: A depiction of components in Controlled semantic cognition framework proposed by Ralph et al. (2017). Their theory suggests an interaction between two semantic systems: one of representation and one of control. The dark blue areas are representational systems - the ATL is a single heteromodal hub which represents both taxonomic and thematic relations. The AG is responsible for automatic retrieval. Areas responsible for semantic control are in light blue - pMTG and IFG, they both work together in order to support semantic control processes. According to Badre and Wagner (2007) in IFG are located important parts for semantic control - pars orbitalis, which supports controlled access to stored conceptual representations and pars triangularis, which supports a domain-general selection process that operates post-retrieval to resolve competition among active representations. ATL, anterior temporal lobes. pMTG, posterior middle temporal gyrus. AG, angular gyrus. IFG, inferior frontal gyrus.

# Chapter 2

# Working memory

Working memory is a short term storage of information. However, it differs from short term memory by its ability to manipulate the information. The first studies of working memory come from the distinction between short term and long term memory in the multi-modal model by Atkinson and Shiffrin (1968). This model proposes that the short-term memory gets input from sensory memory and on the basis of repeated usage of information in short-term memory the information is stored in long-term memory. Also, after recall from long-term memory to short-term memory the representation is strengthened. When information is not used it leads to the decay of that particular information in long-term memory. Short-term memory (STM) is a very limited storage of small capacity for a short period of time. Long-term memory (LTM) in contrast is long term storage of unlimited capacity which works on learning - which is the change of neural connections and by recall of these memories, the activation of specific synapses strengthen the remembered representation in long-term memory.

The first distinction between STM and working memory (WM) was proposed by Baddeley and Hitch (1974). The distinction was described in his multi-component model, where he also suggested that WM can effectively manipulate information held within WM. Baddeley proposed various components of WM : phonological loop, visuo-spatial sketchpad and the episodic buffer, which was added to this model later (Baddeley, 2000). The need for various STM buffers came from the finding that the phonological loop and visuo-spatial sketchpad could operate separately, even independently from long term memory. They investigated it with a dual-task paradigm and the performance was similar as in the single-task conditions.

All these subsystems of working memory are governed by the central executive, which is a system responsible for choosing which information enters WM; it activates or inhibits representations based on current demands and controls slave systems (e.g. phonological loop, visuo-spatial sketchpad and episodic buffer). The central executive also binds information from various sources into coherent representations and shifts between tasks or employs different retrieval strategies. It interacts very closely with attentional systems and is responsible for selective attention.

Each slave system serves a different purpose.

## 2.1 Phonological loop

The phonological loop is the system which contains storage of auditory information or the phonological store and is a component which facilitates rehearsal of auditory memory traces (Baddeley, 2012). If you are asked to remember a phone number you repeatedly silently articulate the digits in your working memory. It is something like an inner voice, which prevents the repeated information from decaying. Additionally, the phonological store serves as an inner ear, which helps to remember the sounds or any auditory input in temporal order. There is various evidence proving the existence of the phonological loop. The effect could be seen when you are asked to remember words which sound very similar. It is often more difficult than to remember distinctly sounding words. This effect is called the effect of phonological similarity. Another effect is the effect of articulatory suppression (Baddeley et al., 1975) and this happens when a person is asked to complete a verbal task but concurrently they have to say out loud irrelevant words. It is assumed that such a task impairs the articulatory rehearsal process which allows the decay of phonological information in working memory.

## 2.2 Visuo-spatial sketchpad

Given the task of describing one's own room, the engagement of a visuo-spatial sketchpad is inevitable. The visuo-spatial sketchpad is the storage of visual and spatial information and enables the manipulation of the information. This system closely interacts with visual pathways according to the task. When a spatial location of a person is needed, the system recruits spatial short-term memory. This memory is in the dorsal stream of the visual pathway. On the other hand, while recognizing objects or learning what an object is, the object memory is involved, which is in the ventral stream of the visual pathway.

## 2.3 Episodic buffer

The episodic buffer is the latest component of working memory added in 2000 by Baddeley (2000). The episodic buffer was found based on the studies with amnesiac patients, which lost the ability to form new memories, which is connected with the impairment of short-term memory. These patients however, were good in short-term recalling of stories. The stories were longer than if they just remembered it with a phonological loop, which led to the creation of this new subsystem of working memory. The episodic buffer thus integrates information across domains from visual, spatial and verbal information and forms such integrated units. It is assumed it also has links to the LTM and semantic systems.

All these subsystems of working memory together with the central executive are involved in the successful execution of everyday behavior. It is a very complex system which engages various cognitive domains facilitating expected behavior. Devinsky and D'Esposito (2003) found that when the functioning of working memory is impaired, it results in disordered behavior and so it is not sufficient to carry out every day tasks.

## 2.4 Cognitive models of working memory

Nowadays the working memory is often described using state-based models. D'Esposito and Postle (2015) describe it in their review on working memory:

> *"These models assume that the allocation of attention to internal representations - be they semantic long-term memory (LTM; e.g., letters, digits, words), sensory, or motoric - underlies the short-term retention of information in working memory."*

Therefore when an information is held in working memory, it must be in one of the states of activation which are produced by the allocation of attention to the information. D'Esposito and Postle (2015) organize state based models into two categories: activated LTM models and sensory-motor recruitment models.

Activated LTM models are treated as one for the semantic domain which means letters, words or digits, whereas sensory-motor recruitment models are applied for perceptual stimuli – such as visual stimuli of colours and orientations, auditory stimuli and tactile stimuli of vibrational frequencies. Both of these models deal with properties of working memory as capacity limitations and proactive interference. It is based on the idea of attentional selection involved in bringing mental representations into working memory and it is the consequence of attentional prioritization which results in above mentioned properties of working memory.

## 2.5 Neural mechanisms of working memory

What brain regions are involved in working memory is one of the questions asked by the ongoing research. In 1964 Pribram et al. had already suggested that the crucial part supporting working memory is the prefrontal cortex (PFC).

The neural structure underlying working memory is suggested to consist of various processes. The literature describes 5 neural mechanisms involved in WM, several of them act in parallel.

### 2.5.1 Persistent neural activity

Persistent neural activity was discovered in studies with monkeys (Fuster and Alexander, 1971). They used extra-cellular recordings which show an ongoing neural activity while monkeys performed a delay response task. The delay response task consisted of actively maintaining information which was no longer available, but the information was needed to complete the task successfully. Later they found similar activity in the human PFC with the use of fMRI. In some of the cases they found that persistent neural activity is involved in coding task-relevant information during WM tasks (Sreenivasan et al., 2014).

It is suggested that persistent neural activity could be a mechanism in working memory which endures throughout the entire length of a delayed period until it can be of use when guiding a response and also that this mechanism directly relates to behavior. Both of these suggested mechanisms are a subject of research and fMRI data have not shown the actual mechanisms underlying persistent neural activity.

### 2.5.2 Hierarchical representations in prefrontal cortex

The prefrontal cortex putatively shows very coarse selectivity for representations maintained in WM. Various studies investigated the nature of representations maintained in the PFC in comparison to posterior brain regions (Constantinidis et al., 2001; D'Esposito and Postle, 2015). They suggest that the PFC is mostly activated by higher-order information, such as task rules, goals or abstract representations, whereas posterior areas are more activated with stimulus specific representations. These propose top-down control of the PFC onto brain regions which store the information, and can guide the activation of task-relevant representations.

### 2.5.3 Top-down signaling

The top down signaling mechanism was for a long time connected to the brain region of the PFC (Duncan, 2001). The mechanism which suppresses task-irrelevant inputs and enhances relevant information to be searched for is very crucial for our everyday behavior. D'Esposito and Postle (2015) have conducted a study by investigating the nature of top -down signaling and under what circumstances it is engaged in task-solving. In their research they presented subjects with faces and scenes and had three trials: one for remembering faces and ignoring scenes, another for ignoring faces and remembering scenes and the last one for passive view of faces and scenes. In each of the trials there was equal bottom-up visual stimuli – faces and scenes, so they could focus on the engagement of top-down signaling. The passive viewing served as a baseline. The results revealed the possibility of employment of two top-down signals. One for activation or enhancement of task relevant information and the other for inhibition or control of task-irrelevant information. The top-down signaling may be one of the core mechanisms of the central executive in working memory.

