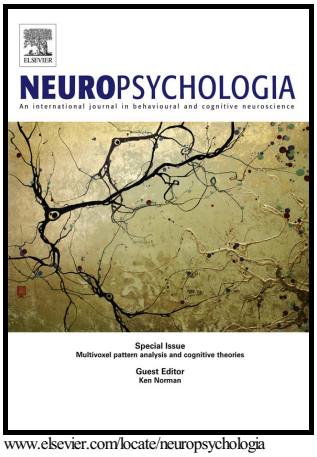
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The Role of the Ventro-Lateral Prefrontal Cortex in Idiom Comprehension: An rTMS Study

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Abstract

Previous research is equivocal with respect to the neural substrates of idiom processing. Particularly elusive is the role of the left ventro-lateral prefrontal cortex (VLPFC), a region implicated in semantic control generally. Although fMRI studies have shown that the left VLPFC is active during idiom processing (see Rapp et al., 2012, for review), rTMS studies have failed to corroborate a clear role of this prefrontal region (e.g., Oliveri et al., 2004).

We investigated this issue using a semantic meaningfulness judgment task that compared idiom comprehension following rTMS-stimulation to the left VLPFC relative to a control site (vertex). We also investigated whether individual differences in general cognitive capacity among comprehenders modulated the effects of rTMS.

The results indicate that left VLPFC stimulation particularly affected the processing of low-familiar idioms, possibly because these items involve a maximal semantic conflict between a salient literal and less-known figurative meaning. Of note, this pattern only emerged for comprehenders with higher cognitive control capacity, possibly because they were more likely to activate or maintain multiple semantic representations during idiom processing, which required VLPFC integrity. Taken together, the results support the importance of the left VLPFC to idiom processing.

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1. Introduction

One aspect of language processing that is particularly challenging is the resolution of semantically ambiguous information across many linguistic levels, including words, phrases and sentences. In this paper, we are interested in how this challenge plays out during the comprehension of idiomatic phrases, such as kick the bucket. According to classic definitions, idioms are relatively more complex than "normal" literal language because their figurative meanings (to die) are often distinct from the compositional meaning created by the combination of their constituents (to strike a pail with one's foot; Nunberg, Sag, & Wasow, 1994). Indeed, according to the traditional view, idioms are long words with arbitrarily stipulated meanings (Bobrow & Bell, 1973; Swinney & Cutler, 1979; reviewed in Libben & Titone, 2008).

However, as noted by many investigators, the traditional view of idioms may be an oversimplification, given that many idioms have internal semantic structure (Gibbs & Nayak, 1989; Gibbs, Nayak, & Cutting, 1989; Gibbs & O'Brien, 1990), and can be modified both semantically and syntactically (e.g. convicted minimalist spills bean, or by and not so large; Gibbs & Nayak, 1989; McGlone, Glucksberg, & Cacciari, 1994). For example, in idioms such as pop the question, the component words can be semantically analyzed to contribute in a metaphorical way towards the figurative meaning (e.g. pop refers to a sudden act and the question refers to a marriage proposal; Gibbs, Nayak, & Cutting, 1989). That literal constituent words of idioms have an actual psychological reality has been demonstrated by several psycholinguistic studies using lexical-decision tasks (e.g. Cacciari & Tabossi, 1988; Cacciari & Glucksberg, 1991; Tabossi, Fanari, & Wolf , 2009; Titone & Connine, 1994). Interestingly, these studies showed that both figurative and literal meanings become activated during idiom processing, supporting a more configurational view of idiom processing, which is not compatible

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with the traditional, holistic view on idioms. Thus, to accommodate both the dual holistic and compositional nature of idioms, hybrid or constraint-based views have attributed both word-like and phrase-like qualities to idioms (e.g., Titone & Connine, 1999; Libben & Titone, 2008; Sprenger, Levelt & Kempen, 2006; see also the configuration model of Cacciari & Tabossi, 1988).

According to such models, idiom processing involves the simultaneous co-activation of figurative and literal meanings, and the speed with which these representations become available is determined by several constraints (Titone & Libben, 2014; Titone & Connine, 1999). One such constraint of great relevance to the present investigation is idiom familiarity, which is typically defined as the degree to which an idiomatic sequence is known in a linguistic community, irrespective of its meaning. Accordingly, high-familiar idioms (e.g., spill the beans, meaning reveal a secret) are over-learned and deeply entrenched within a given linguistic community, and can be recognized as holistic units very quickly, in a way that might potentially trump activation of literal word meanings (Cronk & Schweigert, 1992; Titone & Connine, 1994). In contrast, low-familiar idioms (e.g., take the veil, meaning become a nun) are less known within a language community, thus the literal meanings of the constituent words are more likely to remain active in memory during comprehension.

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1.1 Cognitive control and idiom processing

A hybrid or constraint-based characterization of idiom processing implies that people automatically activate potentially conflicting semantic representations when they encounter idioms. The implication of this view is that idiom processing should be computationally more demanding compared to other non-idiomatic aspects of language, given that it requires the additional recruitment of general cognitive control capacity to resolve the semantic ambiguity

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that arises (Galinsky & Glucksberg, 2000; Glucksberg, Newsome, & Goldvarg, 2001; Papagno & Vallar, 2001; Titone, Holzman, & Levy, 2002; Papagno & Caporali, 2007). In neuropsychology, cognitive control has been defined as the top-down regulated and resource-limited capacity of the cognitive system to configure its own performance through appropriate adjustments in behavior (Wood & Grafman, 2003; Botvinick, Braver, Barch, Carter, & Cohen, 2001). For example, increased demands on cognitive control are associated with detecting cognitive conflicts (Botvinick et al., 2001), inhibiting irrelevant information (Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004), enhancing activation of relevant information (Aron, Robbins, & Poldrack, 2004), as well as monitoring and sending feedback about performed actions and behavior (Wood & Grafman, 2003).

Applied to idiom processing, cognitive control can be used to describe the effortful actions of the cognitive system when faced with evaluating literal and figurative meanings of an idiom against the discourse or sentence context, enhancing activation for figurative meanings, and suppressing activation for literal meanings. For example, when people encounter the idiom spill the beans, they automatically activate its component word meanings (spill, beans), its figurative sense (to die), and then have to use cognitive control to select some aspects of meaning into an unfolding discourse context, while inhibiting or suppressing others.

Thus, it is possible to study the relationship between idiom processing and cognitive control by directly probing activation of the prefrontal cortex (PFC), a neural region generally associated with cognitive control (Norman & Shallice, 1986; Miller & Cohen, 2001; Duncan, 2001; Goldman-Rakic, 1995; Baddeley & Della Sala, 1996; for reviews, see Wood & Grafman, 2003; Ridderinkhof, van den Wildenberg, Segalowitz, & Carter, 2004; Miller, 2000; Braver, Paxton, Locke et al., 2009; MacDonald et al., 2000). Many studies describe the PFC as a neural

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convergence zone for cognitive control, as it upholds, directs and manipulates representations in working memory to configure the cognitive system in its own performance, according to external and internal demands (Thompson-Schill, Bedny, & Goldberg, 2005; Miller, 2000; Duncan, 2001; Yeung, 2013). As such, the PFC is active during response conflicts, selective attention, or context updating (for reviews see Tanji & Hoshi, 2008; Koechlin, Ody, & Kouneiher, 2003; West, 2003; Braver, 2012). These cognitive actions are consistent with a common metaphor that describes the function of this cortical area as a switch operator, which determines which railway track a train will use at any given point in time (Miller, 2000; Wood & Grafman, 2003). Given that idiom processing involves the sustained co-activation of conflicting semantic representations in working memory (Titone, Columbus, Whitford et al., 2015), this cortical region may also be involved in the processing of idioms as well, a topic to which we now turn in more detail.

1.2 Idiom processing and the prefrontal cortex

Several neuroimaging studies have implicated the prefrontal cortex in idiom processing. In a recent fMRI study (Hillert & Buračas, 2009), participants were asked to silently read idioms (e.g. She held the torch) and non-idiomatic literal control phrases (e.g. He met her in the mall) for comprehension. The contrast involving idiomatic vs. literal phrases activated cortical areas in the dorsolateral prefrontal cortex (DLPFC, BA 9 and 46, see Petrides & Pandya, 1999; Yeung, 2013; Tanji & Hoshi, 2008), and also in the ventro-lateral prefrontal cortex (VLPFC; BA 44 and 45 in that study), a prefrontal site slightly inferior to the DLPFC. The results suggest that the semantic conflict between literal and figurative meanings inherent in idioms requires controlled processing mediated by the PFC in general, and the VLPFC, in particular.

Several other fMRI studies have also shown involvement of the left VLPFC during idiom processing (see Zempleni, Haverkort, Renken, & Stowe, 2007; Mashal, Faust, Hendler &

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Jung-Beeman, 2008; Lauro, Tettamanti, Cappa & Papagno, 2008). For example, Lauro and colleagues (2008) used a sentence-to-picture matching task in Italian, in which they asked participants to verify whether a picture correctly depicted a simultaneously displayed idiomatic phrase (e.g. He has a green thumb) or a literal control phrase (e.g. The boy is eating an apple). Correct performance on idiom trials activated the VLPFC (BA 44 and 45) bilaterally, whereas literal trials activated bilateral parietal areas (BA 40). Thus, this study not only suggests that idioms and literal phrases may be processed in non-overlapping cortical areas, but also that idioms primarily activate the VLPFC, potentially because of the semantic conflict inherent in these expressions. This view is consistent with the conclusions of two recent meta-analyses, which found that idiomatic compared to literal phrases activate a left-lateralized network, with strongest activation in the left middle temporal gyrus (BA 21) and the left VLPFC (Bohrn, Altmann, & Jacobs, 2012; Rapp, Mutschler, & Erb, 2012). Thus, even though the meta-analyses and the Lauro et al. (2008) study are not in complete agreement as to the hemispheric lateralization of idiomatic language processing, they both converge on the view that idioms activate the ventro-lateral PFC.

