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UNIVERSITY OF CALIFORNIA SAN DIEGO

SAN DIEGO STATE UNIVERSITY

The influence of semantic context on lexical retrieval in individuals with and without aphasia

A dissertation submitted in partial satisfaction of the requirements for the degree of Doctor of Philosophy

in

Language and Communicative Disorders

by

Elizabeth Anderson

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The dissertation of Elizabeth Anderson is approved, and it is acceptable in quality and form for publication on microfilm and electronically.

Chair

University of California San Diego San Diego State University

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ABSTRACT OF THE DISSERTATION

The influence of semantic context on lexical retrieval in individuals with and without aphasia Elizabeth Anderson Doctor of Philosophy in Language and Communicative Disorders University of California San Diego, 2024 San Diego State University, 2024

Professor Stephanie Riès, Chair

Anomia is a pervasive deficit across individuals with left hemisphere stroke-induced aphasia. Although lexical retrieval is often impaired in individuals with aphasia, the driving forces behind lexical retrieval deficits are not well understood. Lexical activation and selection are key processes enabling us to retrieve words as we speak. Lexical activation occurs through spreading activation from semantic to lexical representations and is facilitated in semanticallyrelated contexts. Lexical selection is the selection of the target word from activated semanticallyrelated alternatives and can be slowed in semantically-related contexts. Lexical retrieval stages can be differently affected depending on the type of semantic context. Taxonomically-related words (e.g., wolf-dog) have been linked with semantic interference. However, thematicallyrelated words (e.g., dog-leash) have been linked with facilitation. Across four studies, this dissertation analyzes the spatiotemporal dynamics of lexical retrieval to further characterize the neural regions and processes underlying lexical retrieval and how these may be differentially impacted depending on the type of semantic context. The results show that taxonomically-related contexts cause semantic interference and are associated with a larger negative-going component in the 300-500 ms time window restricted to a left frontal recording site in both young and older control participants. This component is absent in individuals with aphasia regardless of their lesion site. However, individuals with brain lesions including the left posterior temporal cortex showed impairments in lexical activation, preceding lexical selection, and inner speech monitoring as indicated by an impaired medial frontal error-related electrophysiological component. Intracranial data revealed that medial and superior frontal regions typically associated with conflict resolution are also engaged during spreading activation during picture naming. The results of these studies provide a key step towards understanding the brain dynamics of lexical retrieval in stroke-induced aphasia, including how different lexical retrieval deficits interact with semantic contexts, and providing a knowledge basis for the future development of clinical tools for lexical retrieval.

INTRODUCTION

Anyone who has experienced the tip-of-the-tongue phenomenon knows how frustrating it can be when your brain fails to find the word you are searching for. You might be in the kitchen and turn to ask someone to pass you a spatula and find yourself stuck when the only word you can think of is *spoon*. We can often navigate this setback without too much difficulty, but the older we get the more common this becomes (Salthouse & Mandell, 2013), and for a person with damage to their lexical retrieval system it may be like living in a perpetual state of tip-of-the-tongue.

Language production is a complex task that many adults perform efficiently, retrieving 2-3 words per second from over 50,000 words in their lexicon (Levelt et al., 1999). Despite the ease with which we speak, identifying the neural processes underlying word retrieval during language production is a complex task. After a left hemisphere stroke, these underlying neural processes are often disrupted, resulting in anomia, or the inability to name objects or people. Anomia is one of the most common characteristics of aphasia (<u>Goodglass & Wingfield, 1997</u>). Approximately 180,000 people in the United States have a stroke resulting in aphasia every year and there are about 1 million people with aphasia in the United States currently (NIDCD, 2015). Across four studies, the current dissertation (1) explores the mechanisms underlying lexical retrieval in adults with and without left hemisphere stroke-induced aphasia and (2) discusses the impact of semantic context on these mechanisms, arguing that semantic context plays an important role in word retrieval. In this introduction I will first discuss lexical retrieval and associated cognitive models and the variable influence of semantic context on lexical retrieval followed by an exploration of lexical retrieval disorders. Then, I will discuss the existing

knowledge of the neural underpinnings of lexical retrieval. To conclude, I will give an overview of the chapters of the dissertation.

Lexical retrieval

Several models have been proposed to describe the cognitive processes occurring during language production (Dell, 1986; Dell et al., 1997, 2013; Indefrey & Levelt, 2004; Rabovsky et al., 2016). Such models consistently feature several recognized stages of processing including semantic, lexical (or *lemma*, a nonphonological representation of a word), and phonological stages (Dell et al., 1997). The semantic level contains semantic concepts and features that pertain to the target word/image which are then mapped to a lemma. Then, the lemma maps onto the phonological form of the word, which is then mapped onto articulatory representations leading to the articulation of the word (Dell, 1986; Dell et al., 1997) These levels of language production are often considered interactive and cascading, meaning that semantic processing does not need to be entirely completed before phonological processing and information can flow freely between levels. For this dissertation, the focus is on the intersection between the semantic and lexical layers.



Figure i.1. (a) Serial processing model (Levelt et al., 1999; Indefrey, 2011). (b) Interactive activation model adapted from Dell et al., 1997.

All production models agree upon the idea that semantically related words are coactivated when we produce language. For example, semantically related words such as "bee" and "wasp" share semantic features (e.g., antennae, wings, stingers, etc.). Once a semantic feature is activated this can lead to the activation of multiple lexical items that are connected to that feature (i.e., the activation of the semantic feature antennae can lead to the activation of lexical representations for both bee and wasp). However, regardless of the number of activated lexical representations the goal is still to produce a single response.

Our semantic networks consistently activate as we speak, making them an integral part of lexical retrieval. As a result, the impact of semantic co-activation is often used as a method to understand lexical retrieval. There is a general consensus that lexical activation in production (Alario et al., 2000; Bloem et al., 2004; Costa et al., 2005) and comprehension (Meyer & Schvaneveldt, 1971) is facilitated in semantically related contexts as a result of spreading activation from semantic representations (e.g., insect, flying, etc.) to lexical representations that share these semantic attributes (e.g., *bee, wasp*, etc.) and to frequently co-activated representations (e.g., honey for bee). However, previous language production studies have demonstrated that the behavioral outcome of this co-activation during lexical retrieval depends on the type of semantic relationship tested (Alario et al., 2000; Bloem et al., 2004; Costa et al., 2005; Landrigan & Mirman, 2018). Thematic and taxonomic semantic relationships are two types of semantic relationships that have been studied in the context of language production. Thematic relationships, based on co-occurrence in scenarios (e.g., bee-honey), generally lead to semantic facilitation (Alario et al., 2000; Bloem et al., 2004; Costa et al., 2005; de Zubicaray et al., 2013). Taxonomic relationships, related based on category membership (e.g., bee-wasp),

generally lead to semantic interference in language production (Alario et al., 2000; Bloem et al., 2004; Costa et al., 2005; de Zubicaray et al., 2013).

Rabovsky et al. (2016) proposed a possible explanation for these effects by linking them to a varying number of semantic features and intercorrelational feature density across contexts. Taxonomically-related words tend to share a large number of semantic features, which is associated with an increased activation of semantic neighbors that share these features during language production. This increased co-activation is assumed to be the cause of the semantic interference effect observed in taxonomic contexts, as there will be many activated lexical representations to select from. Since thematically-related words belong to different semantic categories they do not typically share a large number of features. As a result, they tend not to activate as large of a lexical cohort as taxonomic contexts do.

Lexical retrieval in production has most frequently been investigated through the lens of semantic interference. Indeed, there is often an increase in naming latencies and error rates in semantically related compared to unrelated conditions (Damian et al., 2001; Howard et al., 2006; Lupker, 1979). This effect has traditionally been interpreted as reflecting increased difficulty in lexical retrieval (Damian et al., 2001; Howard et al., 2006; Lupker, 1979). However, there are different explanations concerning the origins of this semantic interference effect, including increased competition at the level of lexical selection (e.g., Damian et al., 2001; Howard et al., 2006; Roelofs & Piai, 2013), incremental changes in connection weights between semantic and lexical representations (e.g., Oppenheim et al., 2010; Harvey et al., 2019), and conflict at the level of response preparation (e.g., Caramazza & Costa, 2000; Blackford et al., 2012; Costa et al., 2005; Giezen & Emmorey, 2016; Mahon et al., 2007; Mahon & Navarrete, 2014).

According to Nozari & Hepner (2018), the concept of a flexible criterion for selection has been missing from the debate regarding whether lexical selection is competitive. The inclusion of a flexible criterion means that lexical selection will be impacted by task goals and the level of conflict between activated representations. The flexible criterion theory seeks to answer the question of how the production system determines the difference criterion (α_0), i.e., the point at which one lexical representation is selected over another. Conflict is defined here as "the inverse of the difference between the most highly activated representation and that of the next highest" (Nozari et al., 2011; Nozari & Hepner, 2018). For instance, if the activation level of the target word bee is .02 and the activation level of its nearest competitor wasp is .01, then the conflict level is 100. The difference criterion is typically placed between the conflict distributions of potential correct and error responses, meaning that the placement of this criterion determines whether a response is detected as an error as well. The criterion placement process is dynamic and can vary both within and across individuals (Cox & Shiffrin, 2012; Nozari & Hepner, 2018; Singer & Wixted, 2006). Due to the flexible nature of the model, it is able to account for both competitive and non-competitive selection (see Figure 1 for response distributions).



Figure i.2. Flexible-criterion model, figure adapted from Nozari & Hepner (2018). (a) Lowconflict situation with difference criterion placed at a₀. (b) If the criterion is placed at the intersection of the two distributions, both error rates (dark purple area) and latencies (dark blue area) will increase. (c) The criterion shifts right and away from the a0 from (a), resulting in maintained latencies but an increase in overt errors. (d) The criterion shifts to the left and away from the a0 in (a), overt error rate is maintained but latencies will increase.

In a low conflict situation, the flexible criterion model places the criterion by optimizing performance through balancing between reaction time latency and accuracy. In a high conflict situation, the system recalibrates to find a new optimal criterion, either shifting to the right in favor of faster responses but at the expense of accuracy, or to the left in favor of accuracy but at the expense of speed (Nozari & Hepner, 2018). When faced with this level of high conflict, a healthy speaker's system will typically automatically shift the criterion to the left to avoid making errors.

Of interest for the current work is what individuals with impaired language production systems, particularly those who have stroke-induced lesions, do when required to retrieve words in different contexts inducing varying amounts of conflict. If, as suggested, lexical retrieval can be separated into lexical activation and lexical selection, the impact of lesions on lexical retrieval as a whole as well as on each stage of lexical retrieval must be considered.

Lexical retrieval deficits

Aphasia primarily occurs after left-hemisphere stroke-induced lesions, resulting in impairments in language expression and/or reception. Although there is a broad range in type and severity of language impairments resulting from aphasia, a commonality amongst most individuals with aphasia is anomia, a deficit in lexical retrieval. Despite the high rates of lexical retrieval deficits, the driving forces behind lexical retrieval deficits are not well understood.

Although two individuals with aphasia may both have lexical retrieval deficits, the characteristics of their deficits can differ (e.g., the speed of retrieval, the predominant type of errors they produce, etc.). To account for this variance, different underlying causes have been proposed to underlie lexical retrieval deficits. When lexical-semantic processes are damaged, there is an increase in conflict between active lexical representations, which in turn leads to a decrease in distance between the conflict distribution of errors and correct trials as shown in Figure 2 (Nozari & Hepner, 2018). As a result, an individual with a lexical retrieval deficit is essentially in a continuous state of high conflict that they are unable to resolve interference between representations with the same efficacy as a neurotypical speaker (Nozari & Hepner, 2018). In the flexible criterion model, there are two possible outcomes when an individual with impaired lexical-semantic mapping produces words: they unconsciously shift their criterion to prioritize accuracy (at the cost of speed) or they unconsciously shift their criterion to prioritize speed (at the cost of accuracy). When individuals with brain lesions shift their difference criterion to prioritize accuracy the result is an increase in omission errors due to the decreased efficiency of the damaged system (Nozari & Hepner, 2018). If individuals with lesioned systems shift their criterion to prioritize quick responses, then they will produce more overt errors (e.g., "truck" instead of "bus" during related blocks in blocked cyclic naming). A remaining question is what the underlying cause of differences in criterion setting is and resultant differences

observed in the type of error produced in individuals with aphasia. In a case study by Nozari (2019) that will be discussed in further detail in Chapter 4, two individuals with aphasia displayed the two patterns of behavior described above.



Figure i.3. Flexible criterion model from Nozari & Hepner 2018 showing a high-conflict situation in a production system with damage to the semantic-lexical mapping process. The distributions of conflict for potential correct and error responses overlap significantly, so performance optimization is difficult no matter where the criterion is placed. (a) The criterion is placed at the intersection of the two distributions. (b) The criterion is shifted to the right, away from the original $\alpha 0$, resulting in many commission errors (mostly semantic) but few delays. (c) The criterion is shifted to the left, towards the original $\alpha 0$, resulting in many delayed responses. (d) Critically, the delayed responses are unlikely to reach the desired criterion in a reasonable time because of the poor state of semantic–lexical mapping, leading to many omission errors and, in severe cases, near-mutism.

Nozari (2019) suggests that the variance in pattern of results is due to a dissociation between lexical activation and lexical selection processes. The results (Figure 3) suggest that activation and selection are separable and therefore can be selectively damaged in individuals with aphasia. When the process of lexical activation is damaged, individuals are no longer able to activate lexical items from semantic features. This makes it difficult for any lexical item to cross the threshold necessary for selection, leading to single-word responses, long delays, and an overall increase in omission errors (Nozari, 2019). When the deficit is instead in the ability to suppress incorrect responses, lexical selection is disrupted. Production may be faster, but there is an increase in multiple semantically-related errors per target lexical item. (Nozari, 2019). Neuropsychological and neuroimaging studies suggest that one possible cause for the dissociation of activation and selection deficits in individuals with aphasia is the location of their lesion and the role these regions serve in the stages of lexical retrieval.

	Activation deficit (XR)	Inhibition deficit (QD)
Picture naming	Longer RT, often a single semantically-related response	Shorter RT, multiple semantically-related responses
Modified Category Probe task	Impaired	Unimpaired
Simon task	Unimpaired	Impaired
Miscue task	Few miscue errors	Lots of miscue errors
Word-pair Stroop task	Helped by semantic similarity	Hurt by semantic similarity
Lexical perseveration	Significantly above chance	Marginally above chance

Figure i.4. Summary of findings adapted from Nozari (2019).

Neural underpinnings of lexical retrieval

Several regions of the posterior lateral temporal cortex (pLTC; Figure 4) have been associated with lexical retrieval, including the MTG, inferior temporal gyrus (ITG), and superior temporal gyrus (STG), due to the link between these regions and word meanings (<u>Dronkers et al.</u>, <u>2004; Indefrey & Levelt, 2004; Riès et al., 2017; Trebuchon-Da Fonseca et al., 2009</u>).



Figure i.5. Posterior lateral temporal cortex (pLTC) including the superior temporal gyrus (STG) and middle temporal gyrus (MTG), and inferior temporal gyrus (ITG).

Indeed, individuals with lesions in the pLTC have been shown to struggle to recognize the correct word even when presented to them as an option to choose from (Dronkers et al., 2004), despite their preserved ability to demonstrate object use, indicating that the link between lexical representations and underlying concepts are damaged (Dronkers et al., 2004). The STG and MTG are important for semantic memory (Binder et al., 2009; Bonner & Price, 2013; Patterson et al., 2008; Visser et al., 2010) and mapping concepts onto words during language production (Indefrey & Levelt, 2004; Schwartz et al., 2009). In fMRI (Piai et al., 2013) and MEG (Piai et al., 2014) studies examining the effect of distractors on picture naming in healthy adults, increased activity in the left STG and MTG for unrelated compared to related distractorpicture conditions was found. Spreading activation in the semantically-related condition leads to the picture and word priming each other (Finkbeiner & Caramazza, 2006; Levelt et al., 1999; Roelofs, 2003). Semantic features of a word will activate during production, and the activated semantic features for the target word will also spread activation to all other lexical representations that share those features. The same process occurs during picture naming. Therefore, when a word (e.g., *bee*) and a picture (e.g., *wasp*) share semantic features, the activated semantic features from the word (e.g., stinger, black, yellow, etc.) are contributing to increased activation for the picture and vice versa. The result of this spreading activation is in an attenuation of activity for the related condition relative to the unrelated condition, also referred to as semantic priming (Piai et al., 2013, 2014). This pattern of activity suggests that the left temporal cortex plays a role in lexical activation.

Damage to the MTG in chronic stroke patients is associated with picture naming difficulties (Baldo et al., 2013) and word-level comprehension deficits (Bates et al., 2003; Dronkers et al., 2004). Reperfusion of these regions is correlated with improved naming within 3-5 days post stroke onset, indicating that the MTG is crucial for naming (Hillis et al., 2006). This evidence suggests that their retrieval deficit likely originates at the level of the activation of lexical representations rather than at the level of word selection.

After spreading activation, speakers are tasked with selecting from the set of active lexical representations. As established, this is particularly difficult amongst semantically related alternatives; some neural mechanism is necessary to help speakers correctly select the desired target item. The left prefrontal cortex (LPFC; Figure 5), particularly the left inferior frontal gyrus (LIFG; Riès et al., 2014; Riès et al., 2015; Schnur et al., 2009; Thompson-Schill et al., 1997), middle frontal gyrus (MFG ; <u>Piai et al., 2013</u>) and superior frontal gyrus (SFG; Alario et al., 2006) have been proposed to play a role in overcoming semantic interference (Ries et al., 2014; Schnur et al., 2006; Schnur et al., 2009; Thompson-Schill et al., 1998). The SFG (<u>Piai et al.,</u> <u>2014</u>) and anterior cingulate cortex (ACC; de Zubicaray et al., 2001; Piai et al., 2013) have also been proposed to support cognitive control processes involved in lexical selection.



Figure i.6. Left prefrontal cortex (LPFC), including the left inferior frontal gyrus (LIFG), middle frontal gyrus (MFG), and superior frontal gyrus (SFG).

When the LPFC is damaged, individuals with aphasia have an impaired ability to retrieve semantically related words, suggesting that their deficit lies in the ability to suppress coactivated lexical items during selection (Nozari, 2019; Riès et al., 2015; Schnur et al., 2009; Thompson-Schill et al., 1998). Unlike individuals with damage to the pLTC, individuals with lesions in the LIFG can generally immediately identify the word they are looking for when given a choice between options (Buckner et al., 1996). Indeed, the pattern of behavior exhibited by individuals with LPFC damage, difficulty suppressing semantically-related alternatives with minimal difficulty identifying items, likely reflects a lexical selection deficit rather than a lexical activation deficit. For an example of behavior exhibited by an individual with an inhibition deficit we refer to Nozari (2019). As seen in Figure 3, one of the differences between XR and QD is the effect of semantic similarity on their performance. QD (hypothesized to have an inhibition deficit) was impaired in semantically related conditions, similar to the individuals described above who had increased semantic interference effects with LPFC damage. Semantic context clearly has an impact on individuals with stroke-induced left hemisphere brain lesions, but to understand the nature and extent of this impact it is necessary to consider the role of semantic context in the language production system.

Semantic context

Every time we produce a word, our language production system draws from our semantic knowledge. Since this knowledge is so integral to the functioning of our language system, it logically follows that a greater understanding of the organization and neural implementation of our semantic knowledge will bolster our understanding of the processes underlying word retrieval. As discussed earlier, during language production lexical representations that are semantically related to the target item co-activate. This is why lexical activation is often facilitated in semantically related contexts (Alario et al., 2000; Bloem et al., 2004; Costa et al., 2005). Lexical selection, however, is often studied through semantic interference effects (Damian et al., 2001; Howard et al., 2006; Lupker, 1979). By studying the effects of taxonomic (e.g., bee-wasp) and thematic (e.g., bee-honey) semantic contexts, facilitation effects associated with lexical activation, and interference effects associated with lexical selection, we can develop a better understanding for the mechanisms underlying word retrieval.

Research discussing the processing and representation of taxonomically-related items is substantial, but there is a lack of conclusive work on thematically-related items and how they influence word retrieval in language production (Landrigan & Mirman, 2018; Mirman et al., 2017; Mirman & Graziano, 2012b, 2012a; Schwartz et al., 2011; Thye et al., 2021). Mirman and colleagues have conducted a series of behavioral, eye tracking, and fMRI studies to explore the differences between taxonomic and thematic semantic systems. Notably, they have claimed that taxonomic relations are processed along the ventral processing route, specifically with the anterior temporal lobe serving as the processing hub (Mirman & Graziano, 2012; Schwartz et al., 2011; Thye et al., 2021). They point to the dorsal processing route as being associated with the processing of thematic relations (Kalénine et al., 2009; Mirman et al., 2017; Mirman &

<u>Graziano, 2012; Schwartz et al., 2011</u>). If taxonomic and thematic relationships are in fact separable entities, probing the semantic network through studying these relationships can reveal more about the processes underlying word retrieval. In particular, an exploration of the temporal dynamics of taxonomic versus thematic semantic contexts is missing from the current literature.

Overview of the dissertation

The overarching goals of this dissertation are to (1) investigate the mechanisms underlying word retrieval in adults with and without left hemisphere stroke-induced aphasia and (2) discuss the impact of semantic context on these mechanisms, arguing that semantic context plays an important role in word retrieval in individuals with and without aphasia. The central hypothesis is twofold: (1) the pLTC is crucial for accessing lexical representations and individuals with lesions in this region are more likely to have lexical activation deficits, and increased semantic priming from taxonomic and thematic compared to unrelated contexts will enhance performance; (2) the LPFC is crucial for resolving semantic interference and individuals with lesions in this region are more likely to have lexical selection deficits, and to be impaired in semantically related, particularly taxonomic, compared to unrelated contexts. The behavioral component of this dissertation includes manipulating semantic relationships and observing the resultant effect on reaction time and error rate across participants. The **neuroimaging** component of this dissertation includes measuring differences in activity between conditions across time windows of interest using scalp electroencephalography (EEG) as well as intracranial electroencephalography. The dissertation contains experimental approaches to study lexical retrieval in individuals with and without aphasia with a focus on the impact of semantic context on activation and selection retrieval deficits.

Chapter 1 focuses on the impact of taxonomic and thematic <u>semantic contexts</u> on <u>lexical</u> <u>retrieval</u> in healthy young speakers. I will present findings from an EEG PWI naming task. Pictures were paired with distractor words that were either taxonomically-related (e.g., cowbear), thematically-related (e.g., cow-milk), or unrelated (e.g., cow-pen). It was hypothesized that the presence of taxonomically-related words would require greater cognitive control as reflected by slower reaction times, increased error rates, and increased ERP amplitude compared to the unrelated condition. Thematically-related words should lead to faster reaction times, decreased error rates, and decreased ERP amplitude compared to the unrelated condition. This chapter demonstrates that there is a left frontal semantic interference effect that occurs concurrently with semantic priming for taxonomically-related words. This chapter provides high temporal resolution, but a less defined spatial resolution as to the exact left frontal regions involved in language production. Additional research using a method with high spatial resolution is necessary to further identify the frontal regions involved in lexical retrieval.

Chapter 2 focuses on further characterizing the <u>neural underpinnings of lexical retrieval</u> as discussed above with data from individuals with intractable epilepsy who completed an intracranial EEG PWI task that compared taxonomically-related, unrelated, and identity conditions. This experiment utilized stereotactic EEG, allowing direct access to implanted brain regions while participants named pictures. The primary finding from this study was that frontal regions traditionally associated with cognitive control (ACC, SFG, etc.) are integral in the processes underlying lexical retrieval and are particularly involved in lexical activation in addition to controlled lexical selection. In subsequent research, we were interested in exploring the impact of damage to frontal or temporal regions on language production subprocesses (e.g., lexical activation, interference resolution, speech monitoring, etc.).

Chapter 3 examines conflict monitoring abilities in individuals with lexical retrieval deficits due to damage to frontal or temporal regions that serve as the neural underpinnings of lexical retrieval. We investigated the impact of pLTC lesions on conflict-based monitoring in the medial PFC as reflected by the error-related negativity, a fronto-centrally distributed electrophysiological correlate of speech monitoring. Individuals with aphasia divided into two groups of individuals with left hemisphere lesions, those with damage to the pLTC and those without damage to the pLTC, and age-matched control participants participated in a blockedcyclic naming task. We hypothesized that interactions between the posterior lateral temporal cortex (pLTC) and the medial frontal conflict monitoring system are necessary for inner speech monitoring given that our speech monitor requires access to lexical representations to detect potential conflict and errors. Individuals with a lesion in the pLTC had longer reaction times and produced more errors compared to individuals with left anterior lesions sparing the pLTC. Additionally, they did not show a significant error-related negativity (ERN) unlike control participants or individuals with lesions not including the pLTC. The results from this chapter indicate that the mediofrontal monitoring system that supports inner speech monitoring appears to rely on posterior temporal cortex regions necessary for accessing lexical representations. The subsequent chapter explores how lesions to the pLTC versus LPFC may differentially impact lexical retrieval, as well as the interaction between the effects of different types of semantic context and lesion location on lexical retrieval.

Chapter 4 combines the topics of interest from Chapters 2-4 with a study that examines the relationship between <u>semantic context</u> and <u>lexical retrieval</u> as it applies to individuals with left hemisphere stroke-induced <u>lexical retrieval deficits</u>. The central hypothesis for this study is that the impact of semantic context on lexical retrieval subprocesses in individuals with left

hemisphere stroke-induced lesions depends on the nature of the lexical retrieval deficits these individuals may present with and their brain lesion location. More specifically, I hypothesize that individuals with pLTC lesions will have a deficit in lexical activation and thus will benefit from semantic co-activation, particularly with taxonomically-related words. Taxonomically-related semantic networks are typically denser than thematically-related networks (<u>Rabovsky et al.</u>, <u>2016</u>). Therefore, this dense network of co-activation should increase the likelihood that individuals with cross the threshold for activation. Contrastively, individuals with LPFC lesions will have a deficit in lexical selection and thus will be hurt by semantic co-activation because of their inability to inhibit co-activated alternatives, this will be particularly the case in taxonomically-related contexts because of the higher number of alternatives compared to thematic contexts. This study examines reaction time, error rate, error type, and ERPs to investigate group differences and semantic context effects on lexical retrieval.

Finally, I will present a general discussion of the results of these studies and whether and how these increase our understanding of lexical retrieval mechanisms in speakers with and without stroke-induced aphasia.

CHAPTER 1

Taxonomic and thematic semantic relationships in

picture naming as revealed by Laplacian-transformed event-related potentials

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ORIGINAL ARTICLE

Taxonomic and thematic semantic relationships in picture naming as revealed by Laplacian-transformed event-related potentials

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Abstract

Semantically related concepts co-activate when we speak. Prior research reported both behavioral interference and facilitation due to co-activation during picture naming. Different word relationships may account for some of this discrepancy. Taxonomically related words (e.g., WOLF-DOG) have been associated with semantic interference; thematically related words (e.g., BONE-DOG) have been associated with facilitation. Although these different semantic relationships have been associated with opposite behavioral outcomes, electrophysiological studies have found inconsistent effects on event-related potentials. We conducted a picture-word interference electroencephalography experiment to examine word retrieval dynamics in these different semantic relationships. Importantly, we used traditional monopolar analysis as well as Laplacian transformation allowing us to examine spatially deblurred event-related components. Both analyses revealed greater negativity (150-250 ms) for unrelated than related taxonomic pairs, though more restricted in space for thematic pairs. Critically, Laplacian analyses revealed a larger negative-going component in the 300 to 500ms time window in taxonomically related versus unrelated pairs which were restricted to a left frontal recording site. In parallel, an opposite effect was found in the same time window but localized to a left parietal site. Finding these opposite effects in the same time window was feasible thanks to the use of the Laplacian transformation and suggests that frontal control processes are concurrently engaged with cascading effects of the spread of activation through semantically related representations.

