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# Left Ventrolateral Prefrontal Cortex in Processing of Words and Sentences

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## 46.1 INTRODUCTION

Left ventrolateral prefrontal cortex (VLPFC) has attracted much attention in cognitive neuroscience, not only for its involvement in numerous cognitive operations but also for its historical significance as one of the first brain regions to be formally linked to a specific function. In the mid 19th century, Pierre Paul Broca called this area (later to be called "Broca's area") the locus for production of articulate language and the seat of motor speech (Broca, 1861, 1865).

Although modern theories of language production (i.e., the dual stream model) have revived the notion that this area might be involved in motor production by proposing its involvement in storing articulatory representations, phonetic encoding, and retrieving or generating the articulatory codes (Hickok & Poeppel, 2004, 2007), much more has come to light about VLPFC in the past few decades. These new findings do not negate the possible role of this region in motor production, but rather call for an expansion of its role in the processing of language and perhaps even in nonlinguistic tasks. For instance, VLPFC has been implicated in semantic processing (Buckner et al., 1995; Demb et al., 1995; Démonet et al., 1992; Fiez, 1997; Kapur et al., 1994; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995; McCarthy, Blamire, Rothman, Gruetter, & Shulman, 1993; Petersen, Fox, Snyder, & Raichle, 1990; Raichle et al., 1994), phonological/phonetic processing, especially when phonological segmentation and sequencing is required (Démonet et al., 1992; Démonet, Price, Wise, & Frackowiak, 1994; Fiez et al., 1995; Newman, Twieg, & Ca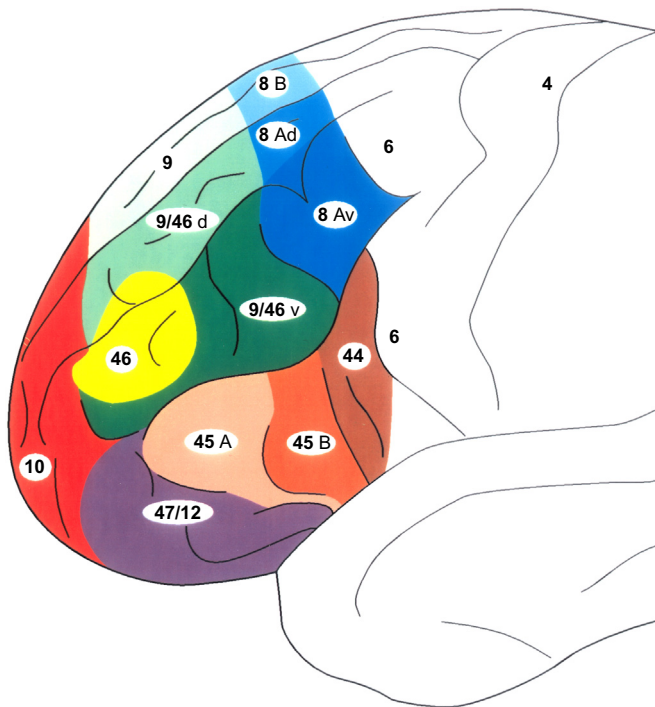rpenter, 2001; Paulesu, Frith, & Frackowiak, 1993; Price et al., 1994; Shaywitz et al., 1995; Zatorre, Evans, Meyer, & Gjedde, 1992), phoneme-to-grapheme conversional processes (Fiebach, Friederici, Müller, & Von Cramon, 2002), syntactic processing (Ben-Shachar, Hendler, Kahn, Ben-Bashat, & Grodzinsky, 2003; Embick, Marantz, Miyashita, O'Neil, & Sakai, 2000; Grodzinsky, 2000), and domain-general processes such as temporal sequencing regardless of the specific stimulus type (Gelfand & Bookheimer, 2003). Also, the term "working memory" appears frequently in the VLPFC literature (Awh et al., 1996; Paulesu et al., 1993).

Moreover, within each domain there is more than one view. For example, even among researchers who agree on VLPFC's involvement in semantic processing, there has been disagreement about whether it is involved in semantic retrieval (Demb et al., 1995; Démonet et al., 1992; Martin et al., 1995), conflict resolution (Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997), or controlled semantic processing (Wagner, Paré-Blagoev, Clark, & Poldrack, 2001). Similarly, there have been debates among proponents of VLPFC's role in syntactic processing, some of whom had a strong hypothesis for the region's involvement in a specific syntactic operation (Grodzinsky, 2000; Musso et al., 2003) whereas others argued for multiple syntactic functions being mediated by the region (Friederici, Meyer, & von Cramon, 2000). The discussion of all these functions is obviously beyond the scope of this chapter. Therefore, we focus on the role of VLPFC in semantic processing, especially in the context of language. In most of what we discuss, the nature of the tasks addresses semantic-lexical mapping; however,

some of the concepts could apply to semantic processing without lexical retrieval.

Because it is our goal to discuss not only single-word but also sentence-level processing, it is inevitable to discuss syntactic theories of VLPFC as well. We review evidence from language comprehension and production studies and, whenever possible, present converging evidence from multiple sources (neuroimaging studies, patient studies, and transcranial magnetic stimulation (TMS) studies) to build a complete picture of the circumstances that lead to VLPFC recruitment and operations that are crucially dependent on this region. The chapter begins with an overview of the anatomy of VLPFC, followed by two main sections, discussing the debates on the region's role in (semantic) the processing of single words and (semantic–syntactic) the processing of sentences. We close by offering a unifying account that best summarizes the body of evidence in the earlier sections, with some future questions to consider.