### 2.5.4 Long-range connectivity

A mechanism important for working memory is synchronization of activity among distributed brain regions. It is still a subject of research how these communications or interactions support working memory. Some authors propose a distributed synchronized activity to be the result of synaptic reverberations (Wang, 1999; Durstewitz et al., 2000). Others propose synchronous oscillations between neuronal populations (Fries, 2005; Singer, 2009). Neural oscillations are involved in communication between regions. The use of electroencephalographic (EEG), magnetoencephalographic (MEG) and elecrtocorticographic (ECoG) recordings defined the specific oscillation for working memory. All of the frequencies (theta, alpha, beta and gamma) were found to be connected to working memory tasks (Roux and Uhlhaas, 2014). However, each of the frequency bands have different functions. Gamma band is suggested to be involved in active maintenance of working memory, theta band in temporal organization of working memory and alpha in the suppression of the task-irrelevant representations (Roux and Uhlhaas, 2014). Although, there already are studies ascribing different functions to these oscillation bands, contrary to temporal organisation of working memory, the theta band is suggested to be responsible for binding of semantic information (Umrianová, 2019). The long-range synchronization of these oscillations plays a crucial role in the functioning of working memory.

### 2.5.5 Brainstem neuromodulators

The neuromodulatory neurons influence cognitive functions. Cools and D'Esposito (2010) found, that dopaminergic modulation of fronto-striatal circuitry is critical for the functioning of working memory. Other authors studied the importance of dopamine in working memory in studies with monkeys. They found that depletion of PFC dopamine or blockade of dopamine receptors impaired working memory functions (Brozoski et al., 1979; Sawaguchi and Goldman-Rakic, 1991). Other studies showed that administration of dopamine receptor agonists to humans improved the performance of working memory (Kimberg et al., 1997; Kimberg and D'Esposito, 2003). Braver and Cohen (1999) suggested that tonic dopamine effects may increase the stability of maintained representations in working memory. For phasic dopamine effects they propose they may serve as a signal for new representations or a need for the update of maintained representations.

## 2.6 The role of WM in semantic processing

The ability to think and reason about a variety of inputs is also due to the functions of working memory. There has been ongoing research about to which degree is the working memory and its capacity responsible for retrieval from LTM. Unsworth et al. (2013) have suggested in their work, that the individual differences in working memory capacity (WMC) affect the ability to retrieve information from LTM. After conducting various experiments focused on prolonged verbal fluency tasks, they found that high-capacity individuals have better performance than low-capacity individuals when they are asked to name as many items from some category (in their experiment, they used naming animals). However, when participants had retrieval cues (e.g. pets, birds etc), the difference was eliminated. Furthermore, they found that high-capacity and low-capacity individuals have different search strategies from LTM. For high-capacity individuals, it was mostly controlled strategic search from LTM, whereas low-capacity individuals reported random access of information from LTM. Unsworth's (2007) experiments indicate that working memory mediates semantic retrieval. Nevertheless, it is not clear whether the contribution of WM to semantic retrieval in fluency-like tasks is related to automatic, controlled or both modes of semantic retrieval.

Other authors (Sabb et al., 2007) suggest that WM and semantic retrieval share neural resources which are part of "a finite capacity system underlying cognitive control" (p. 211). In their study they investigated these systems using a task on semantic priming under different WM loads. They found that the effect of semantic priming was reduced under enlarged WM set size. Similarly with Sabb and his colleagues, Heyman et al. (2015) found that high WM load eliminated effects of semantic priming for asymmetric associated pairs in a forward direction (e.g., panda-dog). However, for other pairs (symmetrically associated or asymmetric associated in backward direction) the semantic priming was not disrupted by WM load, thus it suggests that some forms of priming depend on WM capacity. The semantic priming effect is described as spreading activation from prime to target (Collins and Loftus, 1975). This may suggest that the WM load may affect activation spreading and thus affect semantic priming. However Heyman et al. (2015) indicate that the process of semantic priming is more complex and not just spreading activation is disrupted by WM load, but the whole process is not "capacity free". In a study by Amunts et al. (2020), they investigated the prediction of verbal fluency scores from executive function measures. Working memory being one of the core executive functions was also part of their investigation. Their study did not find a relationship between WM and verbal fluency tasks. They explain it by focusing on different variables describing verbal fluency performance. They focused on the sum of correctly produced words, although the indicator of WM performance is usually showed by the perseveration error. Even though the previous study did not find any relationship of verbal fluency and working memory, participants used working memory for successful completion of the tasks. They must remembered the instructions and keep the earlier responses in their working memory. Also they must suppress prepotent and irrelevant responses and avoid repetition. Shao et al. (2014) also focused on the components of executive control, but in working memory they focused on the ability to update representations held in WM. With the use of the OSPAN task, they found that good performance in the OSPAN task contributed to good performance in the verbal fluency task. It is currently poorly understood to what degree WM load disturbs semantic processing. Further research is needed to address this question using a rigorous experimental methodology.

When it comes to brain regions involved in semantic priming under low WM load, who discovered activity in the inferior frontal gyrus, anterior VLPFC - pars orbitalis (BA 47). The activity was modulated by the concurrent working memory load and the semantic activation of the primed word. As proposed earlier, this area of the IFG is often called the semantic executive system (Badre and Wagner, 2007) and seems to be affected by the working memory system (Sabb et al., 2007). The working memory system is suggested to be mostly located in the dorso-lateral prefrontal cortex (DLPFC) interacting with pars orbitalis as it was discovered that more activity in the DLPFC leads to less activity in pars orbitalis during semantic priming. This leads to the suggestion that the middle frontal gyrus inhibits the activity of the IFG under high WM load and thus the working memory system supports controlled semantic processing.

However, studies investigating the relationship between working memory and semantic processing were not able to definitely determine the underlying mechanisms and interactions with their data. One of the objectives of our research is to understand the relationship between general domain WM and semantic-specific processing (both automatic and controlled).

# Chapter 3

# Research problem

## 3.1 General objective

The main objective of this study is to investigate the interaction of the domain-general working memory system and the semantic-specific system. The research is focused on the employment of the general-domain executive system in supporting the controlled (and automatic) semantic retrieval when a task is demanding. In this study we manipulate the load of the task with the dual-task paradigm - adding a concurrent working memory task to a lexical-semantic retrieval task (ACT).

## 3.2 Methodological approach

For this purpose we conducted a behavioral experiment that included:
(1) the main task assessing the lexical-semantic processes together with concurrent working memory load in order to manipulate the cognitive load effectively and to investigate the functional determinants of domain-general capacities in semantic retrieval,
(2) control measures of working memory (backward digit span, operation span) to investigate the correlations between semantic cognition and working memory capacity.

## 3.3 Hypotheses

Thus, we hypothesised, that loading working memory would increase the average latency in both associative (automatic) and dissociative (controlled) semantic retrieval conditions, but the impairment would be higher for the dissociative condition.

# Chapter 4

# Method

## 4.1 Participants

We recruited participants via advertisement on social networks and leaflets in the faculty building. We estimated the required sample size using an a priori power analysis (5% Type I error rate, 20%Type II error rate, and expected effect size $R^2$ .10, one-sided test). Eventually we had 44 healthy young adults (26 female; age 22 years, SD = 3) participating in the study (we had to exclude one participant due to outlying values in multiple measures). Participants were Slovak native speakers and three of them were left-handed. They have not reported any cognitive disabilities (multiplex sclerosis, learning disorders, ADHD). They received a monetary compensation of 10 euros for participation in the research. In the beginning of the experiment they signed a written informed consent. The experiment was conducted according to the Declaration of Helsinki and approved by the institutional review board.

## 4.2 Procedure

The procedure took place at the FMPH UK lab. In each session one participant sat in front of a computer, signed an informed consent and was instructed about receiving the monetary compensation after fulfilling the task. After this, the participant completed a questionnaire on demographic data. During the task, one administrator was always present in the room, to explain instructions and answer possible questions. The procedure lasted approximately one hour, the participant was informed to take a break after half of the session and was offered refreshments. The procedure consisted of two control measures of working memory at the beginning and the main task.

The main task consisted of four steps:

1. a short practice period prior to testing - Associative and Dissociative condition without WM load,

2. practice period - Associative and Dissociative condition together with concurrent WM load,

3. testing period - Associative and Dissociative condition with various WM loads, randomised.

### 4.2.1 Associative chain test

The test concentrates on continuous generating of words following two rules (Response type factor): *the associative* chain condition and *dissociative* chain condition. In the associative chain condition the participants were asked to produce a chain of associates[1] (e.g., *Sky*$_{[the\ starting\ word]}$ *Cloud* *Data* *Computer*...).