KEYWORDS

ERPs, language production, Laplacian transformation, semantics

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1 | INTRODUCTION

Speech production is a key facet of daily communication, and speakers are typically able to select the correct words to convey their thoughts with ease. Despite the ease with which we speak, identifying the neural processes underlying speech production is a complex task. Several models have been proposed to describe the cognitive processes occurring during language production (Dell et al., 2013; Indefrey & Levelt, 2004; Rabovsky et al., 2016). Such models consistently feature recognized stages of processing such as phonological, morphological, and semantic stages, and all agree upon the idea that semantically related words are co-activated when we produce language. Semantic co-activation refers to the fact that during word retrieval, the target word will receive activation as will its semantic neighbors. The speaker is then tasked with selecting the correct word from the activated options. However, how and when representations are activated at each of the stages and how activation at one stage impacts activation at another stage remains unclear. Here, we address the impact of semantic co-activation during language production by using two complementary electroencephalography (EEG) analysis methods to study the retrieval of unrelated and related nouns.

1.1 Thematic versus taxonomic semantic relationships

Although the existence of semantic co-activation is largely undisputed, the effect of this co-activation on language production and associated brain dynamics currently remains under examination. Evidence exists to support both semantic interference and facilitation on behavior following semantic co-activation (Alario et al., 2000; Bloem et al., 2004; Costa et al., 2005). Semantic interference corresponds to an increase in naming latencies and error rates, whereas semantic facilitation corresponds to a decrease in naming latencies and error rates as the result of the increased activation of semantically related words. These opposing effects of semantic interference and facilitation can be observed in the context of taxonomically related versus thematically related stimuli, respectively (e.g., Alario et al., 2000; Costa et al., 2005; de Zubicaray et al., 2013). Taxonomically related words belong to the same semantic category and have shared features, such as BEE and WASP. Thematically related words occur together in events or scenarios, such as BEE and HONEY. This dissociation between semantic interference in taxonomically related stimuli versus facilitation in thematically related stimuli has been observed in Picture-Word Interference (PWI) tasks where participants name pictures

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with overlapping to be-ignored semantically related distractor words (Abdel Rahman & Melinger, 2007; Alario et al., 2000; Costa et al., 2005; de Zubicaray et al., 2013; La Heij et al., 1990; Sailor et al., 2009), and more recently in the blocked cyclic picture naming paradigm where participants name pictures in blocks of related or unrelated pictures which are repeated for several cycles (McDonagh et al., 2020; although see Roelofs, 2018 and Rose & Abdel Rahman, 2016 for reports of similar interference effects across the different types of semantic relationships in blocked-cyclic and continuous naming tasks). Several explanations have been proposed to account for these opposing effects.

There is a consensus that semantic facilitation is the result of spreading activation from semantic representations (e.g., insect, flying.) to lexical representations that share these semantic attributes (e.g., bee, wasp.) and to frequently co-activated representations (e.g., honey for bee) (Alario et al., 2000; Bloem et al., 2004; Costa et al., 2005). However, there are different explanations concerning the origins of interference, including increased competition at the level of lexical selection (e.g., Damian et al., 2001; Howard et al., 2006; Roelofs & Piai, 2013), incremental changes in connection weights between semantic and lexical representations (e.g., Harvey et al., 2019; Mahon et al., 2012; Mahon & Navarrete, 2014; Oppenheim et al., 2010), and conflict at the level of response preparation (e.g., Blackford et al., 2012; Caramazza & Costa, 2000; Costa et al., 2005; Giezen & Emmorey, 2016; Mahon et al., 2007).

These theories were formulated with evidence compiled from several picture naming paradigms, primarily including the blocked-cyclic, continuous naming, and PWI tasks. Blocked-cyclic (Damian et al., 2001; Oppenheim et al., 2010) and continuous naming (Harvey et al., 2019; Howard et al., 2006) tasks have both been used as evidence to support the idea that semantic interference originates in links between concepts and lexical items and manifests at the stage of lexical selection (Belke & Stielow, 2013; Howard et al., 2006; Oppenheim et al., 2010; Roelofs, 2018). There is debate surrounding the locus of the semantic interference effect in the PWI task. For example, the response exclusion hypothesis (Mahon et al., 2007) theorizes that semantic interference originates from late post-selection monitoring processes during articulation in response to the structure of the task rather than lexical retrieval processes (Blackford et al., 2012; Caramazza & Costa, 2000; Costa et al., 2005; Giezen & Emmorey, 2016; Mahon et al., 2007; Navarrete et al., 2014). Alternatively, a comparison of the three paradigms from Roelofs (2018) suggests that all three tasks are examining word retrieval with semantic interference occurring at the stage of lexical selection.

Roelofs cites overlapping times windows of semantic effects in electrophysiological studies (Aristei et al., 2011; Blackford et al., 2012; Costa et al., 2009; Dell'Acqua et al., 2010; Janssen et al., 2015; Maess et al., 2002; Piai et al., 2014; Rose & Abdel Rahman, 2016) and similar increases in semantic error rates in individuals with left MTG lesions across paradigms (Harvey & Schnur, 2015; Piai & Knight, 2018; Schwartz et al., 2009) to support this claim.

Although all of these proposed theories are in agreement that interference emerges after or concurrently with initial lexical activation, what remains unclear is the relative timing of these processes and possible co-occurrence of facilitation and interference effects. The current study investigates the relative timing and potential cooccurrence of facilitation and interference effects by using both traditional ERP analysis as well as Laplacian transformation providing an estimate of the current source density to examine how different semantic relationships affect the spatio-temporal dynamics of word retrieval during word production.

1.2 | Electrophysiology of language production

Electrophysiological studies provide evidence on the timing of processes required to produce single words that cannot be understood from behavioral data alone. The manipulation of semantic context has been used as a means to probe when brain activity is associated with different processes leading to word production. Several ERP components have been found to be sensitive to semantic context in PWI tasks, including the N1 (Hirschfeld et al., 2008; Wamain et al., 2015), P3 (Wamain et al., 2015), and N400 components (Blackford et al., 2012; Kutas & Federmeier, 2011). In particular, ERP studies of word production have generally converged on two time windows associated with semantic context effects. The first window being between 150 and 250 ms after stimulus onset and associated with visual processing and lexical access based on the observation of semantic context effects in this early time window (Aristei et al., 2011; Blackford et al., 2012; Costa et al., 2009; De Cesarei et al., 2013; Eddy et al., 2006; Eddy & Holcomb, 2010; Strijkers et al., 2010). The second window being centered on the N400, between 300 and 500 ms poststimulus onset, as this established component in language research has been shown to be sensitive to lexico-semantic processing (Kutas & Federmeier, 2011; Kutas & Hillyard, 1980) and to semantic context in the direction of semantic facilitation (larger N400 in unrelated vs. related blocks). In line with facilitatory effects PSYCHOPHYSIOLOGY

found on behavioral measures, thematic relationships have been consistently associated with facilitation effects on ERPs in PWI studies (i.e., smaller amplitudes for semantically related than unrelated stims in all of the aforementioned time windows; Hirschfeld et al., 2008; Wamain et al., 2015). However, results have been less consistent for taxonomic relationships. Whereas some of these studies have reported no difference in amplitude between related and unrelated conditions (Hirschfeld et al., 2008; Wamain et al., 2015), other studies have reported reduced N400 in related versus unrelated conditions for taxonomic pairs (Blackford et al., 2012; Roelofs et al., 2016; see Kutas & Federmeier, 2011). Possible reasons for these inconsistencies include inconsistent study designs, individual differences in semantic knowledge and access, ambiguous interpretations of findings, and the types of ERP analysis techniques used.

In particular, concerning study design, previous studies have not always analyzed taxonomic and thematic relationships against a baseline unrelated condition in order to independently and systematically compare the neurological and behavioral effects of each relationship (e.g., Aristei et al., 2011). Only two of the above-mentioned studies explicitly discussed controlling for the degree of relatedness between pairs in each condition (Blackford et al., 2012 with pairwise comparison values and Wamain et al., 2015 with surveys). In addition, while several electroencephalographic studies have examined the impact of semantic relatedness on the brain dynamics underlying picture naming, few of these studies have directly compared different types of semantic relatedness using EEG (Aristei et al., 2011; Hirschfeld et al., 2008; Wamain et al., 2015). In order to optimize the comparison of semantic context effects between taxonomic and thematic conditions, it is important to directly compare these conditions to ensure that the results are not due to confounding factors such as differences in relatedness strength between conditions. Indeed, the variable ERP effects observed across taxonomic and thematic relationships could be linked to individual differences in similarity judgments between taxonomic and thematic relationships. Taxonomic and thematic similarity judgment has been shown to predict ERP amplitude during passive word reading (Honke et al., 2020). In the current study we controlled for group level differences in stimulus perception prior to the onset of the study through a norming survey to ensure matched ratings of relatedness across conditions and corpus linguistics analysis (see Section 3.2).

Concerning result interpretation, using difference waves has led to debatable interpretations of taxonomic semantic context effects. In particular, using a blocked cyclic naming task with taxonomically related and unrelated items, Janssen et al. (2015) claimed to report both

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an early facilitation (300–400 ms) and later interference effect (500–750 ms) in their ERP data. However, for both the early and late effects the waveforms were larger for unrelated than related condition, except that the early effect was found on a negative-going waveform and the late effect was found on a positive-going waveform. Therefore, analyzing difference waves led to incorrectly interpreting these effects as being opposite. In order to avoid this issue in the present study, we will focus on analyzing waveforms in the individual conditions rather than solely focusing on the difference waves.

A fourth possible reason for the inconsistent ERP findings may be linked to the type of ERP analysis techniques used. Interestingly, previous studies have found that the effects seen on electrophysiological components are not always in the same direction as the effects found on behavioral results. Indeed, the blocked picture naming and the PWI paradigms using taxonomically related stimuli typically elicit semantic interference on behavior, but opposite effects have often been found on associated ERP components. Blackford et al. (2012) used the PWI paradigm and demonstrated varying dissociations between behavior and ERPs based on the characteristics of presented stimuli. In particular, the semantically related condition, in which the picture was primed by a taxonomically related word, led to semantic interference but electrophysiological priming (i.e., decreased amplitude in the related compared to unrelated condition). This suggests that semantic priming may be taking place in the brain even if semantic interference is the outcome on behavioral measures. However, ERP effects associated with semantic interference have been harder to find across language production paradigms (Blackford et al., 2012; Hirschfeld et al., 2008; Wamain et al., 2015; for a review see Nozari & Pinet, 2020). A possibility for the absence of this effect may be linked to several reasons including the analysis techniques used. Previous studies using scalp EEG have mainly focused on monopolar types of analyses, where the signal at each electrode is compared to one predefined reference electrode and where spatial resolution is typically relatively low. This traditional approach to visualizing ERPs might have led to missing more focal effects, resulting in an incomplete description of the brain mechanisms engaged in processing different kinds of semantic relationships. The varying ERP findings here (e.g., the inconsistent taxonomic ERP effects in particular) may in part be due to the inability of monopolar analysis to tease apart inhibitory and facilitatory effects that may co-occur. Using traditional EEG as well as Laplacian transformation, we probe semantic interference and facilitation as associated with taxonomic and thematic semantic relationships to elaborate on the spatio-temporal dynamics of these processes during word production.

1.3 | Laplacian analysis

To counteract the poor spatial resolution in traditional EEG, we used Laplacian transformation in the current study. This technique provides an estimate of the current source density using a double spatial derivative, thus improving the topographical localization of the monopolar EEG recording (Babiloni et al., 2001; Nunez, 1981). The goal of this method is to decrease the spatial blurring of recorded electrical potentials that occur due to the different conduction distortions caused by the cerebrospinal fluid, meningeal layers, skull, and scalp (Babiloni et al., 1996, 2001). As a consequence of this deblurring process, Laplacian analysis can reveal co-occurring effects that may have been obscured in the monopolar analysis. This technique has been previously used in language production studies (Riès et al., 2011, 2015, 2020; Riès, Janssen, et al., 2013; Riès, Xie, et al., 2013) and outside of language (Roger et al., 2010; Tandonnet et al., 2003; Vidal et al., 2000, 2003, 2011) to reveal components occurring at different recording sites and with overlapping time-courses. Laplacian analysis should therefore allow us to observe different semantic effects (i.e., priming and interference) at different recording sites that may be occurring in overlapping time windows.

1.4 | Current study

This study focuses on clarifying the impacts of semantic co-activation on word retrieval in taxonomic versus thematic contexts using electroencephalography. In particular, we focus on the interference and facilitation effects that are tied to taxonomic and thematic relationships, and where these effects stem from in terms of the different stages leading to word production as reflected in ERP components. We directly compare online processing of taxonomic and thematic relationships by analyzing differences in amplitude between conditions in traditional monopolar event-related potentials (ERPs) derived from mastoid referenced EEG, as well as in Laplacian-transformed ERPs with the goal of dissociating temporally overlapping EEG components sensitive to semantic interference from those sensitive to semantic priming. The use of both analysis methods provides us with the advantage of viewing our data from two perspectives.

More specifically, using a PWI paradigm, we compare both taxonomically related and thematically related pairs to their respective matched unrelated word-picture pairs. Importantly, the unrelated pairs consist of the same words and images as the related counterparts but scrambled in order to prevent any possible confounding effects from including different items across conditions. As discussed earlier, the PWI has been used to study taxonomic and thematic relationships previously with mixed findings that are possibly linked to differences in experimental design. In this study, we carefully controlled for these differences as detailed below. Using the PWI paradigm in the current study presents with several benefits including allowing for the creation of 110 carefully controlled stimulus pairs in each condition while still limiting repetition effects in comparison to other paradigms. Crucially, the existence of prior PWI tasks examining taxonomic and thematic relationships (though limited) ensures that we can compare our results to test the efficacy of our methodology and stimuli design.

In order to optimize the comparison between taxonomic and thematic pairs, we use the same pictures in both conditions paired with different distractor words. To circumvent the previously discussed issue of inconsistent stimuli design and to optimize the comparison of semantic context effects between taxonomic and thematic conditions, we will conduct two norming studies prior to running the EEG experiment as well as a corpus linguistic analysis. Our surveys are designed to collect name agreement information for the images as well as relatedness information for the taxonomic and thematic pairs. The aim is to select pictures with high name agreements and pairs considered to be equally highly related in the taxonomically- and thematically related conditions. We use corpus linguistic analysis to quantify the relatedness of the taxonomic and thematic pairs in our study from multiple angles. In particular, we use Resnik scores (Resnik, 1995) based on WordNet's (Miller, 1995) hierarchical organization of semantic networks, and Pointwise Mutual Information (PMI) based on the probability of cooccurrence within text (as in McDonagh et al., 2020). We expect Resnik scores to be higher for taxonomic compared to thematic pairs, given that taxonomic relationships are defined by being part of the same semantic category. By contrast, we expect PMI values to be higher for thematic compared to taxonomic pairs, indicating a higher likelihood of co-occurrence for thematic versus taxonomic pairs given that thematically related words tend to cooccur in scenarios.

Consistent with previous studies, we hypothesize that taxonomic pairs will lead to behavioral interference (Alario et al., 2000; Costa et al., 2005; de Zubicaray et al., 2013) and that thematic pairs will lead to behavioral - PSYCHOPHYSIOLOGY

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facilitation on naming latencies (Alario et al., 2000; Bloem et al., 2004; Costa et al., 2005). As in previous language production studies investigating the impact of semantic relationships using the PWI paradigm, we expect that taxonomically related pairs will be associated with less negative ERPs in time-windows associated with visual processing and early lexical access (i.e., between 150 and 250 ms poststimulus onset, Blackford et al., 2012; De Cesarei et al., 2013; Eddy et al., 2006; Eddy & Holcomb, 2010; Strijkers et al., 2010), indicating less effortful processing. Items in the same category often share visual features, therefore participants' visual processing of a picture may be aided by a previously presented taxonomically related concept. Thematically related concepts may not share the same visual feature overlap but early lexical access is also expected to be facilitated in the case of thematically related concepts, although not as strongly as for taxonomically related concepts. Therefore, we also expect to see a difference in ERP amplitude in this early time-window between the related and unrelated pairs in the thematic condition, although this difference should be smaller than for the taxonomically related pairs. Finally, we expect the effects on ERP amplitude to differ between the taxonomic and thematic conditions in the N400 time window associated with word retrieval processes beginning after initial lexical activation such as lexical selection (i.e., between 300 and 500 ms, Holcomb et al., 2002; Kutas & Federmeier, 2011; Kutas & Hillyard, 1980; Piai et al., 2012). In particular, we expect to replicate previous results showing smaller amplitude in the N400 time window using monopolar analyses (Blackford et al., 2012; Kutas & Federmeier, 2011). In addition to this priming effect, we expect to benefit from the increased topographical localization afforded through Laplacian analyses and find simultaneous opposite effects in the N400 time window. In particular, in the taxonomic condition, we predict increased amplitude in the related compared to unrelated condition over cortical regions previously associated with semantic interference resolution such as the left inferior frontal cortex (i.e., Riès et al., 2015, 2017; Schnur et al., 2009). This effect should not be present in the thematic condition.

2 | METHOD

2.1 Naming survey

During the formulation of our stimuli, we conducted two surveys. The first, discussed here, was a picture norming survey to ensure high naming agreement for the experimental images.



For the picture norming survey, we recruited 21 participants (14 females; average age = 38.3 years; SD = 20.4 years; IQR = 22-60).

2.1.2 | Materials

A total of 177 color images were initially selected for this experiment from the BOSS database (Brodeur et al., 2014) and the internet. The images consisted of animals, food, household items, body parts, and other easily imageable items.

2.1.3 | Procedure

A Qualtrics online survey was created for the norming experiment. Ten participants (six females; average age = 30.4 years; SD = 18.2 years) named list 1 (89 images) and 11 participants (nine females; average age = 48.6 years; SD = 19.6 years) named list 2 (the remaining 88 images). The images were presented one at a time and participants could proceed through the survey at their own pace.

2.1.4 Results

Naming agreement for both lists combined was 92.64% on average (SD = 13%). After norming, we removed images that had less than 70% naming agreement.

2.2 | Relatedness survey

We conducted a survey to examine whether there was a difference in the degree of perceived semantic relatedness of taxonomic versus thematic pairs. The relatedness survey was performed to make sure that the picture-word pairs in both related conditions in our main experiment would be strongly related pairs. In addition, we wanted to ensure that our results would not be linked to differences in relatedness strength between conditions.

2.2.1 | Participants

For the prime-target word relatedness survey, we recruited 41 participants (34 females; average age = 38.1 years; SD = 20.3 years; IQR = 23-62).

2.2.2 | Materials

Each of the selected images were paired with four words, a taxonomically related word (a word that belongs to the same semantic category and associated with shared semantic features, such as WOLF and DOG), a thematically related word (a word that occurs together in events or scenarios with the target picture name, such as LEASH and DOG), an unrelated word drawn from the list of taxonomic primes (to be compared to the taxonomically related pairs), and an unrelated word drawn from the list of thematic primes (to be compared to the thematically related pairs). The related pairs were chosen using the South Florida Free Association Norms database (Appendix B; Nelson et al., 2004) and by our research group. When choosing the prime-target pairs we ensured that none of the prime words began with the same phoneme as the target. Additionally, we avoided thematic prime words indicating elements that could be visible on the target picture (e.g., we would not use the prime-target pair "mane-lion" because a mane is often visible on an image of a lion).

2.2.3 | Procedure

A Qualtrics survey was created to collect relatedness ratings between primes and targets. Each participant rated the association between 179 prime-target pairs on a 7-point Likert scale ranging from highly unrelated to highly related. Participants received one of four lists containing half of the thematically related pairs and half of the taxonomically related pairs. We included moderately related (ranging from 3 to 5 points) filler items, so that not all items would be strongly related or unrelated. First, the prime appeared on the screen for 1 s and was then replaced by the target word. We used word–word relationship rating instead of word-picture relationship rating in order to avoid any possible ambiguity linked to the picture name.

2.2.4 | Results

We found that there was a significant difference in relatedness rating based on type of prime; thematic primes were rated as significantly more related than taxonomic primes (t[311.34] = 5.371, p < .01; thematic: average = 6.52, SD = .31; taxonomic: average = 6.34, SD = .35). For the purposes of the ERP experiment, we controlled for relatedness difference between taxonomic and thematic primes. In order to maximize the number of stimuli for accuracy in EEG output, we maintained a minimum of 100 target images and their primes. To balance the relatedness of the lists, we removed thematic pairs that were more than 1.4 standard deviations higher in relatedness rating than taxonomic pairs, as well as taxonomic pairs that were more than two standard deviations higher in relatedness rating than thematic pairs. This allowed for the creation of a stimulus list both balanced in relatedness and sufficient in size.

The finalized stimuli for the experiment included 110 target pictures each paired with a taxonomic prime, thematic prime, and two matched unrelated primes (Table A1). Taxonomic and thematic primes were not significantly different in length (measured in number of letters; t[207.47] = -0.05, p = .96; thematic: average = 5.12, SD = 1.21; taxonomic: average = 5.13, SD = 1.52) or frequency (zipf log word frequency scale based on SUBTLWF (Brysbaert & New, 2009); t(209.71) = 1.78, p = .08; thematic: average = 4.07, SD = 0.75; taxonomic: average = 3.91, SD = 0.61).

3 | EEG EXPERIMENT METHOD

3.1 | Participants

We recruited 30 (25 females; average age = 23.1 years; SD = 3.3 years; IQR = 21-25) native English-speaking current and former students of San Diego State University between the ages of 18-30. All participants were right handed, had no history of neurological damage or hearing loss, and had normal or corrected-to-normal vision. The data of two participants were rejected due to technical issues. The data of two more participants were rejected from the analyses due to high EEG artifact rejection rates (>40% of all trials) linked to excessive movement and interference from heartbeat. A fifth participant's data were rejected due to average reaction time more than two standard deviations above the mean of the RTs for the group (average = 781 ms, SD = 175 ms). We therefore performed our analyses on the remaining 25 participants (20 females; average age = 23.2 years; SD = 3.3 years; IQR = 21-25).

3.2 | Design

The order of presentation of the stimuli was mixed pseudorandomly using Mix (van Casteren & Davis, 2006) which controlled for distance between identical target pictures, identical prime words, relationship type of pairs, semantic category, and phonological onset. We created 12 different lists, each of which were used at least twice across participants. Pictures had an average name agreement of 95.73% (SD = 8.04%). The average relatedness rating for taxonomic PSYCHOPHYSIOLOGY SPR

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pairs was 6.42 (SD = .30), and 6.48 (SD = .30) out of seven for thematic pairs. The average relatedness rating for unrelated taxonomic pairs was 1.73 (SD = 1.04), and 1.64 (SD = .94) for unrelated thematic pairs. To further quantify taxonomic and thematic relatedness we used both Resnik scores (Resnik, 1995) and Pointwise Mutual Information (PMI) (as in McDonagh et al., 2020). Resnik scores were calculated on word pairs in WordNet (Miller, 1995). This measurement evaluates taxonomic similarity because it is based in WordNet's hierarchical organization of semantic networks. The Resnik similarity score represents how related two words are in a taxonomic hierarchy, with 0 indicating no relationship and higher scores indicating more closely related words (McDonagh et al., 2020). PMI serves as an appropriate index for thematic similarity because it calculates the probability that two words co-occur in text. PMI = 0 is a chance level co-occurrence of two terms, a positive PMI score is greater than chance, and a negative PMI score is less than chance. PMI was calculated using Natural Language Toolkit for Python, using a window of five words excluding punctuation on the spoken language data in the Corpus of Contemporary American English (COCA). As predicted, we found a double dissociation between our taxonomic and thematic pairs: taxonomic pairs had higher Resnik scores than thematic pairs (taxonomic: average = 4.54, SD = 3.58; thematic: average = 1.50, SD = 1.66; F[1218] = 65.1, p < .01) and lower PMI scores (taxonomic: average = 2.00, SD = 3.23; thematic: average = 2.90, SD = 3.57; F[1218] = 6.73, p = .01).

3.3 | Procedure

Each participant saw all 110 images four times with each of the possible word primes: taxonomic, thematic, unrelated taxonomic (i.e., taxonomic picture-word pairs scrambled), and unrelated thematic (i.e., thematic picture-word pairs scrambled). Participants were seated comfortably approximately 140 cm from the stimulus monitor in a dimly-lit room separate from the experimenter. Each trial consisted of a prime word presented for 200 ms followed by the target image presented for 300 ms and then a blank screen for 1800 ms during which the participant named the image aloud (they were told to ignore prime words; Figure 1). The stimulus onset asynchrony (SOA) between the prime and target was therefore 200 ms. This SOA was chosen after considering semantic interference and semantic facilitation findings in previous PWI literature, which indicated that both interference and facilitation effects should be observed with an SOA of 200 ms (Alario et al., 2000; Aristei et al., 2011; Blackford et al., 2012; Bloem et al., 2004; de Zubicaray et al., 2013; Hirschfeld et al., 2008; Sailor



FIGURE 1 Example trial. Each trial consisted of two fixation crosses, a prime word, and the target image. Participants were instructed to blink during the purple fixation cross and to name the image during the white screen



FIGURE 2 EEG recording array. Thirty-nine active electrodes, an electrode on each mastoid (A1, A2), under the left eye (LE), and at the outer corner of the right eye (HE). The left mastoid (A1) served as the reference during recording and analyses. The 15 channels used for the ANOVAs are indicated on the array

et al., 2009). Images subtended a visual angle of 2.1 degrees in the horizontal and vertical directions. Primes were presented in lowercase black Courier New font at the center of a white screen and subtended a horizontal visual angle of 1.85 degrees or less. Between each trial, a purple fixation cross was displayed for 800 ms followed by a black fixation cross also displayed for 800ms. Participants were instructed to try and blink only during the purple fixation crosses as well as during longer blink breaks that occurred approximately every 10-15 trials. There were also five self-paced breaks throughout the experiment. Participants underwent a practice trial with 16 prime-picture pairs before the beginning of the experiment (these pairs were not included in the experiment). We did not familiarize participants with the images to minimize possible effects from repetition priming.

| EEG recording 3.4

Participants were fitted with an elastic electrode cap with 39 active electrodes (Figure 2). EEG was amplified with SynAmpsRT amplifiers (Neuroscan-Compumedics) with a bandpass of DC to 100 Hz and was sampled continuously at 500 Hz. By using a 39-channel cap, we are able to maintain a basis of comparison to previous work in the field that commonly uses 32-channel caps (Chauncey et al., 2009; Declerck et al., 2021a, 2021b; Grainger et al., 2006; McGarry et al., 2021; Meade et al., 2018, 2022).

We also placed an electrode on each mastoid, under the left eye, and at the outer corner of the right eye. The left mastoid served as the reference during recording and analyses. The electrode under the left eye in combination with the electrodes on the forehead were used to identify blinks and the electrode to the side of the right eye

identified horizontal eye movements. All electrode impedances were maintained below 2.5 k Ω (with the exception of one participant who had impedances of below 20 k Ω) by using saline gel (Electro-Gel).