Such work linking the left VLPFC to idiom processing is interesting in light of other studies that link the VLPFC to the cognitive control of semantic memory more generally (Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Thompson-Schill, D'Esposito, & Kan, 1999; Gabrieli, Poldrack, & Desmond, 1998; Badre, Poldrack, Pare-Blagoev, Insler, & Wagner, 2005; Wagner, Pare-Blagoev, Clark & Poldrack, 2001; Whitney, Kirk, O'Sullivan, et al., 2011; Whitney, Kirk, O'Sullivan, et al., 2012; for reviews see Badre & Wagner, 2002, 2007; Thompson-Schill et al., 2005). For example, the VLPFC has been associated with tasks that require the controlled retrieval of semantic representations that are not activated automatically

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through strong cue-target associations. Such situations include when a target word needs to be retrieved that is only weakly semantically related to a cue word (Badre & Wagner, 2007; Thompson-Schill et al., 1997). Similarly, the VLPFC is also active in tasks that require post-retrieval selection, for example, when the subordinate meaning of a lexically ambiguous word competes for activation with automatic activation of its dominant meaning (Whitney et al., 2011). In both cases, the VLPFC is thought to guide the retrieval of task-relevant semantic information from storage sites in the temporal cortex, either by enhancing activation of task-relevant knowledge or inhibiting task-irrelevant representations (Thompson-Schill et al., 1997; Badre et al., 2005). In light of these observations, the VLPFC may also support the mechanisms that guide the retrieval of figurative and literal meanings of idioms from temporal storage sites, maintain such representations in working memory, and engage in meaning selection by up-regulating activation of figurative meanings while simultaneously down-regulating activation of literal meanings.

One potential concern with past studies linking the VLPFC to idiom processing is that they are inherently correlational insofar as they exclusively rely upon the pattern of brain activation measurable when people encounter idioms. Such patterns of activation may be a cause or consequence of comprehension, thus limiting the ability to develop a decisive mechanistic account. A more direct means of experimentally testing the role of the VLPFC in idiom processing is through the use of cortical stimulation paradigms, such as repetitive transcranial magnetic stimulation or rTMS (Pascual-Leone, 1999; Wassermann, 1998). In rTMS, a coil with a rapidly changing current is held above the skull and produces a strong, focal magnetic field, thus creating an ‘artificial lesion’ in underlying brain tissue (Wassermann, 1998). The magnetic field passes painlessly through the skull and transiently introduces noise into neural performance,

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which in turn can be measured in behavioral tasks. In contrast to research with fMRI, rTMS leads to changes in cognitive performance, which can be causally related to a dysfunction or inhibition of the stimulated neural region (Devlin & Watkins, 2007).

Several rTMS studies have shown that stimulation to the prefrontal cortex impairs idiom comprehension (e.g., Fogliata, Rizzo, Reati, Miniussi, Oliveri, & Papagno, 2007; Rizzo, Sandrini & Papagno, 2007; see also Sela, Ivry, & Lavidor, 2012). However, whereas past fMRI studies implicated both the dorso- and the ventro-lateral PFC, rTMS evidence to date has only supported a role for the dorso-lateral PFC (Rizzo et al., 2007; Fogliata et al., 2007; Sela et al., 2012). For example, two studies found that idiom comprehension was impaired when rTMS was applied to the left (Fogliata et al., 2007) and right DLPFC (Rizzo et al., 2007). In both studies, participants showed a greater bias to choose the literal distractor of an idiom in a sentence-to-picture matching paradigm, suggesting an impaired inhibitory mechanism (guided by the DLPFC), which would normally suppress literal word meanings during idiom comprehension. A similar conclusion was drawn from another idiom study that used transcranial direct current stimulation (tDCS) to simultaneously increase and decrease neural excitability. Sela and colleagues (2012) showed that, when facilitating the left DLPFC and inhibiting the right DLPFC, participants were more accurate relating idioms (bite the bullet) with figurative target words (accept) than with literal target words (flavor). This pattern did not emerge when tDCS stimulation was reversed (i.e. facilitation of the right and inhibition of the left DLPFC), which suggests that the left DLPFC may be particularly crucial to processing figurative meanings of idioms. Thus, previous rTMS and tDCS studies are consistent in demonstrating that a stimulation-induced enhancement of prefrontal control mechanisms leads to more successful inhibition of the literal meaning of the idiom.

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In contrast to prior work on the dorso-lateral PFC, the only rTMS study examining the VLPFC failed to find any idiom-specific effects (Oliveri et al., 2004). In that investigation, a sentence-to-picture matching task was used to compare the comprehension of idiomatic and matched literal phrases following stimulation to the VLPFC compared to a baseline without rTMS. Stimulation to the VLPFC led to a general decrease in accuracy for both idiomatic and literal sentences. Thus, it is difficult to interpret these findings specifically with respect to the role of the VLPFC in idiom processing, as opposed to language processing more generally. For example, cortical stimulation to the VLPFC could have caused global performance deficits in a multiple-choice task with several response options. As well, differences among idioms could have led to differential patterns of VLPFC recruitment, however this was not investigated.

In sum, existing research on the role of the VLPFC in idiom comprehension is divided: fMRI studies support the view that this cortical area is associated with idiom processing, whereas rTMS studies do not clearly support its involvement.

1.3 The present study

The goal of the present study was to make use of rTMS to investigate whether idiom processing relies on neural substrates in the left VLPFC. The experiment addressed three primary questions. First, we examined whether the left VLPFC is specifically implicated in idiom comprehension. Several previous rTMS and fMRI studies (Fogliata et al., 2007; Rizzo et al., 2007; Oliveri et al., 2004; Lauro et al., 2008) used sentence-to-picture matching tasks to assess idiom comprehension. However, such tasks may be problematic due to the overt presence of the literal response option and the visuo-spatial difficulties associated with depicting abstract figurative meanings (Papagno & Caporali, 2007; Cacciari & Papagno, 2012). The present study instead used a semantic meaningfulness judgment task in an effort to avoid these concerns.

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Second, we investigated whether VLPFC demands are modulated by differences among idioms, particularly familiarity, which is known to influence idiom processing in general (Schweigert, 1986; Titone & Libben, 2014; Titone & Connine, 1999). We expected that low-familiar idioms (e.g., take the veil), in particular, would be prone to rTMS-induced disruptions, because these phrases involve a maximal semantic conflict between a less-known figurative meaning and a more salient literal meaning. In contrast, rTMS should only minimally disrupt high-familiar idioms (e.g., spill the beans), because they have a highly salient figurative meaning that likely represents a dominant interpretation.

Third, we investigated whether inherent differences among participants in cognitive control capacity (as reflected by the Simon task; Simon & Berbaum, 1990) influence idiom processing. Previous studies supporting the role of executive functions in idiom processing had primarily addressed clinical patient groups, such as individuals with Alzheimer's disease or schizophrenia (Papagno, Lucchelli, Muggia, & Rizzo, 2003; Schettino, Lauro, Crippa et al., 2010; Rassiga, Lucchelli, Crippa, & Papagno, 2009; Titone, Holzman & Levy, 2002). These individuals usually exhibit a range of co-morbid cognitive impairments (for example, memory loss, depression, anxiety or paranoia), making it difficult to attribute any deficits that emerge specifically to reductions in cognitive control. Here, we addressed these concerns by using a technique that experimentally manipulates VLPFC function in healthy younger adults.

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2. Method

2.1 Participants

Sixteen native English speakers from the Montreal community between the ages of 18 and 28 years participated in the experiment (9 female; mean age = 22.63 years). They were

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screened for any relative or absolute contraindications for rTMS (Wassermann, 1998) upon their arrival at the laboratory. Informed written consent was obtained from all participants. Participants had no history of speech/language or hearing impairments, as well as no personal or family history of seizures, epilepsy, and psychiatric or neurological disorders. All participants were strongly right-handed, with a mean right-handedness score of 86 (range: 67 – 100) on the Edinburgh Handedness Inventory (EHI; Oldfield, 1971).[1] The study was approved by the local research ethics committee. A recent brain scan (T1-weighted, structural scans) and participants' consent to its release were mandatory in order to take part in the study.

2.2 Design and Procedure

The design of the study consisted of four predictors, stimulation site (VLPFC vs. vertex, a control site which has no function in language), sentence type (idiomatic vs. literal), idiom familiarity (a scaled variable; obtained from Libben & Titone, 2008), and cognitive control (another scaled variable; assessed through the Simon task; Simon & Berbaum, 1990, see below). Our dependent variables were the speed and accuracy with which participants completed the experimental task (meaningfulness judgments on idiomatic and matched literal sentences). Participants came to our lab twice, corresponding to two sessions of rTMS stimulation (to be detailed below), and performed the experimental task immediately after rTMS stimulation had ceased. The testing sessions were separated by at least one week. The Simon task was only administered once to each subject, during the first testing session prior to the rTMS-paradigm.

[1] On the EHI a person is right-handed if they have a right-handedness score of more than 40.

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2.3 Experimental Task

We employed a meaningfulness judgment task for auditorily presented sentences that contained idioms or matched literal phrases (e.g., spill the beans vs. cook the beans). Participants heard idiomatic and literal stimuli over closed earphones and indicated, by pressing one of two buttons on a response pad, whether the item they heard was meaningful or not. Task instructions (presented on a screen) read: “In this experiment you will listen to spoken English sentences. Your task is to indicate, by pressing a button, if each sentence is meaningful or not. Before the presentation of a sentence, a fixation cross will appear on the screen in front of you. Once the sentence has ended, the question < Meaningful – NO / YES ? > will appear. Make your judgment by pressing the RIGHT ARROW button for YES (MEANINGFUL), and the LEFT ARROW button for NO (NOT MEANINGFUL). Try to respond as quickly and accurately as possible. Please press Enter to indicate that you are ready to begin the experiment."

All trials began with a fixation cross, displayed in the middle of the screen for 1000 ms, followed by the auditory presentation of the stimulus sentence through closed headphones (Sennheiser HD 280 pro) in front of a white screen. Time-locked to the offset of the auditory item, the response prompt “Meaningful - NO / YES ?” was displayed on the screen (the order of NO / YES corresponded to the fact that the left arrow button indicated no, non-meaningful and the right arrow button indicated yes, meaningful). The response prompt stayed on the screen until the participant made a response, with the maximal response time set to 4000 ms. If a participant failed to make a response during this time, the computer automatically initiated the next trial.