The terms Broca's area, left inferior frontal gyrus (LIFG), left inferior prefrontal cortex (LIPC), and VLPFC have sometimes been used interchangeably. It is generally accepted that Brodmann area (BA) 44 and BA 45 (corresponding roughly to pars opercularis and pars triangularis) are the cytoarchitectonic correlates of Broca's region (Aboitiz & García, 1997; Uylings, Malofeeva, Bogolepova, Amunts, & Zilles, 1999; Figure 46.1),



FIGURE 46.1    Anatomy of the VLPFC. *Figure adapted from Petrides and Pandya (2002). Reproduced with permission from Michael Petrides and Wiley-Blackwell publishing.*

although there are finer subdivisions in these areas as well, with the dorsal part of BA45 (BA45B in Figure 46.1) resembling BA44 more closely than its ventral part (BA45A in Figure 46.1; Amunts et al., 2004). VLPFC also includes BA47 (pars orbitalis), the ventral cortical area inferior and anterior to the horizontal ramus of the lateral fissure. Most of the findings in this chapter concern BA44 and/or BA45.

## 46.2  VLPFC IN SINGLE-WORD PROCESSING

Although classic psycholinguistic studies primarily conceived of VLPFC as involved in either motor processing (following Broca's suggestion) or syntactic processing, memory researchers had an altogether different idea. In PET and fMRI studies, VLPFC activation has been consistently found in a variety of tasks requiring semantic processing. Among these are living/nonliving classification (Demb et al., 1995; Gabrieli et al., 1996; Kapur et al., 1994), feature-based similarity judgment (Thompson-Schill et al., 1997; Whitney, Kirk, O'Sullivan, Ralph, & Jefferies, 2011), global similarity judgment (Thompson-Schill et al., 1997; Wagner et al., 2001), and category-based verbal fluency (Basho, Palmer, Rubio, Wulfeck, & Müller, 2007; Birn et al., 2010; Gurd et al., 2002; Paulesu et al., 1997). VLPFC activation in a wide variety of tasks requiring semantic access points strongly to its role in some aspect of semantic processing. Initially, this was hypothesized to be semantic retrieval (Demb et al., 1995; Martin et al., 1995). Starting in the late 1990s, a series of experiments pointed out the region's particular sensitivity to the *control demands* of semantic retrieval as opposed to retrieval *per se*.

The first in this series was the study by Thompson-Schill et al. (1997) in which, through three experiments, the authors showed that activation of VLPFC was much more prominent in conditions with high-selection demands. Two of these experiments concerned single-word comprehension. In the first task, subjects had to judge whether a word matched a picture either in its identity (e.g., the word CAR matching the picture of a car; low selection) or in a feature belonging to it (e.g., the word EXPENSIVE matching the picture of a car; high selection). In the second task, subjects had to judge the similarity of a probe word to a number of alternatives. In the low-selection condition, judgment was to be based on global similarity (e.g., TICK–FLEA/WELL), whereas in the high-selection condition, selection based on a specific feature—and ignoring other attributes—was necessary for making the correct choice (e.g., TOOTH–BONE/TONGUE). The third experiment was a production task. Subjects had to generate verbs in

response to nouns that induced either low competition (e.g., SCISSORS, which strongly evokes the verb CUT) or high competition (e.g., CAT, which could be associated with a number of verbs, like MEOW, PLAY, EAT, etc.) between response alternatives. In the same group of subjects, in all three tasks an overlapping area of VLPFC was found to respond more to conditions that placed higher demands on selection. Wagner et al. (2001) extended these findings by showing that it was possible to manipulate control demands even within the global similarity judgment task. Increased VLPFC activation was found when global similarity was probed for low-association items (e.g., CANDLE-HALO) compared with high-association items (e.g., CANDLE-FLAME).

Although the pattern of activation in these neuroimaging studies was suggestive of a role for VLPFC in semantic control, it remained to be seen if such control depended crucially on this prefrontal region. It was Thompson-Schill et al. (1998) who showed that patients with lesions encompassing VLPFC had trouble with the verb generation task described, but only when the noun was not strongly associated with a unique verb. They further showed that the percentage of damage to BA 44 (but not overall lesion volume or damage to dorsolateral prefrontal regions) was a significant predictor of errors in the trials with high-selection demand.

These early studies convincingly demonstrated that the picture was incompatible with VLPFC's role in pure semantic retrieval but pointed to a role in enforcing top-down control when stimulus-response associations were weak (Miller & Cohen, 2001; Norman & Shallice, 1986). Following Desimone and Duncan (1995), it was proposed that when bottom-up association is not strong enough to pick a clear "winner" among the alternatives, competition must be resolved by top-down control to bias selection toward a single representation, and VLPFC was a likely candidate for implementing this bias (Kan & Thompson-Schill, 2004; Miller & Cohen, 2001; Wagner et al., 2001). Since that time, this idea has been tested using various tasks and paradigms; some of which that are related to word processing are reviewed later.

## 46.2.1 Deciphering Words with Multiple Meanings

Every tongue contains words that carry more than one meaning, and efficient processing of language requires that speakers and listeners would be able to handle this ambiguity by flexibly retrieving the relevant meaning and suppressing the irrelevant meaning in different contexts. As such, these types of words provide a good opportunity for investigating which brain region is involved in biasing selection. Bedny, McGill, and Thompson-Schill (2008) had participants

judge the relatedness of word pairs, with some subsequent pairs containing ambiguous words (e.g., SUMMER-FAN → CEILING-FAN [same meaning]; ADMIRER-FAN → CEILING-FAN [different meaning]). Whereas posterior temporal cortex proved to be sensitive to semantic overlap regardless of ambiguity, VLPFC activity depended on the amount of semantic ambiguity.