3.5 Behavioral data analysis

For the remaining 25 participants, we analyzed mean naming latencies on correctly answered trials in each condition. Correct responses were defined as answers matching the picture name with the highest name agreement for a given item. We accepted as correct semantically identical names for an item (e.g., plane for airplane, bunny for rabbit, etc.). Any response that included anything besides the name of the item was considered an error (e.g., stutter, semantically different word, hesitation such as "uh"). Responses outside of 300-1800 ms after target onset were excluded from analysis. Statistical analysis was performed within R version 3.6.0 using the packages "Ime4" to compute the mixed effect models (Bates et al., 2014a, 2014b) and "car" to compute analysis of deviance tables for the fixed effects of the mixed effect models (Fox & Weisberg, 2011). We report Wald chi-square values and p values from the analysis of deviance table, as well as raw β estimates (β_{raw}), standard errors, Wald Z, and associated p values for significant and marginally significant effects. The individual reaction times (RTs) were inversetransformed to reduce skewness and approach a normal distribution. The analyses were performed on inversetransformed RTs. Naming latency data were analyzed with linear mixed-effects models, testing for main effects of Type (Taxonomic, Thematic) and Relatedness (Related, Unrelated) and their interaction as within-participant factors and we had intercepts for participants and picture name as random effects as well as by-subject and by-target random slopes for Type by Relatedness. We analyzed the accuracy data using logistic mixed-effects models (Baayen et al., 2008; Jaeger, 2008). We tested for main effects of Type and Relatedness and their interaction as withinparticipant factors and we had intercepts for participants and picture name as random effects as well as by-subject and by-target random slopes for Type by Relatedness.

3.6 | ERP data analysis

The ERP analyses presented in this paper are time-locked to the onset of the presentation of the target image presented to participants. We examine the 150–250 and 300– 500 ms epochs as it has been established that the effect of semantic manipulations can be observed on the amplitude of ERP components such as N100, N400, P100, etc. (Blackford et al., 2012; Kutas & Hillyard, 1980). Both monopolar and Laplacian analyses were conducted on the data collected in this experiment. We will discuss each in turn in the following sections.

3.6.1 Monopolar analysis

Across the 25 participants, artifact contamination from eye movement and speech led to the rejection of 7.6% of trials on average. As in a number of previous language processing studies from our research group, the ERP data from a representative sub-array of 15 channels were used for analysis (Chauncey et al., 2009; Grainger et al., 2006). This sub-array consisted of three columns over left, center, and right hemisphere locations, each with five electrode sites extending from the front to the back of the head (Figure 2).

The data were analyzed using repeated measures omnibus ANOVAs with the within-participant factors of Relatedness (Related, Unrelated), Prime Type (Taxonomic, Thematic), Laterality (left, midline, right), and Anteriority of electrode sites (Prefrontal, Frontal, Central, Parietal, and Occipital). Planned follow-up ANOVAs with the within-participant factors of Prime Type (Taxonomic Related OR Thematic Related, Taxonomic Unrelated OR Thematic Unrelated), Laterality (left, midline, and right), and Anteriority (Prefrontal, Frontal, Central, Parietal, and Occipital) were also conducted. Only correct trials were used during ERP analyses. The dependent measures were the mean amplitude measurements in the time windows: 150-250 and 300-500 ms poststimulus (target image) onset. This 150-250 ms time window captures components associated with early visual feature processing (Blackford et al., 2012; De Cesarei et al., 2013; Eddy et al., 2006; Eddy & Holcomb, 2010) and early lexical access (Blackford et al., 2012; Eddy et al., 2006; Eddy & Holcomb, 2010; Strijkers et al., 2010). The 300-500 ms time window is centered on the N400, which is an established component in language research and has been shown to be sensitive to lexico-semantic processing (Kutas & Federmeier, 2011; Kutas & Hillyard, 1980). According to prior language research involving images, an early N300 may be present in addition to the N400 and may be more sensitive to early semantic processing involving semantic features (Blackford et al., 2012; Eddy et al., 2006; Eddy & Holcomb, 2010). As in these previous studies, the epochs we have selected are relevant time frames for the detection of these components.

3.6.2 Laplacian analysis

In speech production EEG experiments, experimenters have to take artifacts from speech articulation into account

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on top of the artifacts produced from blinking, horizontal eye movements, etc. Speaking in particular induces large amounts of EMG activity that heavily contaminates the EEG signal (Vos et al., 2010). Articulation-related EMG activity predominantly occurs closer to vocal onset (van der Linden et al., 2014). Our chosen analysis windows, 150-250 and 300-500 ms, end earlier than two standard deviations below the mean voice onset time (average = 781 ms, $SD = 125 \,\mathrm{ms}$). This makes it unlikely that there was any significant articulation-related artifact in the monopolar ERPs up to the point of analysis. However, Laplacian transformation is particularly sensitive to artifacts (Tandonnet et al., 2005; Vidal et al., 2003), therefore we implemented additional processing steps prior to Laplacian analyses. We used Blind Source Separation based on Canonical Correlation Analysis, or BSS-CCA (using the AAR toolbox for EEGlab by Gómez-Herrero, 2007), to reduce the impact of EMG artifacts from speech articulation in the EEG signal as in (De Clercq et al., 2006; Hallez et al., 2009; Riès et al., 2011, 2015, Riès, Janssen, et al., 2013; Riès, Xie, et al., 2013; Vos et al., 2010). Any artifacts remaining after BSS-CCA were rejected by hand on a trial-by-trial basis. See Supplementary Information for analyses conducted on monopolar data after artifact rejection with BSS-CCA.

After artifact rejection, we then used Laplacian transformation (providing an estimate of the current source density, CSD) in BrainVision Analyzer 2.1 (BrainVision Analyzer, Brain Products GmbH, Gilching, Germany). Laplacian transformation has been shown to increase the spatial resolution of the EEG signal, providing a good estimation of the corticogram (Nunez & Srinivasan, 2006).

As in previous studies (Riès et al., 2011, 2015, 2020; Riès, Janssen, et al., 2013; Riès, Xie, et al., 2013), Laplacian transformation was applied to each participant's individual averages. Then, a grand average was created from those individual averages. Because the voltage distribution is only known at the electrodes, the spherical spline interpolation method is used prior to the application of the spherical Laplace operator in order to estimate the entire voltage distribution (Perrin et al., 1989). Then, second derivations in two dimensions of space were computed (Legendre polynomial: 15° maximum). We chose three for the degree of spline because this value best minimizes errors (Perrin et al., 1987). We assumed a radius of 10 cm for the sphere representing the head. The resulting unit was μ V/cm².

The enhanced topographical localization from Laplacian transformation allowed us to examine ERPs at each electrode site of interest. Linguistic processes involved in picture naming are often described as leftlateralized and have been described at temporoparietal, lateral frontal, and medial frontal sites (Riès, Janssen, et al., 2013; Riès, Xie, et al., 2013), therefore we chose to conduct our main analysis on the pre-identified electrode sites which showed indication of differences between conditions on the grand averages (T3, CP5, and FC5). In particular, a rising negative component has been previously described during picture naming at the left frontal site FC5 (Riès, Janssen, et al., 2013). We also conducted statistical analyses on the sites contralateral to these electrodes (T4, CP6, and FC6) but observed no effects at the contralateral sites. Accordingly, we present the results from the analysis conducted at the left lateral sites T3, CP5, and FC5.

To allow for easier comparison with the monopolar results, we used the same epochs that were used in the monopolar analysis in the analysis of the Laplacian-transformed ERPs: 150-250 and 300-500 ms. The surface area under the curve was calculated in all four conditions for each participant at the electrodes of interest. The EEG data were analyzed using Student's *t* tests or ANOVAs for comparisons of more than two means.

4 | RESULTS

4.1 | Behavioral results

Overall, the naming latencies in the taxonomic conditions (related and unrelated) were slower than the naming latencies in the thematic conditions (related and unrelated) $(X^{2}[1,25] = 30.44, p < .01; \beta_{raw} = 4.24 \times 10^{-5},$ $SE = 7.69 \times 10^{-6}$, Wald Z = 5.52; mean RTs = 784.2 ms, 771.2 ms). In addition, there was a significant interaction between relatedness (related and unrelated) and type of prime (taxonomic and thematic), indicating the relationship between the taxonomic related and unrelated conditions was different from the relationship between the thematic related and unrelated conditions $(X^2[1,25] = 18.33, p < .01; \beta_{raw} = -4.06 \times 10^{-5},$ $SE = 9.48 \times 10^{-6}$, Wald Z = -4.28). Planned followup analyses were used to break down this interaction. Specifically, for taxonomic pairs, naming latencies were significantly slower (by on average 14ms) for related than unrelated pairs (F[1, 25] = 5.96, p < .05; taxonomicrelated: mean RT = 791.4 ms; SD = 94.2 ms; taxonomic unrelated: mean RT = 776.99 ms; SD = 84.64 ms), in the direction of semantic interference. By contrast, naming latencies for thematic pairs were significantly faster (by on average 10 ms) for related than unrelated conditions (F[1, 25] = 7.99, p < .01; thematic related: mean RT = 766.4 ms; SD = 90 ms; thematic unrelated: mean RT = 776.1 ms; SD = 83.1 ms), in the direction of semantic facilitation. Participants had high accuracy rates (average = 92.3% correct; SD = 25.9%). Only a marginal effect of type of prime was found on accuracy rates $(X^{2}[1,25] = 2.82, p = .093)$, which was due to accuracy



FIGURE 3 (a) Reaction times for relatedness by prime type interaction. (b) Accuracy rates for relatedness by prime type. Taxonomic conditions are depicted in red and thematic conditions are depicted in blue. Standard error bars are included on each average

rates being higher for thematic pairs versus taxonomic pairs ($\beta_{raw} = 0.325$, SE = 0.193, Wald Z = 1.61, p = .093). There was no main effect of relatedness ($X^2[1,25] = 2.36$, p = .12) and no interaction between relatedness and type ($X^2[1,25] = 2.49$, p = .11) (see Figure 3b).

4.2 | Monopolar EEG results

Voltage maps in the 150–250 and 300–500 ms time windows, as well as grand averages, time-locked to the presentation of target images are plotted in Figure 4.

4.2.1 | Early effects: 150–250 ms

The omnibus ANOVA showed a main effect of relatedness (F[1,24] = 16.78, p < .01), as well as a three-way interaction between relatedness, laterality, and anteriority (F[8192] = 7.34, p < .01). This indicated that unrelated conditions elicited a greater negativity than related conditions, overall, but especially at anterior midline sites. There was no significant main effect of type of prime (F[1, 24] = 3.01, p = .096) nor interaction of prime type and relatedness (F[1, 24] = 3.26, p = .084). In the follow-up ANOVA for the taxonomic condition alone, there was an effect of relatedness (F[1,24] = 15.77, p < .01); unrelated pairs elicited a greater negativity than related pairs. Again, there was a three-way interaction in relatedness, laterality, and anteriority (F[8192] = 6.8, p < .01). Similarly, as in the general analysis, the difference in relatedness occurred especially at the anterior midline sites. In the analysis of the thematic condition, there was no main effect of relatedness (F[1, 24] = 2.75, p = .11). However, there was a three-way interaction between relatedness, laterality, and anteriority, which indicated that the relatedness effect was in fact limited to left lateral anterior electrodes (F[8, 192] = 3.13, p < .05). For these electrode sites, unrelated pairs elicited a greater negativity than related pairs.

4.2.2 | The N400: 300–500 ms

The omnibus ANOVA in this window revealed a main effect of relatedness (F[1,24] = 23.97, p < .01) as well as a three-way interaction between relatedness, laterality, and anteriority (F[8192] = 3.89, p < .01). As in the earlier window, there was no main effect of prime type (F[1, 24] =.97, p = .33) nor interaction between prime type and relatedness, suggesting that the relationship between the related and unrelated pairs did not differ significantly between the taxonomic and thematic conditions (F[1, 24] =.75, p = .39). In the taxonomic condition, there was a main effect of relatedness with the unrelated pairs eliciting a significantly larger negativity than the related pairs (F[1,24] = 10.65, p < .01). There was also a three-way interaction between relatedness, laterality, and anteriority (F[8192] = 2.07, p < .05). The effect was pronounced at left anterior electrode sites. Unlike in the earlier time window, there was a main effect of relatedness (F[1,24] = 20.07,p < .01) in the thematic condition; unrelated pairs elicited a greater negativity than related pairs. There was also a three-way interaction between relatedness, laterality, and anteriority (F[8192] = 2.77, p < .01). Again, the effect was most pronounced at left anterior electrode sites.

4.3 | Laplacian EEG results

Voltage maps in the 150–250 and 300–500 ms time windows, as well as waveforms, time-locked to the presentation of target images are plotted in Figures 5 and 6.

4.3.1 Early effects: 150–250 ms

At electrode T3, during the 150-250 ms time window, in the taxonomic condition, unrelated pairs elicited a greater negativity than the related pairs (t[25] = -2.86, p < .01). In the thematic condition, there was no significant difference in amplitude between the related and unrelated



pairs (t[25] = -1.67, p = .11). This is in agreement with the early results we observed in our monopolar analysis.

4.3.2 The N400: 300-500 ms

The same effects reported in the monopolar analysis were found at electrode CP5 after Laplacian transformation (Figure 6): the unrelated pairs elicited greater negativity than the related pairs in both the taxonomic and thematic conditions (t(25) = -3.04, p < .01 and t(25) = -2.94, p < .01,respectively). However, a different effect was observed at electrode FC5 (Figure 6), a more anterior electrode site. In the taxonomic condition, the related pairs elicited a greater negativity than the unrelated pairs (t(25) = 2.73, p < .05).

DISCUSSION 5

The aim of the present study was to investigate how different conceptual relationships influence the different stages of speech production through measuring ERPs and naming latencies to pictures in a PWI paradigm. Importantly, we used traditional monopolar analysis as well as



FIGURE 5 Laplacian-transformed ERP waveforms at electrode T3, pictured on scalp (right); in the 150–250 ms epoch, unrelated pairs elicit greater negativity than the related pairs in the taxonomic condition, as seen in the monopolar analysis. Taxonomic conditions are depicted in red and thematic conditions are depicted in blue. Related conditions are depicted by solid lines; unrelated conditions are depicted by dotted lines. Note that negative is plotted up in this diagram



FIGURE 6 Laplacian-transformed ERP waveforms at electrode CP5 (top) and FC5 (bottom). At CP5, pictured on scalp (left, posterior), unrelated conditions elicit greater negativity than the related conditions, as seen in the monopolar analysis. At FC5, pictured on scalp (left, anterior), the taxonomic-related condition elicited significantly greater negativity than the unrelated condition (left). Taxonomic conditions are depicted in red and thematic conditions are depicted in blue. Related conditions are depicted by solid lines; unrelated conditions are depicted by dotted lines. Note that negative is plotted up in this diagram

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Laplacian transformation allowing us to examine spatially deblurred event-related components. Similar to previous studies (Alario et al., 2000; Bloem et al., 2004; Costa et al., 2005), we found opposite effects of taxonomic and thematic relationships on naming latencies. Taxonomic relationships led to semantic interference while thematic relationships led to semantic facilitation. Monopolar EEG analyses showed that unrelated pairs elicited a greater negativity than related pairs in the taxonomic condition in both time windows (150-250 ms, 300-500 ms). In the thematic condition, unrelated pairs also elicited a larger early negativity but over a more spatially restricted left lateral group of electrodes (150-250 ms). This effect became widespread in the later time window (300-500 ms). Laplacian analyses revealed similar findings in these time windows with the exception of an additional greater left frontal negativity for related than unrelated pairs in the taxonomic condition at electrode FC5 (300-500 ms). We address the implications of our behavioral, monopolar, and Laplacian analysis findings in turn.

5.1 | Behavioral analysis

Naming latency results showed a 14 ms average increase for the taxonomically related pairs compared to the unrelated pairs. This interference effect presumably reflects more effortful processing when naming images preceded by a taxonomically related word. Conversely, there was a 10 ms average decrease in naming latencies for the thematically related pairs compared to the unrelated pairs. This facilitation effect presumably reflects easier processing when naming images preceded by a thematically related word. These findings replicate those of previous naming studies (e.g., Alario et al., 2000; Bloem et al., 2004; Costa et al., 2005; Rabovsky et al., 2016).

Whether the end result of our speech production processes is facilitation or interference is dependent on the characteristics of the semantic relationships between the words being studied. The model proposed by Rabovsky et al. (2016) places the number of semantic features (NOF) and intercorrelational feature density at the core of the different behavioral outcomes observed in thematic versus taxonomic contexts. Taxonomically related words tend to share a large number of features because they belong to the same semantic category. This important number of shared features has been associated with increased activation of semantic neighbors sharing these features during production. This co-activation of semantically related neighbors is assumed to be the cause of the semantic interference effect observed in taxonomic contexts. Conversely, thematically related words belong to different semantic categories and do not typically share

a large number of features. Therefore, thematic relationships do not typically activate as large of a lexical cohort as taxonomic relationships (Rabovsky et al., 2016; Rose et al., 2019).

However, another complementary interpretation for the facilitation effect in thematic contexts may be linked to predictability. Indeed, our stimuli showed a double dissociation between Resnik scores (Resnik, 1995), which measure relatedness based on WordNet's hierarchical network of semantic relations (Miller, 1995), and PMI, which measures relatedness based on the probability of two words co-occurring in a text. Thematically related words were found to be more likely to co-occur in text within five words of one another compared to taxonomically related words. This higher co-occurrence may allow participants to form expectations which will be met when seeing a word followed by an image representing a thematically related concept, hence the facilitation effect observed on reaction times. For taxonomic pairs, these expectations may not be as strong and instead the large co-activated cohort of semantically related alternatives makes selecting the correct response more difficult (McDonagh et al., 2020).

5.2 | Monopolar analysis

In the early time window, 150-250 ms post target image presentation, the results showed a widespread greater negativity for unrelated than related pairs in the taxonomic condition. In the thematic condition, this effect was more localized and restricted to left anterior sites. Previous picture naming studies demonstrated that early components were associated with early visual feature processing in epochs overlapping with our 150-250 ms time window (Blackford et al., 2012; De Cesarei et al., 2013; Eddy et al., 2006; Eddy & Holcomb, 2010). In addition, access to the structural semantic features that are specific to visual objects and early lexical access have also been proposed to occur within this same time window (Blackford et al., 2012; Eddy et al., 2006; Eddy & Holcomb, 2010; Strijkers et al., 2010). According to language production models, the prime word activates a cohort of semantic features which are shared with other words. This allows for an initial spreading of activation to lexical representations in the same semantic cohort. Taxonomically related words share a larger cohort of shared perceptual and semantic features than thematically related words as proposed by Rabovsky et al., 2016 and as demonstrated through our Resnik score analysis. Our results are therefore in agreement with this proposal.

Then, we considered the N400 time window spanning between 300 and 500 ms poststimulus presentation (Kutas & Federmeier, 2011). The N400 is a negative-going

waveform that peaks around 400 ms poststimulus presentation. This ERP component is frequently modulated by changes in the semantic context of stimuli. When stimuli are preceded by semantically related content, whether words or images, the N400 has been shown to be attenuated in amplitude in comparison to when stimuli are preceded by unrelated content (Bentin et al., 1985; Johnson et al., 1996; Kutas & Federmeier, 2011). Unrelated, semantically inappropriate, or difficult to process content tends, on the contrary, to increase the amplitude of the N400 (Kutas & Hillyard, 1980). In our study, we found that in this 300-500ms time window, unrelated pairs elicited a greater negativity than related pairs in both the taxonomic and thematic conditions. This is in agreement with the idea that related semantic context helps lexical processing for both taxonomic and thematic relationships. These findings from monopolar analyses suggest highly similar processing for taxonomic and thematic relationships and thus would need to be represented by a model that accounts for this similarity. The controlled semantic cognition (CSC) framework (Jefferies et al., 2020) proposes an equivalent response for taxonomic and thematic relationships in the anterior temporal lobe (ATL). However, when semantic control demands are high the CSC predicts a stronger response in the posterior middle temporal gyrus (pMTG) and inferior frontal gyrus (IFG). We must consider the more focal effects from Laplacian transformation before drawing conclusions regarding the CSC framework. However, the allowance for simultaneous engagement of overlapping and distinct brain regions is promising.

The effect in the taxonomic condition persisted from the 150 to 250 ms window we examined. This is in agreement with EEG studies that have shown that activity associated with early processes does not necessarily stop when activity associated with downstream processes begin (Hassan et al., 2015; Janssen et al., 2020), supporting an interactive view of processing stages in language production (Dell et al., 2013). The amplitude reduction in the related versus unrelated conditions for thematic pairs was more widespread than in the earlier time window. A possible interpretation of this effect could be linked to predictive processing. Indeed, we found in our PMI analysis that thematically related words were found to be more likely to co-occur in text compared to taxonomically related words. The N400 has been shown to be attenuated in contexts where participants are able to predict the upcoming piece of information, such as in sentence completion or priming studies (Kutas & Federmeier, 2011; Lau et al., 2013). This would support the more widespread ERP amplitude reduction in the thematic condition in the 300-500 ms time window compared to the taxonomic condition.

At this point however, it is unclear which process may be sensitive to semantic interference in the taxonomic - PSYCHOPHYSIOLOGY

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condition given that all observed effects on the monopolar ERPs suggest less effortful visual and lexico-semantic processing in the related than unrelated conditions. As mentioned in the introduction, mixed ERP findings have been reported as a result of semantic context manipulation. Reduced ERP amplitudes in related versus unrelated conditions have been found in thematic relationships, but not in taxonomic relationships in the few studies directly comparing these relationships (Hirschfeld et al., 2008; Wamain et al., 2015); although there has also been evidence of reduced ERP amplitudes in taxonomically related compared to unrelated conditions in other studies (e.g., Blackford et al., 2012; Kutas & Federmeier, 2011). One possible reason explaining these differences may be linked to the methods used. In particular, in traditional monopolar analyses spatial resolution is usually low due to the diffusion of the electrical currents through the tissue layers and cerebrospinal fluid separating the brain from the recording sites. In order to investigate these semantic context effects further, we conducted analyses on the Laplacian-transformed ERPs in order to separate neighboring components potentially sensitive in opposite ways to semantic contexts (Nunez & Srinivasan, 2006; Riès et al., 2011).

5.3 Laplacian analysis

Laplacian transformation increases topographical selectivity by effectively filtering out spatially diffuse features of the EEG data (Cohen, 2014). This technique has been shown to increase the topographical localization of the ERPs, providing a good estimation of the corticogram, which allowed us to examine more focal components that may have been undetectable in the monopolar analyses (Luck, 2014; Nunez & Srinivasan, 2006; and as in Riès et al., 2011). In the Laplacian analysis, we focused on the same time windows as in the monopolar analysis to facilitate the comparison of the results. In the early time window, between 150 and 250 ms, we found results consistent with our findings on the monopolar ERPs. We found a similar relatedness effect, meaning a larger amplitude for unrelated pairs than related pairs localized to a left temporal recording site in the taxonomic condition. The left temporal cortex has often been associated with lexical access (Baldo et al., 2013; DeLeon et al., 2007; Trebuchon-Da Fonseca et al., 2009). Patients with lesions in the left posterior temporal cortex have been shown to have lexical access deficits in both production (Baldo et al., 2013; DeLeon et al., 2007) and comprehension (Dronkers et al., 2004). Although the spatial resolution remains limited even following Laplacian transformation, the fact that the activity we found at this left temporal site during speech

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production is sensitive to semantic relatedness suggests that this activity is an indicator of early lexical access.

In the N400 time window, there were differences between related and unrelated pairs that varied between the taxonomic and thematic conditions. In the thematic condition, unrelated pairs elicited a greater negativity than related pairs. This effect was localized to a left parietal recording site (CP5). Previous fMRI and eye tracking research have found links between the processing of thematic relationships and structures along the dorsal processing route (Kalénine et al., 2009; Mirman et al., 2017; Mirman & Graziano, 2012; Schwartz et al., 2011).¹ In particular, using eye tracking, individuals with lesions in BA 39 and the surrounding temporo-parietal cortex regions have been shown to have reduced and delayed activation of thematic relationships and no difference in activation of taxonomic relationships when compared to the control group, indicating that the temporoparietal cortex may play an important role in the processing of thematic relationships (Mirman & Graziano, 2012). Interestingly, the inferior parietal cortex is also involved in forming expectations and prediction during language comprehension (Obleser & Kotz, 2010), anticipatory processes and predictive mechanisms during early action planning (Fontana et al., 2012), and discourse level prediction (Kandylaki et al., 2016). The observed attenuated negativity at a left parietal recording site in the same time window as the N400 (also shown to be sensitive to predictability, see above) for thematically related compared to unrelated pairs may indicate that participants are forming an expectation for the picture name following the word in the thematic condition.

Our results showed that both taxonomically- and thematically related conditions were associated with reduced ERP amplitude compared to unrelated conditions at CP5. The dual-hub theory would however anticipate this effect to be exclusive to thematic relationships. The CSC framework (Jefferies et al., 2020), mentioned earlier, predicts equivalent responses for both types of semantic relationships in the temporoparietal region as we see here. The CSC framework allows for the possibility that different semantic relationships simultaneously engage overlapping and distinct regions. Specifically, the CSC proposes an equivalent response for taxonomic and semantic relationships in the anterior temporal lobe (ATL) and a stronger response in the posterior middle temporal gyrus (pMTG) and inferior frontal gyrus (IFG) when semantic control demands are high.

Finally, in the 300–500 ms time window, at a left frontal recording site (FC5), related pairs elicited a greater negativity than unrelated pairs in the taxonomic condition. Left frontal activity at the FC5 site has been previously described in the context of language production (Riès, Janssen, et al., 2013). The function of this EEG component has not been agreed upon, but we can consider different possibilities by examining the functions typically associated with the left frontal region. From previous fMRI and lesion study research, activity in the left frontal region has been associated with cognitive control processes allowing individuals to overcome interference from semantically related alternatives for lexical selection (Riès et al., 2015, 2017; Schnur et al., 2005, 2006, 2009; Thompson-Schill et al., 1998). The nature of the left frontal cognitive control mechanism proposed to be involved differs between studies, with some suggesting a booster mechanism helping to tease representations apart (Oppenheim et al., 2010), a task biasing mechanism (Belke & Stielow, 2013), a more domain general proactive control mechanism (Jonides & Nee, 2006; Kan & Thompson-Schill, 2004; Riès et al., 2014), or a decision threshold adjustment mechanism (Anders et al., 2015, 2017). The Laplacian-transformed activity we observed at this left frontal site may be reflecting the engagement of left frontal regions to overcome interference. This left frontal effect was only observed in the context of taxonomically related pairs, and not thematically related pairs. This suggests that the left frontal cognitive control mechanism involved to overcome interference between semantically related representations may be necessary particularly in the taxonomically related context but not in the thematically related context. This is also in agreement with dissociations in the processing of taxonomic and thematic relationships between patients with anterior versus posterior lesions (Mirman & Graziano, 2012; Schwartz et al., 2011).

It is also a possibility that ERP effects observed across taxonomic and thematic relationships could be impacted by individual differences in semantic network organization, reading and language ability, and individual variances in similarity judgments between taxonomic and thematic relationships (as seen in Honke et al., 2020). Taxonomic and thematic similarity judgment have been shown to predict ERP amplitude during passive word reading (Honke et al., 2020). This could be contributing to the differences observed between the conditions and is important to take into consideration when developing future studies.

Most notably, using Laplacian transformation allowed us to dissociate opposite effects in the same time window

¹This parietal (dorsal) versus more ventral distribution of effects in thematic versus taxonomic conditions respectively is in agreement with the notion that thematic pairs often contain more manipulable items whereas taxonomic pairs often contain more non-manipulable and living items (Mirman et al., 2017). In our study, there were indeed more living concepts in the taxonomic condition ($X^2(1, 220) = 10.10$, p < .01, $\rho_{raw} = 1.12$, SE = 0.35, Wald Z = 3.18, p < .01; see Table A2 in Appendix), but there were more non-manipulable than manipulable items in the thematic condition ($X^2(1, 220) = 5.93$, p < .05, $\rho_{raw} = 0.67$, SE = 0.28, Wald Z = 2.44, p < .05; see Table A2 in Appendix).

that were not visible on traditional monopolar ERPs which is a novel finding. We note that the spatial resolution of the Laplacian-transformed ERPs would have been better with a higher number of channels but that it was already increased with the number of channels we used compared to monopolar ERPs as shown by Babiloni et al. (1996).