In the dissociate chain condition they were asked to produce a chain of dissociates[2] (e.g., *Sky*$_{[the\ starting\ word]}$ *Teacher* *Tree* *Car*...).

In both conditions participants were asked to follow these rules, preserving fluent word flow, avoiding the repetition of the same words in each word chain and also in the whole task. They were asked not to focus on grammatical correctness of the words, nor on accents. Strategies for easing the word production were not allowed.

Participants were asked to type in as many words as possible in both chains (associative and dissociative) in the duration of 20s. They used a computer keyboard for typing the words. At the beginning of each word-chain, participants received a word (i.e. starting word). The starting word was randomly selected from a group of words. Then they started to type in the word-chains according to the given condition.

All the responses were evaluated by two independent raters and any related word or word not following given rules was considered an error. Response time (RT) was measured for every response word. RT was measured for initiation of response writing, each letter of the world and total RT until participants pressed enter on the keyboard for the completed response word (Fig. 4.1). Another measure - Inhibition cost was computed as the RT difference between Dissociates and Associates (D-A), across all load conditions.

[1] an associate is considered a word relating to the target word, participants were instructed to type-in the first word that came into their mind

[2] a dissociate is considered a word with no functional, semantic or contextual connection to the target word

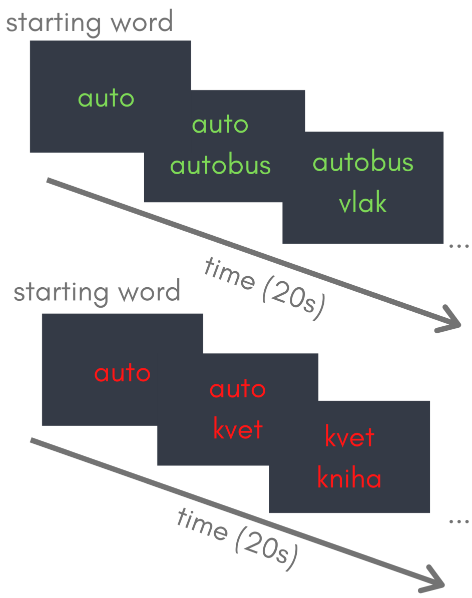


Figure 4.1: The figure represents associative and dissociative (green and red, respectively) conditions of the associative chain test. The starting word *"auto"* (means car) is presented on the screen and a participant is asked to type in an associative word - if the starting word is green, and a dissociative word - if the starting word is red. Then they continue in producing words according to the given condition for a given time - 20 seconds. They always produce a word regarding the previous one. As depicted in the figure, the starting word was car, then for associative condition is word *"autobus"* (means bus) and then an associative word for bus is *"vlak"* (means train). Opposite for the dissociative condition.

### 4.2.2 Dual-task paradigm

For our experimental approach we chose the dual-task paradigm, which allows specific manipulation of cognitive load. As proposed by D'Esposito et al. (1995) the dual-task paradigm employs prefrontal brain areas which are crucial for the executive system.

In our research we manipulated the cognitive load of working memory capacity, by imposing a secondary working memory task to ACT.

A concurrent working memory task was added to the ACT, this task was performed under 3 conditions (no-load, low load, high load). The no-load condition was the basic ACT. In the low load and the high load conditions, participants were asked to remember a sequence of digits presented at the beginning of a trial (new word-chain). For low load, they were presented with 3 digits, for high load with 6 digits (Fig. 4.2). After the end of the word chain they were asked to type-in the digits in the same order as presented, using the computer keyboard. They were asked not to repeat the digits to themselves out-loud during the duration of the word-chain block. Only blocks with correctly remembered sequences of digits for low load were used in data analysis. The criteria for inclusion into the statistics for high load were different, they could make one mistake (remember 5 correct out of 6 digits).

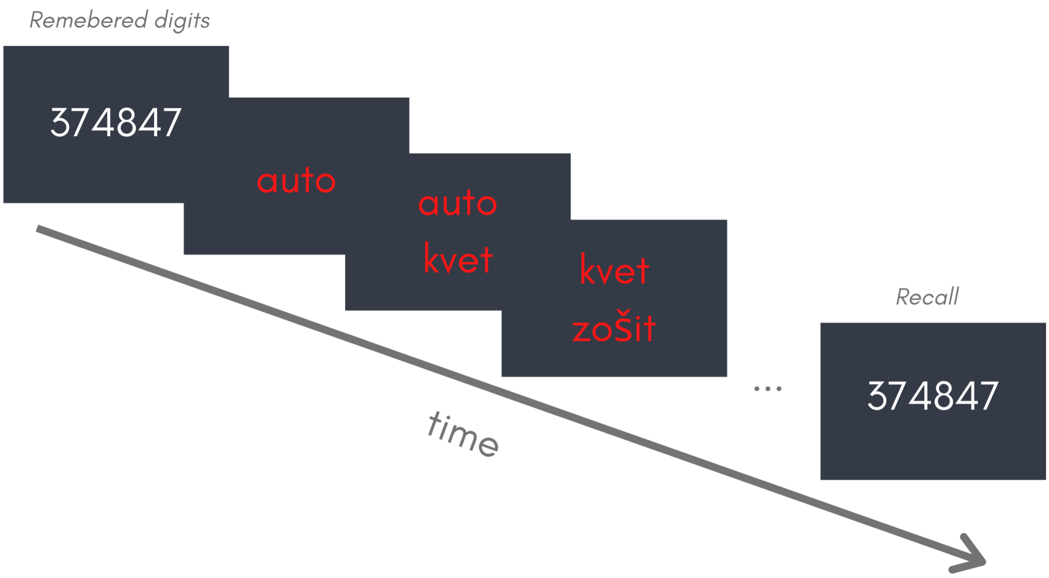


Figure 4.2: In this figure is depicted a dissociative condition of the ACT with a concurrent working memory task in high load condition. At the beginning of a word chain, participants were presented with 0,3 or 6 digits (no load, low load, high load, respectively), which they were asked to remember. Then they produced word chains according to the given condition (associative, dissociative). At the end of the word chain, they had to type in the digits presented at the beginning of the word chain. In the figure the words are *auto* - a car, *kvet* - a flower, *zošit* - a notebook.

The task included a short practice for each condition, then a practice for low load and high load conditions [3]. Testing consisted of 21 chains in two conditions (associative, dissociate) with different load manipulations (no load, low load, high load). There were 9 chains for associative (3 under no load, 3 under low load and 3 under high load) and 12 chains for dissociative (4 under no load, 4 under low load and 4 under high load). The order of conditions and load manipulations were in random order.

When evaluating the semantic retrieval performance in the ACT, we focused on two factors: one determining the relative contribution of automatic and controlled semantic processing (Response type: Associative, Dissociative) and another determining the WM load (Load: no, low, high). These two factors were used in the statistics as main effects to model the retrieval RTs.

[3] in practice participants were asked to remember 2 and 4 digits in low and high load, respectively

### 4.2.3 Working memory measures

To assess an individual performance of working memory capacity, two working memory tasks were situated at the beginning of the research task.

**Digit Span Task** The Digit Span Task is a simple behavioral measure of working memory capacity from the Wechsler Intelligence Scale for Children–III (Wechsler, 1949). This task can have 3 variants, forward, backward and sequencing. In this research we used a backward Digit Span Task and this task was administered via computer. In each trial participants were presented with a sequence of digits in 500ms intervals on the computer screen (e.g., 3, 7, 4, 9, 0). At the end of each trial participants were asked to recall as many digits as possible but in the opposite order from the presented order by typing them using a computer keyboard without a comma or space. After each successfully completed trial (i.e., they remember correctly the sequence of the digits and typed them in the opposite order - e.g., 09473), the number of digits presented increased by one for the next trial. If the trial was not successful (i.e., if any digits are missing and/or the order of digits is wrong), the number of digits presented was lowered by one. The task ended after participants made an error for four trials. The dependent measure was the average number of digits in the four unsuccessful trials minus one, to estimate the working memory capacity.