This finding is mirrored by VLPFC patients' difficulty in efficiently selecting the appropriate meaning of ambiguous words. Bedny, Hulbert, and Thompson-Schill (2007) chose three groups of participants, patients with VLPFC damage, patients with frontal damage sparing VLPFC, and matched controls, and asked them to determine the lexicality of the third word in a triplet of words, with the second word being either a homonym or a polysemous word. Both homonyms and polysemous words have more than one meaning, although these meanings are unrelated in the case of homonyms (e.g., ceiling FAN, vs. football FAN) and related in the case of polysemous words (e.g., live CHICKEN, vs. food CHICKEN). In the triplet, the first and the third words were related to either the same meaning of the second word (e.g., BACK, PACK, BAG; consistent condition) or a different meaning (WOLF, PACK, BAG; inconsistent condition). Unlike controls and patients with non-VLPFC frontal lobe lesions, VLPFC patients' performance did not show a reliable difference between the consistent and inconsistent conditions. These patients did, however, show priming in the consistent condition compared with an unrelated baseline. This finding suggests that, in all likelihood, both meanings of the words were activated, and the activation of the context-relevant meaning benefited performance. However, the context-irrelevant meaning was not properly suppressed. This is consistent with the distinction we made earlier between semantic retrieval versus biasing competition; only the latter of which seems to depend critically on VLPFC.

Event-related potentials (ERP) findings are consistent with the results of Bedny et al. (2007). Swaab, Brown, and Hagoort (1998) presented participants with sentences that primed either the dominant or the subordinate meaning of a homonym, or was unrelated to the target (e.g., target word: RIVER; consistent prime: "The man planted a tree on the bank"; inconsistent prime: "The man made a phone call to the bank," and unrelated prime: "The boy petted the dog on the head"). The target word (RIVER) was always related to the subordinate meaning of the homonym (BANK) and followed the sentence with either a short (100 ms) or a long (1,250 ms) ISI. N400 (as a measure of violation of semantic expectancy) was measured in response to the target word. The logic was that proper priming of the meaning should decrease the amplitude of N400 in the

consistent, but not in the inconsistent, condition. Healthy controls showed this pattern. Broca's patients, the majority of whom had prefrontal lesions, however, showed evidence of reduced N400 under *both* conditions for the short ISI, meaning that context had not successfully abolished the irrelevant meaning. In the longer ISI, some of the patients no longer exhibited this abnormal pattern, implying that given enough processing time, suppression of the irrelevant meaning was slowly achieved, perhaps through a complementary/compensatory network. More recently, Vuong and Martin (2011) supported this position by showing that a patient with damage that included VLPFC damage was considerably slower than two patients with non-VLPFC lesions in using context to bias toward the subordinate meaning of an ambiguous word. However, when tested using balanced ambiguous words, this patient, similar to the other two patients and healthy controls, was unimpaired in using context to resolve ambiguity.

## 46.2.2 Verbal Fluency

Verbal fluency tasks are among the oldest neuropsychological tasks for assessing the integrity of memory and language. There are two categories of verbal fluency tasks. In the *semantic* verbal fluency task a semantic cue is provided, based on which the individual must search for as many words as possible in a short duration of time (e.g., "Name all the animals you can."). In the *phonological* variant, the cue is phonological (e.g., "Name all the words you can that start with B."). Given the very different nature of the search in these two tasks, it is not surprising that semantic and phonological verbal fluency tasks rely, at least in part, on different cognitive architectures. For example, Martin, Wiggs, Lalonde, and Mack (1994) found that the semantic verbal fluency task is subject to interference from object recognition, whereas phonological verbal fluency task performance is sensitive to motor sequence tasks. Likewise, each variant of the task induces preferential activation in a certain frontal region (Birn et al., 2010). However, despite their unique elements, both tasks have been shown to activate VLPFC, although there is disagreement on whether they activate the same or different subpopulation of neurons in this region (Frith, Friston, Liddle, & Frackowiak, 1991; Mummery, Patterson, Hodges, & Wise, 1996; Paulesu et al., 1997).

The verbal fluency task provides a unique opportunity to study two cognitive operations within the verbal fluency task. At any given point during this task it is possible to continue retrieving names from the same subcategory as the previous item or to switch to a new subcategory. For example, when prompted to name as many animals as you can, you may cue yourself by starting with the subcategory of farm animals. The ability to retrieve many names in one subcategory is called *Clustering*. Even when you have good clustering abilities, at some point you will run out of names of farm animals, and to maximize your output you must switch to a new subcategory, for example, wild animal. The ability to switch from one subcategory to another is called *Switching*. It has been proposed that clustering reflects the intactness of semantic knowledge, whereas switching reflects the biasing ability. In tandem with this proposition, damage to the temporal cortex typically causes clustering deficits and damage to the left prefrontal cortex is associated with switching deficits (Chertkow & Bub, 1990; Troyer, Moscovitch, & Winocur, 1997). In two experiments, Hirshorn and Thompson-Schill (2006) showed that it was the switching aspects of the task that elicited VLPFC activation. In Experiment 1, subjects were told either to switch on every trial or to freely produce words given a category cue. In Experiment 2, they were given instructions for free category-based name generation while pushing a button but were asked to push a different button whenever they switched to a new category. In both cases, VLPFC activation was linked directly to switching.

On the lesion side, lesions in the frontal cortex have long been known to cause impairments in performing verbal fluency tasks (Baldo & Shimamura, 1998; Janowsky, Shimamura, Kritchevsky, & Squire, 1989; Owen, Downes, Sahakian, Polkey, & Robbins, 1990; Perret, 1974; Robinson, Shallice, Bozzali, & Cipolotti, 2012; Stuss et al., 1998; Troyer, Moscovitch, Winocur, Alexander, & Stuss, 1998), and some have specifically pinned the effect down to the VLPFC (Novick, Kan, Trueswell, & Thompson-Schill, 2009).