The presence of both effects in the same time window is in agreement with the idea that facilitation and interference occur concurrently during speech production, as suggested by Rabovsky et al. (2016). Our electrophysiological results are also in agreement with those of Piai et al. (2014) who used magnetoencephalography (MEG) to compare brain responses to taxonomically related and unrelated prime word-picture pairs. Their results showed that activity phase-locked to the stimulus (evoked activity) was larger on unrelated than related trials, occurring in the left temporal cortex and peaking at 400 ms. This effect was in the same time window as the effect we observed in the monopolar analysis and at the left temporal site in the Laplacian analysis. Non-phase-locked activity (induced activity), alternatively, was larger on related than unrelated trials from approximately 350 to 650ms poststimulus onset and localized to the left superior frontal gyrus. These results, which are largely aligned to our present results, suggested that different types of brain activities are sensitive to semantic relatedness in different ways in similar time windows but different brain regions. Finally, these results also parallel those of Riès et al. (2017), which showed concurrent semantic context effects in both the direction of facilitation and interference using intracranial EEG and the blocked cyclic picture naming paradigm contrasting taxonomically related versus unrelated contexts. This is again in agreement with a more interactive rather than strictly serial view of processing stages in language production. Importantly, this study showed a large semantic interference effect at left frontal recording sites (Riès et al., 2017).

Interestingly, the results from the Laplacian analyses follow the pattern of results from the traditional monopolar analyses in many aspects. The greater negativity for unrelated pairs in the taxonomic condition prior to 300 ms was consistent between analysis methods. However, the ability to examine more focal effects following Laplacian transformation led to a divergence in results. Results from the monopolar analysis did not show different effects for the thematic and taxonomic conditions in the time window spanning from 300 to 500 ms poststimulus presentation. However, Laplacian analyses revealed opposite effects in the same time window at different recording sites. The left temporoparietal results were in agreement with the monopolar finding in that both unrelated conditions elicited a greater negativity than related conditions. Contrastively, at the left frontal recording site, taxonomically related - PSYCHOPHYSIOLOGY SPR

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pairs elicited a greater negativity than unrelated pairs. This was not the case for the thematically related pairs. These results demonstrate that it is not simply that taxonomic relationships are associated with more processing difficulty than thematic relationships at every stage of the word production process. The results reveal that overlapping effects are occurring during lexical retrieval: left frontal cognitive control engages to support the resolution of semantic interference associated with the processing of taxonomic relationships while left posterior regions simultaneously support lexical activation facilitated by the presence of semantically related neighbors. These simultaneous effects would not have been documented without the use of Laplacian transformation. The results from monopolar analysis were not invalidated by the introduction of a second analysis method but supplemented and further clarified.

6 | CONCLUSION

In conclusion, our results suggest that when we speak, spreading activation between semantically related concepts facilitates lexical access in the brain whether or not the relationship is thematic or taxonomic, as indicated by the early ERP effects between 150 and 250ms. Following these early effects, the facilitation effects persists into the N400 time-window suggesting facilitated semantic processing in both conditions, possibly linked to increased predictability of the upcoming picture name in the thematic condition as supported by the parietal distribution of this effect in the Laplacian analysis. Critically, in the case of taxonomic relationships, the Laplacian analysis also revealed a concurrent interference effect in the N400 window at a left frontal recording site. This effect likely reflects more effortful processing in lexical retrieval processes beginning after initial lexical activation (such as lexical selection) when placed in the context of taxonomically related words, leading to the engagement of left frontal cognitive control not seen in the thematic context. These results illustrate the importance of considering Laplacian transformation when studying the brain dynamics of language production using ERPs.

AUTHOR CONTRIBUTIONS

Elizabeth Jane Anderson: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; visualization; writing – original draft; writing – review and editing. Katherine Midgley: Conceptualization; funding acquisition; methodology; resources; software; supervision; validation; writing – review and editing. Phillip Holcomb: Conceptualization; funding acquisition; methodology; resources; software; 18 of 26



supervision; validation; writing – review and editing. **Stephanie K Ries:** Conceptualization; funding acquisition; methodology; resources; software; supervision; validation; writing – review and editing.

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APPENDIX

TABLE A1 Full list of target images and prime words (taxonomic, thematic, taxonomic unrelated, and thematic unrelated) for each image

Target image (picture name)	Taxonomic prime (written word)	Thematic prime (written word)	Unrelated prime (taxonomic) (written word)	Unrelated prime (thematic) (written word)
acorn	pecan	squirrel	package	stamp
airplane	helicopter	pilot	pie	oven
angel	devil	halo	blender	bread
apple	pear	core	screw	hammer
arm	leg	sleeve	peas	husk
armor	suit	shield	sink	drain
arrow	dart	target	concrete	wall
baby	child	crib	crate	farm
bacon	sausage	eggs	vault	lock
ballerina	gymnast	tutu	rag	shampoo
balloon	kite	air	wasp	honey
banana	kiwi	monkey	torch	flame
basket	hamper	picnic	dentures	floss
bee	wasp	honey	kite	hole
beer	wine	keg	ship	anchor
boat	ship	anchor	pear	keg
bottle	jar	cork	mule	desert
box	crate	gift	child	crib
bracelet	necklace	wrist	tiger	roar
brick	concrete	wall	dart	target
bridge	road	river	elbow	glove
bus	train	driver	priest	convent
button	zipper	shirt	coral	ocean
cake	pie	oven	helicopter	pilot
camel	mule	desert	boot	laces
candle	torch	flame	plow	harvest
canoe	raft	oar	spoon	vine
car	truck	engine	ribbon	loom
castle	palace	moat	stool	desk
cat	leopard	meow	wheat	brake
chair	stool	desk	palace	moat
cherry	plum	blossom	leg	sleeve
church	mosque	altar	koala	bamboo
cliff	hill	rock	truck	engine
clock	watch	time	toe	ring
comb	brush	hair	hawk	night
corn	peas	husk	sailor	treasure
cracker	biscuit	salt	raft	saddle
crown	tiara	jewel	shark	hook
dragon	unicorn	fire	jar	cork
ear	chin	wax	hill	rock
elephant	zebra	tusk	knee	sandal

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Target image (picture name)	Taxonomic prime (written word)	Thematic prime (written word)	Unrelated prime (taxonomic) (written word)	Unrelated prime (thematic) (written word)
envelope	package	stamp	pecan	squirrel
eye	nose	glasses	cushion	mattress
finger	toe	ring	wine	time
fireplace	chimney	soot	cabbage	dressing
fish	shark	hook	coat	neck
flask	jug	whiskey	stairs	rung
foot	knee	sandal	clam	pearl
frog	turtle	pond	toast	syrup
gate	fence	latch	mop	dirt
grapes	peach	vine	tiara	jewel
grass	lawn	weeds	necklace	wrist
hand	elbow	glove	road	river
hay	wheat	farm	leopard	meow
heart	lung	blood	tire	garden
horse	donkey	saddle	detergent	bubble
hose	sprinkler	garden	cabin	pole
house	cottage	garage	kiwi	air
knife	spoon	butcher	squash	seeds
ladder	stairs	rung	jug	whiskey
lettuce	cabbage	dressing	chimney	soot
lion	tiger	roar	ах	wood
map	globe	compass	brush	hair
mask	costume	face	dolphin	blubber
moon	sun	eclipse	cigar	smoke
moth	beetle	cocoon	hammock	rope
mouse	rat	cheese	pin	thread
nail	screw	hammer	hurricane	wind
needle	pin	thread	rat	cheese
nun	priest	convent	train	driver
owl	hawk	night	suit	shield
oyster	clam	pearl	purse	movie
panda	koala	bamboo	mosque	altar
pencil	crayon	eraser	radio	cable
penny	dime	copper	zipper	shirt
pillow	cushion	mattress	nose	glasses
pipe	cigar	smoke	sun	eclipse
pirate	sailor	treasure	zebra	tusk
pumpkin	squash	seeds	watch	butcher
rabbit	hamster	carrot	chin	wax
rose	tulip	thorn	glue	paper
safe	vault	lock	peach	oar
saw	ax	wood	plum	blossom
scarf	coat	neck	lawn	weeds

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TABLE A1 (Continued)

Target image (picture name)Taxonomic prime (written word)Unrelated prime (taxonomic) (written word)Unrelated prime (thematic) (written word)shellcoraloceangymnasttutushoebootlaceshamstercarrotshovelrakeholedoorcurtainsoapdetergentbubbledonkeycorestaplergluepapertulipthornswinghammockropebeetlecocoonteethdenturesflosshamperpicnic
shellcoraloceangymnasttutushoebootlaceshamstercarrotshovelrakeholedoorcurtainsoapdetergentbubbledonkeycorestaplergluepapertulipthornswinghamnockropebeetlecocoonteethdenturesflosshamperpiping
shoebootlaceshamstercarrotshovelrakeholedoorcurtainsoapdetergentbubbledonkeycorestaplergluepapertulipthornswinghammockropebeetlecocoonteethdenturesflosshammerpicnic
shovelrakeholedoorcurtainsoapdetergentbubbledonkeycorestaplergluepapertulipthornswinghanmockropebeetlecocoonteethdenturesflosshamperpicnic
soapdetergentbubbledonkeycorestaplergluepapertulipthornswinghammockropebeetlecocoonteethdenturesflosshammerpicnic
stapler glue paper tulip thorn swing hammock rope beetle cocoon teeth dentures floss hammer pionic
swing hammock rope beetle cocoon
teeth dentures floss hamper picnic
dentites not namper preme
tent cabin pole sprinkler gift
theater arena movie biscuit salt
toaster blender bread devil halo
tornado hurricane wind bell referee
towel rag shampoo dime copper
tractor plow harvest globe compass
tree bush leaf medal winner
trophy medal winner bush leaf
tub sink drain sausage eggs
tv radio cable crayon eraser
vacuum mop dirt fence latch
waffle toast syrup turtle pond
wallet purse money unicorn fire
whale dolphin blubber costume face
wheel tire brake lung blood
whistle bell referee cottage money
window door curtain rake monkey
yarn ribbon loom arena garage

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 TABLE A2
 Percentage of targets, taxonomic primes, and thematic primes that belong to each semantic category

Category	Target %	Taxonomic %	Thematic %
Non-living versus Living			
Living	29.09	30.00	12.73
Non-living	70.91	69.09	87.27
Non-manipulable versus Manipulable			
Manipulable	47.27	51.82	35.45
Non-manipulable	52.73	48.18	64.55
Semantic categories			
Activities and sports	10.00	10.00	5.45
Animal	8.18	8.18	2.73
Body part	7.27	7.27	4.55
Building and infrastructure	6.36	6.36	4.55
Clothing and accessories	5.45	9.09	10.91
Financial	2.73	1.82	1.82
Food and drink	11.82	11.82	10.00
Household items	15.45	14.55	9.09
Nature	7.27	6.36	22.73
Person	4.55	4.55	4.55
Tool	11.82	11.82	12.73
Transportation	6.36	5.45	2.73
Miscellaneous	2.73	2.73	8.18

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CHAPTER 2

Examining the brain dynamics of control processes during language production using

intracranial electroencephalography

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1. Introduction

Typical language production involves retrieving 2-3 words per second from over 50,000 words in the mental lexicon (Levelt et al., 1999), a complex task that speakers complete easily. Speakers retrieve approximately 16,000 words every day on average (Mehl et al., 2007). The result of impaired lexical retrieval is ubiquitous as it impacts all daily interactions from meetings at work to conversations with friends and interactions at the checkout line at the grocery. Despite the prevalence and necessity of lexical retrieval in daily life, there is still much unknown about its neurological basis. The current study seeks to add to the existing knowledge about the neurological basis of lexical retrieval by exploring the spatiotemporal dynamics involved in lexical retrieval subprocesses via intracranial electroencephalography.

Semantic context has been shown to impact lexical retrieval (Alario et al., 2000; Blackford et al., 2012; Bloem et al., 2004; Costa et al., 2005; de Zubicaray et al., 2013; Dell, 1986). Therefore, lexical retrieval is often investigated through manipulating semantic contexts. Semantically-related contexts typically lead to semantic facilitation or priming, especially in language comprehension (Kutas & Federmeier, 2011; Kutas & Hillyard, 1980). However, in language production, semantically-related contexts have been shown to lead to semantic interference on behavioral outcomes, especially when the semantic context is taxonomicallyrelated (i.e., of the same semantic category, Alario et al., 2000; Bloem et al., 2004; Costa et al., 2005; de Zubicaray et al., 2013). The psycholinguistic literature converges in postulating the existence of spreading activation from semantic representations (e.g., fruit, tart, juicy, etc.) to lexical representations that share these semantic features (e.g., *lemon, apple*, etc.). Therefore, activating the features associated with *lemon* will also prime *apple* for retrieval. Semantic facilitation or priming is theorized to stem from this spreading activation and therefore can be

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tied to the lexical activation stage of lexical retrieval. However, there is debate regarding which stage of lexical retrieval may be indexed by semantic interference. An initial interpretation of the semantic interference effect is that it reflects competition at the level of lexical selection (e.g., Caramazza, 1997; Roelofs, 1992; Damian et al., 2001; Howard et al., 2006; Roelofs & Piai, 2013). Alternative accounts have since argued that semantic interference may instead reflect incremental changes in connection weights between semantic and lexical representations (e.g., Harvey et al., 2019; Mahon et al., 2012; Mahon & Navarrete, 2014; Oppenheim et al., 2010) or conflict at the level of response preparation (e.g., Blackford et al., 2012; Caramazza & Costa, 2000; Costa et al., 2005; Giezen & Emmorey, 2016; Mahon et al., 2007). In the current study our goal is not to adjudicate between these theories, but to contribute to our understanding of the timing and location of neural processes involved in lexical retrieval.

A network of frontal and temporal brain regions has been associated with lexical retrieval. Medial frontal regions such as the presupplementary motor area (pre-SMA; Alario et al., 2006; Tremblay & Gracco, 2009) and the anterior cingulate cortex (ACC; de Zubicaray et al., 2001; Piai et al., 2013) have been shown to play a role in semantic interference resolution and response selection both inside and outside of language production (e.g., Barch et al., 2000; Botvinick et al., 1999; Christoffels et al., 2007; Debener, 2005; Dehaene et al., 1994; Piai et al., 2013). The left inferior frontal gyrus (LIFG) also appears to play a significant role in semantic interference resolution as seen in the blocked-cyclic naming task where individuals with LIFG damage had a greater semantic interference effect than controls (Riès et al., 2014; Schnur et al., 2006; Schnur et al., 2009) or individuals with right IFG damage (Riès et al., 2014). Schnur et al. (2009) also observed that the magnitude of the semantic blocking effect (i.e., the number of errors produced in semantically related vs. unrelated blocks) increased across naming cycles in

individuals with damage to the LIFG in comparison to controls or individuals with damage in the left temporal cortex. With evidence from their PWI magnetoencephalography (MEG) study, Piai and colleagues proposed that the superior frontal gyrus (SFG) also supports cognitive control processes involved in resolving semantic interference during word retrieval (Piai et al., 2014).

The middle temporal gyrus (MTG) and superior temporal gyrus (STG) are important for semantic memory (Binder et al., 2009; Bonner & Price, 2013; Patterson et al., 2008; Visser et al., 2010) and mapping concepts onto words during language production (Indefrey & Levelt, 2004; Schwartz et al., 2009). FMRI (Piai et al., 2013) and MEG (Piai, Roelofs, Jensen, et al., 2014) studies examining the effect of distractors on picture naming in healthy adults have reported increased activity in the left STG and MTG for unrelated compared to related distractor-picture conditions. Additionally, damage to the MTG in chronic stroke patients is associated with picture naming difficulties (Baldo et al., 2013) and word-level comprehension deficits (Bates et al., 2003; Dronkers et al., 2004). Reperfusion of these regions correlated with improved naming within 3-5 days, indicating that the MTG is crucial for naming (Hillis et al., 2006).

The picture-word interference (PWI) paradigm has often been used to study language production, as it probes characteristics of stimuli that can affect the speed and accuracy of picture naming (e.g., semantic relatedness). The picture-word interference (PWI) task has been used to study lexical retrieval through eliciting the semantic interference effect (Blackford et al., 2012; Bloem et al., 2004; Costa et al., 2005). In this paradigm, pictures are presented along with a distractor word. The task commonly contains conditions where the distractor word is semantically unrelated and semantically related to the target images. However, the brain dynamics of this semantic interference effect have been more difficult to pin down using EEG. Some EEG studies of language production have reported no difference in amplitude between

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related and unrelated conditions (Hirschfeld et al., 2008; Wamain et al., 2015) while others have reported electrophysiological priming with related conditions eliciting a reduced N400 in comparison to unrelated conditions (Blackford et al., 2012; Roelofs et al., 2016). One possible reason for these inconsistent findings is the type of ERP analysis technique used. Indeed, the spatial resolution of scalp EEG signal is heavily distorted as it travels through the cerebrospinal fluid and skull to the electrodes. In a previous study, we used Laplacian transformation to reduce spatial blurring and were able to detect a left lateral frontal semantic interference effect occurring simultaneously with the widespread semantic priming effects (Anderson et al., 2022). By having direct access to brain regions through intracranial EEG we will be able to circumvent spatial blurring issues and be able to precisely examine the nature of the activity of the neural regions involved in lexical retrieval.

In the current study, we explore the brain regions associated with lexical retrieval during language production by analyzing direct cortical recordings in neurosurgical patients that offer millisecond- and centimeter-scale resolution.

1.1. Current study

Much of the existing literature thus far examining brain regions associated with word retrieval has used noninvasive techniques (e.g., EEG, MEG, fMRI). Intracranial EEG recordings are well-suited to determine which brain regions are involved in lexical retrieval subprocesses because they are one of the few brain imaging techniques usable in humans that combine excellent spatial and temporal resolution and enable us to access deeper focal neural activity not accessible using noninvasive techniques. In the current study, using a PWI paradigm we used distractor words that were taxonomically-related, unrelated, and identical to the picture names as a means to identify the spatiotemporal dynamics of lexical retrieval. We investigate both the left

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and right hemispheres as language has been shown to be more bilaterally organized in individuals with epilepsy (Anders et al., 2019; Hamberger & Cole, 2011; Janszky et al., 2006; Riès et al., 2017). We expect to observe widespread sematic facilitation effects (Anders et al., 2019; Riès et al., 2017) as well as semantic interference effects that are more restricted in space, likely originating in the left prefrontal cortex (Anderson et al., 2022).

2. Methods

2.1. Participants

Thirteen individuals (7M; mean age = 29.5 years; SD = 8.1 years) undergoing neurosurgical evaluation for intractable epilepsy in the UC San Diego Health were recruited. Eight individuals (5M; mean age = 29.4 years; SD = 7.9 years) had intracranial data to be included in the electrophysiological analyses as one participant had only a single depth electrode and the localization data from four participants is not yet available through UC San Diego Health. All participants were native English speakers. Participants completed a series of neuropsychological tests administered as part of their clinical evaluation (see Table 2.1.). Importantly, all participants performed within two standard deviations of the average naming score on the Boston Naming Test, indicating within-normal picture naming abilities (Kaplan et al., 2016). All participants provided informed consent according to the Declaration of Helsinki.

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Table 2.1.	Standardized	neurops	ychological	test scores

Participant ID	IQ (standard score)	Naming ^a	Category fluency ^b	Letter Fluency ^c	Verbal learning ^d	Verbal recall ^d	Visual learning ^e	Visual recall ^e	Attention/ working memory ^f	Set- shifting ^g	Cognitive flexibility/ problem solving ^h
SD026	101	49	55	43	49	60	53	53	53	48	47
SD027	80		27*	23*	27*	20*	<20	<20	33	47	52
SD028	98	35	49	51	51	40	40	32	35	35	36
SD029	117	46	43*	37*	45	35	60	63	53		53
SD030	116	36	48	40	61	60	60	61	39	66	43
SD031	81	35	44	49	20	25	27	25	56	31	47
SD033	77	35	30	38	47	55	39	41	40	31	56
SD034	99	31	43*	44*	35	20	34	39	50	43	
60006											

SD036

Note. All scores reported as T-scores except for IQ which is reported as a standard score. T-scores were obtained from an interpretive manual from each test and represent how far an individual's performance differs from the healthy normative sample (adjusted for age, and sometimes sex and education). A T-score of 50 means that about half of the individuals in the normative sample scored higher and half scored lower. T-scores have a mean of 50 and a standard deviation of 15.

^aT-score based on performance on the Boston Naming Test (BNT)

^bT-score based on animal fluency from Halstead Reitan Expanded norms unless marked with an asterisk (tested on the D-KEFS version of category fluency)

^cT-score based on FAS fluency from Halstead Reitan Expanded norms unless marked with an asterisk (tested on the D-KEFS version of letter fluency)

^d Verbal learning and recall T-scores based on the California Verbal Learning Test-2nd edition (CVLT-2) unless marked with an asterisk (tested on the Hopkins Verbal Learning Test) ^e T-scores based on the Brief Visuospatial Memory Test-Revised (BVMT-R)

^fT-scores based on Digit Span from WAIS-IV

^gT-scores based on the Trail Making Test Part B (TMT-B) from the Halstead Reitan Expanded norms

^hT-scores based on total number of errors produced on the Wisconsin Card Sorting Test (WCST)

2.2. Design

The order of presentation of the stimuli was mixed pseudorandomly using Mix (van Casteren & Davis, 2006) which controlled for distance between identical target pictures, condition, semantic category, and phonological onset. All participants saw the same list containing 180 trials (with the exception of sd26 who saw 133 trials because of clinical time constraints outside of our control). Participants named pictures in a picture-word interference paradigm where words were superimposed over pictures in three conditions: semantically related, semantically unrelated, and identity. A stimulus onset asynchrony (SOA) of 0 ms was chosen after considering previous findings that the semantic interference effect is observed when distractor words are presented before (-160 ms), simultaneously with (0 ms), and shortly after (+200 ms) the target image (Blackford et al., 2012; Bloem et al., 2004; Mahon et al., 2007). The stimuli consisted of 60 colored photographs with above 80% naming agreement issued from the BOSS database (Brodeur et al., 2014) belonging to ten different semantic categories (six members per categories) superimposed with the name of another member in three conditions

(i.e., related, unrelated, identity) as shown in Figure 2.1. Importantly, all three conditions contain the same words and images but scrambled in order to prevent any possible confounding effects from including different items across conditions.



Figure 2.1. Example stimuli from each condition. Each target picture appeared once with its identity word superimposed, once with a semantically-related word, and once with a semantically-unrelated word.

2.3. Procedure

Experimental instructions and stimuli were presented to participants in their hospital rooms on a Windows 10 desktop PC (Dell XPS 8910; Mai et al., 2024). Participants were seated approximately one meter from the stimulus monitor. The experiment was controlled by Presentation, allowing online recording of the participants' verbal response. Each trial consisted of an image overlaid with a prime word (0 ms SOA) for 2000 ms and then a blank screen for 2000 ms during which the participant named the image aloud (they were told to ignore prime words). Between each trial, a fixation cross was displayed for 1000 ms. Images subtended a visual angle within 5 degrees in the horizontal and vertical directions. There were five self-timed breaks throughout the experiment (one break every 30 trials).

2.4. iEEG recording

Testing was conducted at the UCSD Medical Center in collaboration with Dr. Jerry Shih, Neurologist, Director of the Epilepsy Center. Electrophysiological data was collected through depth electrodes placed perpendicularly to the cortical surface to target deep brain structures (stereoencephalography, sEEG) in patients suffering from intractable epilepsy undergoing intracranial monitoring for localization of epileptic foci (3-10 days). Electrodes were distributed across left and right hemispheres (see Figure 2.2. and Supplementary Table 2.S1.). Each electrode had between ten to sixteen 2 mm contacts. iEEG activity was recorded using a clinical EEG recording system (Natus Xltek NeuroWorks, Natus Medical Incorporated, San Carlos, CA). Post-operative CT scans and pre-operative T1-weighted MRI scan (~1mm voxel isotropic SPGR or MPRAGE sequences, 3R GE or Siemens scanners) were collected on all participants as part of the normal clinical routine.

Intracranial EEG signals were amplified using a multi-channel amplifier system (Natus Quantum) and recorded using Natus NeuroWorks software. In addition to the Presentation recordings, oral responses were recorded simultaneously with the EEG data by feeding the output of a Zoom H2n microphone as an additional input channel to the Natus Quantum amplifier as in (Mai et al., 2024).

2.5. Electrode localization

Stereo EEG electrodes were localized by registering each patient's preoperative T1weighted MR volume to an intraoperative CT in 3D Slicer (Fedorov et al., 2012; Kikinis et al., 2014) and manually marking each contact. Telemetry channel names to the marked centroids were assigned by a team of neurosurgeons at UCSD Medical Center. Volumetric anatomical

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labels were retrieved following the Desikan-Killiany atlas (Desikan et al., 2006) with additional segmented volumes for the thalamic nucleus (Iglesias et al., 2018), amygdala (Saygin & Kliemann et al., 2017), and hippocampal (Iglesias et al., 2015) subfields.



Figure 2.2. sEEG electrode placement. The placement of sEEG electrodes in each of the eight individuals who participated in the current study normalized to the MNI space. Each participant's electrodes are depicted in a different color.

2.6. *iEEG data pre-processing (cleaning and segmentation)*

After recording, neural data were de-identified and exported from the clinical NeuroWorks system in .edf (European Data Format) format for pre-processing using MatLab. The iEEG data was then filtered at 60 Hz and resampled to 1024 Hz. Channels showing epileptic activity, excessive artifacts, or line noise were removed prior to segmentation. Although weaker compared to scalp EEG, all other artifacts (eye movements and muscle artifacts) were rejected
based on a trail-by-trail visual inspection of monopolar recordings (Ball et al. 2009; Jerbi et al. 2009; Kovach et al. 2011; Nejedly et al. 2019). All channels were then bipolar referenced. All iEEG analysis was performed using custom analysis scripts using Matlab v.9.9.0 (R2020b, The Math Works, Inc). Our analyses focused on Local Field Potential (LFP; 0.1 - 30 Hz) and High Frequency Broadband (70-150 Hz) signal. For all patients, a scalp electrode is used as a local reference and ground. We will first determine which electrodes show significant activity (>10% increase compared to baseline on the average of all trial types for at least a duration of 100ms).

2.7. Significant electrodes

A consistent increase in LFP or HFB power for an electrode's data with respect to stimulus onset over all trials of the naming task was taken to be indicative of the corresponding region's involvement in the task. An electrode was deemed significant if its amplitude significantly increased above the -500 to 0 baseline window average. A z-test was conducted on each electrode sample with respect to the baseline mean and variance. If the window of analysis presented with significant z-scores (p < 0.05) for over 100ms, the electrode was regarded as containing significant activity relative to the baseline. Electrodes with continuous significant z-scores for 100ms or more following FDR correction were considered to be significant.

As in Haller et al. (2018), we used Principal Component Analysis (PCA, using correlation matrix and varimax rotation) on stimulus-locked HFB and LFP time series averaged across correct trials for each active channel in order to reduce dimensionality of the signal. This allowed us to identify channels with common temporal HFB or LFP patterns. We analyzed each participant's dataset separately since the temporal profile of the signal depends on reaction time parameters (mean, range, distribution), which vary for each participant. The number of significant principal components (PCs) was determined using a variant of parallel analysis, whereby comparison data were generated for increasing numbers of components until the observed eigenvalues failed to show significant improvement (Haller et al., 2017). We then performed hierarchical data clustering based on temporal features of the data and blind to spatial distribution of the signal to group the clustering space.