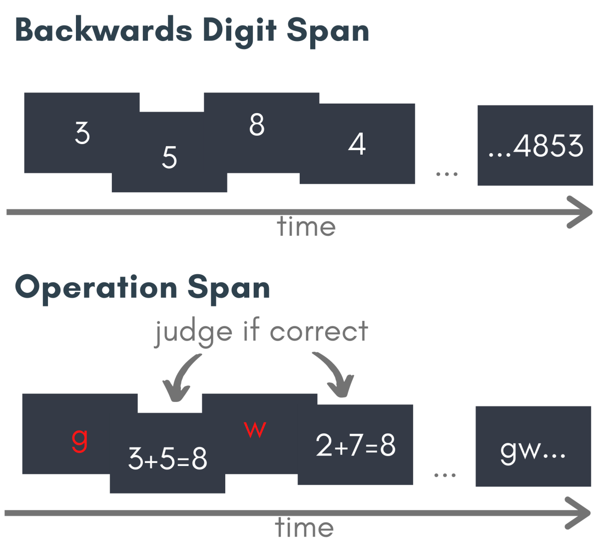


Figure 4.3: Working memory capacity measures: Backward Digit Span and Operation span.

**Operation Span Task** The Operation Span Task developed by Turner and Engle (1989) utilizes solving mathematical operations. In our research the participant is asked to remember a sequence of letters, but in-between the presented letters the participant is asked to judge whether a presented mathematical equation is correct or wrong (e.g., 25+4=29) by pressing a letter 'A' or 'N' on the keyboard, 'A' for correct and 'N' for incorrect mathematical equation. At the end of the task the participant is asked to type in the remembered sequence of letters in the order as presented. The task ends after 4 incorrectly remembered sequences of letters. The working memory span is defined as the average number of digits in the four unsuccessful trials minus one.

## 4.3 Data analysis

After acquisition of the data, they were merged separately for each task. For the main task - the associative chain test (ACT), prior to statistical analyses $<$ 0.1% of responses were removed, because they had large response times (RTs > 20s). The rest of responses was evaluated by two independent raters, in order to check and exclude the errors (i.e. responses that did not conform the rule: for associative condition unrelated words and for dissociative condition related words, also when they used verbs, or proper nouns instead of common nouns). Responses not conforming the rules were removed (less than 3%). There was no further analysis of the responses due to the high accuracy of them ($i.e., >$ 97%), so only analyses on RT were performed. Prior to statistical analyses, the data were winsorized (10% trimming, two-sided) to replace extreme values, because there were several outlying observations among the RT values in the dataset. This was done separately for each participant and the ACT factor (associative and dissociative condition). The data were processed in R studio (RStudio Team, 2018) using R language and R environment (R Core Team, 2018).

For analyses of retrieval RTs from the experimental ACT task we used linear mixed effect models (LMEM; R package lme4, (Bates et al., 2015)). This method allowed us to analyze individual RTs nested within a participant by estimating a random intercept for each participant (default unstructured covariance matrix). The LMEM included the main effects of Response type [associative, dissociative] and Load [no, low, high] and their interaction effect. Notably, data from the ACT chains involving >1 error in the memory recall (i.e., more than one missing digit or wrong digit) were excluded from the analyses.

LMEMs were fitted using restricted maximum likelihood (REML) and due to a smaller sample, we derived p-values with Satterthwaite approximation for degrees of freedom, since these were shown to produce optimal estimates even for smaller samples (Luke, 2017). Post-hoc pairwise comparisons between the experimental conditions

(Response type and Load) were evaluated using Wald's statistic and Satterthwaite approximation of degrees of freedom. To account for family-wise error rate (Type I error) we corrected the p-values of the post-hoc tests with Tukey HSD adjustment (adjusted p-values are reported). Furthermore, for each participant, the individual data points (RTs) were averaged, separately for each task and condition (or combination of conditions). Using the averages, two derived measures were computed: inhibition cost (dissociative RT – associative RT) and WM load effect (high WM load RT – no WM load RT).

The basic and derived (average) measures from ACTs and averaged measures from the control tasks (Working Memory Capacity measures) were then used in a correlation analysis.

# Chapter 5

# Results

## 5.1 Main experiment

To evaluate retrieval response times (RTs), a LMEM analysis was used for the main factor Response type (associative, dissociative) and working memory load (no, low, high). The LMEM showed a significant main effect of Response type, $F(1, 3866) = 600.93, p < .001$, and significant main effect of Load, $F(2, 3865) = 44.47$, $p < .001$. However, the interaction of these two main effects was not significant, $F(2, 3865) = 0.29, p = .746$ (5.1). As depicted in the Fig. 5.1, the latency of responses in the dissociative condition was substantially higher than in the associative condition. Both associative and dissociative retrieval was similarly affected by WM load, whereas high WM load (6 digits) disrupted retrieval more substantially than low WM load (3 digits); (see Fig. 5.1 for more details).

Table 5.1:
*Effects of Response type and Working memory load and their interaction effect.*

| Effect | $F$ | $p$ |
|---|---|---|
| Response type | 600,9297 | $<$ 0.001 *** |
| Working memory load | 44,47 | $<$ 0.001 *** |
| Response type x WM load | 0,2927 | 0, 746 |

*Note.* Effects of Response type and Working memory load were both strongly statistically significant. However, their interaction effect (Response type x WM load) was not significant. The analyses of each effect of the ACT measures were conducted using ANOVA F-statistics.

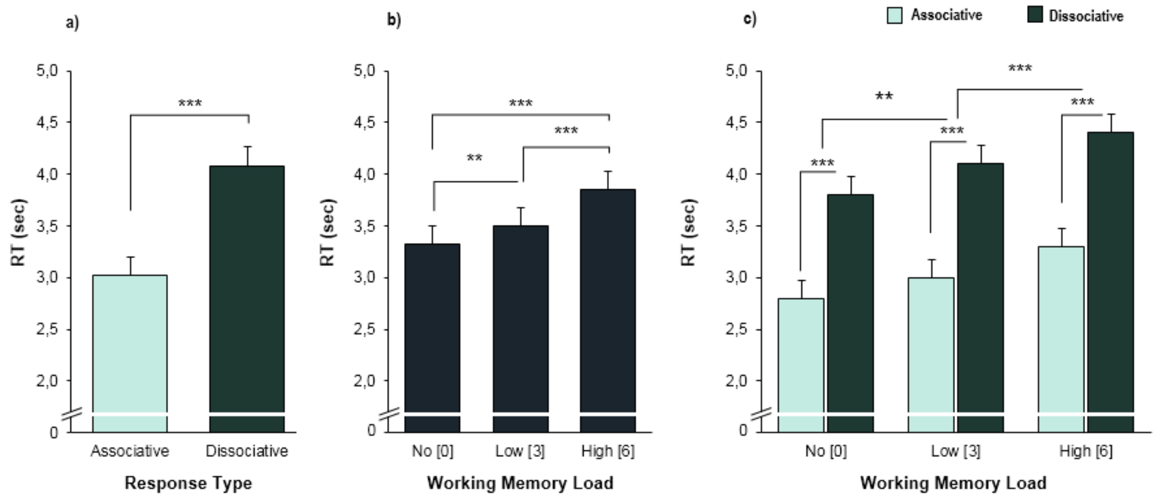


Figure 5.1: Mean RT ( $1SE$) of the ACT measures.
a) *associative* (light blue bars) and *dissociative* (dark green bars) condition of Response type factor across all working memory load conditions, showing strongly significant diﬀerence in RTs for dissociative condition;
b) the comparison of response time latency due to the diﬀerent WM loads [no, low (3 digits) high (6 digits)] regardless of the response type, showing also strongly significant diﬀerences between loads, with high load being the most disrupting;
c) response type conditions under WM load, the response latency is significantly higher for both conditions under load.
Tukey adjusted post-hoc $p < .01$ (two-sided),
Tukey adjusted post-hoc $p < .001$ (two-sided).

## 5.2 Working memory correlation results

The correlation analysis showed strong correlation between WM load eﬀect (derived measure representing diﬀerence between high and no WM load RT) and Inhibition cost (derived measure for diﬀerence between dissociative and associative RT) $r(42) = .655$, $p < .001$ (Fig. 5.2d). The positive correlation between the Inhibition cost and WM load eﬀect was stronger for dissociative condition $r(42) = .647$, $p < .001$ (Fig. 5.3f) than for associative condition (Fig. 5.3e). However, the inhibition cost was not significantly correlated with WM capacity. Furthermore, negative correlation was found between Response initiation and WM capacity $r(42) = -.273$, $p = 0.077$, thus individuals with higher WMC have more rapid production of associative responses (Fig.5.2c).

A positive correlation was also observed between Response initiation (overall Associate RT averaged across the three load conditions) and WM load eﬀect total $r(42) = .392$, $p = .009$ and also only for the dissociative condition $r(42) = .333$, $p = .029$ (see Tab. 5.2 for more details).