## 46.2.3 Picture Naming and the Need for Control

This discussion raises the question of where the boundary is for the need for top-down control. Does naming pictures, for example, require top-down control? This question is particularly important because picture naming is the single most important neuropsychological test in localizing deficits in lexical retrieval. Furthermore, in many cases a patient's response pattern in picture naming allows for predictions to be made about their other production abilities, such as word repetition (Nozari & Dell, 2013; Nozari, Kittredge, Dell, & Schwartz, 2010). But is picture naming measuring lexical-semantic retrieval or controlled selection? The reports are mixed. Although some have found activation of VLPFC in picture naming (Murtha, Chertkow, Beauregard, Dixon, & Evans, 1996; Murtha, Chertkow, Beauregard, & Evans, 1999), some have not (Etard et al., 2000). We briefly discuss two factors, name agreement and context, that speak directly to the

control aspect of picture naming, and help reconcile these seemingly disparate findings. Novick et al. (2009; Experiment 2) showed that a patient with VLPFC lesion was significantly impaired in naming pictures with low name agreement (e.g., COUCH/SOFA) compared with controls and patients with frontal lesions sparing VLPFC. However, the same patient showed no marked deficits in naming pictures with high name agreement. Given what has been discussed earlier in this chapter, the explanation for this finding should be clear. When bottom-up cues are not strong enough to unequivocally select a unique representation, VLPFC is needed to implement top-down control and help with selection.

But even when the picture itself is associated with a unique label, the context in which the name is to be retrieved can modulate retrieval demands. When pictures are named in the context of same-category items (e.g., DOG, HORSE, LION), they are named more slowly in the neurologically intact adults (Belke, Meyer, & Damian, 2005; Damian, Vigliocco, & Levelt, 2001; Kroll & Stewart, 1994) and with more errors in aphasic patients with left frontal lesions (McCarthy & Kartsounis, 2000; Schnur, Schwartz, Brecher, & Hodgson, 2006). These tasks control for pure lexical retrieval because picture naming in a semantically heterogeneous context (e.g., DOG, TRUCK, APPLE) is also assessed and acts as a baseline for comparison. While the exact mechanisms of this *semantic blocking effect* are disputed (Howard, Nickels, Coltheart, & Cole-Virtue, 2006; Oppenheim, Dell, & Schwartz, 2010), there is consensus that competition is higher in the semantically homogenous context, and both neuroimaging and lesion studies link the effect to VLPFC (Schnur et al., 2009). Incidentally, the Murtha et al. (1996, 1999) picture naming study administered only a homogenous block of animals to subjects to name, whereas Etard et al. (2000) used a heterogenous block. Given the well-established semantic blocking effect, it is not surprising that picture naming designs that strongly tap into the effect activate VLPFC. In summary, picture naming seems to require top-down support from VLPFC primarily under conditions of high competition.

## 46.2.4 TMS Studies

So far, we have shown that neuroimaging and patient studies converge on the biasing role of VLPFC in semantic/lexical retrieval. We end this section by providing a brief review of the TMS studies related to this issue. Devlin, Matthews, and Rushworth (2003; Experiment 2) presented subjects with single words and asked them to make a natural/man-made judgment for each word. In a control perceptual task, subjects judged whether the horizontal line above the word was shorter than the word. They showed that TMS to the anterior portion of VLPFC interfered with the semantic, but not the perceptual, decision. This finding, along with higher activation of anterior VLPFC in making semantic versus phonological judgments (Devlin et al., 2003; Experiment 1), was taken as evidence for this region's contribution to making semantic judgments. Gough, Nobre, and Devlin (2005) provided additional support for this finding by showing that TMS over the anterior VLPFC caused a selective impairment in a semantic (synonym judgment) as opposed to a phonological (homophone judgment) task, whereas the opposite pattern was found when posterior VLPFC was stimulated (see also Wig, Grafton, Demos, & Kelley, 2005) for a demonstration of eliminated priming as a function of encoding under TMS).

The direct involvement of VLPFC in biasing semantic selection was also demonstrated in a number of recent TMS studies. Hindy, Hamilton, Houghtling, Coslett, and Thompson-Schill (2009) used TMS and computer-mouse tracking to examine the role of VLPFC in semantic processing. In each trial, two words appeared on the screen, one of which was better matched to a probe word that appeared with some delay, and participants had to move the mouse toward the correct response. Either the probe was strongly associated with the response (e.g., KING-HOOK; probe = QUEEN) or this association was weak (e.g., CARDS-HOOK; probe = QUEEN). Repetitive TMS was delivered soon after the onset of the first two words and before the appearance of the probe item. The results showed greater deviation of mouse movement trajectories toward the incorrect response when the association was weak, compatible with the hypothesized role of VLPFC in biasing competition toward the correct meaning (however, the effect was not found when the congruency between the stimuli and the probe item was manipulated). Importantly, when the delay between the response and target words was removed (and TMS was delivered afterwards), the effect disappeared. Hindy et al. (2009) suggested that the disappearance of the effect with this timing manipulation implies that the contextually appropriate association is formed, and conflict is already resolved before receiving TMS. In a conceptually similar study, Whitney et al. (2011) used a design similar to that of Wagner et al. (2001), in which subjects had to select a word that had either a strong (e.g., PEPPER) or a weak (e.g., GRAIN) association with the probe word (SALT). Although performance in the strong-association condition was unaffected by TMS over VLPFC, stimulation disrupted performance in the low-association condition. Similar to the results of Devlin et al. (2003), a control (nonsemantic) judgment task was insensitive to TMS effects in this area (see also Whitney, Kirk, O'Sullivan, Ralph, & Jefferies, 2012).