2.8. Behavioral data analysis

For the thirteen participants included in behavioral analysis, we analyzed mean naming latencies on correctly answered trials in each condition. Correct responses were defined as answers matching the picture name with the highest name agreement for each item. We accepted as correct semantically identical names for an item (e.g., bike for bicycle, bunny for rabbit, etc.). Any alternative response outside of the name of the target item was considered an error (e.g., stutter, semantically different words, hesitation such as "uh"). For error rate analyses, only incorrect responses that included a complete incorrect response were included (i.e., semantic and phonological errors were included while hesitations and no responses were excluded). Statistical analysis was performed within R version 3.6.0 using the packages "lme4" to compute mixed effect models (Bates et al., 2014a, 2014b) and "car" to compute analysis of deviance tables for the fixed effects of the mixed effect models (Fox & Weisberg, 2011). We report Wald chi-square values and p values from the analysis of deviance table, as well as raw β estimates (β raw), standard errors, Wald Z, and associated p values for significant and marginally significant effects. The individual reaction times (RTs) were inverse-transformed to reduce skewness and approach a normal distribution. The analyses were performed on inverse-transformed RTs.

Naming latency data were analyzed with linear mixed-effects models, testing for the main effect of Condition (Related, Unrelated, Identity) on reaction time measured in milliseconds with intercepts for Item and Participant as random effects as well as by-participant random slope for Condition. We analyzed the accuracy data using logistic mixed-effects models (Baayen et al., 2008; Jaeger, 2008). We tested for the main effect of Condition (Related, Unrelated, Identity) on error rate with intercepts for Item and Participant as random effects as well as such as the su

2.9. iEEG data analysis

We used the output from the PCA and clustering analyses to determine the latency of the peak of amplitude of each principal component for each individual. This led us to focus our subsequent analyses on 5 different time windows: 150 - 250 ms (Time Window 1), 300 - 500 ms (Time Window 2), 550 - 750 ms (Time Window 3), 800 - 1000 ms (Time Window 4), and 1100 ms onwards (Time Window 5). For example, if Principal Component #5 for participant sd26 peaked at 800 ms it would be assigned Time Window 4. Following this example, Principal Component #5 is composed of activity from four electrodes (DRIA04-03/Insula, DRIA05-04/Insula, DRCA02-01/dACC, and DRHT12-11/Superior Temporal) for sd26. Therefore, the activity from each of those four channels was assigned to Time Window 4. After assigning electrodes to distinct time windows, we conducted a linear mixed effects model analysis to examine the interaction effect between Condition (Related, Unrelated), Electrode Location, and Time Window on the dependent variable of surface area under the curve for LFP and HFB activity. We controlled for random effects of Item and Participant and by-participant random slope for Condition. Only correct trials were used in the iEEG analysis. All reported results

include significant activity from at least two participants as is standard practice in SEEG studies (Mercier et al., 2022).



Figure 2.3. Depiction of components extracted from LFP data for participant sd26 after Principal Component Analysis and clustering. (Left) Nine clusters of Principal Components were identified from the whole signal for each participant. (Right) The time-course of each of the nine Principal Components is presented with amplitude on the y-axis and time on the x-axis.

3. Results

3.1. Behavioral Results

There was a main effect of Condition on reaction time ($\chi^2(2, 13) = 40.33$, p < .001). Participants were significantly slower in the related than in the unrelated condition (Effect Size = +32 ms, $\beta_{raw} = 3.076e-05$, SE = 1.245e-05, t = 2.47, p = 0.019), and in the related than in the identity condition (Effect Size = +145 ms, $\beta_{raw} = 1.381e-04$, SE = 2.645e-05, t = 5.22, p < .001). They were also significantly slower in the unrelated versus identity condition (Effect Size = +113 ms, $\beta_{raw} = -1.074e-04$, SE = 3.145e-05, t = -3.42, p = 0.005). Effect size is defined here as the difference in averages between groups. There was a main effect of Condition on accuracy ($\chi^2(2, 13) = 6.69, p = .035$). There was no significant difference between the related and unrelated conditions (Effect Size = 0.73%, β_{raw} = 0.130, SE = 0.328, z = 0.396, p = 0.692), but participants were significantly more accurate in the identity than in the related (Effect Size = - 4.41%, β_{raw} = -1.26, SE = 0.530, z = -2.38, p =0.018) and unrelated conditions (Effect Size = -5.14%, β_{raw} = 1.39, SE = 0.549, z = 2.53, p =0.012).



Figure 2.4. (Left) Reaction times in milliseconds across conditions. Average reaction time per condition depicted inside of each bar. (Right) Error rate (%) across conditions. Average error rate per condition depicted inside of each bar. Standard error bars are shown on each average.

3.2. iEEG Results

3.2.1. LFP

There were main effects of Condition ($\chi^2(1,1) = 4.24$, p < .05), Electrode Location ($\chi^2(1,24) = 60.71$, p < .001), and Window ($\chi^2(1,4) = 22.27$, p < .001). There was also a two-way interaction between Condition and Window ($\chi^2(1,4) = 11.05$, p < .05) as well as a three-way interaction between Condition, Location, and Window ($\chi^2(2,30) = 44.59$, p < .05). These results

indicated that the effect of condition varied significantly across location when comparing different time windows. The effect of Condition was strongest from 800 – 1000 ms post-stimulus onset (β_{raw} = -118921.2, SE = 43792.6, *t* = -2.716, *p* = 0.0066). Without controlling for electrode location, the related condition elicited greater negativity than the unrelated condition from 800 – 1000 ms. However, when considering Condition effects over time by specific brain regions, the unrelated condition elicited significantly greater activity than the related condition in three brain regions: the caudal anterior cingulate cortex, insula, and superior frontal gyrus. This effect occurred in the 550 - 750 ms post-stimulus time-window in four individuals in the dACC (β_{raw} = -144251.4, SE = 68698.9, *t* = -2.100, *p* = .036), in the 800 - 1000 ms post-stimulus time-window in two individuals in the insula (β_{raw} = 151922.0, SE = 58234.3, *t* = 2.609, *p* = 0.0091), and in the same 800 - 1000 ms post-stimulus time-window in three individuals in the SFG (β_{raw} = 131425.2, SE = 53225.3, *t* = 2.469, *p* = 0.014). All SFG and dACC effects occurred in the right hemisphere and the insula effects occurred bilaterally.











Figure 2.5. Activity reported from three brain regions where the unrelated condition elicited greater activity than the related condition. (a) Average surface area under the curve of activity in the caudal anterior cingulate cortex from 550 to 750 ms post-stimulus onset in participant sd36. (b) Average surface area under the curve of activity in the insula from 800 to 1000 ms post-stimulus onset in participant sd26. (c) Average surface area under the curve of activity in the superior frontal gyrus from 800 to 1000 ms post-stimulus onset in participant sd28.

3.2.2. HFB

The linear mixed effects model showed a main effect of Location ($\chi^2(1,27) = 812.12, p < .001$) and of Window ($\chi^2(1,4) = 39.17, p < .001$) as well as a two-way interaction between Location and Window ($\chi^2(1,39) = 715.56, p < .001$). There was no main effect of Condition ($\chi^2(1,1) = 0.076, p = 0.78$) nor any interaction effects between Condition and either Location or Window. There were no regions that showed significant difference between related and unrelated conditions across any of the five windows for two or more participants.

4. Discussion

The aim of the present study was to utilize a technique with high temporal and spatial resolution to shed light on the spatio-temporal dynamics of lexical retrieval. We tested the performance of individuals with intractable epilepsy in a picture-word interference naming task after their electrode implantation in UCSD Medical Center. Participants were slower to name semantically related than unrelated picture-word pairs, although there was no difference in accuracy between these conditions. The analysis of the iEEG data indicates the involvement of several frontal brain regions in lexical retrieval.

Lexical retrieval consists of the complementary processes of spreading activation and then selection from co-activated lexical representations. The behavioral outcome of choosing from amongst co-activated items is often semantic interference, which is indeed what we observed in the behavioral data, specifically in the reaction time results. Participants were slower in the semantically related condition compared to the unrelated condition (Alario et al., 2000; Bloem et al., 2004; Costa et al., 2005; de Zubicaray et al., 2013). This indicates that they struggled more when tasked with selecting, for example, drum in the presence of the

semantically related distractor word guitar than when in the presence of the unrelated distractor word bench.

The interference effect observed in the behavioral data was not observed in the intracranial data. This is not uncommon as it often requires fine-grained analysis techniques to disentangle interference effects from neural data. For example, in Anderson et al. (2022) no interference effect was detected during a PWI task using traditional monopolar EEG analysis (as in Blackford et al., 2012; Hirschfeld et al., 2008; Roelofs et al., 2016; Wamain et al., 2015), but with the use of Laplacian transformation (a spatial filter that increases topographical localization) a left frontal interference effect was found occurring simultaneously with the widespread priming effect. Anders and colleagues conducted a blocked cyclic naming task and examined intracranial data from 84 brain regions. Of the investigated regions, 39 showed significant deviation from baseline, nine of the 39 regions showed a facilitation effect, and only one region, the pre-SMA, showed an interference effect (Anders et al., 2019). The findings suggest that the pre-SMA plays a role in resolving semantic interference, possibly at the stage of response selection directly before articulation (Anders et al., 2019). Riès et al. (2017) also observed overlapping semantic facilitation and interference effects in the left posterior inferior temporal gyrus and the left prefrontal cortex during an intracranial language production study. These studies importantly support semantic facilitation and semantic interference coexisting simultaneously in the signal, but that the interference effect may be more highly restricted spatially and more difficult to detect in iEEG data. It remains plausible that this interference effect does exist in the current study and was not detected due to a variety of reasons such as variable electrode coverage across participants, the necessity of dimensionality reduction to analyze a dataset of this scale, etc.

As mentioned, although picture naming studies often find behavioral interference in the presence of semantic context, semantic priming is often the effect observed in the corresponding neural data (Blackford et al., 2012; Roelofs et al., 2016; see Kutas & Federmeier, 2011). The presence of this effect indicates that lexical-semantic activation was more effortful in the unrelated than in the related condition due to the decreased semantic priming in the unrelated condition. The precise mechanisms underlying the involvement of brain regions in lexical retrieval is still unclear, but there is evidence that the frontal lobe supports top-down control processes that allow speakers to narrow their search for the target word (Piai et al., 2013, 2014; Riès et al., 2017). We observed semantic facilitation in three primary regions: the ACC (550 - 750 ms post-stimulus), the SFG (800 - 1000 ms post-stimulus), and the insula (800 - 1000 ms post-stimulus).

The ACC is linked to general action monitoring and conflict resolution both in and outside of language (e.g., Barch et al., 2000; Botvinick et al., 1999; Christoffels et al., 2007; Debener, 2005; Dehaene et al., 1994; Piai et al., 2013). The ACC has been associated with speech monitoring with evidence from fMRI studies without distorted auditory feedback (Christoffels et al., 2007; Gauvin et al., 2016; van de Ven et al., 2009). Electrodes located in the ACC recorded greater activity in the unrelated than in the related condition from 550 to 750 ms post-stimulus. This suggests that spreading activation from semantically related items facilitates semantic processing with the assistance of control processes housed in the ACC.

The same pattern of activity was observed in the SFG in a later time window, from 800 to 1000 ms post-stimulus onset. The SFG supports cognitive control processes linked to resolving semantic interference (Piai et al., 2014) as well as response selection, inhibition, response switching, and conflict monitoring (Anders et al., 2019; George et al., 1994; Ridderinkhof et al.,

2004; Simmonds et al., 2008; Verbruggen & Logan, 2008). The observation of greater activity for unrelated than related conditions persisting to the 800-1000 window suggests that spreading activation from semantic co-activation continues on past initial lexical activation and semantic processing, facilitating semantically related items throughout the remaining stages of language production.

The insula has traditionally been associated with motor processing and articulation (Ackermann & Riecker, 2004, 2010; Ardila et al., 2014; Baldo et al., 2011; Oh et al., 2014). There is continuing debate as to the exact functions associated with the insula and the extent and manner to which the insula is involved in language processing. A meta-analysis from Oh et al., (2014) provided a summary of functional neuroimaging data that described the involvement of the insula during a variety of speech and language tasks. Oh and colleagues stated that the activation of the insula during language tasks is unsurprising due to the functional connectivity of the insula to brain regions often cited as playing a role in language processing such as the inferior frontal gyrus. A second meta-analysis from Ardila and colleagues focused on exploring the connections between the insula and regions associated with various language processing functions (Ardila et al., 2014). Regions Ardila and colleagues found to be connected to the insula included BA44 (Broca's area, associated with language production), BA9 (left MFG, associated with language production and complex language organization), BA37 (posterior ITG, MTG, fusiform gyrus, associated with lexico-semantic associations), and BA22 (STG, associated with naming and language understanding). The highly central and interconnected nature of the insula makes it difficult to pinpoint the precise role the insula plays in language production, whether it supports processes related to articulation and/or response selection, or if it is a control center that connects to and strengthens the network of language processing regions. Research from

Dronkers (1996) has shown that damage to the insula results in speech apraxia, or an impaired ability to plan and coordinate speech movements with a preserved ability to perceive speech sounds. This supports the insula's involvement in programming complex articulation sequences (Dronkers, 1996). The insula's involvement in the current study suggests that semantic priming percolates downwards to this later stage of language production.

In conclusion, the current study sheds light on the spatiotemporal dynamics of lexical retrieval in language production. Our results show that a network of frontal regions facilitates lexical retrieval and subsequent stages of language production. Superior and medial frontal control may therefore be key for selecting from unrelated lexical items that lack significant co-activation to assist with response selection. Additional research is however necessary to determine if the semantic interference effect can be detected in an alternative type of analysis of intracranial data in order to reconcile the behavioral results with those observed in the iEEG data. Functional connectivity analyses in particular will bolster the information presented in the current study by defining the regions that work in concert to execute the stages of lexical retrieval.

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Patient	LH	RH
sd26	1	167
sd27	77	79
sd28	20	96
sd29	127	99
sd30	34	120
sd33	12	126
sd34	46	154
sd36	102	120

Table 2.S1. Distribution of electrodes across left and right hemispheres for each individual with intractable epilepsy.

CHAPTER 3

The role of the left posterior temporal cortex in speech monitoring

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Abstract

Speech monitoring abilities vary in individuals with stroke-induced aphasia, brain lesion location being one possible contributing factor. Left posterior temporal (pLTC) regions have been proposed to be central to lexical access. We tested whether lesions in the pLTC would affect the medial frontal action monitoring system indexed by the Error-Related Negativity (ERN), previously proposed to play a role in inner speech monitoring. We recorded electroencephalography in 7 individuals with lesions including the pLTC, 7 individuals with lesions sparing the pLTC, and 20 matched controls during picture naming. Individuals with pLTC lesions were slower and less accurate than the other groups. Individuals with lesions sparing the pLTC showed the expected ERN pattern, whereas individuals with pLTC lesions did not. The medial frontal monitoring mechanism may therefore be compromised if regions central to lexical access are damaged, as interactions between the pLTC and the medial frontal cortex may support inner speech monitoring.

Keywords: Speech monitoring, medial prefrontal cortex, error-related negativity, stroke-induced aphasia

1. Introduction

Although language production is complex, healthy adult speakers can select words from a mental dictionary of more than 50,000 words to produce 2-3 words per second and only err about once every 48.5 seconds (Alderete & Davies, 2019). Several theories have been proposed to describe the process by which we monitor our speech production. Theories of speech monitoring propose that speech can be monitored overtly, as we hear ourselves speak, and covertly, before speech output. The "inner loop" of speech monitoring is responsible for monitoring speech production online, before production. The "outer loop" monitors speech after production and relies primarily on auditory feedback (for reviews, see Gauvin & Hartsuiker, 2020; Postma, 2000). While cognitive models agree that the outer loop of speech monitoring relies on speech comprehension mechanisms, the mechanisms underlying the inner loop of speech monitoring have been a matter of debate (Nozari, 2020; Nozari et al., 2011; Roelofs, 2020; Zheng et al., 2018), and are the focus of the current study.

1.1. Speech Monitoring Models

Several theories have been proposed to account for the fact that we are able to catch our speech errors before hearing ourselves speak. One of the first theories to have been proposed is the Perceptual Loop Theory (PLT, Levelt et al., 1999). According to this model, the inner loop receives the output of the language production system before articulation once the phonetic plan has been prepared, feeds this output to the speech comprehension system, which then feeds back into the conceptual level of the speech production system. While parsimonious because contained within the language system, the implications of the PLT have been challenged with various types of data. Neuropsychological data from individuals with acquired language disorders have shown dissociations between error detection in language production and

perception (Nozari et al., 2011), which is not reconcilable with the PLT because it assumes a dependence of speech monitoring on speech comprehension. Dissociations have also been found between how speakers detect errors in their own speech vs. in other's speech (Nooteboom & Quené, 2013, 2017), which is also incompatible with the assumptions of the PLT.

Another influential model is the conflict-based model of speech monitoring proposed by Nozari and colleagues (Nozari et al., 2011). The overarching concept behind this theory is that errors are detected within the language production system when two or more alternatives are activated at the time of responding, generating a conflict signal. That conflict signal can then be monitored by a domain-general cognitive control system. This theory was tested with error data from natural speech production in individuals with aphasia and showed a strong correlation between error-detection and the individuals' production skills rather than comprehension measures, accounting for the dissociations between self-monitoring and comprehension abilities found in these individuals. This model therefore postulates that the speech comprehension system is not necessary for the inner loop of speech monitoring and that this inner loop instead relies on the speech production system, in a similar vein as the production-based monitors initially proposed (Laver, 1973, 1980; for a review see Postma, 2000).

A third and more recent model proposed by Gauvin and Hartsuiker (2020) builds upon the conflict-based model by proposing mechanisms for error detection and repair as well as error detection in other's speech, which were not included in the conflict-based model. Similarly, as the conflict-based model proposed by Nozari et al. (2011), Gauvin and Hartsuiker's model (2020) proposed that a domain-general cognitive control system is involved in speech monitoring of self-produced speech and in speech produced by others. Other models have also been proposed, including the hierarchical state feedback control (Hickok, 2012) model or forward

model theory (Pickering & Garrod, 2014; Pickering & Garrod, 2013a, 2013b). However, these models tend to focus on specific aspects of speech monitoring or fail to account for dissociations between error detection in language production and perception in data from individuals with aphasia (Gauvin & Hartsuiker, 2020).

1.2. Brain regions associated with speech monitoring

The neurological bases of speech monitoring have been investigated with multiple brain imaging techniques and paradigms (e.g., Behroozmand et al., 2015; Christoffels et al., 2007; Fu et al., 2006; Hashimoto & Sakai, 2003; McGuire et al., 1996), and can shed light on the cognitive architecture of speech monitoring as well. In particular, external manipulation of verbal auditory feedback in fMRI and PET paradigms have shown that overt speech monitoring (i.e., the outer loop of speech monitoring) leads to activation in an array of brain regions including in particular the bilateral superior temporal gyrus (STG; e.g., Fu et al., 2006; Hashimoto & Sakai, 2003; McGuire et al., 1996; Tourville et al., 2008). Hemodynamic signal in the STG has been shown to increase when auditory feedback during self-produced speech is distorted (e.g., pitch elevation of the participant's voice, masking with pink noise, etc., Behroozmand et al., 2015; Hashimoto & Sakai, 2003). By contrast, when speech is not distorted during production, the STG is not always reported to be active (Christoffels et al., 2007; van de Ven et al., 2009). A recent fMRI study examining internal speech monitoring during masked production in fact found no activation of the STG, suggesting that the STG is not involved in the inner loop of speech monitoring but rather only in the outer loop of speech monitoring (Gauvin et al., 2016). If we admit that the STG plays a crucial role in speech comprehension, these neuroimaging results are therefore not in agreement with the premise of the PLT (Gauvin & Hartsuiker, 2020)

Several brain regions have been associated with general action monitoring, including the anterior cingulate cortex (ACC) and/or supplemental motor area (SMA, Debener, 2005; Dehaene et al., 1994), thalamus (Falkenstein et al., 2001; Peterburs et al., 2011), and basal ganglia (Falkenstein et al., 2001; Ullsperger & von Cramon, 2006). Importantly, these regions have also been associated with speech monitoring using fMRI in paradigms without auditory distortion (Christoffels et al., 2007; Gauvin et al., 2016). Of particular interest here, medial frontal regions, such as the ACC, have been associated with action monitoring and conflict resolution both in and outside of language (e.g., Barch et al., 2000; Botvinick et al., 1999; Christoffels et al., 2007; Debener, 2005; Dehaene et al., 1994; Piai et al., 2013). This functional and anatomical overlap supports the idea that a domain-general medial frontal monitoring process is necessary for speech monitoring, as implemented in Nozari et al. (2011) and Gauvin and Hartsuiker's (2020) models.

However, a commonality of all cognitive models of speech monitoring is that the language production system is always involved as the cognitive processes upstream of speech monitoring need to happen to have a speech output to monitor. Indeed, speech monitoring theoretically relies on input from the language representational system where conflict between linguistic representations can arise. Nevertheless, how the medial frontal speech monitoring system may interact with brain regions involved in core language functions is unknown. These regions include left posterior temporal regions associated with lexical access, including the left posterior middle temporal gyrus (MTG, Baldo et al., 2013; Dronkers et al., 2004), the left posterior STG (DeLeon et al., 2007; Hillis et al., 2006), and the posterior inferior temporal cortex (ITG, Trebuchon-Da Fonseca et al., 2009). Indeed, individuals with stroke-induced brain lesions in the left posterior temporal cortex often struggle to recognize the correct name of an image

even when it is presented to them as an option to choose from, despite their preserved ability to demonstrate object use. This has been interpreted as indicating that the link between lexical representations and underlying concepts is damaged in these individuals (Dronkers et al., 2004). In individuals with temporal lobe epilepsy, hypoperfusion in the left posterior STG and ITG have been associated with word finding difficulties (DeLeon et al., 2007; Trebuchon-Da Fonseca et al., 2009). These results suggest that the left posterior temporal cortex in general plays an important role in accessing linguistic representations. Therefore, we hypothesize that interactions between the left posterior temporal cortex and the medial frontal cortex are necessary for efficient speech monitoring to happen.

In addition, the close temporal relationship between "inner" and "outer" speech monitoring requires a technique with high temporal resolution to further define the network of brain regions involved in these different aspects of speech monitoring. Therefore, electrophysiological analyses are required to investigate event-related activity tied to action monitoring.

1.3. Electroencephalography

Of particular interest in the current study is the error-related negativity (ERN or Ne; first reported by Falkenstein et al., 1991 and Gehring et al., 1993). This component has a frontocentral distribution, typically best seen at electrode FCz or Cz in the 10-20 electrode positioning system, with the ACC and/or the SMA as possible sources (Bonini et al., 2014; Debener, 2005; Dehaene et al., 1994). The ERN was originally discovered in non-linguistic contexts following an incorrect response (Falkenstein et al., 1991; Gehring et al., 1993), hence its name, and has since then been observed in linguistic tasks involving speech production (Masaki et al., 2001; Riès et al., 2011, 2013a, 2020). Laplacian transformation has been used in both

linguistic (Riès et al., 2011; Riès et al., 2021; Riès et al., 2020) and non-linguistic (Vidal et al., 2000, 2003) studies to reveal that the ERN is also present in correct trials, only it typically has a smaller amplitude and is masked by a large posterior positivity in traditional monopolar EEG recordings. In speech production studies, the ERN peaks between vocal onset and around 100 ms post vocal onset (Acheson et al., 2012; Riès et al., 2011, 2013b, 2020). Using intracranial EEG, Bonini et al. (2014) found an intracranial EEG activity similar to the ERN in both incorrect and correct responses during a Simon task in the SMA (Bonini et al., 2014). In addition, Roger et al. (2010) found that the same component underlies the ERN in error and correct trials using ICA and source localization on scalp EEG data (Roger et al., 2010). The presence of the ERN on both error and correct trials indicates that it does not reflect error detection, but instead a more general action monitoring system. Previous work from our group has demonstrated that the ERN in both errors and correct trials in picture naming begins to rise before the verbal response onset in speech and in sign language production (Riès et al., 2011, 2013b, 2020). This indicates that the ERN reflects a speech monitoring mechanism involved before auditory (in speech) or visual (in sign production) feedback can be perceived. This supports the idea that the ERN reflects a general-purpose action monitoring system that is involved in inner language output monitoring and constitutes one of the bases for the conflict-based monitoring model proposed by Nozari et al., 2011.

1.4. Current Study

In this study, we explore the impact of stroke-induced brain lesions to posterior temporal regions on conflict-based monitoring in the medial PFC as reflected by the ERN. We propose that interactions between the posterior lateral temporal cortex (pLTC) and the medial frontal conflict monitoring system are necessary for the domain-general monitoring system to interact

with the language production system, and in particular linguistic representation access. We expect that individuals with a stroke-induced brain lesion in the pLTC will be impaired on speech monitoring compared to individuals with left frontal lesions. Specifically, we expect them to show higher error rates and an impaired medial frontal ERN pattern, with possibly an absence of amplitude difference between correct and error trials as found in individuals with lateral PFC lesions in rule-based cognitive control tasks (Gehring & Knight, 2000; Riès et al., 2013b).

To address this hypothesis, we recorded EEG in individuals with lesions including the pLTC or with LPFC lesions excluding the pLTC and in a group of age-matched control participants as they performed a blocked-cyclic naming task (Damian et al., 2001; Kroll & Stewart, 1994). We are expecting that individuals with lesions in the pLTC will have impaired access to lexical representations and thus should have impaired inner speech monitoring. They should have lower accuracy than the individuals with LPFC lesions and controls, and they should show no amplitude difference between errors versus correct trials on the ERN in this naming task.

2. Methods

2.1. Participants

We recruited 34 native English-speaking adults between the ages of 50 and 80 from the San Diego area, 14 individuals with left hemisphere stroke-induced lesions (mean age = 59.8 years, $\sigma = 12.6$ years; 4 females; mean years of education = 17.3 years, $\sigma = 2.3$ years) and 20 age-matched controls (mean age = 60.7 years, $\sigma = 8.12$ years; 8 females; mean years of education = 16.5 years, $\sigma = 2.3$ years). All participants were right-handed before stroke, had no history of additional neurological damage or hearing loss, and had normal or corrected-to-normal vision. Control participants were not included in the behavioral error analyses or EEG analyses due to low error rates but were included in the behavioral analyses examining semantic interference on RTs.

Individuals with aphasia were divided into two groups for analysis: 7 individuals with left anterior lesions (i.e., focal unilateral frontal lesions excluding the pLTC) and 7 individuals with left posterior lesions (i.e., focal unilateral posterior lesion including the pLTC). The posterior lesion group includes individuals with lesions that extended anteriorly, therefore we are not differentiating these groups based on LPFC involvement, but instead on pLTC involvement (see Figure 1). This area is the area of interest in the current study and hence the damage including or excluding this region was used as the differentiating factor. Importantly, there was no significant difference in lesion size between the two groups (lesion size calculated by percent volume t(10.6) = -1.23, p = .24 and lesion size calculated by cubic millimeters t(9.88) = -1.20, p = .26).



Figure 3.1. Lesion overlays for the included participants: (a) Individuals with lesions including the pLTC (n=4). (b) Individuals with LPFC lesions excluding the pLTC (n=6). The brighter the red, the more participants had a lesion including this area.

All individuals with aphasia were tested at least 6 months post-stroke. All individuals with aphasia had overall good production abilities as indicated by their scores on the confrontational naming subtest of the Cognitive Linguistic Quick Test (CLQT; Helm-Estabrooks, 2001), scores were not available for one participant, see Table S1 in the supplementary materials). Participants with aphasia performed within normal limits on the confrontational naming section of the CLQT, had a mild to moderate aphasia based on the Aphasia Quotient on the WAB-R, and tested as having mild to no apraxia of speech on the Apraxia Battery for Adults (ABA; Dabul, 2000). Scores were comparable across groups for the subtests of interest although the posterior patient group had a lower overall AQ (78.2, SD=9.7) than the anterior patient group (93.6, SD=4.8). More nuanced results are available through the Western Aphasia Battery-Revised (WAB-R; Kertesz, 2007) which was run on a subset of the participants (see Table S1).