The individual data points (averaged RTs) for each participants are depicted in the correlation plots Fig. 5.2 and Fig. 5.3, separately for each task and condition (or combination of conditions). They depict the correlations between each WM task, Working memory capacity, Response initiation and Inhibition cost (see Fig. 5.2a,b,c for more details); and the correlation between Inhibition cost and WM load effect (see Fig.5.2d and Fig.5.3 for more details) (total, for associative condition and dissociative condition, separately).

Table 5.2:
*Correlation results of Working memory measures and the ACT*

Pearson Correlations

| | | IC | RI |
|---|---|---|---|
| WM effect (total) | *r* (42) | .655 | .392 |
| | *p*-value | < .001 | .009 |
| WM effect for A | *r* (42) | .304 | .294 |
| | *p*-value | .048 | .056 |
| WM effect for D | *r* (42) | .647 | .333 |
| | *p*-value | <.001 | .029 |

*Note.* The *Working memory load effect* is a derived measure computed as the difference between no WM load RT and high WM load RT. *IC* = Inhibition cost, derived measure computed as difference between associative RT and dissociative RT. *RI* = Response initiation is overall associative RT averaged across the three load conditions (no, low, high).

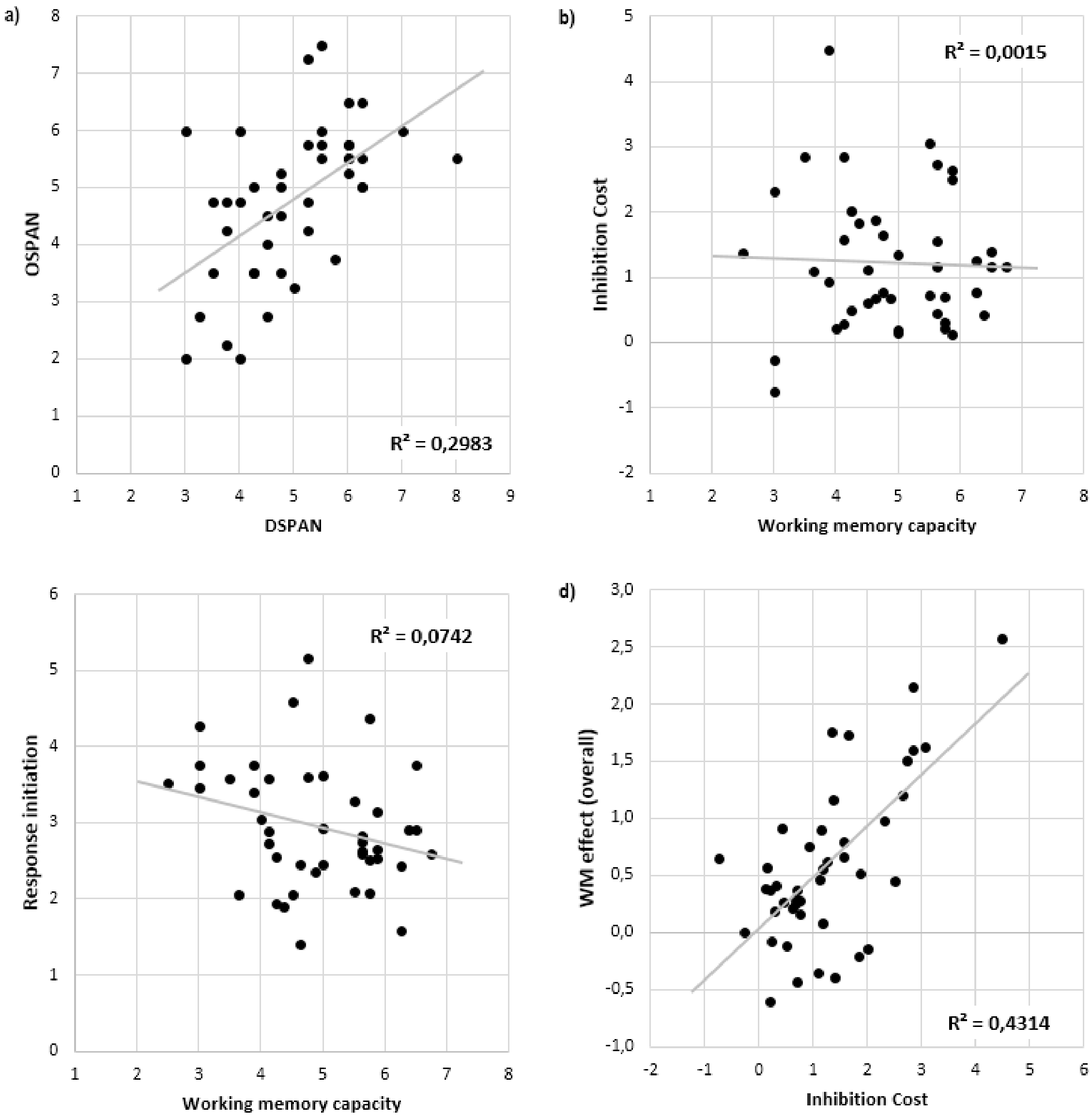


Figure 5.2: Correlation analysis of working memory measures and derived measures from the ACT. Each data point is averaged RTs for each participant. a) correlation between two WM measures: DSPAN - Backward digit span, OSPAN - Operation span. b) Averaged working memory capacity with Inhibition cost (dissociative RT – associative RT). c) Averaged WM capacity and Response initiation (overall associate RT averaged across the three load conditions). d) Inhibition cost and overall WM load effect (high WM load RT – no WM load RT).

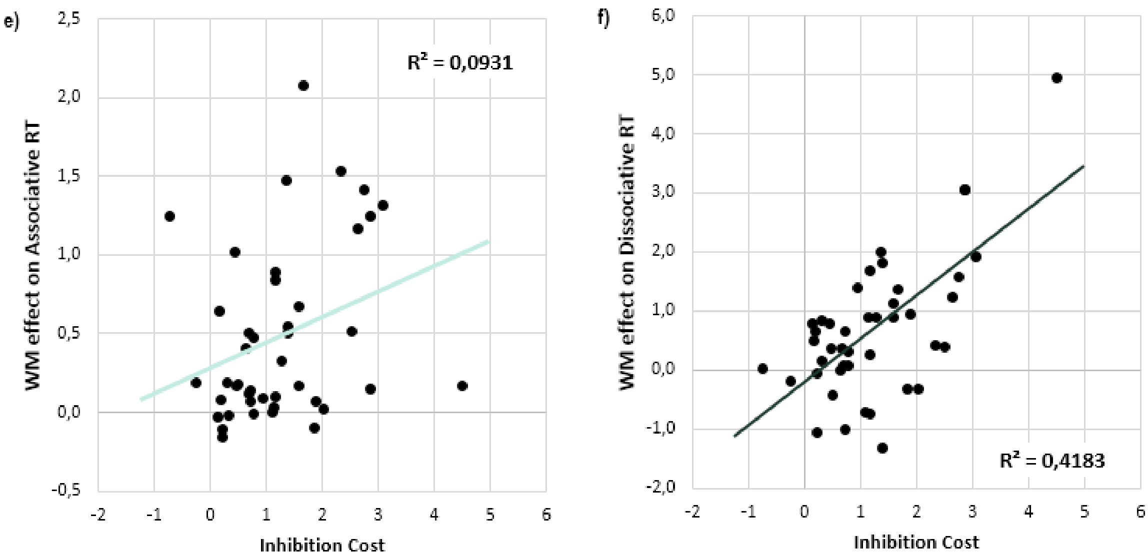


Figure 5.3: Correlation analysis of working memory measures and derived measures from ACT. Each data point is averaged RTs for each participant. e) Inhibition cost and WM load e□ect on associative RT. f) Inhibition cost and WM load e□ect on dissociative RT.

# Chapter 6

# Discussion

The research was conducted in order to investigate the interaction between semantic retrieval and working memory. We wanted to understand the role of working memory as a general-domain system in the semantic-specific system that underpins rapid retrieval from the semantic memory. It was proposed, that a general-domain system aids semantic processing when a task is demanding, thus we focused on a systematic manipulation of the working memory load in automatic and controlled semantic retrieval.