To summarize, we reviewed evidence for the possible role of VLPFC in comprehension and production of single words and showed that while this region does have an involvement in semantic/lexical retrieval, this involvement appears to be specific to situations in which there is a need for biasing competition through top-down control.

## 46.3 VLPFC IN SENTENCE PROCESSING

Although the role of VLPFC was being investigated in semantic processing mostly by memory researchers, many linguists and psycholinguists were attempting to understand the role that VLPFC played in processing syntax. The initial motivation for the various syntactic hypotheses might have stemmed from the clinical profile of Broca's aphasia (Grodzinsky, 2000), an impairment that is characterized by agrammatic speech without marked semantic difficulties. There was a major problem with this inference. Damage to Broca's area is neither sufficient nor necessary for generating symptoms constituting Broca's aphasia. Damage restricted to Broca's area leads only to a transient mutism with spontaneous recovery (Levine & Mohr, 1979; Mohr et al., 1978). However, Broca's aphasics' lesions often extend beyond BA 44 and BA 45 to involve some parts of BA 6, BA 8, BA 9, BA 10, and BA 46, as well as the underlying white matter and basal ganglia (Damasio, 1992; Dronkers, Plaisant, Iba-Zizen, & Cabanis, 2007).

However, regardless of whether the profile of Broca's aphasia is informative about the role of Broca's area, a large number of neuroimaging studies have also implicated VLPFC in "syntactic processing" (see Kaan & Swaab, 2002, for an excellent review). Here, we use the general framework used by Kaan and Swaab (2002) to review the evidence for a syntactic role of VLPFC.

### 46.3.1 Syntactic Complexity

The first group of studies constitutes experiments comparing syntactically simple versus syntactically complex sentences using a variety of manipulations (Caplan, Alpert, & Waters, 1998, 1999; Cooke et al., 2002; Dapretto & Bookheimer, 1999; Fiebach, Schlesewsky, & Friederici, 2001; Inui et al., 1998; Keller, Carpenter, & Just, 2001; Michael, Keller, Carpenter, & Just, 2001; Stowe et al., 1998; Stromswold, Caplan, Alpert, & Rauch, 1996). For example, Caplan et al. (1999) had subjects judge the plausibility of cleft object and cleft subject sentences (e.g., "It was the actress that the award thrilled" vs. "It was the award that thrilled the actress") and found increased VLPFC activation when subjects processed the cleft object sentences. Although these two

sentences are close in meaning in the sense that they both convey that the actress was thrilled by the award, they are different in their syntactic forms, making VLPFC a suspect in processing syntactic complexity. However, Cooke et al. (2002) failed to find increased VLPFC activation in object-relative clauses with short antecedent gaps (e.g., "The flower girl who Andy punched in the arm was 5 years old"), but they did find it when the gap was long (e.g., "The messy boy who Janet, the very popular hairdresser, grabbed was extremely hairy."). In line with this, Fiebach et al. (2001) showed that when the case marker disambiguated the thematic roles in sentences containing relative clauses (as is the case in German), it was only the long-distance dependencies that induced VLPFC activation. This led to the proposal that VLPFC mediates *syntactic working memory*. However, it is unclear how the finding of Caplan et al. (1999) would fit into this account.

Moreover, Chen, West, Waters, and Caplan (2006) showed that when length and syntactic structure were kept constant, higher activation of VLPFC was found when the subject of the relative clause was inanimate (e.g., "The golfer that the lightning struck survived the incident") compared with when it was animate (e.g., "The wood that the man chopped heated the cabin."). Neither syntactic ambiguity nor syntactic working memory can be blamed for this difference. Corroborating the antisyntactic evidence were findings of Keller et al. (2001), who showed that syntactically complex sentence with object-relative clauses (e.g., "The boy who the doctor visited had contracted pneumonia") actually elicited *less* activity in VLPFC compared with syntactically simple sentences that contained a temporarily ambiguous word (e.g., "The desert trains [= noun] usually are late"; "The desert trains [= verb] its inhabitants to conserve their resources"). An innovative study in this genre was conducted by Dapretto and Bookheimer (1999), who claimed that their design allowed for teasing apart semantic from syntactic processing. They asked subjects to make same/different judgments for sentences such as "The bridge is west of the airport" paired with what the authors considered either a semantically different sentence (e.g., "The bridge is west of the river") or a syntactically different sentence ("West of the bridge is the airport"). VLPFC was selectively implicated for the syntactically different sentences. However, the syntactically different sentences also perform different meanings ("The bridge is west of the airport" does not mean that "West of the bridge is the airport"). It is therefore unlikely that this design can single-out syntactic processing.

One of the most famous syntactic accounts of VLPFC, based on syntactic complexity, is its role in syntactic (or *transformational*) movements (Grodzinsky, 1995, 2000). This account proposes that when faced with a sentence

like "Which man did the woman like?", the parser would create a placeholder (trace) to the right-hand side of the verb to simulate an active sentence structure: "[Which man] did the woman like {trace}?". By establishing a common index between the trace and its antecedent (which man), the parser recognizes the antecedent as the theme of the verb "like." Following this proposal, Grodzinsky (2000) claimed that in Broca's aphasia, all traces of movements are deleted and, primarily based on this assumption, concluded that Broca's area handles exclusively intrasentential dependency relations. Grodzinsky's theory has received criticism not only for equating Broca's aphasia with Broca's area, an issue that we touched on earlier in this chapter but also because of its oversight in explaining the full picture of Broca's aphasia that it targets (see Grodzinsky, 2000 for full commentaries). For one thing, there are Broca's patients who perform better than chance in comprehension of certain transformationally derived passives (Balogh & Grodzinsky, 1996; Druks & Marshall, 1995; Hickok & Avrutin, 1995; Saddy, 1995). The most serious criticism for the theory, though, is the finding that the deficits in such patients is not limited to processing sentences with syntactic structures requiring transitional movements. Agrammatic patients can have problems with active sentences, too, as long as the semantic roles are reversible. Schwartz, Saffran, and Marin (1980), among others, have reported such deficits when semantic symmetry is possible around a verb (e.g., "The dancer applauds the clown") or around a spatial preposition (e.g., "The square is above the circle").