2.2. Materials and Design

All individuals participated in a blocked-cyclic naming task. Each semantic category member (e.g., cat in *animals*) was represented by six different items (i.e., six different cats), and was presented within semantically homogenous (HOM) versus heterogeneous (HET) blocks (see Figure 2) in similar fashion as in Damian et al. (2001). All included images had 80% or greater naming agreement.

There was a total of 432 trials (6 items per semantic category with 6 exemplars each). All items appeared an equal number of times in the homogeneous and heterogeneous blocks. The order of presentation of the stimuli was mixed pseudo-randomly using Mix (van Casteren & Davis, 2006) controlling for the distance between identical target names and phonological onset. There was a minimum distance of three items between identical targets and no two phonological onsets occurred in a row including across block boundaries. Lists were counterbalanced across participants.

The stimuli were color photographs of common objects across six semantic categories (instruments, vehicles, furniture, fruit, animals, and clothing). We created six lists that were counterbalanced across participants.



Figure 3.2. Example of semantically related and unrelated blocks. In the homogenous condition participants named a series of semantically related pictures one after the other (e.g., fruit). In the heterogenous condition participants named a series of semantically unrelated pictures.

2.3. Procedure

Participants were seated comfortably approximately 150 cm away from the stimulus monitor in a sound-attenuated, dimly lit room separate from the experimenter. A trial consisted of the following sequence events: (1) a fixation point ("plus" sign presented at the center of the screen) for 500 ms; (2) a picture for 2000 ms (3) a blank screen for 1500 ms. The subsequent trial started automatically. Participants were instructed to try to blink only during the blank screen between trials.

The experiment was controlled using Presentation software (NeuroBehavioral Systems, Inc., Berkeley, CA). Images subtended a visual angle of 2.0 degrees in the horizontal and vertical directions. Participants were asked to provide a one-word response as quickly and as accurately as possible. Participants were familiarized with the picture names before the start of the experiment using a 7th exemplar of each category member. The pictures used for the familiarization were presented one by one in random order and the participant was asked to name each one. The experimenter stood next to the participant and verbally corrected participants when an incorrect or unexpected response was produced. Following the familiarization phase, the experiment began. The experimenter left the room but regularly checked in with the participants during the breaks. Breaks occurred every 72 trials and the participants could rest as long as they wanted during the breaks.

2.4. EEG Recording

Participants were fitted with an elastic electrode cap with 64 Ag/AgCl active electrodes (10-20 system positions). The vertical electrooculogram (EOG) was recorded by means of two surface electrodes just above and below the left eye, respectively. The horizontal EOG was recorded with two electrodes positioned over the two outer canthi. The passive reference was placed over the left mastoid. An ActiChamp system (Brain Products) was used to record EEG with a bandpass of DC to 100 Hz (3 db/octave) and was sampled continuously at 250 Hz.

2.5. Behavioral Data Analysis

Trials were excluded from the analysis of correct responses if the participants did not respond or produced any kind of verbal error: partial or complete production of incorrect words, verbal disfluencies (stuttering, utterances repairs, etc.), and hesitations (e.g., if the experimenter perceived the response to be abnormally lengthened or preceded by an unusually long empty or filled pause). All verbal errors, excluding no responses and hesitations, were included in the analysis of errors. Statistical analysis was performed within R version 3.6.0 (R Core Team, 2012) using the packages "lme4" to compute the mixed effect models (Bates et al., 2014) and "car" to compute analysis of deviance tables for the fixed effects of the mixed effect models (Fox & Weisberg, 2011). We analyzed the accuracy data using logistic mixed-effects models (Baayen et al., 2008). We tested for main effects of Group (individuals with anterior lesions vs. posterior lesions vs. control participants) and Semantic Context (Heterogeneous vs. Homogeneous) and

their interaction on accuracy rates and controlled for random effects of picture names, participants, and by-participant random slope for semantic condition. We report Wald chi-square values and p-values from the analysis of deviance table, as well as raw β estimates (β raw), standard errors, t-values and associated p-values for significant (p<.05) and marginally significant (p<.10) effects. Response latencies were measured from the onset of the stimulus to the beginning of the vocal response using the software CheckVocal (Protopapas, 2007), which displays both the waveforms and the spectrograms of the utterances. Naming latency data were analyzed with linear mixed-effects models, testing for main effects of Semantic Condition and Group and their interaction and controlled for random effects of participants and picture names, as well as random slopes for Semantic Condition within participant.

2.6. ERP Data Analysis

We used Independent Component Analysis (ICA) as implemented in EEGLAB (Delorme & Makeig, 2004) to correct for vertical eye movements. In speech production EEG experiments, experimenters must take artifacts from speech articulation into account on top of the artifacts produced from blinking, horizontal eye movements, etc. Speaking, in particular, induces large amounts of EMG activity that heavily contaminates the EEG signal (Vos et al., 2010). We used Blind Source Separation based on Canonical Correlation Analysis, or BSS-CCA (De Clercq et al., 2006; using the AAR toolbox for EEGlab by Gómez-Herrero, 2007), to reduce the impact of EMG artifacts from speech articulation in the EEG signal as in (Riès et al., 2011, 2013a, 2013b, 2015, 2020; Vos et al., 2010). As in previous studies from our group, we ran BSS-CCA twice: first on non-overlapping 30-second-long time windows to reduce tonic EMG activity from frowning or muscle fatigue, and second on non-overlapping 2-second-long time windows to

target EMG activity from articulation (Anderson et al., 2022; Riès et al., 2011, 2013a, 2013b, 2015, 2020, 2021). Any artifacts remaining after BSS-CCA were rejected by hand on a trial-by-trial basis.

As in previous studies (Anderson et al., 2022; Riès et al., 2011, 2013a, 2013b, 2015, 2020), Laplacian transformation was applied to each participant's individual averages to reduce spatial noise caused by the diffusion of currents from their sources to the electrodes (described below). Then, a grand average was created from those individual averages. Second derivations in two dimensions of space were computed (Legendre polynomial: 15° maximum). We chose 3 for the degree of spline because this value best minimizes errors (Perrin et al., 1987). We assumed a radius of 10cm for the sphere representing the head. The resulting unit was μ V/cm². Grand averages were created for correct and error trials in both groups (individuals with posterior lesions and individuals with anterior lesions) for the participants with more than five error trials remaining after artifact rejection (Steele et al., 2016). This included 6 out of 7 individuals with anterior lesions. Four out of 7 individuals with posterior lesions were included; two individuals were excluded due to high error rate (>50%) and one individual was excluded due to high EEG artifact rejection rates linked to excessive movement.

The enhanced topographical localization from Laplacian transformation allowed us to examine ERPs at each electrode site of interest. We focused our analysis on electrode sites known to be associated with the ERN in speech production, which includes the medial frontal sites FCz and Cz (Riès et al., 2011, 2013b, 2021; Vidal et al., 2000) and performed our analyses per electrode. Following the approach outlined in Riès et al. (2011, 2013b), our analyses centered on (a) the slope of the rising ERN to establish the presence or absence of the component relative

to zero, and (b) on the peak-to-peak amplitudes between the peak of the ERN and the preceding positive-going peak.

3. Results

3.1. Behavioral results

Figure 3 presents accuracy (a) and reaction time (b) data for all three groups. Analyses revealed a main effect of Group ($\chi^2 = 63.81$, p <.001) for accuracy; individuals with aphasia and posterior lesions made more errors (mean error rate: 27.1%, SD = 15.1%) than either the anterior lesion group (z(13) = -2.25, p = .024, mean error rate: 8.2%, SD = 5.2%) or control group (z(22) = -6.31, p < .001, mean error rate: 1.6%, SD = 1.7%) (see Figure 3a). There was also a main effect of Group ($\chi^2 = 32.27$, p <.001) for reaction time; individuals with aphasia and posterior lesions were slower (mean RT: 1271 ms, SD = 420.6 ms) than either the anterior lesion group (t(13) = 2.69, p = .012, mean RT: 1042 ms, SD = 344.9 ms) or control group (t(22) = 6.96, p < .001, mean RT: 820 ms, SD = 218.2 ms) (see Figure 3b).



Figure 3.3. (a) Accuracy rates by group in the blocked cyclic naming task. (b) Reaction times by group in the blocked cyclic naming task. The anterior group includes individuals with lesions excluding the pLTC and the posterior group includes individuals with lesions including the pLTC. Standard error bars are included on each average.

3.2. EEG results

Control participants did not produce a sufficient number of errors to be included in the ERP analyses, thus they are excluded below. For individuals with aphasia who had lesions excluding the pLTC, the slope of the rising negativity was significantly different from zero in error trials (t(5) = 4.43, p = .007) and marginally different from zero in correct trials ((t(5) = -2.21, p = .078)), indicating the presence of an ERN component peaking around 100 ms after the response. In contrast, for individuals with aphasia who had lesions that included the pLTC, the slope of the average EEG activity was not significantly different from zero in either error (t(3) = -0.12, p = .91) or correct trials (t(3) = -1.22, p = .31), indicating the absence of an ERN component.

Error trials were associated with a significantly greater peak-to-peak amplitude than correct trials in the individuals with aphasia who had lesions excluding the pLTC (t(5) = -3.61, p = .015; see Figure 4), but not in the individuals with aphasia who had lesions including the pLTC (t(3) = .231, p = .832; see Figure 5).

Interestingly, we found converging results on a set of four individuals with strokeinduced lesions in the pLTC tested as part of a previous study (Riès et al., 2013b). This previous study however did not include this group of individuals as it was focused on examining the role of the lateral PFC in speech versus domain general action monitoring. We therefore report the results from that pLTC group in the supplementary materials.



Figure 3.4. Laplacian-transformed EEG results at electrode Cz, pictured on scalp (right), for the group with lesions excluding the pLTC. Error trials elicited a significant greater negativity than correct trials (left). Correct trials are depicted in blue and error trials are depicted in red. Note that negative is plotted up in this diagram.


Figure 3.5. Laplacian-transformed EEG results at electrode Cz, pictured on scalp (right), for the posterior group with lesions including the pLTC. There was no significant different in amplitude between correct and error trials (left). Correct trials are depicted in blue and error trials are depicted in red. Note that negative is plotted up in this diagram.

4. Discussion

We tested the performance of individuals with left hemisphere stroke-induced lesions and resulting aphasia and healthy age-matched control participants on a blocked cyclic naming paradigm. Both aphasia groups were slower and less accurate than the control group. Individuals with aphasia who had lesions including the pLTC were slower and less accurate than individuals with aphasia who had anterior lesions excluding the pLTC. The analyses of the EEG data indicated the presence of a frontocentral ERN in those individuals with lesions excluding the pLTC but not in those individuals with lesions including the pLTC.

As has been shown in previous studies (Riès et al., 2013b; 2015), the behavioral results indicate that the individuals with lesions excluding the pLTC showed longer reaction times and increased error rates compared to the control participants. This group had maximum lesion overlap in the left prefrontal cortex. The left PFC houses brain regions which have long been associated with different linguistic and non-linguistic processes, including the left IFG, MFG, and SFG. In particular, the left IFG has been associated with pre-articulatory and semantic interference resolution processes (e.g., Flinker et al., 2015; Schnur et al., 2009), and with proactive interference resolution processes in working memory tasks (Jonides & Nee, 2006). Given these prior reports, it is not surprising that these individuals show worse performance than the control group.

A novel outcome from this study was the finding that lesions that included the pLTC lead to increased error rates and longer reaction times as compared to those individuals where the lesion excluded the pLTC. This pattern is consistent with many studies associating different parts of the pLTC to core lexical access processes in language production and perception. Indeed, individuals with lesions that included the posterior MTG have been shown to have trouble finding the name of an image even when alternatives containing the correct name are presented to them (Baldo et al., 2011; Dronkers et al., 2004). This contrasts with those individuals with left lateral frontal lesions who also have naming difficulties but will typically be able to pick the correct name among presented alternatives (Dronkers et al., 2004). Interestingly, in alignment with our work, it has been shown that in individuals with left posterior temporal lesions who have jargon aphasia (typically associate with Wernicke's aphasia), speech monitoring is affected during picture naming (Marshall et al., 1996).

When we look to word finding difficulties in other, non-aphasic populations, we see that studies exploring word finding problems in individuals with intractable epilepsy have demonstrated hypoperfusion in the parts of the pLTC (left inferior temporal gyrus and superior temporal gyrus) that is associated with anomic states (Trebuchon-Da Fonseca et al., 2009). The importance of the pLTC in core lexical access may explain why the individuals who had lesions that included the pLTC showed overall poorer performance than those whose lesions that excluded the pLTC. Importantly, the two patient groups had comparable lesion sizes and hence, the difference between them cannot simply be explained by a difference in lesion size.

In agreement with our hypothesis, the EEG results revealed a larger ERN in incorrect trials compared to correct trials in individuals with anterior lesions (as in Riès et al., 2013b), but not in individuals with posterior lesions. Individuals with posterior lesions in fact did not show a significant ERN at all as the slope of the component was not statistically different from zero. Convergent results from a previous study (Riès et al., 2013b) are reported in the supplementary materials. These results indicate that individuals with anterior lesions not including the pLTC have a more intact ability to monitor their errors, which would explain why they make less errors overall compared to individuals with posterior lesions. The absence of an ERN component in individuals with posterior lesions indicates an impaired inner speech monitoring mechanism in these individuals. Indeed, the ERN in speech production has been associated with inner speech monitoring as it starts to rise before vocal onset and therefore before the speakers are able to hear themselves (Riès et al., 2011). Its medial frontal topography is also consistent with neuroimaging studies highlighting the role of the ACC and SMA in general action and speech monitoring in the absence of distorted auditory feedback (Christoffels et al., 2007; van de Ven et al., 2009). Intracranial results in a non-linguistic cognitive control task indicate a probable source of the

ERN in the SMA (Bonini et al., 2014). The operation of the medial frontal cortex in inner speech monitoring appears to be relatively unimpaired if the left frontal area is lesioned in simple picture naming (as shown in Riès et al., 2013b). However, if the left posterior region is lesioned, inner speech monitoring appears to be severely impaired. This indicates that medial frontal functioning may be compromised if the access to linguistic representations is affected. This would be in agreement with the conflict monitoring model proposed by Nozari et al., 2011, in which the language production system interacts with a domain-general conflict monitoring system to enable inner speech monitoring independently of the speech comprehension system. It is important to note that the posterior lesions in our patient sample also included the left superior temporal gyrus, known to house essential speech perception mechanisms (e.g., Bhaya-Grossman & Chang, 2022; Chang et al., 2010; Yi et al., 2019), and it is therefore not possible to completely negate the claims of Perceptual Loop Theory of speech monitoring based on our data solely. Indeed, one could argue that it is because this central region for speech perception is damaged that the medial frontal monitoring system is impaired. Although this alternative interpretation may account for our results, the extensive debate between the tenets of these models argues otherwise (Gauvin & Hartsuiker, 2020; Nozari, 2020; Roelofs, 2020). In particular, the PLT does not account easily for the dissociation between error detection in self-produced versus in other's language production that has been reported in patient studies (e.g., Butterworth & Howard, 1987; Marshall et al., 1998; Miceli et al., 1980; Nickels & Howard, 1995). In addition, a recent fMRI study investigating inner speech monitoring during masked production did not find activation of the STG (Gauvin et al., 2016), contrarily to what would be predicted if the speech perception system was involved in inner speech monitoring. The most plausible interpretation explaining our results in the face of the existing theoretical framework and empirical evidence is therefore

that access to linguistic representations via mid- to posterior temporal regions, whether these are shared between language production and perception or not, is key to successful inner speech monitoring as mediated by the medial frontal domain-general action monitoring system. This represents a novel finding as little is known about the network interactions supporting inner speech monitoring.

In conclusion, we argue that inner speech monitoring is supported by interactions between a domain-general action monitoring system housed in the medial frontal cortex and left mid- to posterior temporal regions housing core lexical access processes. Indeed, the medial frontal inner speech monitoring mechanism is compromised if the posterior temporal cortex regions that are critical for accessing lexical representations are damaged.

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Declaration of Interest

No potential conflict of interest was reported by the author(s).

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	Participant	Age (Years)	Gender	Education (Years)	WAB- AQ	CLQT Confrontation Naming (/10)	Apraxia Battery for Adults	
	P9	54	М	18	90.8	10	mild/none	
	P10	66	F	16	93.8	10	mild/none	
or	P12	73	М	17	90.5	10	none	
	P13	36	М	16	88.3	10	mild/none	
iteri	P2	56	М	14	94.5	N/A	mild/none	
an	P6	55	М	20	76- 100	10	mild/none	
	P18	38	F	18	81.2	10	mild/ moderate	
	P5	59	М	18	71.6	10	atypical	
	P7	64	М	16	90.4	10	none	
ior	P11	62	М	15	71.5	10	mild/none	
poster	P14	84	F	20	72.5	10	mild	
	P1	56	М	18	67.7	10	none	
	P4	68	М	22	82.6	10	mild	
	P16	66	F	14	90.9	10	mild/none	

Table 3.S1. Demographics and neuropsychological scores for the individuals with aphasia in our study.

Convergence data from previous project

Four individuals with left hemisphere stroke-induced lesions including the pLTC (3M; mean age = 69.8 years, σ = 5 years; mean years of education = 17.3 years, σ = 3 years) participated in the same study as reported in Ries et al. (2013b). They completed a similar blocked cyclic picture naming task as in the current study (see methods in Ries et al., 2013b).

Their EEG results show that the slope of the average EEG activity between -150 ms pre-vocal onset and vocal onset was not significantly different from zero in either errors (t(3) = 1.32, p = .28) or correct trials (t(3) = 1.52, p = .23). There was also no difference between slopes in errors versus correct trials (t(3) = -.36, p = .74). Finally, the surface area under the curve between vocal onset and 150 ms post-response was not different between errors and correct trials (t(3) = .273, p = .80).



Figure 3.S1. Laplacian-transformed EEG results at electrode FCz for the posterior group of participants from Ries et al. (2013) with lesions including the pLTC. There was no significant different in amplitude between correct and error trials (left). Correct trials are depicted in blue and error trials are depicted in red. Note that negative is plotted up in this diagram. Topographies at the expected window for the ERN peak (right) do not show any fronto-central negativity.

Chapter 3, in full, is a reprint of material as it was submitted as Anderson, E.J., Love, T., & Riès, S.K. (submitted). The role of the left posterior temporal cortex in speech monitoring. Cognitive Neuropsychology. The dissertation author was the primary investigator and author of this paper.

CHAPTER 4

Lexical retrieval deficits across semantic contexts in stroke-induced aphasia

Elizabeth J. Anderson & Stephanie K. Riès

1. Introduction

Approximately 180,000 people in the United States have a stroke resulting in aphasia every year and there are about 2 million people with aphasia in the United States (*Aphasia*, 2015; Ivanova & Dronkers, 2022). Aphasia primarily occurs after left-hemisphere stroke-induced lesions, resulting in impairments in language expression and reception. The inability to retrieve the names of everyday objects is a key characteristic of aphasia. Although lexical retrieval is a central component of daily communication, there is still much unknown about the underlying causes driving lexical retrieval deficits in individuals with aphasia. With the growing numbers of individuals with aphasia each year, it is crucial to understand where the language network is breaking down in order to formulate treatment plans that target the most impactful areas for recovery. Speech-language pathologists often use semantic relatedness as a tool to treat individuals with lexical retrieval deficits (Boyle & Coelho, 1995; Renvall et al., 2007), but the impact of semantic relationships on lexical retrieval subprocesses in individuals with left hemisphere stroke-induced lesions remains uncertain.

1.2. Activation and selection lexical retrieval deficits

Lexical retrieval can be decomposed into two complementary processing stages: lexical activation and lexical selection (Caramazza & Costa, 2000; Damian et al., 2001; Howard et al., 2006; Oppenheim et al., 2010; Piai et al., 2014). Lexical activation occurs through spreading activation from semantic to lexical representations during speech production; lexical selection is the act of choosing the target word from amongst the network of activated lexical representations (Caramazza & Costa, 2000; Damian et al., 2001; Howard et al., 2006; Oppenheim et al., 2010).

Lexical retrieval is often impaired in individuals with aphasia, but the driving forces behind lexical retrieval deficits are not well understood. Anomia is a universal deficit for

individuals with aphasia (Laine & Martin, 2006), but the resultant speech patterns that occur can vary from person to person. For example, one person may have effortful speech full of long pauses and omitted words that they are not able to produce while another person has more fluent speech filled with neologisms or incorrectly selected alternatives (see Damasio, 1992 for a review). Both individuals would be considered to have a deficit in their ability to retrieve words, but the nature of this deficit is not identical. Therefore, lexical retrieval deficits at the level of lexical representation can likely occur due to breakdowns in different subprocesses of lexical retrieval.

Computational models of aphasia (e.g., Dell et al., 1997; Schwartz et al., 2006) that have explained the error patterns in individuals with aphasia have demonstrated the crucial nature of spreading activation during lexical retrieval. These models include a bidirectional connection between semantic and lexical levels referred to as "*parameter s*" (Figure 4.1). When parameter s is lower this indicates a weaker transmission of information from the semantic to the lexical



Figure 4.1. Adaptation of Dell et al. (1997)'s model of lexical activation.

layer is in the model. Practically, this results in behavioral patterns that include semantic errors, mixed errors, and occasionally unrelated lexical errors (Nozari, 2019; Schwartz et al., 2006).

Low levels of activation that prevent any item from reaching the threshold for selection may be the primary cause of semantic errors as described by these models. However, it is possible that the issue does not lie with activation itself (Nozari, 2019). It is a possibility that items receive enough activation to pass the threshold and then the issue lies with selecting from the activated items. There are multiple theories about the outcomes that occur in a system with high enough levels of lexical activation for lexical items to reach the selection threshold. Theories supporting lexical selection by competition (e.g., Roelofs, 1992; Damian et al., 2001; Howard et al., 2006; Roelofs & Piai, 2013) state that production is delayed until competition is resolved and one item is selected, likely through the use of inhibitory control. Non-competitive accounts of lexical selection (e.g., Mahon et al., 2007; Navarrete et al., 2012, 2014) claim that the first item to reach threshold is selected for production and the presence of "competitors" therefore does not affect production. Therefore it remains to be seen if deficits to inhibitory control can be one cause of an increase in semantic errors, suggesting that inhibition of competing responses is a crucial aspect of lexical selection (Nozari, 2019).

	Activation deficit (XR)	Inhibition deficit (QD)
Picture naming	Longer RT, often a single semantically-related response	Shorter RT, multiple semantically-related responses
Modified Category Probe task	Impaired	Unimpaired
Simon task	Unimpaired	Impaired
Miscue task	Few miscue errors	Lots of miscue errors
Word-pair Stroop task	Helped by semantic similarity	Hurt by semantic similarity
Lexical perseveration	Significantly above chance	Marginally above chance

Figure 4.2. Summary of findings adapted from Nozari (2019).

In a case study from Nozari (2019), two individuals with aphasia demonstrated separate patterns of lexical retrieval deficits (Figure 4.2). Nozari presented the hypothesis that there are two distinguishable lexical retrieval deficits: an activation deficit and an inhibition deficit (referred to as a selection deficit from here on). An activation deficit involves a deficit in the ability to activate the target lexical item from semantic features, while a selection deficit involves an impaired ability to inhibit co-activated lexical items. In Nozari's study, the individual with an activation deficit tended to have longer reaction times and lower interference caused by semantic miscues during the Miscue Task when the first letter of a taxonomically-related picture name was superimposed on top of a picture. Indeed, the co-activation of semantically-related items increased their chance of reaching the selection threshold for the target word and producing a correct response. Since an activation deficit is characterized by a difficulty in maintaining the activation of lexical items and their connection to their semantic features, additional activation of lexical items that share semantic features should in turn reinforce the activation of the target lexical item. The individual with a selection deficit, on the other hand, tended to have shorter reaction times and produce multiple incorrect semantically-related responses. Their inability to inhibit semantically co-activated items resulted in an increased impairment in semantically related conditions. Of particular interest for the current study is the possible variable impact of semantic similarity on lexical retrieval based on the presence of either an activation or a selection deficit.

1.3. Semantic Context

Prevalent language production models, such as the interactive activation model discussed above (Dell et al., 2013) and the serial processing model (Indefrey, 2011; Levelt et al., 1999), agree upon the fact that semantically related items are co-activated during language production

(Dell et al., 1997; Indefrey & Levelt, 2004; Roelofs, 2003). Previous language production studies, have demonstrated that the behavioral outcome of this co-activation during lexical retrieval depends on the type of semantic relationship tested. For example, taxonomic relationships, related based on category membership (e.g., bee-wasp), generally lead to semantic interference in language production (Alario et al., 2000; Anderson et al., 2022; Bloem et al., 2004; Costa et al., 2005; de Zubicaray et al., 2013). However, thematic relationships, based on co-occurrence in scenarios (e.g., bee-honey), generally lead to semantic facilitation (Alario et al., 2000; Anderson et al., 2022; Bloem et al., 2004; Costa et al., 2005; de Zubicaray et al., 2013). Research discussing the processing and representation of taxonomic relationships is substantial, but there is a lack of conclusive work on the integration and processing of thematic relationships (Landrigan & Mirman, 2018). If taxonomic and thematic relationships can further shed light on the probing the semantic network through studying these relationships can further shed light on the

1.4. Neurological underpinnings of lexical retrieval

One way to shed light on the causal roles of the brain regions supporting lexical retrieval is to examine the impact of lesions to these brain regions on language production and lexical retrieval dynamics. Here, we propose that the nature of the lexical retrieval deficits observable after left hemisphere stroke, namely whether those stem from activation versus selection impairments, is associated with the location of the brain lesion.

We hypothesize that activation deficits are associated with posterior lateral temporal cortex (pLTC) lesions as the left posterior superior, middle, and inferior temporal gyri (STG, MTG, and ITG) have been associated with word meaning access (DeLeon et al., 2007; Dronkers et al., 2004). Individuals with lesions in the pLTC, and in particular the left mid to posterior

MTG, have been shown to struggle to recognize the correct word even when presented to them as an option to choose from (Dronkers et al., 2004), despite their preserved ability to demonstrate object use. This suggests that their retrieval deficit likely stems from the fact that the links between semantic and lexical representations are damaged leading to a lexical activation deficit (Dronkers et al., 2004). When the left MTG is damaged in chronic stroke patients, the result is often picture naming difficulties (Baldo et al., 2013) and word-level comprehension deficits (Bates et al., 2003; Dronkers et al., 2004). Reperfusion of this region is correlated with improved naming within 3-5 days post-stroke, indicating that the left MTG is crucial for lexical access (Hillis et al., 2006).

The STG and MTG are important for semantic memory storage and access bilaterally (Binder et al., 2009; Bonner & Price, 2013; Patterson et al., 2008; Visser et al., 2010) and these regions in the left hemisphere also support the mapping of concepts onto lexical representations during language production (Indefrey & Levelt, 2004; Schwartz et al., 2009). Studies examining the effect of distractor words on picture naming in healthy adults using fMRI (Piai et al., 2013) and MEG (Piai et al., 2014) found increased activity in the left STG and MTG for semantically unrelated compared to related distractor-picture conditions, which was interpreted as reflecting semantic priming. In semantically related contexts, activated semantic features linked to the target representation will spread to other lexical representations that share those features. This spread of activation results in increased lexical activation as compared to semantically unrelated contexts. Therefore, in priming studies with a related word (e.g., *rat*) and picture (e.g., *mouse*) that share semantic features, the activated semantic features from the word (e.g., whiskers, tail, rodent, etc.) are increasing the activation for the picture and vice versa. As a result, the picture and word are priming each other (Finkbeiner & Caramazza, 2006; Levelt et al., 1999; Roelofs,

2003), leading to an attenuation of brain activity for the related compared to the unrelated condition (Piai et al., 2013, 2014). This pattern of activity further suggests that left temporal cortex regions play a role in lexical activation.