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Task instructions and response prompts appeared on a 17" (43 cm) by 24" (61 cm) Dell 32-bit computer monitor with a 60 Hz refresh rate and a screen resolution of 1680 x 1050 pixels; participants were seated at a distance of about 60 cm from the screen.

2.4 Stimuli

To create the experimental stimuli, we selected 54 verb-determiner-noun idioms (kick the bucket, break the ice) from the Libben and Titone (2008) idiom corpus. The idioms ranged between high and low-familiar on a scale from 1-7 (1 meaning that the idiom is never encountered, and 7 meaning that the idiom is frequently encountered; mean familiarity = 3.37; SD = 0.82). Both literally plausible (e.g., pull the plug) and literally implausible idioms (e.g., hedge one's bets) were included (mean literal plausibility of the idioms = 3.81; min = 1.5; max = 4.86). Literal control phrases were created for each idiom by replacing the main verb of the idiom with a verb of approximately the same length that fit the noun semantically; for example, spill the beans (idiomatic) was matched with cook the beans (literal control).

Subsequently, each idiomatic and literal phrase was embedded in a sentence. Each sentence consisted of two clauses: the first clause always started with an agent (a name; e.g. Dolan ...), followed by the idiom / matched literal phrase in the past tense (e.g. ... spilled / cooked the beans ...), followed by a supporting context (e.g. ... when he mentioned the surprise party to his friend / before he started adding vegetables to the soup pot). Non-meaningful versions of each sentence were created by replacing one word in the sentence context with a semantically anomalous word of the same grammatical class, which made a meaningful interpretation of the sentence impossible (e.g. Dolan spilled the beans when he returned the surprise party to his friend / Dolan cooked the beans before he started adding duration to the soup pot).

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In total, there were 216 experimental items counterbalanced over four experimental conditions: idiomatic meaningful, idiomatic non-meaningful, literal meaningful, literal non-meaningful. For an example of the experimental items, see Table 1.

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Idiomatic – Meaningful	Josh bore his cross the entire flight and didn't complain about the snoring man.
Literal – Meaningful	Josh lost his cross when he dropped it in the grass on the way home from church.
Idiomatic – Not Meaningful	Josh bore his cross the entire flight and didn't stockpile about the snoring man.
Literal – Not Meaningful	Josh lost his cross when he dropped it in the stork on the way home from church.

Table 1: Experimental items for the four sentence conditions: idiomatic/literal meaningful, idiomatic/literal non-meaningful.

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To create auditory versions of each experimental sentence, we recorded the 216 items in a sound-attenuated booth using an AKG C 420 III PP condenser microphone and a Marantz professional digital recorder. A native female speaker of North American English was asked to read out every sentence with a natural-sounding intonation, with the microphone positioned about 5 cm from her mouth. To keep prosodic differences between the recordings minimal, the speaker was instructed to use the same prosodic pattern for each sentence. Upon recording, the 216 auditory items were transferred to a computer and edited using Praat (version 5.3.44; Boersma & Weenink, 2013) to ensure that sentence onset and offset were standardized. In order to ensure there were no significant differences in the average length of the experimental items, we compared the average sentence length of all auditory stimuli across the four conditions. A one-way ANOVA revealed no significant differences [$F(3, 212) = 0.39$, $p = 0.76$].

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To determine the order in which the 216 auditory items were presented during the task, all items were randomized using a Latin square randomization (Edwards, 1951) with sentence type and meaningfulness as blocking factors, and were distributed evenly across two experimental lists (corresponding to VLPFC and vertex stimulation sites). Each list contained two items of any given idiom quadruplet. The same number of idiomatic and literal, as well as meaningful and non-meaningful, sentences occurred in each list. Finally, as a precautionary measure, we re-created both experimental lists with reversed item order, resulting in a total of four experimental lists. The order of stimulation site (VLPFC or vertex first) and list administration was counterbalanced across participants.

2.5 rTMS Protocol

We used a standard virtual lesion rTMS protocol, compatible with established TMS safety guidelines (Wassermann, 1998). Repetitive trains of TMS at 1 Hz (600 in total) were delivered to the neural target area for about 10 minutes, which was expected to induce a transient decrease in corticospinal excitability and concurrent disruption of cognitive tasks associated with the stimulated brain region, lasting for about 10-15 minutes (Pascual-Leone, 1999; Rossi, Hallet, Rossini & Pascual-Leone, 2009). In preparation for each testing session, before participants came to the lab, their brain scans were imported into Brain Sight 2 software (Rogue Research, Montreal, Canada) to determine the two sites of cortical stimulation (VLPFC/experimental, and vertex/ control), as well as the left hand motor area. Upon a participant's arrival at the laboratory, we performed MRI-to-head co-registration, using three anatomical landmarks on the head (tip of the nose, bridge of the nose, as well as superior lateral edge of the tragus of the left and right ear) whose position was assessed using an infrared tracking system (Polaris, Northern Digital, Waterloo, Canada). Upon successful co-registration, infrared tracking was used to monitor the

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position of the coil with respect to the participant's brain. For all stimulations, we used a 70mm figure-of-eight coil, driven by a high-speed magnetic stimulator that produced short duration biphasic pulses (Magstim Rapid 1400, Wales, U.K). The stimulator was controlled through Presentation software (Neurobehavioral Research), installed on a Dell Precision M 60 laptop, driven by an Intel® Core ™ 2 CPU T 7600 processor.

To ascertain the maximal strength that could be used for the experimental stimulation, prior to the rTMS session, we determined the resting motor threshold (RMT) for each participant. Two EMG surface electrodes were placed over the first dorsal interosseus muscle of a participant's right hand. Single TMS pulses were then delivered to their left motor cortex hand area, with the TMS coil aligned tangentially to the skull and the coil's handle pointing posteriorly. Stimulation intensity and coil position were adjusted until the EMG electrodes recorded a signal greater than 50μV for a minimum of five trials out of ten.

After RMT was determined, the experimental stimulation began. The intensity level was set to 110% of the RMT value. As noted, rTMS stimulation was applied to the target site (VLPFC or vertex) in trains of 600 pulses at 1 Hz. Five participants reported mild discomfort during rTMS stimulation to the VLPFC, caused by muscle twitches in the jaw. For these subjects, the intensity level was reduced accordingly. Participants reported no adverse side effects during or after rTMS stimulation.

Based on past work from our group, we estimated that rTMS stimulation at the frequency level we used should yield a 10 – 15 min inhibitory effect (see Boroojerdi, Prager, Muellbacher & Cohen, 2000; Gerschlager, Siebner & Rothwell, 2001; Shum, Shiller, Baum & Gracco, 2011), which we determined to be sufficient to complete the idiom task. To confirm that participants indeed had enough time to finish the idiom task before any rTMS effects trailed off, we

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conducted a post-hoc analysis of the logfiles created for each experimental run. The mean completion time of the experimental task was 10.25 minutes across subjects and sessions (maximum = 11.25 min.; minimum = 9.32 min.; SD = 0.44 min).

Based on prior work (Pascual-Leone, 1999; Walsh & Cowey, 2000), we expected that the TMS protocol used should primarily slow a participant's reaction times, rather than lead to a decline in accuracy. However, past rTMS and tDCS studies on idiom comprehension consistently reported effects on accuracy (Rizzo et al., 2007; Fogliata et al., 2007; Sela et al., 2012), suggesting that rTMS not only slows cognitive performance, but also makes it more prone to errors. Thus, our expectation was somewhat open as to whether rTMS effects should arise for both reaction times and accuracy.

2.6 Localization of Stimulation Sites

For stimulation to the left VLPFC, we used the Montreal Neurological Institute (MNI) coordinates (x = -54, y = 21, z = 12), corresponding to the left mid ventral prefrontal cortex or pars triangularis, BA 45. We chose this site specifically because it has been reported to be maximally sensitive to distant semantic relationships in studies on semantic retrieval in the context of competing alternatives (Badre & Wagner, 2007; Whitney et al., 2011, 2012).

For vertex–rTMS we used the MNI coordinates x = 0, y = -30, z = 80 (Ko, Monchi, Ptito et al., 2008) to guide rough coil placement, and then adjusted the stimulation sites individually for each participant, determining vertex as the highest point of the skull located medially between both hemispheres (Leitão, Thielscher, Werner, et al., 2012). The mean MNI coordinates for Vertex-rTMS across subjects were [x = 0.16, y = -23.37, z = 80.19].

The cortical site for the left hand motor area was also determined individually for each participant, as the knob-like structure in the pre-central gyrus of the left hemisphere that is

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shaped like an omega in the axial plane and looks like a hook in the sagittal plane (see Yousry, Schmid, Alkadhi, et al., 1997). The mean MNI coordinates across subjects for the hand motor area were [x = -35.08, y = -17.94, z = 51.23].

2.7 Simon Cognitive Control Task

The Simon task is a computer-based interference task (for a review, see Lu & Proctor, 1995), and is based on the observation that participants execute a motor response more quickly and more accurately if the response is spatially congruent to the stimulus location, even when stimulus location is not relevant to the task. The original Simon effect was obtained with auditory stimuli (Simon & Small, 1969), but it has also been replicated with color as the relevant dimension (Simon & Berbaum, 1990; Zorzi & Umiltá, 1995), as in the current adaptation.

Participants saw red and blue squares appear on the left or right side of a screen. Each trial started with a fixation cross, displayed for 500 ms at the centre of the computer monitor, followed by the appearance of the colored square. When the square was blue, subjects were instructed to press a button on the left side of the keypad with their left hand. When the square was red, they were instructed to press a button on the right side with their right hand. The maximal response time was set to 1700ms. In congruent trials, the screen location of the square and the response side determined by the square color were identical, whereas in incongruent trials, they were not. Cognitive control load is proportionally greater in incongruent trials, since participants need to overcome the pre-potent response to press the button on whichever side they saw the stimulus appear (Hommel, 1993).

We computed the mean correct response times for each participant in congruent and incongruent trials, excluding outliers that were more than 2 standard deviations from the mean (166 out of 3841 cells in total; 4.32 % of all data points). Based on these values, we computed a

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cognitive control cost score for each participant, by subtracting the average reaction time on congruent trials (easy trials, i.e. low demand on cognitive control) from the average reaction time on incongruent trials (hard trials, i.e. high demand on cognitive control). Thus, a higher Simon cost score reflects a greater difference between hard and easy trials, and thus lower levels of cognitive control.