For assessing the semantic retrieval we used the lexical-semantic task ACT requiring continuous production of responses (Marko et al., 2019b). To understand the interactions between semantic cognition and working memory we manipulated the working memory load using the dual-task paradigm. Participants were asked to concurrently perform a working memory task while being engaged in the retrieval task, employing both automatic (associative) and controlled (dissociative) semantic processes. The experiment consisted of 2 conditions (automatic, controlled) under 3 WM load manipulations (no load, low load, high load). The WM tasks (Backward DSPAN and OSPAN) served as a control measure for WM capacity.

For our experiment, we hypothesized that the simultaneous working memory task would disrupt both retrieval processes, but with higher impairment in the controlled semantic task. Our hypothesis was based on depleting the domain-general resources pertaining to the working memory system, which is also considered to involve general-domain executive control. According to Miyake et al. (2000) there are three core executive functions or controls: updating, shifting, and inhibition. Other authors agreed on di�erent core executive functions, which are cognitive flexibility, working memory and inhibition (Diamond, 2013; Karr et al., 2018; Friedman and Miyake, 2017). With our research we focused on the controlled processes related to inhibition (Collette et al., 2001; Allen et al., 2008). We measured the inhibition cost as a derived measure from response time (dissociative RT – associative RT), thus reflecting the efficacy of suppressing prepotent/habitual associations during semantic retrieval.

We first discuss the results of the main experiment, how WM affected automatic and controlled semantic cognition. We also interpret the results in the scope of other research. Then we discuss the results of the correlation analysis. The role of individual working memory capacity in semantic processing.

## 6.1 The contribution of working memory in semantic retrieval

Our experiment showed a statistically significant main effect of Response type. The latency of responses in the dissociative condition was substantially higher than in the associative condition. We also found significant main effect of Load. The WM load on all three levels (0,3,6) impaired both conditions (associative, dissociative). With higher load, the impairment was higher. The first expectation, that WM impairs both automatic and controlled semantic processes, was confirmed. However, in opposition to our expectations, the interaction effect was not significant. The impairment in the dissociative condition was not higher than in associative. WM affected both conditions similarly.

The result showing higher response time for the dissociative condition than for associative condition is in agreement with the previous findings (Marko et al., 2019a; Marko et al., 2019b). Producing dissociative responses requires the inhibition of automatic responses to target words and shifting the focus to a semantically unrelated cluster of words in memory. Such an additional process is more time consuming than just producing automatic associations to semantic cues. According to previous research (Allen et al., 2008) response suppression (producing dissociates) has been linked to the prefrontal regions that also participate in working memory functioning - the left dorsolateral prefrontal cortex and orbitofrontal cortex (Diamond, 2013).

The finding that the WM load parametrically disrupted semantic memory retrieval is in favor of our hypothesis and in line with the previous studies on verbal fluency (Rosen and Engle, 1997; Rende et al., 2002; Unsworth et al., 2013). However, our findings importantly extend previous discovery, revealing that working memory supports both the automatic and the controlled processes in semantic retrieval. The reason why the other studies did not provide similar evidence using verbal fluency tasks, is that verbal fluency ability is ambiguous with regard to the nature of processes it involves, as argued in the previous research (Henry and Crawford, 2004; Shao et al., 2014; Whiteside et al., 2016).

On the contrary to our expectations there was a non-significant difference between the impairment of automatic and controlled conditions, suggesting that the working memory load affected both of the assessed retrieval modes in a similar fashion. Thus, we can conclude that the working memory is engaged in semantic processes which are crucial for both associative and dissociative tasks. One of the possible accounts for this finding is that WM is required for maintaining task goals (i.e., task-oriented behavior) as well as semantic cues of the presented stimuli, which facilitates the memory search for correct responses. Since maintaining retrieval targets is needed across various retrieval tasks, this account is in line with the observation that both associative and dissociative retrieval was influenced by load manipulation. Moreover, such an explanation is also consistent with the models of verbal fluency, namely the global-slowing (Mayr and Kliegl, 2000; Mayr, 2002) and the cue – maintenance models (Hills et al., 2015; Hills et al., 2013) . These models describe maintenance and dynamic updating of the search goal to be crucial for the paced retrieval from semantic memory. In line with these accounts, we could speculate that WM may play a role in the regulation of semantic activation via sustaining and updating of retrieval cues, and could effectively support priming (predicting) of likely associates or inhibiting/suppressing prepotent responses. This may lead to the hypothesis that WM supports the process of automatic spreading activation, by amplifying or attenuating the activation within the semantic network. With the regulation of activation spreading it may control semantic search according to maintained goals or semantic features in working memory (Diamond, 2013). The impairment of WM thus should lead to less efficient control over automatic (but task-irrelevant) responses and increased response latency of likely associates, making semantic retrieval less goal-oriented. Both these accounts are in line with our data. Notably, the functional link between working memory and the semantic system is also implied by neuroimaging data (Sabb et al., 2007). For instance, Sabb et al. (2007) found that increased working memory load decreases activity in the prefrontal circuits that underpin controlled semantic retrieval. Thus, our findings are consistent with this evidence, indicating that the working memory and the semantic processing may share or even compete for limited neural resources. Another line of evidence provided by Rende et al. (2002) suggests that the semantic processing underlying fluent retrieval from the semantic memory may be supported by the phonological loop, i.e., a ”verbal” component of the WM memory model proposed by Baddeley and Logie (1999). In their experiments, Rende et al. (2002), investigated an articulatory suppression using a dual-task paradigm. The performance in the letter fluency task was impaired when a concurrent task was present. Following the findings by Rende et al. (2002), it could be proposed that remembering the digits in the load conditions depleted the capacity of the phonological loop that is important for semantic processing of the words during retrieval. In particular, in trials including WM loads the participants had to subvocally rehearse the digits to maintain them throughout the prolonged period of time, which could induce a similar articulatory suppression effect as described in Rende et al.

(2002). This effect of WM load could therefore translate into more shallow processing of the stimulus words, hindering a proper semantic analysis that would guide the semantic search for correct responses (associations or dissociations). Similarly, Miyake et al. (2004) suggest that the inner speech is crucial for maintaining and recalling the task goal, thus important for strategic cueing in memory search. They propose, that when instructions are less explicit, or we may say less automatic, the effect of articulatory suppression is higher. Thus, according to this view, the load should induce a larger articulatory suppression effect in the dissociative condition, as compared to the associative, because this mode of retrieval is less automatic and requires control over prepotent responses to stimulus words, which must be suppressed in order to produce dissimilar words. Further research is needed to account for this effect in lexical-semantic tasks using the dual-task paradigm.

## 6.2 The effect of Working memory capacity in semantic cognition

In our experiment, we measured individual WM capacity as a control measure. Before the main lexical-semantic task, participants completed the Backward Digit span task and Operation span task. The individual WM capacity was then averaged from these two tasks. We used this measure in correlation analysis to study the effect of WM capacity on two derived measures - Response initiation (RI) and Inhibition cost (IC). Inhibition cost is the difference between associative and dissociative response time. Response initiation is the overall associate RT averaged across the three load conditions. Another derived measure used in the correlation analysis was the overall WM effect, which was the difference between response time under no WM load and response time under high WM load.

This exploratory analysis hinted that slowing of retrieval due to WM load (WM effect) was positively correlated with the inhibition cost (Fig. 5.2). In particular, this correlation was stronger for dissociates (Fig. 5.3) than for associates (Fig. 5.3). Such findings may suggest that individuals with less efficient inhibitory processing employ more of the limited WM resources during retrieval (if the WM resources are available) to support the demanding dissociative task and to prevent uncontrollable triggering of automatic associates. Indeed, further research is still needed to address and critically evaluate these proposed accounts and whether WM interacts with automatic and dissociative processing via the same or partially distinct means.

The correlation analysis showed a negative correlation between WMC and RI (Fig. 5.2). Our result suggests, that individuals with high WMC are faster in delivering associations than low WMC individuals, regardless of WM load. This may indicate that

WM contributes to automatic retrieval. It is also in line with other studies (Unsworth et al., 2013; Unsworth, 2007) showing that high-WMC individuals retrieve more correct responses than low-WMC individuals. They argue with the choice of searching strategies. While high-WMC individuals reported using general-specific strategy, the low-WMC individuals did not use any strategy- they retrieved words in random order. Unsworth et al. (2013) thus propose, that WMC is not needed in the whole search process, but is crucial when individuals must select a search strategy, to produce suitable cues. This could also be a situation in controlled mechanisms when a dominant automatic response must be suppressed in order to retrieve a task-relevant response. However, further research is needed to evaluate these proposed interactions of WM and automatic and dissociative semantic processing.