We propose that while pLTC lesions will be associated with lexical activation deficits, left prefrontal cortex (LPFC) lesions will be associated with lexical selection deficits. Indeed, the LPFC, particularly the left inferior frontal gyrus (<u>LIFG; Riès et al., 2014, 2015; Schnur et al.,</u> <u>2009; Thompson-Schill et al., 1997</u>), middle frontal gyrus (MFG; Piai et al., 2013), and superior frontal gyrus (Piai et al., 2014) have been proposed to play a role in overcoming semantic interference (T. Schnur et al., 2006; Thompson-Schill et al., 1998).

After the initial spreading of activation between semantic and lexical representations during language production, speakers are then tasked with selecting from the set of active lexical representations. This can be difficult amongst semantically related alternatives as more than one item in the lexicon is receiving activation. A cognitive control mechanism is thus necessary to help speakers select the target item. The LPFC, including the LIFG ((T. T. Schnur et al., 2009; Thompson-Schill et al., 1997), MFG (Piai et al., 2013), and SFG (Piai et al., 2014) have been theorized to play a role in overcoming semantic interference

During blocked-cyclic naming tasks, in which participants name pictures in semanticallyrelated vs. unrelated blocks, individuals with PFC damage have larger semantic interference effects than control participants (<u>Schnur et al., 2006; Schnur et al., 2009</u>) or individuals with right PFC damage (Riès et al., 2014). The magnitude of this semantic interference (i.e., the number of errors produced in semantically related vs. unrelated blocks) was found to increase across naming cycles in individuals with LIFG damage in comparison to control participants or individuals with left temporal cortex damage (T. T. Schnur et al., 2009). Activity in the MFG has

been associated with selecting words during language production (Jeon et al., 2009; Riès et al., 2016; Spalek & Thompson-Schill, 2008). With evidence from a picture-word interference (PWI) MEG study, Piai and colleagues proposed that the SFG also supports cognitive control processes involved in resolving semantic interference during word retrieval (Piai et al., 2014). The SFG has also been linked to response selection, inhibition, response switching, and conflict monitoring (George et al., 1994; Ridderinkhof et al., 2004; Simmonds et al., 2008; Verbruggen & Logan, 2008). These results demonstrate that these prefrontal regions (i.e., LIFG, MFG, SFG, pre-SMA) are necessary for successfully navigating high conflict contexts, such as semantically related contexts.

When the LPFC is damaged, individuals with aphasia have an impaired ability to select from semantically related lexical representations, suggesting that their deficit lies in the ability to suppress or overcome the co-activation of semantically related lexical items during selection (Nozari, 2019; Riès et al., 2015; T. T. Schnur et al., 2009; Thompson-Schill et al., 1998). Unlike individuals with damage to the pLTC, individuals with lesions in the LIFG can generally immediately identify the word they are looking for when given a choice between options (Buckner et al., 1996). The results observed likely point to a deficit in the lexical selection stage rather than lexical activation stage, therefore the behavior exhibited by individuals with LPFC lesions should reflect that of the individual with an inhibition deficit in Nozari (2019).

Because lexical activation and selection stages occur on a rapid timescale and can be overlapping in time, shedding light on the spatio-temporal dynamics underlying lexical retrieval can help further our understanding of these processes.

1.5. Electrophysiology of lexical retrieval

EEG provides a means to examine the processes underlying language production at a time-scale that more closely aligns with language processing compared to fMRI studies. Event-related potentials (ERPs) are used to measure the electrical activity recorded at the scalp during EEG tasks. These ERPs have been shown to reflect different underlying cognitive processes. For example, the N1 is a negative-going ERP that closely follows stimulus presentation and has been associated with visual processing and attention (Vogel & Luck, 2000). The P3 is a positive-going ERP that has been associated with decision making difficulty and the processing of unexpected stimuli (Fabiani et al., 1986; Luck, 2014; Twomey et al., 2015). Notably, the N400 is a negative-going ERP that indexes the degree of semantic processing occurring during linguistic tasks (Kutas & Federmeier, 2011). The amplitude of the N400 has shown to be sensitive to semantic context and it is typically larger in unrelated vs. related contexts. Its amplitude is also larger in in conditions that require an increased amount of semantic processing (e.g., trials with more semantically complex or unexpected semantic stimuli Kutas & Federmeier, 2011; Kutas & Hillyard, 1980).

These established ERP components guide the analysis process of EEG studies. In language production EEG studies, it is common practice to select time windows of analyses that capture the components that have been linked to semantic context effects. A window centered around the N400, between 300 and 500 ms post-stimulus onset, is typically investigated to focus on lexico-semantic processing in production and in comprehension (Kutas & Federmeier, 2011; Kutas & Hillyard, 1980).

In the context of language production EEG studies, thematically-related contexts have consistently been associated with facilitatory effects on the amplitude of ERPs associated with lexical access and lexical selection in PWI studies (i.e., smaller amplitudes for related compared to unrelated conditions; Anderson et al., 2022; Hirschfeld et al., 2008; Wamain et al., 2015). However, studies examining taxonomically-related have reported a variety of results, including no difference in amplitude between related and unrelated conditions (Hirschfeld et al., 2008; Wamain et al., 2015), reduced N400 amplitude in related versus unrelated conditions (Blackford et al., 2012; Roelofs et al., 2016; see Kutas & Federmeier, 2011), and increased ERP amplitude in the N400 time-window in related vs. unrelated conditions (Anderson et al., 2022). Few studies have directly compared the effect of taxonomically- to thematically-related contexts on lexical retrieval using EEG (Anderson et al., 2022; Aristei et al., 2011; Hirschfeld et al., 2008; Wamain et al., 2015), and no studies have done so in the context of lexical retrieval in individuals with aphasia.

Using traditional monopolar analyses and Laplacian transformation (i.e., a double spatial derivative of the EEG signal providing increased topographical localization of ERPs; Babiloni et al., 1996, 2001; Riès, 2013a), Anderson et al., (2022) found that taxonomically versus thematically-related contexts differentially impact the brain dynamics supporting lexical retrieval in picture naming in healthy young adults. Critically, in the case of taxonomically-related contexts, Laplacian transformation revealed a concurrent facilitation effect at a left parietal recording site and interference effect at a left frontal recording site during the N400 time window. This interference effect likely reflects more effortful processing during lexical retrieval processes that begin after initial lexical activation (such as lexical selection) when placed in the context of taxonomically related words. This concurrent effect was not visible without the increased topographical localization afforded by Laplacian transformation and illustrates the

importance of considering Laplacian transformation when studying the brain dynamics of language production using ERPs.

1.6. Current study

The current study investigates whether different semantic contexts impact lexical retrieval during speech production in different ways across individuals with LPFC vs. pLTC lesions. This work (1) examines the subprocesses of lexical retrieval in individuals with aphasia by using complementary tasks to establish a possible dissociation between activation vs. selection lexical retrieval deficits in relation to lesion location; and (2) examines the impact of taxonomic vs. thematic semantic contexts to establish how different semantic relationships may impact lexical retrieval in different ways depending on the nature of lexical retrieval deficits. We use Laplacian transformation to investigate the spatio-temporal brain dynamics of lexical retrieval processes in individuals with left hemisphere stroke-induced aphasia. Laplacian transformation allows us to deblur ERPs recorded at neighboring sites that may have been averaged together due to the conduction distortions caused by the cerebro-spinal fluid, meningeal layers, skull, and scalp, and hence enhance the spatial resolution of EEG (Babiloni et al., 1996, 2001). Our central hypothesis is that individuals with more pronounced lexical activation rather than selection deficits are more likely to have lesions involving the pLTC, while individuals with more pronounced lexical selection vs. activation deficits are more likely to have lesions involving LPFC. In addition, while lexical activation will be reduced in individuals with pLTC lesions, impacting performance overall compared to controls, both thematic and taxonomic contexts should provide semantic priming and hence enhance performance compared to unrelated contexts. On the contrary, increasing the activation of semantic neighbors should impair performance in individuals with pLTC lesions more than controls. This should be

particularly visible in the taxonomic compared to thematic condition. We use tasks adapted from Nozari (2019) and Anderson et al. (2022) to test these hypotheses.

1.6.1. Behavioral hypotheses

Individuals with activation deficits will struggle on tasks that require sustained activation of lexical items, such as the Category Probe task (detailed below in section 2.2.1.). We predict that they will have significantly impaired performance compared to control participants, only reaching 75% accuracy on lists 2 to 3 words in length (Nozari, 2019), indicating impaired lexical activation. Individuals with selection deficits will successfully reach 75% accuracy on lists 4 to 6 words in length on the Category Probe task, performing within two standard deviations of controls (Nozari, 2019), indicating relatively preserved lexical activation.

By contrast, individuals with selection deficits will struggle to inhibit semantically related co-activated items during lexical retrieval. Therefore, the presence of semantically related distractors will impair their performance in comparison to controls or individuals with activation deficits who should not have an issue with inhibition to the same extent. When tasked with naming items in the presence of a semantically-related miscue (see section 2.2.2.), individuals with selection deficits will produce more miscue errors following a miscue than individuals with pLTC lesions or controls, indicating impaired lexical selection in the face of competing distractors. Individuals with activation deficits will produce more omission errors following a miscue than individuals with LPFC lesions or controls, indicating intact inhibition and impaired activation in the face of competing distractors.

Individuals with pLTC lesions will benefit from the increased co-activation in the related conditions. We hypothesize that their lexical retrieval deficit stems from a deficit in activating any word in a semantic network, and by providing them with multiple words in the same

semantic network, we will increase the odds that they will be able to activate lexical representations and select a response, particularly in the more densely co-activated taxonomically-related semantic network (Rabovsky et al., 2016). Any semantically-related item will help these individuals significantly more than unrelated items (Nozari, 2019), leading to facilitation in the PWI taxonomically-related condition as well as in the thematically-related condition compared to the unrelated condition. In the Picture-pair Stroop task, individuals with pLTC lesions will have a smaller Stroop effect (the difference between their performance in the regular and reversed trials will be larger) than individuals with LPFC lesions, though this effect will still be larger than in controls.

Spreading activation causes semantically related items to co-activate during language production. In the related conditions, individuals with LPFC lesions will struggle to inhibit the other highly active items and select the target response in comparison to controls and individuals with pLTC lesions (Nozari, 2019). This will be particularly difficult in the taxonomic condition because the taxonomically-related semantic networks are typically denser than the thematicallyrelated ones (Rabovsky et al., 2016). The less dense thematically-related semantic networks will lead to a smaller interference effect in the thematic compared to taxonomic condition, though individuals with LPFC lesions will still struggle to inhibit the semantically-related alternative. Similarly, these individuals will demonstrate a larger Stroop effect than controls and individuals with pLTC lesions, especially in taxonomically-related conditions.

1.6.3. EEG hypotheses

As in our previous work (Anderson et al., 2022), we expect that control participants will show a facilitation effect in thematically-related contexts and a concurrent left frontal interference effect for taxonomically-related contexts in the N400 time window (300-500 ms) in Tasks 3 and 4.

We expect to observe an N400 effect (lower left frontal amplitude in the 300 – 500 ms time window for related vs. unrelated items) that will be reduced in individuals with pLTC lesions in comparison to controls or individuals with LPFC lesions, in line with their underlying lexical activation deficits.

2. Methods

2.1. Participants

Eight individuals with aphasia (2 female; mean age = 61.3 years, SD = 16.3 years; mean years of education = 17, SD = 2.9 years) and twelve age-matched controls (9 female; mean age = 63.1 years, SD = 9.3 years; mean years of education = 16.2, SD = 1.8 years) participated in the current study. All participants were right-handed (pre-stroke), had no history of additional of additional neurological damage or hearing loss, and had normal or corrected-to-normal vision.

All individuals with aphasia tested were at least 2 years post-stroke. Participants performed within normal limits on the confrontational naming section of the Cognitive Linguistic Quick Test (CLQT; Helm-Estabrooks, 2001), had mild to moderate aphasia based on the Aphasia Quotient on the WAB-R, and tested as having mild to no apraxia of speech on the Apraxia Battery for Adults (ABA; Dabul, 2000). See Table 4.1 below for the score on these tests of our individual with aphasia.

Individuals with aphasia were divided into two groups for analysis: 4 individuals with left anterior lesions (i.e., focal unilateral frontal lesions excluding the pLTC) and 3 individuals with left posterior lesions (i.e., focal unilateral posterior lesion including the pLTC). One individual

with a pLTC lesion was excluded from EEG recording as EEG could not be recorded in this participant. The posterior lesion group includes individuals with lesions that extended anteriorly, therefore we are not differentiating these groups based on LPFC involvement, but instead on pLTC involvement. This area is the area of interest in the current study and hence the damage including or excluding this region was used as the differentiating factor. Importantly, there was no significant difference in lesion size between the two groups (lesion size calculated by percent volume t(2.29) = -0.46, p = .68 and lesion size calculated by cubic millimeters t(2.46) = -0.43, p = .70).

Table 4.1. Demographics and neuropsychological scores for the individuals with aphasia in our study.

Participant	Group	Gender	Age	Education	WAB- AQ	CLQT Naming	ABA-2
PT1	Anterior	М	78	17	90.5	10	None
PT2	Posterior	М	67	15	71.5	10	Mild/None
PT3	Anterior	М	60	20	89	10	Mild/None
PT4	Anterior	F	39	18	81.2	10	Mild/Mod.
PT5	Posterior	Μ	74	22	82.6	10	Mild
PT6	Posterior	F	67	14	90.9	10	Mild/None
PT7	Anterior	М	72	16	93.8	10	Mild/None
PT8	Posterior	М	34	14	74	10	Mild/None



Figure 4.3. Lesion overlays for included participants. (a) For this overlay, n = 7 as the lesion reconstructions for PT8 (pLTC lesion) are currently in progress. (b) Lesion overlays for individuals with LPFC lesions excluding the pLTC (n = 4). (c) Lesion overlays for individuals with lesions including the pLTC (n = 3). The brighter the red, the more participants had a lesion including this area.

2.2. Design

Three of the four tasks included in this study have been adapted from Nozari (2019)'s case study that demonstrated a dissociation between activation and selection deficits in two individuals with aphasia.

2.2.1. Category Probe

The Category Probe task (Nozari, 2019) requires participants to keep sustained the activation of lexical items and their semantic categories in order to have the semantic information necessary to compare items and make a decision. Participants heard a series of nouns, and then were presented with a target noun and asked whether the target noun belongs to

the same semantic category as any of the preceding nouns. All items were pre-recorded and presented at a rate of 1/second via E-Prime with the probe word following after a two second pause. The list of nouns grew from 1 to 6 words throughout the task if an accuracy of 75% or higher was met to move on to the next list length. For example, for a 4-item list they could hear "dog, house, car, book", followed by the probe word "monkey", and then answer "yes" because monkey and dog belong to the same semantic category (animal). The full task contained 96 trials and consisted of six lists of varying lengths (List 1 = 12 trials, List 2 = 12 trials, List 3 = 12 trials, List 4 = 16 trials, List 5 = 20 trials, List 6 = 24 trials).

2.2.2. Miscue Task

In this miscue task (Nozari, 2019), 20 images were presented once with a visuallypresented cue (the correct first letter of the picture name) and once with a miscue (the first letter of a taxonomically-related picture name, e.g., a picture of a lion with a "T" for "tiger"). Pictures were presented within a 4" x 4" white square and all cues/miscues were overlaid centrally on top of the pictures in 66-point Calibri font. Participants had ten seconds to respond to each picture after which the presentation automatically progressed forward to the next picture.

2.2.3. Picture-word interference

The picture-word interference task consisted of taxonomically-related, thematicallyrelated, and unrelated pictures and prime words. The design and selection of the stimuli is detailed in Anderson et al., 2022 (Chapter 1). Individuals with aphasia can have reading difficulties (Dickens et al., 2021), therefore the visual prime words were changed to auditory prime words with a stimulus onset asynchrony of -200 ms.

2.2.4. Picture-pair Stroop

Participants named two target images per block (e.g., bee and phone), then learned to invert the names of the two images (e.g., in the reversed condition, when participants see a picture of a bee they say "phone"). There were 3 types of blocks: unrelated, taxonomically-, and thematically-related. In each condition, participants first named the pictures with their appropriate names. The pictures were pseudorandomized to not occur more than three times consecutively within or across blocks. Then the participants performed a reversed naming block consisting of the same pictures as in the first block. The participants named images in a total of 36 blocks with 12 trials in each block for a total of 432 trials to reach a sufficient number for Laplacian analyses (216 trials unreversed and 216 trials reversed). The unreversed trials constitute a miniature version of the blocked cyclic picture naming paradigm, and has been shown to elicit comparable effects as the traditional version (Nozari, 2019). This paradigm is also designed to elicit a Stroop-like effect where speakers must suppress the urge to name the image with its original name in order to produce the alternative response (Nozari, 2019). The Stroop effect size measures the extent to which the reversal condition impacts participants in comparison to the non-reversal condition and will be used to further identify selection deficits (Nozari, 2019).

2.3. Procedure

Participants completed three to four experimental sessions, each lasting approximately two hours. The first session included neuropsychological testing including a hearing screening, three subtests (pointing digit span, synonymy triplets, and picture category judgment) of the Temple Assessment of Language & Short-term Memory in Aphasia (TALSA, see Table 4.2.; Martin et al., 2018), the Miscue Task, and the Category Probe task. In addition, individuals with

aphasia completed the Wisconsin Card Sorting Task and were scheduled for a separate testing session to complete the Western Aphasia Battery-Revised (Kertesz, 2007), Cognitive Linguistic Quick Test (Helm-Estabrooks, 2001), and Apraxia Battery for Adults (Dabul, 2000) if those scores were unavailable in their records. In the following session, participants completed a PWI EEG task and in their final session they completed the Picture-pair Stroop EEG task. Each EEG trial consisted of: (1) a fixation cross for 1000 ms each; (2) an auditory prime word (PWI task) OR a picture, which will remain on the screen until the participants respond or until 2000 ms have passed (Picture-pair Stroop task); (3) a picture, following the previous timing (both tasks); (4) a blank screen for 1000ms. The stimulus onset asynchrony (SOA) for the auditory prime and picture pairs was 200 ms as in our previous PWI study (Anderson et al., 2022). Images subtended a visual angle of 2.0 degrees in the horizontal and vertical directions.

Participant	Group	Picture Category Judgment Score	Synonymy Difference Score	Digit Span Score
PT1	Anterior	24/24	2	4
PT2	Posterior	24/24	0	3
PT3	Anterior	24/24	0	4
PT4	Anterior	24/24	0	3.66
PT5	Posterior	24/24	0	3.33
PT6	Posterior	24/24	0	3
PT7	Anterior	24/24	0	4
PT8	Posterior	23/24	0	2.66

Table 4.2. Scores on the TALSA subtests.
For the PWI task, participants underwent a practice trial with 16 prime-picture pairs before the beginning of the experiment (these pairs were not included in the experiment). For the Stroop task, participants underwent a practice trial with 4 blocks: two standard and two reversed (these blocks were not included in the experiment). Between each block, participants were presented with the two images included in the block as well as a text label indicating their expected response.

2.4. Behavioral Methods and Analysis

The dependent variables were reaction time and accuracy. Statistical analyses of behavioral data were performed using the R packages "lme4" for mixed effect models (D. Bates et al., 2014, 2020) and "car" to compute analysis of deviance tables for the fixed effects of the mixed effect models (Fox & Weisberg, 2011). We report Wald chi-square values and p-values from the analysis of deviance table as well as raw β estimates, standard errors, and t- and Wald Z values for reaction times and accuracy analyses respectively. Naming latency and accuracy data were analyzed using linear and logistic mixed effect models (Baayen et al., 2008) respectively to test for fixed effects of semantic relationship (Related, Unrelated for Tasks 1 and 2; Taxonomic, Thematic, Unrelated for Tasks 3 and 4), participant group (Control, Individuals with LPFC Lesions, Individuals with pLTC Lesions), and their interaction, and controlling for random effects of Participant and Item and random slopes for Condition within Participant. Correct responses are defined as answers matching the picture name with the highest name agreement for a given item. Semantically identical names were accepted as correct (e.g. plane for airplane, bunny for rabbit, etc.). Responses that include anything besides the name of the item will be considered an error (e.g., stutter, semantically different word, hesitation such as "uh").

2.5. EEG Methods and Analysis

We used a 64 active electrode cap (ActiChamp, Brain ProductsTM). In speech production EEG experiments, experimenters must take into account muscular artifacts produced from speech articulation in addition to the artifacts produced from blinking, horizontal eye movements, etc. Speaking is associated with significant electromyographic (EMG) activity that heavily contaminates EEG signal (de Vos et al., 2010) and occurs close to vocal onset (van der Linden et al., 2014). As Laplacian transformation is particularly sensitive to artifacts (Tandonnet et al., 2005; Vidal et al., 2003) we implemented a series of additional processing steps prior to analyzing Laplacian transformed data. We used Blind Source Separation based on Canonical Correlation Analysis, i.e. BSS-CCA (using the AAR toolbox for EEGlab by Gomez-Herrero, 2007), to reduce the impact of EMG artifacts from speech articulation in the EEG signal as previously used in our lab (Anderson et al., 2022; Hallez et al., 2009; Riès et al., 2011, 2013a, 2013b, 2015; Vos et al., 2010; Wim De Clercq et al., 2006). Any artifacts remaining after BSS-CCA were rejected by hand on a trial-by-trial basis.

After artifact rejection we then used Laplacian transformation in BrainVision Analyzer 2.2 (BrainVision Analyzer, Brain Products GmbH, Gilching, Germany). Laplacian transformation estimates current source density using a double spatial derivative, which leads to more focal topographic resolution of the EEG signal therefore allowing to enhance the topographical localization of ERPs in comparison to more traditional monopolar ERP analyses (Babiloni et al., 2001; Riès et al., 2013). Laplacian transformation was applied to each participant's individual averages. Then, a grand average was created from those individual averages. Because the voltage distribution is only known at the electrodes, the spherical spline interpolation method is used prior to the application of the spherical Laplace operator in order to estimate the entire voltage distribution (Perrin et al., 1989). Then, second derivations in two dimensions of space were computed (Legendre polynomial: 15º maximum). We chose three for the degree of spline because this value best minimizes errors (Perrin et al., 1987). We assumed a radius of 10 cm for the sphere representing the head. The resulting unit was μ V/cm². The goal of this method is to decrease the blurring of recorded electrical potentials that occur due to the different conduction distortions caused by the CSF, meningeal layers, skull, and scalp (Babiloni et al., 1996, 2001). This deblurring process can be particularly beneficial in the context of individuals with brain lesions because it can help observe ERPs stemming from brain regions close but not in the lesioned area (e.g., medial frontal cortex; Riès et al., 2013), which is otherwise difficult with traditional ERP analyses. We do not expect to observe any reliable ERPs stemming from the lesioned brain regions. Only correct trials will be included in the ERP analyses. The dependent measures will be the mean ERP amplitude in the analyzed epochs. The 300-500 ms time window is centered around the N400, which is an established component in language research shown to be sensitive to lexico-semantic processing (Kutas & Federmeier, 2011; Kutas & Hillyard, 1980). This is the primary window of interest for this initial set of ERP analyses as it allows us to focus on the point lexico-semantic processing is most likely to diverge across conditions manipulating semantic relatedness.

The enhanced topographical localization from Laplacian transformation allows us to examine ERPs at specific electrode sites of interest. In particular, a rising negative component has been previously described during picture naming at the left frontal site FC5 (Riès et al., 2013a) and specifically tied to an increase in negativity for taxonomically-related compared to unrelated conditions (Anderson et al., 2022). We chose to conduct our analyses on pre-identified

electrode sites which showed indication of differences between conditions on the grand averages. We visually inspected FC5 and the surrounding left frontal electrodes and noted the expected pattern of activity on neighboring electrode F5.

3. Results

3.1. Category Probe

To provide an example of the scoring procedure for the Category Probe task, a score of 3.5 indicates that the participant completed more than 75% of trials correctly in List 3 and 50% of trials correctly in List 4. All control participants except for two scored a perfect score of 6 (they successfully completed at least 75% of all lists); two control participants completed 71% of the final list (group mean = 5.96, SD = .11). A 3-way Anova revealed a main effect of Group (Control, Individuals with pLTC Lesions, Individuals with LPFC Lesions) on Category Probe score (F(2,19) = 24.97, p < .001). A post-hoc Tukey test revealed that Controls scored higher than either individuals with LPFC lesions (p = .035) or individuals with pLTC lesions (p < .0001) and individuals with LPFC lesions scored higher than individuals with pLTC lesions (p = .008). Three out of the four individuals with LPFC lesions a 1.5 and making them an outlier amongst individuals with LPFC lesions. No individual with a pLTC lesion was able to reach a score of 4 or higher.





Figure 4.4. Scores for participants on the Category Probe Task. (Top) Scores for control participants. (Bottom) Scores for each individual with aphasia.

3.2. Miscue Task

3-way ANOVAs revealed an effect of Group (Control, Individuals with pLTC Lesions, Individuals with LPFC Lesions) on number of Miscue Errors (F(2,19) = 9.24, p = .0016), number of Omission Errors (F(2,19) = 4.95, p = .019), Other Errors (F(2,19) = 17.17, p < .001), and Total Errors (F(2,19) = 15.22, p < .001). Individuals with aphasia produced significantly more miscue responses (i.e., respond "tiger" for the trial T-Lion) and more errors overall than controls (see Table 4.X.). Individuals with aphasia made marginally more omission errors than controls. Individuals with aphasia made significantly made more errors classified as Other (i.e., unrelated errors or semantic/phonological errors not directly attributable to the miscue) than either controls or individuals with LPFC lesions.

Error Type	Control vs. Individuals with pLTC Lesions	Control vs. Individuals with LPFC Lesions	Individuals with pLTC Lesions vs. Individuals with LPFC Lesions
Miscue	<i>p</i> = .003*	<i>p</i> = .034*	<i>p</i> = .647
Omission	<i>p</i> = .059	<i>p</i> = .059	<i>p</i> = 1
Other	<i>p</i> < .0001*	<i>p</i> = .633	<i>p</i> = .0024*
Total	<i>p</i> < .001*	<i>p</i> = .047*	<i>p</i> = .095

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Figure 4.5. Scores for each individual with aphasia on the Miscue task.

3.3. PWI behavioral results

There was a main effect of Condition ($\chi^2(3) = 12.35$, p = .0063) and Lesion Site ($\chi^2(2) = 28.71$, p < .001) on reaction time, but no interaction effect ($\chi^2(6) = 2.24$, p = .90). Control participants were faster than individuals with LPFC lesions ($\beta_{raw} = 1.927e-04$, SE = 3.781e-05, t = 5.096, p < .001) and individuals with LPFC lesions were faster than individuals with pLTC lesions ($\beta_{raw} = -1.696e-04$, SE = 4.793e-05, t = -3.539, p < .01). Overall, participants were faster in the thematically-related condition than in the taxonomically-related condition ($\beta_{raw} = -2.268e-05$, SE = 6.584e-06, t = -3.444, p < .001). There was no significant difference between the taxonomically-related and unrelated conditions ($\beta_{raw} = 3.825e-06$, SE = 6.962e-06, t = 0.549, p = 0.59) and participants were marginally faster in the thematically-related than in the unrelated condition ($\beta_{raw} = -1.024e-05$, SE = 5.886e-06, t = -1.740, p = 0.086).