3. Results

We constructed linear mixed-effects (LME) models with random slopes where appropriate, as implemented in the lme4 library (Bates, 2005; Bates & Sarkar, 2005; Barr, Levy, & Scheepers, 2013) within R (R Development Core Team, 2013). The dependent variables were accuracy (a binomial variable) and correct reaction times (RT; in milliseconds), time-locked to the offset of the auditory sentence. The independent variables were sentence type (a categorical variable with two levels: Idiomatic versus Literal), site of stimulation (a categorical variable with two levels: stimulation to VLPFC and vertex), idiom familiarity (a scaled continuous variable based on prior ratings from Libben & Titone, 2008), and the Simon cost score (a scaled continuous variable; see above). Because idiom familiarity and decomposability are often correlated (Libben & Titone, 2008; Titone & Connine, 1994), all models included idiom decomposability as a continuous control variable. In addition, to address potential fatigue in the course of an experimental run, all models included trial number as a continuous control variable. We deviation coded categorical factors for all omnibus models; however, model splits used treatment-coding (with vertex as the reference level for site of stimulation, and the literal condition as the reference level for sentence type). Accuracy and RT analyses reported below were conducted on meaningful items only. Five items out of 108 were excluded from the analysis, since they yielded abnormally long average reaction times (reaction times which were

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more than 2 standard deviations from the mean for meaningful items). Table 2 displays the average RT and accuracy, as well as the standard errors, for meaningful items, split out by sentence type and site of stimulation.

	Correct Reaction Times		Accuracy	
	M	SE	M	SE
Baseline/Vertex				
Idiomatic	501.21	53.16	0.88	0.02
Literal	445.32	38.80	0.93	0.01
Ventro-Lateral PFC				
Idiomatic	547.32	55.10	0.86	0.02
Literal	493.43	40.87	0.92	0.01

Table 2: Means and standard errors (subject-weighted) in idiomatic and literal sentences for correct reaction times (in ms) and percentage of accuracy, depending on site of stimulation.

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3.1 Accuracy

Stepwise log-likelihood model comparisons (Baayen, Davidson, & Bates, 2008; Bates, Kliegl, Vaishth, & Baayen, 2015) showed that by-subject and by-item random slopes were not warranted for this model.

We found a significant main effect of sentence type (b = -1.05, SE = 0.28, z = -3.71), and a significant main effect of familiarity (b = 0.57, SE = 0.15, z = 3.82) in the omnibus accuracy model. In addition, there were trends toward significant interactions between sentence type and familiarity (b = 0.55, SE = 0.28, z = 1.94), and between familiarity and cognitive control (b = -0.21, SE = 0.12, z = -1.82). To investigate what was driving these interactions, we median-split items by cognitive control (as done below in the RT analyses), and computed two new models, one for low-control individuals and another one for high-control individuals.

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In both models, we found a significant main effect of sentence type (low-control individuals: b = -1.24, SE = 0.44, z = -2.81; high-control individuals: b = -1.08, SE = 0.54, z = -2.00), indicating that both low- and high-control individuals responded less accurately to idioms than to literal items. However, only the model for high-control individuals showed a significant main effect of familiarity (b = 0.81, SE = 0.41, z = 1.99), whereas the main effect of familiarity was not significant for low-control individuals (b = 0.02, SE = 0.38, z = 0.04). Thus, only high-control individuals were less accurate for low-familiar relative to high-familiar idioms.

No other main effects or interactions reached significance in the omnibus accuracy model (main effect of site of stimulation: b = -0.09, SE = 0.22, t = -0.40; main effect of cognitive control: b = -0.01, SE = 0.20, t = -0.05). Table 3 shows the statistical results for all model comparisons in the accuracy and reaction time LMER models.

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	Correct Reaction Times			Accuracy		
Fixed Effects	b	SE	t	b	SE	z
Sentence Type	56.51	34.50	1.64	-1.05	0.28	-3.71
Site of Stimulation	56.45	41.49	1.35	-0.09	0.22	-0.40
Idiom Familiarity (scaled)	-11.16	12.45	-0.90	0.57	0.15	3.82
Simon Cost Score (scaled)	-35.99	48.04	-0.75	-0.01	0.20	-0.06
Sentence Type * Site of Stimulation	28.49	33.37	0.85	0.27	0.44	0.62
Sentence Type * Idiom Familiarity	-44.76	23.08	-1.94	0.55	0.28	1.94
Site of Stimulation * Idiom Familiarity	24.52	16.78	1.46	0.04	0.21	0.17
Sentence Type * Simon Cost Score	-21.64	30.35	-0.71	0.08	0.24	0.34
Site of Stimulation * Simon Cost Score	110.92	41.45	2.68	-0.06	0.24	-0.23
Idiom Familiarity * Simon Cost Score	5.26	8.24	0.64	-0.21	0.12	-1.82
Sentence Type * Site of Stimulation * Idiom Familiarity	0.90	33.54	0.03	0.18	0.43	0.43
Sentence Type * Site of Stimulation * Simon Cost Score	70.37	32.52	2.16	0.24	0.48	0.62
Sentence Type * Idiom Familiarity * Simon Cost Score	-0.70	16.46	-0.04	0.16	0.23	0.69
Site of Stimulation * Idiom Familiarity * Simon Cost Score	-14.68	16.55	-0.89	-0.09	0.23	-0.41
Sentence Type * Site of stimulation * Idiom Familiarity * Simon Cost Score	-89.35	33.06	-2.70	-0.55	0.46	-1.19
Control Predictors	b	SE	t	b	SE	z
Idiom decomposability (scaled)	1.78	12.29	0.15	0.10	0.15	0.70
Trial number (scaled)	-33.71	8.20	-4.2	0.02	0.09	0.17
Random Effects		Variance			Variance	
Subject		35979.8			0.42	
Subject | Sentence Type		10583.0			n/a	
Subject | Site of Stimulation		23284.5			n/a	

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Item	6614.9	0.74

Table 3: Linear mixed effects regression results for the deviation-coded four-factor model, including sentence type, site of stimulation, idiom familiarity and Simon cognitive control cost score.

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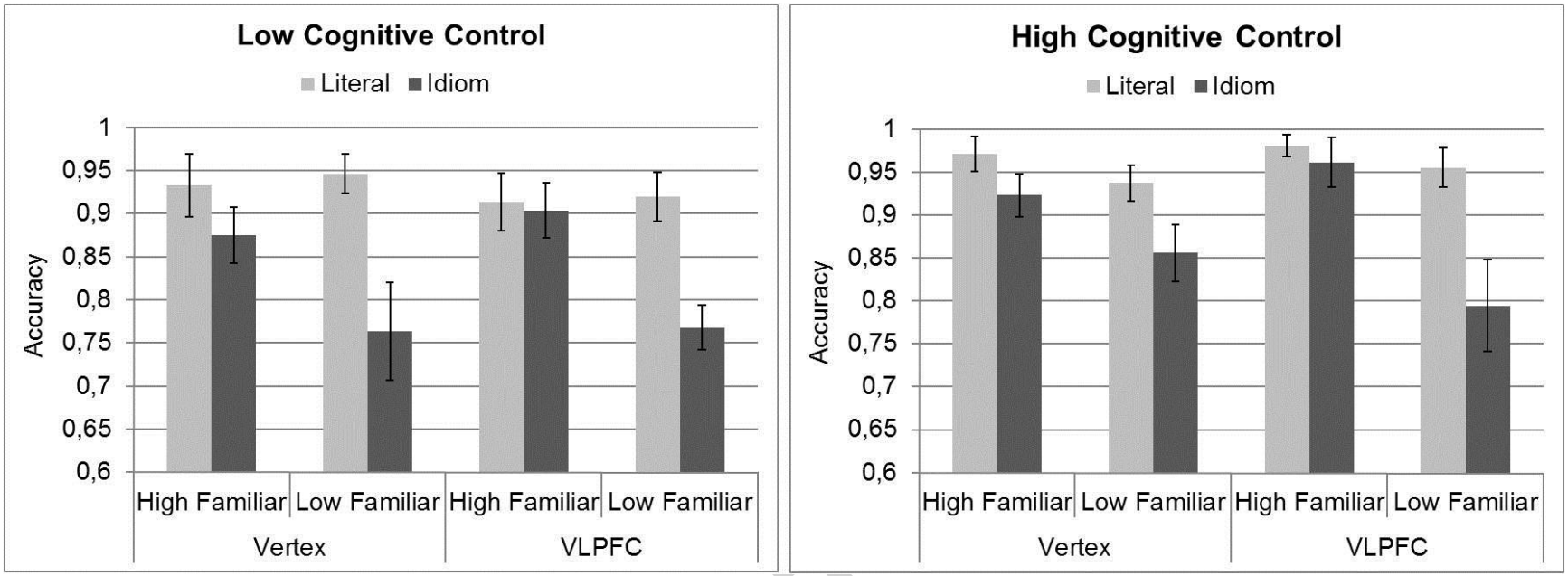


Figure 1: Mean accuracy for meaningful idiomatic and literal sentences in low- and high-control individuals (left and right panel, respectively), depending on site of stimulation and idiom familiarity. Error bars indicate standard errors of the mean (subject-weighted).

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3.2 Reaction Times

Prior to analysis, correct reaction time data were trimmed minimally through exclusion of outliers which were more than 2 standard deviations from the individual's mean (resulting in an exclusion of 170 / 3454 data points, 4.9% of all observations – a justifiable rate according to Ratcliff, 1993). Log-likelihood model comparisons indicated that by-subject random slopes were warranted for sentence type and site of stimulation. By-item random slopes were not warranted for this model.

We found a significant four-way interaction among sentence type, site of stimulation, familiarity and cognitive control (b = -89.35, SE = 33.06, t = -2.70). To investigate what drove this four-way interaction, we median split the data by cognitive control, thus computing two new models, one model for low-control individuals and one model for high-control individuals.