To summarize, VLPFC is recruited for processing of certain syntactic complexities, but its activation does not seem to be either necessary for or limited to all syntactically complex sentences. It is worth mentioning that the activation of VLPFC in difficult sentences has been attributed to subvocal rehearsal, which presumably helps with parsing (Paulesu et al., 1993; Smith & Jonides, 1999). To test this hypothesis specifically, Caplan, Alpert, Waters, and Olivieri (2000) investigated VLPFC activation in subject-relative and object-relative sentences under concurrent articulation conditions (which seriously reduce the chance of subvocal rehearsal) and showed that the differential activation of VLPFC for object-relative sentences survived this manipulation. It is therefore unlikely that this explanation sufficiently justifies the nature of VLPFC's involvement in these cases.

## 46.3.2 Anomalous Sentences

Another category of studies aiming at semantic—syntactic comparison of VLPFC involves presenting anomalous sentences. Many such studies have failed to show a syntax-specific role for this cortical region (Indefrey, Hagoort, Herzog, Seitz, & Brown, 2001; Kuperberg et al., 2000; Newman, Pancheva, Ozawa, Neville, & Ullman, 2001; Ni et al., 2000; Nichelli et al., 1995; cf., Embick et al., 2000). In some cases VLPFC was not recruited when detecting syntactic anomalies such as "Trees can grew," and in some other cases detection of syntactic and semantic anomalies was not dissociable. Also, the choice of baseline should be taken into account when interpreting claims about the exclusivity of VLPFC's processing to syntax. For example, Moro et al. (2001) showed VLPFC's selective activation during detection of syntactic anomalies, but the baseline for comparison was detection of phonotactic and orthographic anomalies. To attribute greater VLPFC activation in detecting syntactic over, for example, phonotactic anomalies, one must assume that the cognitive processes required for detecting these two types of violation are the same, except for the materials. This is very unlikely to be the case because spotting syntactic errors, for example, noun—verb agreement errors, requires keeping track of earlier parts of the utterance, whereas phonotactic violations can be detected without any memory of what has been stated earlier. In fact, there is now ample evidence that semantic and pragmatic violations do recruit VLPFC (Hagoort, Hald, Bastiaansen, & Petersson, 2004; Kiehl, Laurens, & Liddle, 2002; Kuperberg, Holcomb, et al., 2003; Kuperberg, Sitnikova, Caplan, & Holcomb, 2003; Newman et al., 2001; Ni et al., 2000; see also Marini & Urgesi, 2012 for a TMS study). Baumgaertner, Weiller, and Büchel (2002) took this one step further by showing that unexpected sentence endings, even if they do not qualify as violations, elicit activation in VLPFC.

## 46.3.3 Other Semantic—Syntactic Comparisons

Another category of studies speaking to a semantic—syntactic differentiation in the role of VLPFC compared either word lists to sentences or meaningful sentences to jabberwocky and syntactic prose. Kaan and Swaab (2002) point out that the studies in this category that have failed to identify VLPFC (Kuperberg et al., 2000; Mazoyer et al., 1993; Stowe et al., 1998; 1999) outnumber the studies that have reported a positive effect (Bottini et al., 1994) and point to task-specific demands for recruiting VLPFC in the latter cluster.

## 46.3.4 Ambiguity

Although there is simply too much evidence to deny the involvement of VLPFC in some aspect of semantic processing, it is also clear that there are some syntactic structures that elicit VLPFC activation more than others, as pointed out in the *syntactic complexity* section. Here, we separately review a subset of these

studies, focusing on garden path sentences (temporarily ambiguous sentences that initially lead to an incorrect interpretation), because they have been particularly useful in reconciling the semantic−syntactic debate over the role of VLPFC. We mentioned the Keller et al. (2001) study showing VLPFC activation when subjects encountered sentences containing ambiguous words like TRAIN. Minimizing the differences between surface forms of sentences, Mason, Just, Keller, and Carpenter (2003) used a similar logic by using ambiguous words like WARNED in the following sentences and observed the following activation pattern in VLPFC: a > b > c.

**a.** *The experienced soldiers warned about the dangers conducted the midnight raid. (ambiguous verb, subordinate form)*
**b.** *The experienced soldiers warned about the dangers before the midnight raid. (ambiguous verb, dominant form)*
**c.** *The experienced soldiers spoke about the dangers before the midnight raid. (unambiguous verb)*

When there was a single possible interpretation of the verb (i.e., spoke = past tense, active), VLPFC's role in parsing was minimal. When there were alternative meanings to be considered, VLPFC activation increased to bias toward one of the two interpretations (i.e., warned = past tense, active or passive). The maximum involvement of VLPFC was observed when the correct interpretation required biasing toward the subordinate meaning of an ambiguous verb (i.e., warned = passive; see Garnsey, Pearlmutter, & Myers, 1997, for a discussion of verb bias).

A few years after the Mason et al. study, January, Trueswell, and Thompson-Schill (2009) presented the first clear demonstration for the involvement of the same cortical region in processing both syntactic and nonsyntactic high-conflict tasks. These authors demonstrated within-subject overlap in neural substrates of processing garden path sentences and the word Stroop task, localizing both effects to VLPFC. Studies of patients with VLPFC lesions confirm that they have problems recovering from the wrong interpretation of sentences that initially induce a bias toward the incorrect meaning (Novick et al., 2009; Novick, Trueswell, & Thompson-Schill, 2005). The same patients show selective impairment in suppressing interference in a memory task (Novick et al., 2009; see also Hamilton & Martin, 2005).