Task errors correspond to when participants produced the distractor word rather than the target image. There was a main effect of Condition on task errors ($\chi^2(3) = 21.53$, p < .001). Overall, participants made marginally fewer task errors in the unrelated than in the taxonomically-related condition ($\beta_{raw} = .77$, SE = .46, Wald Z = 1.67, p = 0.098).



Figure 4.6. Behavioral results for the picture-word interference task. Left: Reaction time across conditions for individuals with LPFC lesions, control participants, and individuals with pLTC lesions. Right: Task error rate across conditions for individuals with LPFC lesions, control participants, and individuals with pLTC lesions.

3.3.2. Control vs. IWA EEG results

The EEG results revealed a greater negativity in the taxonomically-related condition compared to the thematically-related condition (t(10) = -2.39, p = .038) and to the unrelated condition (t(10) = -2.48, p = .033) for control participants in the 300 to 500 ms post-stimulus time-window at a left lateral PFC site (electrode F5). There was no significant difference between the thematically-related and the unrelated condition at this recording site (t(10) = 1.22, p= .25). There was no significant difference in activity for IWA between any of the conditions (see Table 4.3. for a summary of the results).

3.3.3. Comparison of pLTC vs. LPFC Lesion Groups

Overall, the individuals with aphasia did not have a significant difference in left frontal activity between conditions. Follow-up analyses were conducted to examine whether activity could be observed after dividing IWA into groups based on their lesion locations. This analysis revealed no significant difference between conditions for either individuals with LPFC lesions or individuals with pLTC lesions (see Table 4.3 for a summary of results).

	Individuals with aphasia	Individuals with	Individuals with
	(n = 7)	LPFC lesions $(n = 4)$	pLTC lesions $(n = 3)$
Taxonomic vs.			
Thematic	t(6) = -0.88, p = 0.41	t(3) = -0.15, p = 0.89	t(2) = -0.87, p = 0.48
Taxonomic vs.			
Unrelated	t(6) = -1.19, p = 0.28	t(3) = -1.42, p = 0.25	t(2) = -0.95, p = 0.44
Thematic vs.			(2) 1.50 0.05
Unrelated	t(6) = -0.69, p = 0.52	t(3) = 0.34, p = 0.75	t(2) = -1.59, p = 0.25

Table 4.4. Summary of PWI condition comparison results for individuals with aphasia.



Figure 4.7. Laplacian-transformed ERP waveforms at electrode F5. In the 300-500 ms epoch, the taxonomic condition elicits greater negativity than either the thematic (a, top left) or unrelated condition (b, top right) for controls. There is no significant difference between taxonomic and thematic (c, bottom left) nor unrelated (d, bottom right) for individuals with aphasia.

3.4. Picture-pair Stroop

EEG data has not yet been analyzed for the Stroop task; the focus in this section will be the behavioral results. Participants were slower in the reversed than non-reversed blocks in taxonomic ($\chi^2(1) = 45.64$, p < .001), thematic ($\chi^2(1) = 30.60$, p < .001), and unrelated ($\chi^2(1) =$ 81.17, p < .001) conditions. Individuals with LPFC lesions were slower than controls in taxonomic ($\beta_{raw} = 2.83e-04$, SE = 5.37e-05, t = 5.27, p < .001), thematic ($\beta_{raw} = 2.86e-04$, SE = 5.89e-05, t = 4.86, p < .001), and unrelated ($\beta_{raw} = 2.70e-04$, SE = 5.90e-05, t = 4.58, p < .001) conditions. There was no significant difference between individuals with LPFC and pLTC lesions in the thematic condition ($\beta_{raw} = -1.25e-04$, SE = 7.97e-05, t = -1.57, p = .14). Individuals with LPFC lesions were marginally faster in the unrelated ($\beta_{raw} = -1.37e-04$, SE = 7.65e-05, t = -1.80, p = .09) and taxonomic ($\beta_{raw} = -1.39e-05$, SE = 7.27e-05, t = -1.91, p = .074) conditions than individuals with pLTC lesions.

There was a marginal effect of lesion on task error rate in the taxonomic condition ($\chi^2(1)$ = 3.73, p < .054) and a marginal effect of condition (reverse versus non-reversed) on task error rate in the thematic condition ($\chi^2(1) = 2.76$, p = .096). Individuals with pLTC lesions made more task errors than individuals with LPFC lesions in the taxonomic condition, regardless of whether the block was reversed or non-reversed. In the thematic condition, all participants made more task errors in the non-reversed than in the reversed condition.



Figure 4.8. Behavioral results for the picture-pair Stroop task. Left: Reaction time across conditions for individuals with LPFC lesions, control participants, and individuals with pLTC lesions. Right: Task error rate across conditions for individuals with LPFC lesions, control participants, and individuals with pLTC lesions.

4. Discussion

4.1. Activation and selection deficits: Category probe and miscue tasks

As predicted, individuals with LPFC lesions did not perform significantly differently than control participants in the Category Probe task, indicating that they have a preserved ability to hold lexical items active and make decisions based on that information. Individuals with pLTC lesions performed significantly worse than control participants on average, indicating that their ability to hold lexical items active was impaired. This task requires individuals to keep the list of words and their connections to semantic categories active in their working memory. This task has therefore often been used as a test of working memory. It should be noted that in a digit span pointing task, individuals with pLTC lesions did score significantly lower than individuals with LPFC lesions or control participants, indicating that they may have a greater deficit in nonverbal working memory. However, as stated in Nozari (2019) the Category Probe task is also appropriate for testing for lexical activation deficits as it is not essential to the task that the participants be able to recall the name of the items presented to them (through either repetition or nonverbal pointing). It is only critical that each item is activated and as a result the activation of a semantic category is reinforced (Nozari, 2019). Reinforcing semantic categories requires continuously mapping semantic features to lexical items in inner speech, or "verbal rehearsal" (Baddeley & Hitch, 1974). The verbal rehearsal process should be largely uninterrupted in individuals with selection deficits; therefore, they will be able to continuously map semantic features to lexical items and complete the task just as we observed in the current study. By contrast, there is no clear trend in the pattern of errors in the Miscue task. The prediction was that individuals with LPFC lesions would produce more miscue errors due to their inhibition deficit and individuals with pLTC lesions would produce more omission errors due to their lexical activation deficit. However, we did not observe this dissociation. We did observe a greater number of errors classified as "other" (i.e., primarily phonological errors and semantic errors unrelated to the miscue) produced by individuals with pLTC lesions in comparison to individuals with LPFC lesions. It is likely that due to the presence of a lexical activation deficit, individuals with pLTC lesions are also experiencing downstream effects at the stage of lexical selection and are producing more errors as they struggle to retrieve the target word.

4.2. Taxonomic vs. thematic behavioral results

Regardless of the presence of a lesion or not, all participants were faster in the thematic than in the taxonomic condition in the PWI task and marginally faster in the thematic than in the unrelated condition. The facilitation effect for thematically-related items has been observed in individuals without aphasia (Alario et al., 2000; Anderson et al., 2022; Bloem et al., 2004; Costa et al., 2005; de Zubicaray et al., 2013) and our results suggest that the same effect persists in the presence of a left hemisphere stroke-induced lesion. Rabovsky et al. (2016) proposed a model in which the number of semantic features and intercorrelational feature density are responsible for the different behavioral outcomes in taxonomic versus in thematic contexts. Taxonomically related words tend to share a large number of features because they belong to the same semantic category and tend to be visually, operationally, and behaviorally similar. The higher the number of shared features the higher the activation of semantic neighbors during language production. This dense co-activation is thought to be the cause of semantic interference in taxonomic contexts (Rabovsky et al., 2016). Since thematically related words typically belong to separate semantic categories, they do not share this same dense overlap in semantic features. Therefore, thematic relationships tend to activate a smaller lexical cohort than taxonomic relationships (Rabovsky et al., 2016; Rose et al., 2019).

All participants benefited from the smaller cohort of activated items in the thematic condition. The co-activated items in the thematic condition appear to have reinforced activation of lexical items enough that participants were able to retrieve words more quickly than in the unrelated condition, but without the struggle of selecting from the densely co-activated taxonomic networks. For the PWI task, there was no difference based on lesion location, however, most individuals with aphasia had an error rate of over 50% in all conditions indicating that the task was very difficult for them and perhaps not ideal for our purpose.

While there was no difference based on lesion location in the PWI task, however, individuals with LPFC lesions were marginally faster and made marginally fewer task errors in the taxonomic condition than individuals with pLTC lesions in the picture-pair Stroop task. Individuals with aphasia performed better in the Stroop task than in the PWI task and it is possible that the strenuous nature of the PWI task obscured a potential group effect. The marginal differences in reaction time and error rate between the two groups of individuals with

aphasia observed in the picture-pair Stroop task suggest that further data collection in the less taxing Stroop paradigm may reveal an effect of condition of lesion location.

4.3. Taxonomic vs. thematic EEG results

The control participants in the PWI task demonstrated the same pattern of activity as the young controls in Anderson et al. (2022): an increase in activity at a left PFC location for the taxonomic condition that was not present for the thematic condition, indicating the presence of an interference effect. This suggests that when placed in the context of taxonomically-related items, healthy speakers may utilize cognitive control processes housed in a left PFC region to help them resolve the conflict presented by the co-activation of taxonomically-related items.

Left PFC activity has been reported in previous language production ERP studies (Anderson et al., 2022; Riès, 2013a). The mechanism underlying this EEG component has not yet been agreed upon, but we can consider different possibilities by examining the functions typically associated with the left PFC. Previous fMRI and lesion study research have associated the left PFC with cognitive control processes allowing individuals to overcome interference from semantically related alternatives for lexical selection (Riès et al., 2015, 2017; Schnur et al., 2005, 2006, 2009; Thompson-Schill et al., 1998). Across studies there have been varying proposals of the nature of this left frontal cognitive control mechanism, including a booster mechanism helping to tease lexical representations apart (Oppenheim et al., 2010), a task biasing mechanism (Belke & Stielow, 2013), a more domain general proactive control mechanism (Jonides & Nee, 2006; Kan & Thompson-Schill, 2004; Riès et al., 2014), or a decision threshold adjustment mechanism (Anders et al., 2017). The Laplacian-transformed activity we observed at the left frontal site F5 in the current study may be reflecting the engagement of the left PFC to overcome semantic interference. This left PFC effect was only observed in the context of taxonomically-

related pairs, and not thematically-related pairs. This suggests that the left frontal cognitive control mechanism involved to overcome interference between semantically related representations may be necessary particularly in the taxonomically-related context but not or less so in the thematically-related context.

The individuals with aphasia do not display this left PFC interference effect. Several of the individuals with aphasia included in this analysis have lesions including this region. This may be one reason why we are not observing a clear component in these individuals. We conducted follow-up analysis splitting individuals with aphasia into those with LPFC lesions and those with pLTC lesions. We observed that neither group had a significant effect of condition at this left PFC recording site. However, as individuals with pLTC lesions could also have LPFC involvement, it is unclear whether the generation of this left PFC component would also be affected by the lesion in this group as well.

As mentioned above, individuals with aphasia found this task particularly difficult, so it is possible that the baseline difficulty of the PWI task was too high, overshadowing any possible effect of semantic primes on electrophysiological results. Participants had lower error rates on the Stroop task, so upon further data collection we will be able to determine if a semantic context effect can be observed in EEG in individuals with aphasia within a less strenuous task.

5. Conclusion

Both control participants and individuals with aphasia benefit from the presence of thematically-related contexts during picture naming tasks as seen from faster reaction times compared to taxonomic relationships. In addition, control participants showed a similar left PFC interference effect as previously reported in young control participants in the taxonomicallyrelated context. These preliminary results do not show a difference in the influence of semantic

context on lexical retrieval between individuals with aphasia based on lesion location, but they do support the need for careful consideration of contexts presented to all individuals with aphasia.

Clinical interventions for word-finding deficits often employ treatment techniques based on semantic relatedness that collapse taxonomic and thematically-related items or focus purely on one or the other (e.g., Semantic Feature Analysis, Boyle & Coelho, 1995); contextual priming, Renvall et al., 2007); cueing hierarchies, Wambaugh, 2003). If taxonomic and thematic relationships are processed differently in individuals with aphasia, this could influence the design and choice of treatment approaches. Indeed, taxonomic relationships may not support lexical retrieval as well as thematic relationships for individuals with aphasia and thus scaffolding lexical retrieval through thematic relationships may be more beneficial in a clinical setting.

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GENERAL DISCUSSION

The overarching goal of this dissertation was to examine the brain dynamics of lexical retrieval in adults with and without left hemisphere stroke-induced aphasia. Specifically, we tested whether different types of semantic contexts, namely taxonomic versus thematic, have a varying impact on the processes underlying lexical retrieval. We discuss what brain regions are involved in lexical retrieval and the subsequent impact on lexical retrieval when these regions are lesioned. Of key interest is whether taxonomic and thematic contexts variably impact lexical retrieval based on which region of the brain has been damaged (specifically, the posterior lateral temporal cortex versus the left prefrontal cortex).

Taxonomic versus thematic semantic contexts

In healthy adults there is a difference between the processing of taxonomically-related and thematically-related stimuli (Alario et al., 2000; Anderson et al., 2022; Bloem et al., 2004; Costa et al., 2005). In Chapter 1, we replicated previous findings as young controls were found to have slower reaction times in the taxonomic condition than in the unrelated condition and faster reaction times in the thematic condition than in the unrelated condition. The results presented in Chapter 4 mirrored these effects with older adults; reaction times were slower in the taxonomic condition than in the thematic condition. There was no significant difference in errors by condition in either group as healthy adults did not make many errors on simple picture naming tasks. The PWI intracranial electroencephalography (iEEG) task presented in Chapter 2 focused on taxonomically-related versus unrelated items. The behavioral results from this study also demonstrate semantic interference on reaction time for taxonomically-related compared to unrelated picture-word pairs in individuals with intractable epilepsy.

The behavioral outcome for language production in the context of taxonomic versus thematic or unrelated relationships is different, suggesting that there exists an underlying

processing difference between the two types of semantic contexts. Indeed, when examining lexical retrieval online in these different semantic contexts using EEG, we noted that picture naming in the presence of taxonomically-related items requires the recruitment of left PFC cognitive control resources to resolve conflict, and that these resources do not seem as engaged in the thematically-related condition. An increased negativity in taxonomically-related contexts compared to unrelated and thematically-related contexts was observed both in young controls (Chapter 1) and older adults (Chapter 4) during the 300 to 500 ms time window associated with lexico-semantic processing (Kutas & Federmeier, 2011).

Therefore, lexical retrieval in taxonomically-related contexts appear to require more effortful processing than in thematically-related or semantically unrelated contexts beginning after initial lexical activation and possibly at the level of lexical selection. One possible reason for these effects proposed by Rabovsky et al. (2016) is linked to a varying number of semantic features and intercorrelational feature density across contexts. Taxonomically-related words tend to share a large number of features, which is associated with an increased activation of semantic neighbors that share these features during language production. This increased co-activation is assumed to be the cause of the semantic interference effect observed in taxonomic contexts, as there will be many activated lexical representations to select from. Since thematically-related words belong to different semantic categories they do not typically share a large number of features. As a result, they tend not to activate as large of a lexical cohort as taxonomic contexts do. These differing effects for taxonomic and thematic contexts could also be due to individual differences in semantic network organization, reading and language ability, and individual variance in similarity judgments between taxonomic and thematic relationships (as seen in Honke et al., 2020). In the next section, I will discuss in further detail the possible roles of this

left PFC mechanism as well as the roles of medial PFC and left posterior temporal regions in lexical retrieval.

Neural underpinnings of language production

Over the course of the studies included in this dissertation, several regions were found to be associated with lexical retrieval. The left PFC mechanism that is engaged in taxonomicallyrelated contexts may be a form of cognitive control. Previous fMRI research and lesion studies have tied activity in left PFC regions to cognitive control processes that allow individuals to overcome semantic interference for lexical selection (Riès et al., 2015, 2017; Schnur et al., 2005, 2006, 2009; Thompson-Schill et al., 1998). There are several hypotheses regarding the nature of this left PFC cognitive control mechanism, with some researchers suggesting a booster mechanism that assists in teasing representations apart (Oppenheim et al., 2010), a task biasing mechanism (Belke & Stielow, 2013), a more domain general proactive control mechanism (Jonides & Nee, 2006; Kan & Thompson-Schill, 2004; Riès et al., 2014), or a decision adjustment threshold (Anders et al., 2017).

In addition to the left PFC activity observed during language production in Chapters 1 and 4, in Chapter 2 we observed medial frontal, superior frontal, and insular activity during a picture naming iEEG task. Specifically, we observed semantic facilitation in three primary regions: the anterior cingulate cortex (ACC; 550 – 750 ms post-stimulus), the superior frontal gyrus (SFG; 800 – 1000 ms post-stimulus), and the insula (800 – 1000 ms post-stimulus). In these regions, the unrelated condition elicited larger LFP activity than the taxonomically-related condition, indicating that lexical retrieval was more effortful in the unrelated condition. This is likely due to the reduced spreading activation in the unrelated in comparison to the semanticallyrelated condition. The ACC is linked to general action monitoring and conflict resolution both in and outside of language (e.g., Barch et al., 2000; Botvinick et al., 1999; Christoffels et al., 2007; Debener, 2005; Dehaene et al., 1994; Piai et al., 2013). The ACC has been associated with speech monitoring with evidence from fMRI studies without distorted auditory feedback (Christoffels et al., 2007; Gauvin et al., 2016; van de Ven et al., 2009). The SFG has also been linked to cognitive control processes that aid in semantic interference resolution (Piai et al., 2014) as well as response selection, inhibition, response switching, and conflict monitoring (Anders et al., 2019; George et al., 1994; Ridderinkhof et al., 2004; Simmonds et al., 2008; Verbruggen & Logan, 2008). This suggests that spreading activation from semantically related items facilitates lexical retrieval with the assistance of control processes housed in the ACC and SFG. The role of the insula during language production is less clear due to its highly central and interconnected nature, but it likely supports processes related to articulation and/or response selection or serves as a control center that strengthens the network of language processing regions (Ardila et al., 2014; Oh et al., 2014).

One limitation of intracranial EEG research is the lack of consistency in spatial sampling across participants. Participants typically have electrodes implanted in frontotemporal regions to monitor for their epileptogenic zones, but this varies by hemisphere and exact location across participants. Previous intracranial language studies observed interference effects, but they were more spatially restricted than facilitation effects (Anders et al., 2019; Riès et al., 2017). The semantic interference effect is likely difficult to detect in neurophysiological data as it is more focal in the brain and the slight variance in electrode placement across participants may have led to us missing it in the iEEG study.

As discussed throughout this dissertation, regions of the posterior lateral temporal cortex (pLTC) have also been previously associated with lexical retrieval. This is due to the link between the MTG, STG, and ITG and word meanings (Dronkers et al., 2004; Indefrey & Levelt, 2004; Riès et al., 2017; Trebuchon-Da Fonseca et al., 2009). While chapters 1 and 2 did not provide any evidence of activity sensitive to semantic context in posterior lateral temporal regions, exploring the impact of lesions in the pLTC on lexical retrieval revealed its importance in Chapters 3 & 4.

We hypothesized that different semantic contexts would result in different patterns of behavior and neural activity based on the location of an individual's left hemisphere lesion. In particular, we contrasted groups of individuals based on whether or not their lesion included the pLTC. Individuals with pLTC lesions were hypothesized to have lexical retrieval deficits at the level of the activation of lexical representations. Indeed, pLTC regions have been associated with linking representations to underlying concepts (Dronkers et al., 2004), and mapping concepts onto words during language production (Indefrey & Levelt, 2004; Schwartz et al., 2009). Alternatively, individuals with LPFC lesions excluding the pLTC were hypothesized to have an intact ability to map concepts to words, but an impaired ability to inhibit co-activated lexical items during language production, placing their deficit at the level of lexical selection subsequent to lexical activation.

Impact of left hemisphere lesions on lexical retrieval

Of particular interest for this dissertation was the effect of lesions in the regions identified as necessary for lexical retrieval during language production. Chapters 3 and 4 reported the impact of lesions in the pLTC versus LPFC on lexical retrieval and the associated cognitive control processes.

In Chapter 3, individuals with pLTC lesions had longer reaction times and produced more errors than individuals with LPFC lesions during a blocked-cyclic naming task. In addition, they did not show a significant error-related negativity (ERN) unlike control participants or individuals with left anterior lesions not including the pLTC. This indicated a disruption of their internal speech monitoring loop, which explained why they produced more errors overall. Our results therefore indicate that the medial frontal monitoring system supporting internal speech monitoring appears to rely on posterior temporal cortex regions necessary for accessing lexical representations. This is a novel result in the field and underlines the importance of distant connectivity between left posterior temporal and medial frontal regions in supporting inner speech monitoring.

Chapter 4 explored the differences in lexical retrieval between individuals with pLTC versus LPFC lesions, and particularly how semantic context may differentially impact lexical retrieval in the two groups. The results thus far indicate that there are behavioral and neurophysiological differences between individuals with pLTC lesions and individuals with LPFC lesions. Notably, in comparison with controls and individuals with LPFC lesions, individuals with pLTC lesions scored significantly lower on the Category Probe task that required sustained activation of semantic category information. They also produced more semantic and phonological errors in the Miscue Task that required participants to name an image with an overlapping distractor letter. This suggests that individuals with pLTC lesions do indeed have impaired lexical activation that may be impacting subsequent stages of lexical retrieval, resulting in an impaired ability to select the correct target item. Since the damage to the production system for these individuals likely occurs at the level of lexical activation, they are unable to hold lexical representations active, thereby negatively impacting their ability to select

from active representations as a result. This constitutes another important contribution of this work. Indeed, previous studies have proposed that pLTC regions are crucial for lexical retrieval, and in particular lexical activation (Dronkers et al., 2004; Baldo et al., 2011), and have shown a double dissociation between lexical activation and inhibition in individuals with aphasia (Nozari, CITE). However, our study is the first to demonstrate that lexical activation can be selectively impaired following lesions to the pLTC and not to the LPFC.

There was no difference between the groups of individuals with aphasia in the PWI task. In the Stroop task, individuals with pLTC lesions made marginally more task errors than individuals with LPFC lesions in the taxonomically-related condition. Further data collection specifically in the Stroop task may reveal significant group differences in future analyses.

Mirman and colleagues have conducted several studies exploring the processing differences between taxonomic and thematic semantic contexts (Landrigan & Mirman, 2018; Mirman et al., 2017; Mirman & Graziano, 2012b, 2012a; Schwartz et al., 2011; Thye et al., 2021). Their work has led to proposing different processing routes for taxonomic and thematic semantic systems. Specifically, they observed an association between taxonomic systems and structures along the ventral processing route, particularly the anterior temporal lobe (Mirman & Graziano, 2012a; Schwartz et al., 2011; Thye et al., 2021). By contrast, they linked the processing of thematic relations with structures along the dorsal processing route (Kalénine et al., 2009; Mirman et al., 2017; Mirman & Graziano, 2012a; Schwartz et al., 2011). For example, using eye tracking, individuals with lesions in BA39 and the surrounding temporo-parietal cortex regions were shown to have reduced and delayed activation of thematically-related words and no difference in the activation of taxonomically-related contexts when compared to the control group, indicating that the temporoparietal cortex may play an important role in the processing of thematically-related semantic contexts (Mirman & Graziano, 2012a).

This dissertation provides a unique lens into the study of taxonomic versus thematic contexts by (1) focusing on the impact of these different semantic contexts on the brain dynamics of lexical retrieval during production, which is largely absent from the work presented by Mirman and colleagues and (2) examining the impact of these different semantic contexts on the behavior and brain dynamics of individuals with left-hemisphere stroke-induced aphasia with lesions including or not including the pLTC. The results demonstrate that taxonomically-related contexts impact the brain dynamics of lexical retrieval at a different timepoint and spatial location than thematically-related contexts for control participants. In particular, a left PFC component peaking around 400 ms post-stimulus onset was sensitive to semantic interference in taxonomically-related contexts. This component was not present in individuals with aphasia, regardless of lesion location. Although behavioral semantic interference was observed in taxonomically-related contexts compared to thematically-related contexts in all three participant groups, there was no electrophysiological difference between conditions and the left PFC component of interest was absent for individuals with aphasia regardless of their lesion location. If indeed the impact of semantic context on lexical retrieval can be further dissected by brain lesion location, additional data collection is necessary as this division cannot be observed with the current dataset of eight individuals with aphasia.

Clinical implications

The long-term motivation for this work is rooted in the goal of improving individualized treatment plans for individuals with aphasia. Clinical interventions for word-finding deficits often employ treatment techniques based on semantic relatedness that collapse taxonomic and

thematically-related items or focus purely on one or the other (e.g., Semantic Feature Analysis, Boyle & Coelho, 1995; contextual priming, Renvall et al., 2007; cueing hierarchies, Wambaugh, 2003). Semantic feature analysis (SFA) is a treatment technique designed to improve the retrieval of conceptual information by activating the semantic network of target words (Boyle & Coelho, 1995). Clinicians prompt naming by asking the client with aphasia questions about where the target image can be found, what category it falls into, what it's used for, etc. SFA is typically conducted with a series of testing images that clinicians then test for generalization outside of trained items, but it is unclear in the literature if the chosen set of images are typically semantically-related or randomized testing items. If it is the case that semantic similarity (specifically, taxonomic similarity) negatively impacts performance, then it is possible that treatments that probe this type of semantic similarity may not be optimal. However, SFA also utilizes aspects of thematic relations by prompting clients to think about the situational context within a scenario rather than semantic categorization, which may circumvent potential interference effect associated with taxonomic contexts. Contextual priming is a treatment typically performed with picture sets containing 4-6 items that are taxonomically related, phonologically related, and unrelated (Renvall et al., 2007). Clinicians compare the semantic and phonological conditions to the baseline unrelated condition to observe the effects of priming on their client's performance. Cueing hierarchy treatment incorporates knowledge of both taxonomic and thematic contexts in its design (Wambaugh, 2003). Clinicians administer a prestimulation test where clients must select the target image from one unrelated and two taxonomically related distractors. One stage of the treatment involves the clinician prompting their clients with sentences that do not provide enough semantic context to lead to the exact target (e.g., if the target is "cow" the clinician will say "The farmer fed the"). This cue results

in the client needing to sort through taxonomically-related items (farm animals) to select the correct word. Then, the clinician moves to prompting the client with a thematically-related sentence (e.g., "The farmer went to the barn to milk the ..."). The results of these cues rely heavily on how much the client struggles with semantic contexts, and whether or not they are equally impacted by taxonomic and thematic contexts. The behavioral outcomes of this study thus far indicate that individuals with aphasia do struggle more with taxonomically-related items than thematically-related items. This outcome highlights the necessity of carefully selecting stimuli when developing individualized treatment plans. This individualized treatment structure could range from a clinician focusing on taxonomic items out of a desire to increase the difficulty level of a treatment or avoiding taxonomically-related contexts altogether for individuals with more severe aphasia who are struggling to complete simple naming tasks.

Concluding remarks

Across four studies, this dissertation has analyzed the spatiotemporal dynamics of lexical retrieval and how these dynamics are impacted depending on the type of semantic context. The results show that taxonomically-related contexts lead to semantic interference and are associated with a larger negative-going component in the 300 to 500 ms time window restricted to a left frontal recording site in both young and older control participants. Regardless of lesion site, this component is absent in individuals with aphasia. However, individuals with brain lesions including the left posterior temporal cortex showed impairments in lexical activation, preceding lexical selection, and inner speech monitoring as indicated by an impaired medial frontal error-related electrophysiological component. Intracranial data revealed that medial and superior frontal regions typically associated with conflict resolution are also engaged during spreading activation during picture naming. The results of these studies provide a key step towards
understanding the brain dynamics of lexical retrieval in stroke-induced aphasia, including how different lexical retrieval deficits interact with semantic contexts, and providing a knowledge basis for the future development of clinical tools for lexical retrieval.

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