In examining the data for participants with low levels of cognitive control, analyses showed no significant main effects or interactions, despite patterns that may seem apparent from the left panel of Figure 2 (main effect of sentence type: b = 12.00, SE = 55.67, t = 0.22; main effect of site of stimulation: b = 104.41, SE = 82.37, t = 1.27; main effect of familiarity: b = -15.12, SE = 28.63, t = -0.53; three-way interaction between sentence type, site of stimulation and familiarity: b = -79.55, SE = 51.32, t = -1.55).

In contrast, the model for individuals with high levels of cognitive control showed a significant three-way interaction among sentence type, site of stimulation and idiom familiarity (b = 82.55, SE = 43.02, t = 1.96). To investigate the source of this three-way interaction, we performed another model split, in which we median-split items by familiarity. The results showed a significant interaction between sentence type and site of stimulation only in the model for low-familiar items (b = -126.39, SE = 62.85, t = -2.01) but not in the model for high-familiar

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items (b = 86.27, SE = 56.80, t = 1.50). Another split of the model for low-familiar items by sentence type showed that there was a significant main effect of site of stimulation only for idiomatic (b = -122.37, SE = 56.95, t = -2.15) and not literal items (b = 7.54, SE = 35.79, t = 0.21).

Thus, when rTMS was applied to the VLPFC of high-control individuals, reaction times became faster for low-familiar idioms (in comparison to the reaction times for low-familiar idioms during vertex stimulation). Figure 2 (right panel; high control individuals) illustrates this pattern, and shows a decrease in RT for low-familiar idioms from vertex to VLPFC stimulation.

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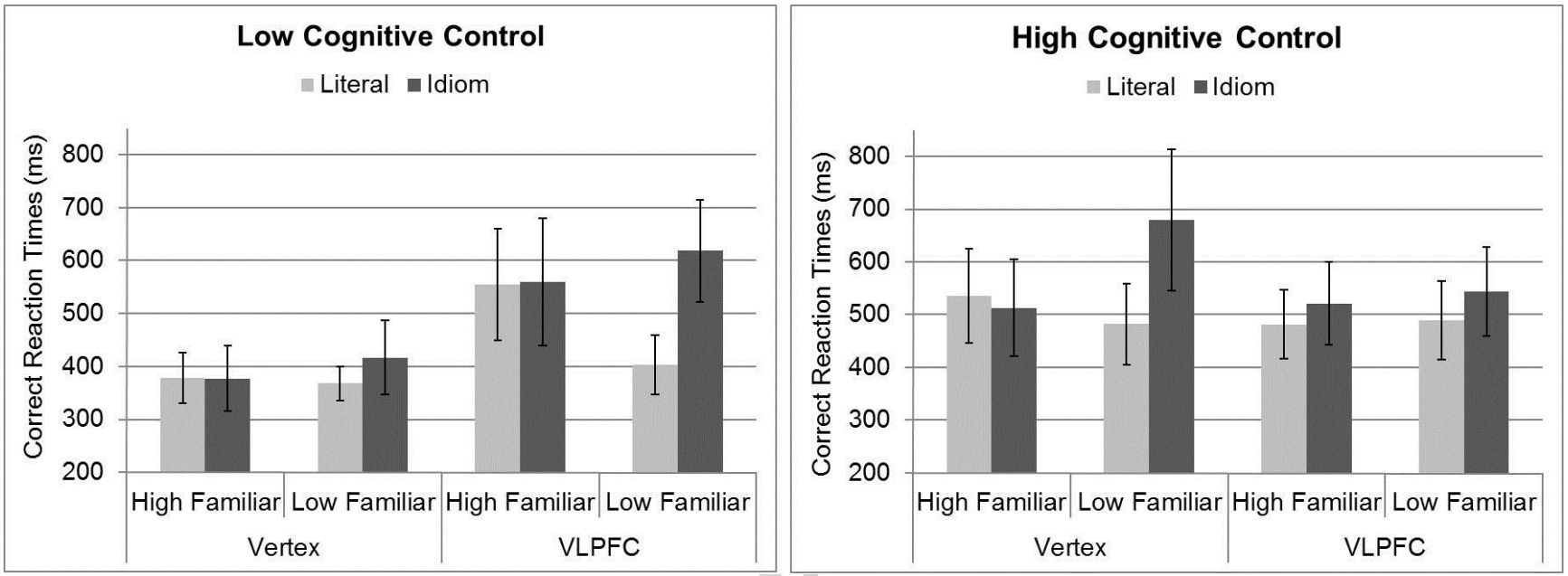


Figure 2: Mean correct reaction times (± standard errors of the mean, subject-weighted) for meaningful items in low- and high-control individuals (left and right panel, respectively), depending on sentence type, site of stimulation and idiom familiarity.

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3.3 Summary

In sum, the accuracy and RT data showed two primary results of interest. First, in the accuracy data, high (and not low-) control individuals were less accurate for low-familiar compared to high-familiar idioms. Second, the reaction time data confirmed this pattern, in that RTs for low-familiar idioms tended to be longer than for high-familiar idioms; the RT data further showed that in high-control individuals, there was a decrease in reaction times to low-familiar idioms when rTMS was applied to the VLPFC.

Taken together, these findings suggest that cortical stimulation of the VLPFC impairs idiom comprehension for a subset of idioms, that is, for low familiar idioms when semantic representations are maximally conflicting. Moreover, this effect emerged only in individuals who have higher levels of cognitive control, perhaps because such individuals are more likely to entertain multiple semantic representations during language processing. This possibility will be further discussed below.

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4. Discussion

Our main question of interest was whether an rTMS-induced 'artificial lesion' to the left VLPFC (specifically, BA 45) would lead to a comprehension disadvantage for idiomatic but not literal sentences. We hypothesized this neural region would be active during idiom comprehension because of its involvement in tasks that require controlled selection among competing representations (Badre & Wagner, 2002, 2007; Badre et al., 2005; Whitney et al., 2011, 2012). According to our hypothesis, such circumstances should apply to idioms because they have semantically conflicting literal and figurative meanings. Our expectation was that low-familiar idioms, in particular, should be prone to rTMS-induced disruptions, because these items involve a maximal semantic conflict between a less familiar figurative meaning and a proportionally more salient literal meaning. Indeed, our findings suggest that the VLPFC is important for the understanding of low-familiar idioms for some individuals. Following stimulation to this neural target site, meaningfulness judgments for low-familiar idioms were significantly faster than responses to matched literal control phrases, primarily for individuals with high levels of cognitive control.

An rTMS-induced speed-up in reaction times has also been reported in previous studies on idiom comprehension. Rizzo et al. (2007), for example, found that, following rTMS stimulation to the left dorso-lateral PFC, study participants responded generally faster to idiomatic and literal items, but showed an idiom-specific increase in error rates that did not occur for literal items.[2] Since the Rizzo et al. (2007) study used a sentence-to-picture matching task which required participants to choose the correct picture among a literal and idiomatic

[2] The authors exclude the possibility of a speed-accuracy trade-off, since the effect did not occur in a control task with the same idiomatic and literal stimuli (see Rizzo et al., 2007).

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representation, the authors interpreted their findings as a 'release from inhibition', suggesting that, as a consequence of TMS stimulation, participants were less able to correctly inhibit the idiom's literal interpretation and more likely to erroneously choose the literal foil. Even though the experimental task of the present study involved no such overt presentation of the literal meaning, our use of low-familiar idioms could have led to a similar behavioral response in participants. Low-familiar idioms involve a maximal semantic conflict between a less known figurative and more salient literal meaning, which normally needs to be resolved by the prefrontal cortex. As in the Rizzo et al. (2007) study, rTMS stimulation to the VLPFC may have caused an impairment in PFC-located circuits which are normally dedicated to controlling activation levels of multiple semantic representations during language processing. As in the Rizzo et al. (2007) paper, this impairment in controlled processing may have led to a drop in accuracy, indicating that participants were now glossing over literal and figurative meanings of idioms. Unlike in the Rizzo et al. (2007) study, which showed a reduction in reaction times for both idiomatic and literal items, the RT results of the present study are in line with this interpretation, as the reduction in reaction times emerged only for idiomatic items.

Of note, the present study indicates that the impairments in idiom comprehension upon prefrontal cortex stimulation were especially pronounced in high-control individuals. Even though accuracy was low for idioms across the board, only high-control individuals showed effects of idiom familiarity - their responses to low-familiar idioms were generally less accurate (regardless of site of stimulation), and cortical stimulation to the left VLPFC led to accelerated responses to low-familiar idioms in these individuals. The fact that only high-control individuals were affected by VLPFC stimulation may indicate that these individuals may be more likely to entertain multiple semantic representations during language processing, which can thus be

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impacted by cortical stimulation. In contrast, low-control individuals may only activate more prominent semantic representations (in the case of low-familiar idioms, the literal meaning), so that VLPFC stimulation interferes only minimally with idiom comprehension. Thus, it seems that high-control individuals may rely more on the integrity of VLPFC substrates in order to use controlled processing to maintain and select among these multiple semantic representations, whereas in low-control individuals, VLPFC input may be only minimal (because they do not activate multiple interpretations).

Support for this interpretation comes from several studies that have linked individual differences in executive functions to white and gray matter variations in the frontal cortex (Fornito, Yücel, Wood, et al., 2004; Forstmann, Jahfari, Scholte et al., 2008). For example, Forstmann et al. (2008) investigated axonal diameter, fiber density and coherence of white matter tracts in the frontal lobes of high- and low-control individuals. Their results showed that high-control individuals (as measured by the Simon task) have a stronger coherence in white matter tracts of the fronto-occipital fasciculus, a fiber tract that connects the lateral frontal cortex with more posterior brain regions, among them the temporal lobe. Importantly, this fiber tract has been implicated by several studies as the main sub-cortical pathway mediating semantic processing (the ventral stream; Duffau, Gatignol, Mandonnet et al., 2005; Saur, Kreher, Schnell, et al., 2008). The results of the present investigation are compatible with such findings; one could assume, for example, that idiom comprehension (and presumably the comprehension of semantic ambiguities in general; Boulenger, Hauk & Pulvermüller, 2009) crucially relies on the VLPFC to balance and evaluate the conflicting meanings, and this process is additionally modulated through the integrity and strength of white matter tracts that ensure the quick and

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efficient information transfer from semantic storage sites in the temporal lobe to the frontal cortex.