But does VLPFC respond to the ambiguous word itself, or to the need for revision (i.e., the disambiguating information)? Fiebach, Schlesewsky, Lohmann, Von Cramon, and Friederici (2005) found greater VLPFC activation when disambiguating information came later, as opposed to earlier, in the sentence. This is expected if VLPFC starts the biasing process at the moment the parser encounters an ambiguity and continues to update the bias as more cues accumulate. If the initial commitment to a meaning is incorrect, then the later the disambiguating information comes in, the farther the bias in the incorrect direction, the more work needed to shift the competition in favor of the alternative meaning, and, hence, the greater activation in the delayed disambiguation condition. Compatible with this interpretation, Rodd, Johnsrude, and Davis (2012) manipulated the relative timing of the ambiguous word and the disambiguating information and showed VLPFC activation by the ambiguous word and by the subsequent disambiguating information. In contrast, left inferior temporal gyrus responded only to the disambiguating information.

The evidence strongly suggests that when there is need for biasing interpretation toward one of the two meanings, VLPFC is activated, especially if the favored meaning turns out to be incorrect. If this is really the role of this region, then the bias need not be induced by syntax; semantics also should be able to create the incorrect bias. Recently, Thothathiri, Kim, Trueswell, and Thompson-Schill (2012) demonstrated that this is true. By keeping the verb constant in an unambiguous syntactic structure and changing the content nouns around the verb, they evaluated parsing of three types of sentences (a−c in the following sentences). The pattern of VLPFC activation was as follows: a > b > c.

**a.** *The journalist was interviewed by the undergraduate. (violation of the usual role of journalist)*
**b.** *The patient was interviewed by the attractive man. (neutral roles)*
**c.** *The celebrity was interviewed by a reporter. (congruent with the usual role of reporter)*

Although there is no ambiguity in these sentences, violation of the usual semantic roles recruits VLPFC proportionally to the degree of violation. Similarly, Saffran, Schwartz, and Linebarger (1998) reported that patients with agrammatic aphasia exhibited high error rates even with syntactically simple sentences when semantic information contradicted the correct thematic role assignment (e.g., "The deer shot the hunter"), but the exact site of lesion was not specified for the patients in this study.

## 46.4 SUMMARY

### 46.4.1 Against a Rigid Semantic−Syntactic Distinction in VLPFC

Our goal for organizing this chapter into two sections was to better classify studies pertaining to the role of VLPFC in single-word versus sentence proessing. In so doing, we also captured the spirit of a

fundamental debate over the role of VLPFC, namely the semantic–syntactic debate. In the first section, we discussed an abundance of evidence from neuroimaging, TMS, and lesion studies converging on the role of VLPFC in biasing competition during semantic/lexical selection in the absence of any syntax-like structure. In the second section, we discussed studies that directly pitted semantic processing against syntactic processing in VLPFC and showed that the evidence for a pure syntactic account is sparse.

Our contention is that drawing a hard line between semantic and syntactic processing in understanding the role of VLPFC in language processing is not very useful. By this assertion, we do not mean to deny that semantic and syntactic aspects of language processing are distinct and can be teased apart, but that given the empirical evidence, this distinction does not seem critical to VLPFC operations. ERP studies have shown that both syntactic violations (e.g., "at breakfast the boys would eats...") and certain semantic violations in the absence of syntactic violations ("at breakfast the eggs would eat...") evoke a positivity called P600 (Kuperberg, 2007; Kuperberg, Caplan, Sitnikova, Eddy, & Holcomb, 2006; Kuperberg, Holcomb, et al., 2003; Kuperberg, Sitnikova, et al., 2003). Interestingly, even though these two sentence types are different from violations of world knowledge, such as "The Dutch trains are white..." (Hagoort et al., 2004), or expected events "...at breakfast the boys would plant...," which elicit N400 instead, all of these violations activate VLPFC (Kuperberg, Sitnikova, & Lakshmanan, 2008).

What is the cognitvie explanation for this? Modern theories of language comprehension (MacDonald, Pearlmutter, & Seidenberg, 1994) propose that on encountering a sentence, multiple sources of information (syntactic, semantic, pragmatic, etc.) are triggered and collaborate to derive the meaning. Activation of information in each domain is probabilistic and frequency-dependent, and convergence of information from these multiple domains leads to proper comprehension of a sentence. Because the ultimate goal is to arrive at a coherent meaning supported by all cues, any type of information, if it creates a bias toward an interpretation that clashes with other types of information, leads to conflict, and this conflict requires top-down control to be resolved. The source of initial incorrect bias could be syntactic (e.g., in the case of less frequent object-relative clauses without strong semantic cues), semantic (e.g., when the world knowledge is incongruent with the thematic roles, like celebraties photographing paparazzi), or perhaps other (e.g., pragmatic and prosodic). Regardless, on encountering potential for multiple interpretations, VLPFC is activated to use the existing information to create the bias and continues to do so until conflict is minimized.

If VLPFC fails, due to lesion or temporary deactivation via TMS, then top-down control is significantly reduced and processing would follow bottom-up cues, giving rise to the difficulty that VLPFC patients have with sentences, the correct interpretation of which requires overriding a strong semantic–syntactic cue. Complementary to this picture are cases where bottom-up cues are limited. Although a sentence bombards the comprehension system with multiple external cues, production is much more internally driven. Thus, the speaker must use top-down control to successfully initiate (and to fluently continue) the generation of concept/linguistic materials, except for cases when a strong bottom-up cue is presented (e.g., a picture of an object with a unique label), eliminating the need for top-down biasing.