## 6.3 Limitations

The present study investigated free associations and controlled inhibition in semantic retrieval with the novel lexical-semantic task ACT (Marko et al., 2019b), whereas most studies focused on semantic cognition using verbal fluency tasks. Having a different methodological approach allowed us to bring a new viewpoint into this area and made an attempt to examine unexplored connections and interactions between WM and semantic cognition. However, there were few studies to compare our results with, so further research is needed to support, refute, or expand our results. In addition, studies with verbal fluency used recordings of participant's responses, thus their results are not affected by possible slow down of the computer keyboard. However, we limited this effect by counting the response times from the initiation of responses, thus the pace of writing should not be taken into account. Nevertheless, during the experiment, we noticed that the participants had problems with fast typing. Even though we asked them not to care about mistakes or accents, they tended to correct their responses which resulted in prolonged time and less produced words in total. It would be interesting to adapt this study for the possible use of a voice recorder instead of a computer keyboard.

Also, another shortcoming needs to be considered. The experiment was administrated by two researchers. One of them was English-speaking, thus all instructions from the researcher were in the English language. There were also written instructions in the Slovak language at the beginning of each task, but it might have produced a little confusion among participants. However, we always tried to ask participants if they understand everything clearly, and before the experiment they have stated their level of English proficiency.

Finally, the findings might not be generalized, because the experiment was focused only on a limited scope of semantic cognition (free associations and controlled inhibition). There is a possibility that the role of working memory is qualitatively (or quantitatively) different in other processes of (controlled) semantic cognition, e.g., when searching for atypical associations or common association of various stimuli. These phenomena need further research.

Future work will investigate the neural correlates of automatic and controlled semantic retrieval under cognitive load with the use of transcranial magnetic stimulation (TMS). This will shed light on possible interactions between working memory and semantic retrieval. The additional concentration on the effect of the concurrent WM load in the semantic network could be studied with the use of functional magnetic resonance imaging (fMRI). This could reveal how WM load affects neural networks implementing semantic cognition (automatic or controlled).

# Conclusion

The semantic system is crucial for context relevant behavior. The controlled semantic cognition framework (Ralph et al., 2017) proposes that this system is not just the storage of conceptual knowledge, but it consists of another system responsible for control. It is suggested that this semantic-specific control system interacts with a general-domain cognitive control and working memory to executively manipulate the retrieval of semantic representations that fit the current demands or situation.

In this research, we administered a behavioral experiment focusing on the investigation of the domain-general executive system and its role in the semantic memory retrieval. For this purpose we employed a dual-task paradigm to effectively manipulate the domain-general demands. Contrary to other previous studies we used a novel lexical-semantic task for assessing semantic retrieval, which enabled us to examine both the automatic (associative) and the controlled (dissociative) retrieval processes. With new methodology we explored the interactions between both retrieval processes and working memory. We hypothesised that a concurrent working memory load will increase the average retrieval latency in both retrieval conditions (automatic and controlled), but this impairment will be more substantial for controlled processing.

Our research showed a significant impairment in both conditions under WM load. This indicates that the working memory contributes to semantic memory retrieval in a more broad sense. Previous research pointed out that active maintainance of representations in WM induces synchronised activations in the domain-specific cortical network, which enables other mental processes such as semantic activation and feature analysis, to have access to the representations held in WM. This is in line with the suggestion that maintained representations in WM intensify the activation of relevant knowledge in long term memory. This leads to deeper processing and strategic access to task-relevant representations. However, when WM load burdens maintenance of representations and processing of semantic stimuli, the task-relevant and goal-oriented retrieval may be impaired.

We believe that our research will serve as a base for future studies on semantic memory retrieval and its interaction with the domain-general executive system. Future studies should examine the differences between automatic and controlled semantic retrieval processes. This path of research is not only important from a psychological perspective, but may also help to unravel the different pathophysiology of its various impairments.

# Bibliography


Allen, P., Mechelli, A., Stephan, K. E., Day, F., Dalton, J., Williams, S., and McGuire, P. K. (2008). Fronto-temporal interactions during overt verbal initiation and suppression. *Journal of Cognitive Neuroscience*, 20(9):1656–1669.

Amunts, J., Camilleri, J. A., Eickhoff, S. B., Heim, S., and Weis, S. (2020). Executive functions predict verbal fluency scores in healthy participants. *Scientific reports*, 10(1):1–11.

Atkinson, R. C. and Shiffrin, R. M. (1968). Human memory: A proposed system and its control processes. *Psychology of learning and motivation*, 2(4):89–195.

Baddeley, A. (2000). The episodic buffer: a new component of working memory? *Trends in cognitive sciences*, 4(11):417–423.

Baddeley, A. (2012). Working memory: theories, models, and controversies. *Annual review of psychology*, 63:1–29.

Baddeley, A. D. and Hitch, G. (1974). Working memory. In *Psychology of learning and motivation*, volume 8, pages 47–89. Elsevier.

Baddeley, A. D. and Logie, R. H. (1999). Working memory: The multiple-component model.

Baddeley, A. D., Thomson, N., and Buchanan, M. (1975). Word length and the structure of short-term memory. *Journal of verbal learning and verbal behavior*, 14(6):575–589.

Badre, D., Poldrack, R. A., Paré-Blagoev, E. J., Insler, R. Z., and Wagner, A. D. (2005). Dissociable controlled retrieval and generalized selection mechanisms in ventrolateral prefrontal cortex. *Neuron*, 47(6):907–918.

Badre, D. and Wagner, A. D. (2002). Semantic retrieval, mnemonic control, and prefrontal cortex. *Behavioral and cognitive neuroscience reviews*, 1(3):206–218.

Badre, D. and Wagner, A. D. (2007). Left ventrolateral prefrontal cortex and the cognitive control of memory. *Neuropsychologia*, 45(13):2883–2901.

Baror, S. and Bar, M. (2016). Associative activation and its relation to exploration and exploitation in the brain. *Psychological science*, 27(6):776–789.

Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software, Articles*, 67(1):1–48.

Becker, C. A. and Killion, T. H. (1977). Interaction of visual and cognitive effects in word recognition. *Journal of experimental psychology: Human perception and performance*, 3(3):389.

Binder, J. R. and Desai, R. H. (2011). The neurobiology of semantic memory. *Trends in cognitive sciences*, 15(11):527–536.

Braver, T. S. and Cohen, J. D. (1999). Dopamine, cognitive control, and schizophrenia: the gating model. In *Progress in brain research*, volume 121, pages 327–349. Elsevier.

Brozoski, T. J., Brown, R. M., Rosvold, H., and Goldman, P. S. (1979). Cognitive deficit caused by regional depletion of dopamine in prefrontal cortex of rhesus monkey. *Science*, 205(4409):929–932.

Collette, F., Van der Linden, M., Delfiore, G., Degueldre, C., Luxen, A., and Salmon, E. (2001). The functional anatomy of inhibition processes investigated with the hayling task. *Neuroimage*, 14(2):258–267.

Collins, A. M. and Loftus, E. F. (1975). A spreading-activation theory of semantic processing. *Psychological review*, 82(6):407.

Constantinidis, C., Franowicz, M. N., and Goldman-Rakic, P. S. (2001). Coding specificity in cortical microcircuits: a multiple-electrode analysis of primate prefrontal cortex. *Journal of Neuroscience*, 21(10):3646–3655.

Cools, R. and D'Esposito, M. (2010). 5.4 dopaminergic modulation of flexible cognitive control in humans. *Dopamine handbook*, page 249.

D'Esposito, M., Detre, J. A., Alsop, D. C., Shin, R. K., Atlas, S., and Grossman, M. (1995). The neural basis of the central executive system of working memory. *Nature*, 378(6554):279–281.

D'Esposito, M. and Postle, B. R. (2015). The cognitive neuroscience of working memory. *Annual review of psychology*, 66.

Devinsky, O. and D'Esposito, M. (2003). *Neurology of cognitive and behavioral disorders*, volume 68. Oxford University Press.

Diamond, A. (2013). Executive functions. *Annual review of psychology*, 64:135–168.

Duncan, J. (2001). An adaptive coding model of neural function in prefrontal cortex. *Nature reviews neuroscience*, 2(11):820–829.

Durstewitz, D., Seamans, J. K., and Sejnowski, T. J. (2000). Neurocomputational models of working memory. *Nature neuroscience*, 3(11):1184–1191.