This interpretation of our findings is also consistent with previous idiom studies focussing on clinical patient groups who frequently present with aberrations in prefrontal cortex areas, such as individuals with schizophrenia and Alzheimer's disease. These individuals often show neural lesions, degeneration or abnormal levels of activation in prefrontal cortex regions (Kaufmann, Pratt, Levine, & Black, 2010; Volk & Lewis, 2002; West, 1996), and there is also evidence that they have difficulties with idiom comprehension. For example, people with Alzheimer's disease are reported to more likely associate an idiom with its literal than with its figurative meaning in a sentence-to-picture or sentence-to-word matching task (see Papagno, 2001; Papagno et al., 2003; Rassiga et al., 2009; Schettino et al., 2010). As well, people with schizophrenia have difficulty generating activation of idiomatic meanings only for expressions that have plausible literal interpretations that could compete with an idiom interpretation (e.g., kick the bucket but not come up roses; Titone, Holzman, & Levy, 2002; also see Iakimova, Passerieux, Denhière et al., 2010, for supporting results). Together, such findings suggest that clinical aberrations in PFC substrates render these patients unable to sufficiently activate figurative meanings during idiom processing, so that they can only understand literal meanings of idioms.

Our finding here that low-familiar (but not high-familiar) idioms involves controlled processing supports the predictions of hybrid views of idiom processing, which argue that idioms are accessed through a network of interconnected nodes whose activation spreads sequentially within and between the component words (Titone & Connine, 1999; Titone & Libben, 2014). Thus, the connection strength among individual constituents depends on the frequency with

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which the unit is activated (Jescheniak & Levelt, 1994; Levelt, Roelofs, & Meyer, 1999). For low-familiar idioms, this connection is most likely weaker than in high-familiar idioms, due to the lack of repeated activation for these less-frequently encountered items. Because low-familiar idioms are less tightly bound as a unit, their literal constituent words should lead to greater interference during processing (Kan & Thompson-Schill, 2004), requiring greater inhibitory capacity during processing. The co-activation of multiple meanings then calls on VLPFC-guided control mechanisms that maintain these meanings in a temporary loop, evaluate them against the sentence context, and finally select the figurative meaning by suppressing all unwanted (in the case of idioms, literal) representations. This interpretation could also explain the absence of an rTMS effect in the one previous rTMS study that investigated the left VLPFC (Oliveri et al., 2004). In that study, only high-familiar idioms were used, that is, items which likely involve very little interference from literal constituents, because their configurations are highly over-learned. Such circumstances should minimize controlled processing demands and, consequently, decrease VLPFC-input.

An alternative interpretation for the inconsistency in results between the present study and the Oliveri et al. (2004) paper is that the Oliveri et al. (2004) study primarily used literally implausible idioms (i.e. idioms which do not allow for a meaningful literal interpretation), while the idioms in the present investigation were both literally plausible (e.g., pull the plug) and literally implausible (e.g., hedge one's bets). Thus, cognitive load could have been minimal for processing the Oliveri et al. (2004) idioms (because of their low probability of a literal interpretation), while cognitive load may have been greater for processing the idioms in the present investigation[3]. However, we specifically checked for the effects of this variable in our data set, by running follow-up models which included literal plausibility instead of idiom

[3] We would like to thank the reviewers for pointing this out.

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familiarity. These models showed no significant main effects or interactions. Thus, the results of the present study seem to be best accounted for by the explanation that low-familiar idioms may increase cognitive load by inducing a maximal semantic conflict, whereas high-familiar idioms may keep cognitive load minimal.

A previous EEG study also supports this view (Rommers, Dijkstra, &Bastiaansen, 2013), as it demonstrates that high-familiar idioms involve only minimal activation of literal constituent words. Rommers et al. (2013) analyzed the N400 EEG component (see Kutas & Federmeier, 2011; for review) to index semantic integration difficulties that participants experienced when they were reading idiomatic and matched literal sentences for comprehension. The experimental sentences were modified in that idioms and matched literal phrases were preceded by a strong biasing context and key constituent words of the idiomatic or literal phrases were replaced with either semantically related or unrelated words (e.g. in the Dutch idiom tegen de lamp lopen, lit. to walk against the lamp, fig. to get caught; 'lamp' was replaced with 'candle' [related] or 'fish' [unrelated]). The results revealed that word substitutions in literal control sentences elicited a graded pattern of N400s, with related words eliciting a significantly smaller N400 than unrelated words, thus suggesting fewer integration difficulties when participants were reading contextually related rather than unrelated words. In high-familiar idioms, in contrast, there was no graded N400; that is, the brain's response was indistinguishable for related and unrelated substitutions. The authors argue that familiar idioms do not require compositional word-by-word processing in the way that literal language does, so that both related and unrelated word substitutions are seen as a violation in high-familiar idioms. In sum, previously obtained evidence (Oliveri et al., 2004; Rommers et al., 2013) and the data from the present investigation indicate that control-related processing demands increase (and involve VLPFC-input to a greater

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extent) when several semantic representations are maximally conflicting (such as in low-familiar idioms), whereas control-related demands are minimal when one representation is highly salient compared to the others (Oliveri et al., 2004; Rommers et al., 2013; also see Thompson-Schill et al., 1997).

In this context, one open question is whether the role of the VLPFC is one specifically dedicated to idiom comprehension, or whether its role is a more general one, indexing increased workload or effortful processing for any instance of selection demands (Boulenger, Hauk & Pulvermüller, 2009). To date there is more evidence in the extant literature to suggest that the role of the VLPFC in idiom comprehension is related to more general effortful processing circumstances, rather than to a specific brain response to idiomaticity. For example, VLPFC-activation has also been observed in lexical ambiguity resolution (Rodd, Davis & Johnsrude, 2005) and the comprehension of semantically unexpected constituent words (Van Petten & Luka, 2006). Thus, it seems that the activation or input of the VLPFC in the present study and in previous investigations may be best explained as a brain response to general instances of cognitive conflict or heavy burden on the language processing system (Boulenger, Hauk, & Pulvermüller, 2009).

Finally, one limitation of the present study is that our data are unable to further dissociate the specific roles of the ventrolateral and the dorsolateral PFC during idiom comprehension. To date, studies have implicated both regions as crucial for idiom resolution: the VLPFC in the present investigation and in several fMRI studies (e.g. Rapp et al., 2012; Lauro et al., 2008), and the DLPFC in three previous rTMS studies (Fogliata et al., 2007; Rizzo et al., 2007; Sela et al., 2012). One possibility is that these two regions are differentially sensitive to manipulations in variables that are known to affect idiom processing, for example familiarity. For example, two

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previous rTMS studies addressing the DLPFC used exclusively high-familiar idioms (Fogliata et al., 2007; Rizzo et al., 2007; the third study did not control for this variable: Sela et al., 2012), whereas the VLPFC effect obtained in the present study emerged only for low-familiar idioms. Thus, an important next step for future rTMS and fMRI studies is to investigate both regions and to determine whether neural activity in these regions is modulated by variables such as idiom familiarity, as in the present study, but also literal plausibility or degree of semantic overlap between the idiomatic meaning and the meanings of an idiom's constituent words.

5. Conclusion

To date, investigations of the role of the ventro-lateral prefrontal cortex (VLPFC) in idiom processing have been equivocal, with fMRI studies consistently demonstrating its involvement (Zempleni et al., 2007; Lauro et al., 2008; for reviews see Rapp et al., 2012; Bohrn et al., 2012), and rTMS studies failing to corroborate this result (Oliveri et al., 2004).

The present investigation used a meaningfulness judgment task to test whether rTMS stimulation to the left VLPFC and a control site (vertex) would differentially affect the comprehension of idiomatic and matched literal sentences. Our prediction was that rTMS should disrupt the comprehension of low-familiar idioms, in particular, as these items involve a maximal semantic conflict between a less known figurative and a more salient literal interpretation. The results corroborated this hypothesis, but individual differences in cognitive control capacity modulated the effect: Only high-control individuals were susceptible to rTMS-induced disruptions, whereas low-control individuals showed no effects of prefrontal cortex stimulation. Thus, high-control individuals may be inherently more likely to activate multiple semantic representations and use controlled processing during idiom processing, whereas low-control individuals may activate only more prominent semantic representations (and rely less on

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left-hemispheric VLPFC integrity). In sum, the present data show that idiom resolution is predicted by both idiom-inherent and listener- or speaker-related characteristics, which supports hybrid or constraint-based views of idiom processing (Titone & Libben, 2014).

Future studies need to disentangle the potentially diverging roles of the dorsolateral (DLPFC) and ventrolateral PFC (VLPFC) during idiom processing, and determine how general cognitive functions (such as cognitive control) interact with idiom-specific factors other than familiarity (for example, decomposability or literal plausibility) in constraining idiom resolution.

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Conflicts of interest:

None declared.

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ACCEPTED MANUSCRIPT

6. References

Aron, A., Robbins, T., & Poldrack, R. (2004). Inhibition and the right inferior frontal cortex. TRENDS in Cognitive Sciences, 8, 170-177.

Baayen, R. H., Davidson, D. J., & Bates, D. M. (2008). Mixed-effects modeling with crossed random effects for subjects and items. Journal of Memory and Language, 59, 390-412.

Baddeley, A., & Della Salla, S. (1996). Working memory and executive control. Philosophical Transactions: Biological Sciences, 351, 1397-1404.

Badre, D., Poldrack, R., Pare-Blagoev, E., Insler, R., & Wagner, D. (2005). Dissociable controlled retrieval and generalized selection mechanisms in ventrolateral prefrontal cortex. Neuron, 47, 907-918.

Badre, D., & Wagner, A. (2002). Semantic retrieval, mnemonic control, and prefrontal cortex. Behavioral and Cognitive Neuroscience Reviews, 1, 206-218.

Badre, D., & Wagner, A. (2007). Left ventrolateral prefrontal cortex and the cognitive control of memory. Neuropsychologia, 45, 2883-2901.

Barr, D., Levy, R., Scheepers, C., & Tily, H. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. Journal of Memory and Language, 68, 255-278.

Bates, D. (2005). Fitting linear mixed models in R. R News, 5, 27-30.

Bates, D., Kliegl, R., Vasishth, S., & Baayen, H. (2015). Parsimonious mixed models. arXiv preprint arXiv: 1506.04967.

Bates, D., & Sarkar, D. (2005). The lme4 library. On-line available: http://lib. stat. cmu. edu/R/CRAN.

Bobrow, S., & Bell, S. (1973). On catching on to idiomatic expressions. Memory & Cognition, 1, 343-346.

Accepted manuscript

ACCEPTED MANUSCRIPT

Boersma, P., & Weenink, D. (2013). Praat: Doing phonetics by computer (version 5.3. 60).

Bohrn, I., Altmann., U., & Jacobs, A. (2012). Looking at the brains behind figurative language: A quantitative meta-analysis of neuroimaging studies on metaphor, idiom, and irony processing. Neuropsychologia, 50, 2669–2683.

Boroojerdi, B., Prager, A., Muellbacher, W., & Cohen, L. (2000). Reduction of human visual cortex excitability using 1-Hz transcranial magnetic stimulation. Neurology, 54, 1529-1531.

Botvinick, M., Braver, T., Barch, D., Carter, C., & Cohen, J. (2001). Conflict monitoring and cognitive control. Psychological Review, 108, 624-652.

Boulenger, V., Hauk, O., & Pulvermüller, F. (2009). Grasping ideas with the motor system: Semantic somatotopy in idiom comprehension. Cerebral Cortex, 19, 1905-1914.

Braver, T. (2012). The variable nature of cognitive control: A dual-mechanisms framework. TRENDS in Cognitive Sciences, 16, 106-113.

Braver, T., Paxton, J., Locke, H., & Barch, D. (2009). Flexible neural mechanisms of cognitive control within human prefrontal cortex. Proceedings of the National Academy of Sciences of the United States of America, 106, 7351–7356.

Cacciari, C., & Glucksberg, S. (1991). Understanding idiomatic expressions: The contribution of word meanings. Advances in Psychology, 77, 217-240.

Cacciari, C., & Papagno, P. (2012). Neuropsychological and neurophysiological correlates of idiom understanding: How many hemispheres are involved? In M. Faust (Ed.), The Handbook of the Neuropsychology of Language, 2, (pp. 368-387). New Jersey: Wiley-Blackwell.

Accepted manuscript

ACCEPTED MANUSCRIPT

Cacciari, C., & Tabossi, P. (1988). The comprehension of idioms. Journal of Memory and Language, 27, 668-683.

Cronk, B. C., & Schweigert, W. A. (1992). The comprehension of idioms: The effects of familiarity, literalness, and usage. Applied Psycholinguistics, 13, 131-146.

Devlin, J., & Watkins, K. (2007). Stimulating language: Insights from TMS. Brain, 130, 610-622.

Duffau, H., Gatignol, P., Mandonnet, E., Peruzzi, P., Tzourio-Mazoyer, N., & Capelle, L. (2005). New insights into the anatomo-functional connectivity of the semantic system: a study using cortico-subcortical electrostimulations. Brain, 128, 797-810.

Duncan, J. (2001). An adaptive coding model of neural function in prefrontal cortex. Nature Reviews Neuroscience, 2, 820-829.

Edwards, A. L. (1951). Balanced latin-square designs in psychological research. The American Journal of Psychology, 64, 598-603.

Fogliata, A., Rizzo, S., Reati, F., Miniussi, C., Oliveri, M., & Papagno, C. (2007). The time course of idiom processing. Neuropsychologia, 45, 3215-3222.

Fornito, A., Yücel, M., Patti, J., Wood, S. J., & Pantelis, C. (2009). Mapping grey matter reductions in schizophrenia: an anatomical likelihood estimation analysis of voxel-based morphometry studies. Schizophrenia Research, 108, 104-113.

Forstmann, B. U., Jahfari, S., Scholte, H. S., Wolfensteller, U., van den Wildenberg, W. P., & Ridderinkhof, K. R. (2008). Function and structure of the right inferior frontal cortex predict individual differences in response inhibition: A model-based approach. The Journal of Neuroscience, 28, 9790-9796.

Accepted manuscript

ACCEPTED MANUSCRIPT

Gabrieli, J., Poldrack, R., & Desmond, J. (1998). The role of left prefrontal cortex in language and memory. Proceedings of the National Academy of Sciences of the United States of America, 95, 906-913.

Galinsky, A., & Glucksberg, S. (2000). Inhibition of the literal: Metaphors and idioms as judgmental primes. Social Cognition, 18, 35-54.

Gerschlager, W., Siebner, H., & Rothwell, J. (2001). Decreased corticospinal excitability after subthreshold 1 Hz rTMS over lateral premotor cortex. Neurology, 57, 449-455.

Gibbs, R. W., & Nayak, N. P. (1989). Psycholinguistic studies on the syntactic behavior of idioms. Cognitive Psychology, 21, 100-138.

Gibbs, R., Nayak, N., & Cutting, C. (1989). How to kick the bucket and not decompose: Analyzability and idiom processing. Journal of Memory & Language, 28, 576-593.

Gibbs, R., & O'Brien, J. (1990). Idioms and mental imagery: The metaphorical motivation for idiomatic meaning. Cognition, 36, 35-68.

Glucksberg, S., Newsome, M., & Goldvarg, Yevgeniya. (2001). Inhibition of the literal: Filtering metaphor-irrelevant information during metaphor comprehension. Metaphor and Symbol, 16, 277-298.

Goldman-Rakic, P. (1995). Cellular basis of working memory. Neuron, 14, 477-485.

Hillert, D., & Buračas, G. (2009). The neural substrates of spoken idiom comprehension. Language and Cognitive Processes, 24, 1370-1391.

Hommel, B. (1993). The relationship between stimulus processing and response selection in the Simon task: Evidence for a temporal overlap. Psychological Research, 55, 280-290.

Accepted manuscript

ACCEPTED MANUSCRIPT

Iakimova, G., Passerieux, C., Denhiere, G., Laurent, J., Vistoli, D., Vilain, J., & Hardy-Bayle, M. (2010). The influence of idiomatic salience during the comprehension of ambiguous idioms by patients with schizophrenia. Psychiatry Research, 177, 46-54.

Jescheniak, J. D., & Levelt, W. J. (1994). Word frequency effects in speech production: Retrieval of syntactic information and of phonological form. Journal of Experimental Psychology: Learning, Memory, and Cognition, 20, 824-843.

Kan, I., & Thompson-Schill, S. (2004). Selection from perceptual and conceptual representations. Cognitive, Affective, & Behavioral Neuroscience, 4, 466-482.

Kaufman, L. D., Pratt, J., Levine, B., & Black, S. E. (2010). Antisaccades: a probe into the dorsolateral prefrontal cortex in Alzheimer's disease. A critical review. Journal of Alzheimer's Disease, 19, 781-793.

Ko, J., Monchi, O., Ptito, A., Bloomfield, P., Houle, S., & Strafella, A. (2008). Theta burst stimulation-induced inhibition of dorsolateral prefrontal cortex reveals hemispheric asymmetry in striatal dopamine release during a set-shifting task–a TMS–[11C] raclopride PET study. European Journal of Neuroscience, 28, 2147-2155.

Koechlin, E., Ody, C., & Kouneiher, F. (2003). The architecture of cognitive control in the human prefrontal cortex. Science, 14, 1181-1185.

Kutas, M., & Federmeier, K. D. (2011). Thirty years and counting: Finding meaning in the N400 component of the event related brain potential (ERP). Annual Review of Psychology, 62, 621–647.

Lauro, L., Tettamanti, M., Cappa, S., & Papagno, C. (2008). Idiom comprehension: A prefrontal task? Cerebral Cortex, 18, 162-170.

Accepted manuscript

ACCEPTED MANUSCRIPT

Leitão, J., Thielscher, A., Werner, S., Pohmann, R., & Noppeney, U. (2013). Effects of parietal TMS on visual and auditory processing at the primary cortical level–a concurrent TMS-fMRI study. Cerebral Cortex, 23, 873-884.

Levelt, W., Roelofs, A., & Meyer, A. (1999). A theory of lexical access in speech production. Behavioral and Brain Sciences, 22, 1-75.

Libben, M., & Titone, D. (2008). The multidetermined nature of idiom processing. Memory & Cognition, 36, 1103-1121.

Lu, C. H., & Proctor, R. W. (1995). The influence of irrelevant location information on performance: A review of the Simon and spatial Stroop effects. Psychonomic Bulletin & Review, 2, 174-207.

MacDonald, A., Cohen, J., Stenger, V., & Carter, C. (2000). Dissociating the role of the dorsolateral prefrontal and anterior cingulate cortex in cognitive control. Science, 288, 1835-1838.

McGlone, M., Glucksberg, S., & Cacciari, C. (1994). Semantic productivity and idiom comprehension. Discourse Processes, 17, 167-190.

Mashal, N., Faust, M., Hendler, T., & Jung-Beeman, M. (2008). Hemispheric differences in processing the literal interpretation of idioms: Converging evidence from behavioral and fMRI studies. Cortex, 44, 848-860.

Miller, E. (2000). The prefrontal cortex and cognitive control. Nature Reviews Neuroscience, 1, 59-65.

Miller, E., & Cohen, J. (2001). An integrative theory of prefrontal cortex function. Annual Reviews Neuroscience, 2001, 167-202.

Accepted manuscript

ACCEPTED MANUSCRIPT

Norman, D., & Shallice, T. (1986). Attention to action: Willed and automatic control of behavior. In R. Davidson, G. Schwartz, & Shapiro, D. (Eds.), Consciousness and Self-Regulation: Advances in Research and Theory (pp. 1-18). New York, NY: Plenum.

Nunberg, G., Sag, I., & Wasow, T. (1994). Idioms. Language, 70, 491-538.

Oldfield, R. (1971). The assessment and analysis of handedness: The Edinburgh inventory. Neuropsychologia, 9, 97-113.

Oliveri, M., Romero, L., & Papagno, C. (2004). Left but not right temporal involvement in opaque idiom comprehension: A repetitive transcranial magnetic stimulation study. Journal of Cognitive Neuroscience, 16, 848-855.

Papagno, C. (2001). Comprehension of metaphors and idioms in patients with Alzheimer's disease. Brain, 124, 1450-1460.