Fedorenko, E. and Thompson-Schill, S. L. (2014). Reworking the language network. *Trends in cognitive sciences*, 18(3):120–126.

Friedman, N. P. and Miyake, A. (2017). Unity and diversity of executive functions: Individual differences as a window on cognitive structure. *Cortex*, 86:186–204.

Fries, P. (2005). A mechanism for cognitive dynamics: neuronal communication through neuronal coherence. *Trends in cognitive sciences*, 9(10):474–480.

Fuster, J. M. and Alexander, G. E. (1971). Neuron activity related to short-term memory. *Science*, 173(3997):652–654.

Henry, J. D. and Crawford, J. R. (2004). A meta-analytic review of verbal fluency performance following focal cortical lesions. *Neuropsychology*, 18(2):284.

Herdman, C. M. (1992). Attentional resource demands of visual word recognition in naming and lexical decisions. *Journal of Experimental Psychology: Human Perception and Performance*, 18(2):460.

Heyman, T., Van Rensbergen, B., Storms, G., Hutchison, K. A., and De Deyne, S. (2015). The influence of working memory load on semantic priming. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 41(3):911.

Hill, H., Strube, M., Roesch-Ely, D., and Weisbrod, M. (2002). Automatic vs. controlled processes in semantic priming—differentiation by event-related potentials. *International Journal of Psychophysiology*, 44(3):197–218.

Hills, T. T., Mata, R., Wilke, A., and Samanez-Larkin, G. R. (2013). Mechanisms of age-related decline in memory search across the adult life span. *Developmental psychology*, 49(12):2396.

Hills, T. T., Todd, P. M., and Jones, M. N. (2015). Foraging in semantic fields: How we search through memory. *Topics in Cognitive Science*, 7(3):513–534.

Jefferies, E., Thompson, H., Cornelissen, P., and Smallwood, J. (2020). The neurocognitive basis of knowledge about object identity and events: dissociations reflect opposing effects of semantic coherence and control. *Philosophical Transactions of the Royal Society B*, 375(1791):20190300.

Karr, J. E., Areshenkoff, C. N., Rast, P., Hofer, S. M., Iverson, G. L., and Garcia-Barrera, M. A. (2018). The unity and diversity of executive functions: A systematic review and re-analysis of latent variable studies. *Psychological bulletin*, 144(11):1147.

Kesner, R. (1973). A neural system analysis of memory storage and retrieval. *Psychological Bulletin*, 80(3):177.

Kimberg, D. Y., D'Esposito, M., and Farah, M. J. (1997). Effects of bromocriptine on human subjects depend on working memory capacity. *Neuroreport*, 8(16):3581–3585.

Kimberg, D. Y. and D'Esposito, M. (2003). Cognitive effects of the dopamine receptor agonist pergolide. *Neuropsychologia*, 41(8):1020–1027.

Luke, S. G. (2017). Evaluating significance in linear mixed-effects models in R. *Behavior research methods*, 49(4):1494–1502.

Marko, M., Cimrová, B., and Riečanský, I. (2019a). Neural theta oscillations support semantic memory retrieval. *Scientific reports*, 9(1):1–10.

Marko, M., Michalko, D., and Riečanský, I. (2019b). Remote associates test: An empirical proof of concept. *Behavior research methods*, 51(6):2700–2711.

Mayr, U. (2002). On the dissociation between clustering and switching in verbal fluency: Comment on Troyer, Moscovitch, Winocur, Alexander and Stuss. *Neuropsychologia*, 40(5):562–566.

Mayr, U. and Kliegl, R. (2000). Complex semantic processing in old age: Does it stay or does it go? *Psychology and aging*, 15(1):29.

Miyake, A., Emerson, M. J., Padilla, F., and Ahn, J.-c. (2004). Inner speech as a retrieval aid for task goals: The effects of cue type and articulatory suppression in the random task cuing paradigm. *Acta psychologica*, 115(2-3):123–142.

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

Neely, J. H. (1977). Semantic priming and retrieval from lexical memory: Roles of inhibitionless spreading activation and limited-capacity attention. *Journal of experimental psychology: general*, 106(3):226.

Posner, M. I., Snyder, C. R., and Solso, R. (1975). Attention and cognitive control. *Information processing and cognition: The Loyola symposium.*

Pribram, K., Ahumada, A., Hartog, J., and Roos, L. (1964). A progress report on the neurological processes disturbed by frontal lesions in primates. In *The frontal granular cortex and behavior*, pages 28–55. McGraw-Hill New York.

Ralph, M. A. L., Jefferies, E., Patterson, K., and Rogers, T. T. (2017). The neural and computational bases of semantic cognition. *Nature Reviews Neuroscience*, 18(1):42–55.

Rende, B., Ramsberger, G., and Miyake, A. (2002). Commonalities and differences in the working memory components underlying letter and category fluency tasks: a dual-task investigation. *Neuropsychology*, 16(3):309.

Rogers, T. T. and McClelland, J. L. (2004). *Semantic Cognition: A Parallel Distributed Processing Approach*. The MIT Press.

Rosen, V. M. and Engle, R. W. (1997). The role of working memory capacity in retrieval. *Journal of Experimental Psychology: General*, 126(3):211.

Roux, F. and Uhlhaas, P. J. (2014). Working memory and neural oscillations: alpha–gamma versus theta–gamma codes for distinct WM information? *Trends in cognitive sciences*, 18(1):16–25.

Sabb, F. W., Bilder, R. M., Chou, M., and Bookheimer, S. Y. (2007). Working memory effects on semantic processing: Priming differences in pars orbitalis. *Neuroimage*, 37(1):311–322.

Sawaguchi, T. and Goldman-Rakic, P. S. (1991). D1 dopamine receptors in prefrontal cortex: involvement in working memory. *Science*, 251(4996):947–950.

Schwartz, M. F., Kimberg, D. Y., Walker, G. M., Brecher, A., Faseyitan, O. K., Dell, G. S., Mirman, D., and Coslett, H. B. (2011). Neuroanatomical dissociation for taxonomic and thematic knowledge in the human brain. *Proceedings of the National Academy of Sciences*, 108(20):8520–8524.

Shao, Z., Janse, E., Visser, K., and Meyer, A. S. (2014). What do verbal fluency tasks measure? Predictors of verbal fluency performance in older adults. *Frontiers in psychology*, 5:772.

Singer, W. (2009). Distributed processing and temporal codes in neuronal networks. *Cognitive neurodynamics*, 3(3):189–196.

Sreenivasan, K. K., Curtis, C. E., and D'Esposito, M. (2014). Revisiting the role of persistent neural activity during working memory. *Trends in cognitive sciences*, 18(2):82–89.

Thompson-Schill, S. L., D'Esposito, M., Aguirre, G. K., and Farah, M. J. (1997). Role of left inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation. *Proceedings of the National Academy of Sciences*, 94(26):14792–14797.

Tulving, E. et al. (1972). Episodic and semantic memory. *Organization of memory*, 1:381–403.

Turner, M. L. and Engle, R. W. (1989). Is working memory capacity task dependent? *Journal of memory and language*, 28(2):127–154.

Umrianová, R. (2019). Role of theta oscillations in prefrontal cortex in semantic retrieval: tACS study. Master's thesis, Comenius University in Bratislava, Mlynská dolina, 842 48 Bratislava. Available from CRZP.

Unsworth, N. (2007). Individual differences in working memory capacity and episodic retrieval: Examining the dynamics of delayed and continuous distractor free recall. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 33(6):1020.

Unsworth, N., Brewer, G. A., and Spillers, G. J. (2013). Working memory capacity and retrieval from long-term memory: The role of controlled search. *Memory & Cognition*, 41(2):242–254.

Wang, X.-J. (1999). Synaptic basis of cortical persistent activity: the importance of NMDA receptors to working memory. *Journal of Neuroscience*, 19(21):9587–9603.

Wechsler, D. (1949). Wechsler intelligence scale for children.

Whiteside, D. M., Kealey, T., Semla, M., Luu, H., Rice, L., Basso, M. R., and Roper, B. (2016). Verbal fluency: Language or executive function measure? *Applied Neuropsychology: Adult*, 23(1):29–34.

Whitney, C., Kirk, M., O'Sullivan, J., Lambon Ralph, M. A., and Jefferies, E. (2011). The neural organization of semantic control: TMS evidence for a distributed network in left inferior frontal and posterior middle temporal gyrus. *Cerebral Cortex*, 21(5):1066–1075.