Papagno, C., & Caporali, A. (2007). Testing idiom comprehension in aphasic patients: The effect of task and idiom type. Brain and Language, 100, 208-220.

Papagno, C., Lucchelli, F., Muggia, S., & Rizzo, S. (2003). Idiom comprehension in Alzheimer's disease: The role of the central executive. Brain, 126, 2419-2430.

Papagno, C., & Vallar, G. (2001). Understanding metaphors and idioms: A single-case neuropsychological study in a person with Down syndrome. Journal of the International Neuropsychological Society, 7, 516-527.

Pascual-Leone, A. (1999). Transcranial magnetic stimulation: Studying the brain-behaviour relationship by induction of 'virtual lesions'. Philosophical Transactions of the Royal Society B: Biological Sciences, 354, 1229-1238.

Accepted manuscript

ACCEPTED MANUSCRIPT

Petrides, M., & Pandya, D. N. (1999). Dorsolateral prefrontal cortex: Comparative cytoarchitectonic analysis in the human and the macaque brain and corticocortical connection patterns. European Journal of Neuroscience, 11, 1011-1036.

R Development Core Team. (2013). R: A Language and Environment for Statistical Computing. (Version 3.0.2) [Computer Software]. Vienna: R Foundation for Statistical Computing.

Rapp, A., Mutschler, D., & Erb., M. (2012). Where in the brain is nonliteral language? A coordinate-based meta-analysis of functional magnetic resonance imaging studies. NeuroImage, 63, 600-610.

Rassiga, C., Lucchelli, F., Crippa, F., & Papagno, C. (2009). Ambiguous idiom comprehension in Alzheimer's disease. Journal of Clinical and Experimental Neuropsychology, 31, 402-411.

Ratcliff, R. (1993). Methods for dealing with reaction time outliers. Psychological Bulletin, 114, 510-532.

Ridderinkhof, K., van den Wildenberg, W., Segalowitz, S., & Carter., C. (2004). Neurocognitive mechanisms of cognitive control: The role of prefrontal cortex in action selection, response inhibition, performance monitoring, and reward-based learning. Brain and Cognition, 56, 129-140.

Rizzo, S., Sandrini, M., & Papagno, C. (2007). The dorsolateral prefrontal cortex in idiom interpretation: An rTMS study. Brain Research Bulletin, 71, 523-528.

Rodd, J. M., Davis, M. H., & Johnsrude, I. S. (2005). The neural mechanisms of speech comprehension: fMRI studies of semantic ambiguity. Cerebral Cortex, 15, 1261-1269.

Accepted manuscript

ACCEPTED MANUSCRIPT

Rommers, J., Dijkstra, T., & Bastiaansen, M. (2013). Context-dependent semantic processing in the human brain: Evidence from idiom comprehension. Journal of Cognitive Neuroscience, 25, 762-776.

Rossi, S., Hallett, M., Rossini, P., & Pascual-Leone, A. (2009). Safety, ethical considerations, and application guidelines for the use of transcranial magnetic stimulation in clinical practice and research. Clinical Neurophysiology, 120, 2008-2039.

Saur, D., Kreher, B. W., Schnell, S., Kümmerer, D., Kellmeyer, P., Vry, M. S., ... & Weiller, C. (2008). Ventral and dorsal pathways for language. Proceedings of the National Academy of Sciences, 105, 18035-18040.

Schettino, A., Lauro, L. R., Crippa, F., Anselmetti, S., Cavallaro, R., & Papagno, C. (2010). The comprehension of idiomatic expressions in schizophrenic patients. Neuropsychologia, 48, 1032-1040.

Schweigert, W. A. (1986). The comprehension of familiar and less familiar idioms. Journal of Psycholinguistic Research, 15, 33-45.

Sela, T., Ivry, R., & Lavidor, M. (2012). Prefrontal control during a semantic decision task that involves idiom comprehension: A transcranial direct current stimulation study. Neuropsychologia, 50, 2271–2280.

Shum, M., Shiller, D., Baum, S., & Gracco, V. (2011). Sensorimotor integration for speech motor learning involves the inferior parietal cortex. European Journal of Neuroscience, 34, 1817-1822.

Simon, J., & Berbaum, K. (1990). Effect of conflicting cues on information processing: The 'Stroop effect' vs. the 'Simon effect'. Acta Psychologica, 73, 159-170.

Accepted manuscript

ACCEPTED MANUSCRIPT

Simon, J., & Small A. (1969). Processing auditory information: Interference from an irrelevant cue. Journal of Applied Psychology, 53, 433.

Sprenger, S. A., Levelt, W. J., & Kempen, G. (2006). Lexical access during the production of idiomatic phrases. Journal of Memory and Language, 54, 161-184.

Swinney, D., & Cutler, A. (1979). The access and processing of idiomatic expressions. Journal of Verbal Learning and Verbal Behavior, 18, 523-534.

Tabossi, P., Fanari, R., & Wolf, K. (2009). Why are idioms recognized fast? Memory & Cognition, 37, 529-540.

Tanji, J., & Hoshi, E. (2008). Role of the lateral prefrontal cortex in executive behavioral control. Physiological Reviews, 88, 37-57.

Thompson-Schill, S., Bedny, M., & Goldberg, R. (2005). The frontal lobes and the regulation of mental activity. Current Opinion in Neurobiology, 15, 219-224.

Thompson-Schill, S., D'Esposito, M., Aguirre, G., & Farah, M. (1997). Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation. Proceedings of the National Academy of Sciences, 94, 14792-14797.

Thompson-Schill, S., D'Esposito, M., & Kan, I. (1999). Effects of repetition and competition on activity in left prefrontal cortex during word generation. Neuron, 23, 513-522.

Titone, D., Columbus, G., Whitford, V., Mercier, J., & Libben, M. (2015). Contrasting bilingual and monolingual idiom processing. Bilingual Figurative Language Processing, 171-207.

Titone, D. A., & Connine, C. M. (1994). Comprehension of idiomatic expressions: Effects of predictability and literality. Journal of Experimental Psychology: Learning, Memory, and Cognition, 20, 1126.

Accepted manuscript

ACCEPTED MANUSCRIPT

Titone, D., & Connine, C. (1999). On the compositional and noncompositional nature of idiomatic expressions. Journal of Pragmatics, 31, 1655-1674.

Titone, D., Holzman, P., & Levy, D. (2002). Idiom processing in schizophrenia: literal implausibility saves the day for idiom priming. Journal of Abnormal Psychology, 111, 313-320.

Titone, D., & Libben, M. (2014). Time-dependent effects of decomposability, familiarity and literal plausibility on idiom priming: A cross-modal priming investigation. The Mental Lexicon, 9, 473-496.

Van Petten, C., & Luka, B. J. (2006). Neural localization of semantic context effects in electromagnetic and hemodynamic studies. Brain and Language, 97, 279-293.

Volk, D. W., & Lewis, D. A. (2010). Prefrontal cortical circuits in schizophrenia. In N. Swerdlow (Ed.), Behavioral Neurobiology of Schizophrenia and Its Treatment (pp. 485-508). Heidelberg: Springer.

Wagner, A., Paré-Blagoev, E., Clark, J., & Poldrack, R. (2001). Recovering meaning: Left prefrontal cortex guides controlled semantic retrieval. Neuron, 31, 329-338.

Walsh, V., & Cowey, A. (2000). Transcranial magnetic stimulation and cognitive neuroscience. Nature Reviews Neuroscience, 1, 73-80.

Wassermann, E. (1998). Risk and safety of repetitive transcranial magnetic stimulation: Report and suggested guidelines from the International Workshop on the Safety of Repetitive Transcranial Magnetic Stimulation, June 5–7, 1996. Electroencephalography and Clinical Neurophysiology, 108, 1-16.

West, R. (1996). An application to prefrontal cortex function theory to cognitive aging. Psychological Bulletin, 120, 272-292.

Accepted manuscript

ACCEPTED MANUSCRIPT

West, R. (2003). Neural correlates of cognitive control and conflict detection in the Stroop and digit-location tasks. Neuropsychologia, 41, 1122-1135.

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

Whitney, C., Kirk, M., O'Sullivan, J., Lambon Ralph, M., & Jefferies, E. (2012). Executing semantic processing is underpinned by a large-scale neural network: revealing the contribution of left prefrontal, posterior, temporal, and parietal cortex to controlled retrieval and selection using TMS. Journal of Cognitive Neuroscience, 24, 133-147.

Wood, J., & Grafman, J. (2003). Human prefrontal cortex: Processing and representational perspectives. Nature Reviews Neuroscience, 4, 139-147.

Yeung, N. (2013). Conflict monitoring and cognitive control. In K. Ochsner & Stephen Kosslyn (Eds.), Oxford Handbook of Cognitive Neuroscience (Vol. 2, pp. 275-299). New York, NY: Oxford University Press.

Yousry, T., Schmid, U., Alkadhi, H., Schmidt, D., Peraud, A., Buettner, A., & Winkler, P. (1997). Localization of the motor hand area to a knob on the precentral gyrus: A new landmark. Brain, 120, 141-157.

Zempleni, M.-Z., Haverkort, M., & Renken, R., & Stowe, L. (2007). Evidence for bilateral involvement in idiom comprehension: An fMRI study. NeuroImage, 34, 1280-1291.

Zorzi, M., & Umiltá, C. (1995). A computational model of the Simon effect. Psychological Research, 58, 193-205.

Accepted manuscript

ACCEPTED MANUSCRIPT

Highlights

- Prior work using fMRI and rTMS conflicts regarding whether the left ventro-lateral PFC (VLPFC), a convergence zone for semantic control, is recruited during idiom comprehension.
- We examined whether a virtual lesion induced by repetitive TMS (rTMS) in the left VLPFC impaired idiom comprehension as a function of idiom familiarity and individual differences in cognitive control.
- rTMS to the left VLPFC impaired the comprehension of low-familiar idioms in individuals with high levels of cognitive control.
- These results cohere with other work showing the left VLPFC to be implicated when multiple semantic representations are viable, as in the case of low-familiar idioms. High-control individuals may be more susceptible to rTMS-induced disruptions because they are more likely to entertain multiple semantic representations during idiom processing.

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