## 46.4.2 A New "Broca's" Aphasia

Earlier in this chapter we alluded to the fact that Broca's aphasia does not necessarily correspond to pathology in Broca's area. In this section, we present other clinical profiles of aphasia that have stronger ties to VLPFC lesions. First, we discuss the revival of an old profile described by Alexander Luria, called "dynamic aphasia" (Luria, 1970, 1973; Luria & Tsvetkova, 1968), which has been directly linked to VLPFC damage. Next, we discuss a syndrome called Semantic Aphasia (SA), also seen in VLPFC patients, although certain temporoparietal regions can induce similar symptoms. Our goal is not to argue that these two are distinct syndromes. In fact, it is quite likely that the patients reported under these two labels have similar clinical deficits; however, to date they have been studied and discussed under different literature.

A typical dynamic aphasic profile is portrayed by a patient described by Robinson, Blair, and Cipolotti (1998). This patient had a frontal meningioma that impinged on BA 45 and presented with no impairment in simple picture naming, word repetition, comprehension, or reading, but who did have markedly decreased spontaneous or propositional speech. In multiple experiments, the authors showed that the patient was unimpaired in generating words or phrases given a strong cue that limited the possible responses, and also was severely impaired under conditions where the cue was not strongly associated with a unique response (see Robinson, Shallice, & Cipolotti, 2005, for a similar report). It is worth mentioning that the patient reported in Robinson et al. (1998) had a lesion that also impacted the dorsolateral PFC (DLPFC). Alexander (2006) has also considered lesions of DLPFC to be relevant to symptoms of dynamic aphasia. To investigate exactly which aspect of the impairment in dynamic aphasia was linked to the VLPFC, Robinson,

Shallice, Bozzali, and Cipolotti (2010) extended their case study to a group study. In this new study, patients with VLPFC damage were compared with patients with frontal lesions sparing VLPFC and patients with posterior lesions. Compared with the other two groups, VLPFC patients showed selective impairment in sentence generation tasks only when stimuli activated multiple conceptual propositions that competed with each other for selection. For example, VLPFC patients were impaired in generating sentences from high-frequency words, but not from low-frequency words and proper nouns, because the latter two are more constraining in their associations. In contrast, when the lesion spared VLPFC (i.e., non-VLPFC and the left temporal groups), the patients did not show sensitivity to the number of possible propositions.

Impairment in this experimental task was shown to be predictive of the clinical problem. VLPFC patients' scores in the high-frequency minus low-frequency and in the high-frequency minus proper noun conditions showed a reliable correlation with their spontaneous speech rate. In keeping with this, Blank, Scott, Murphy, Warburton, and Wise (2002) found that BA 44 showed greater activation under conditions of propositional compared with nonpropositional speech (i.e., counting and overlearned nursery rhymes). However, it must be pointed out that based on these findings, Robinson et al. (2010) concluded that VLPFC has a fundamental role in selection for conceptual propositions, as opposed to selection during lexical retrieval. Given the evidence reviewed in earlier sections, we are skeptical about the exclusivity of the role of VLPFC to conceptual biasing. For instance, under this account, it is unclear why VLPFC lesions would cause impairment in naming a picture COUCH/SOFA when the "concept" is right in front of the patient. However, we concur that profile of dynamic aphasia is compatible with the perspective taken in this chapter on the role of VLPFC.

Another clinical syndrome that has been recently linked to VLPFC is SA (Jefferies & Ralph, 2006), a deficit that is meant to be contrasted with Semantic Dementia (SD). SD, which generally results from bilateral damage (often of the atrophic type) to anterior temporal lobes, affects conceptual knowledge in verbal and nonverbal domains across different sensory modalities (Bozeat, Lambon Ralph, Patterson, Garrard, & Hodges, 2000; Coccia, Bartolini, Luzzi, Provinciali, & Lambon Ralph, 2004; Luzzi et al., 2007). Thus, the hallmark of SD is that failure to activate a concept is stable across tasks and processing modalities (Bozeat et al., 2000; Jefferies & Ralph, 2006). TMS studies on healthy controls corroborate this assertion (Pobric, Jefferies, & Ralph, 2007; Ralph, Pobric, & Jefferies, 2009). In contrast to SD, SA patients have intact

conceptual knowledge, but controlling that knowledge has become dysregulated. These patients usually have poststroke lesions in the VLPFC, although it has been reported that lesions in inferior parietal cortex (i.e., BA 39/40) and posterior temporal (especially temporoparietal junction) can create similar symptoms, suggesting that semantic control is achieved through a distributed network (Whitney et al., 2012). Importantly, SA patients differ from SD patients in their inconsistent performance on the same items when the control demands of the task change, and their picture naming performance shows great sensitivity to constraining or distracting cues.

Deficits of SA patients closely mirror what we discussed as VLPFC's function. For example, Noonan, Jefferies, Corbett, and Ralph (2010) performed four experiments in a group of SA patients, three of which are in line with the studies previously discussed in this chapter. In Experiment 1, participants had to judge which of three alternatives was closest in meaning to a probe item. The semantic distance between the probe item (CHIPMUNK) and the target was manipulated to be low (e.g., SQUIRREL) in half of the trials and high (e.g., BEE) in the other half, whereas the two distractors were kept the same (and unrelated to both the probe and the target). In Experiment 2, they examined synonym and antonym judgments when the associative strength between the probe (e.g., HAPPY/NEAT) and one of the distractors was either stronger or weaker than the association between the probe and the target (e.g., HAPPY−SAD [distractor] > HAPPY−CHEERFUL [target]; NEAT−MESSY [distractor] < NEAT−TIDY [target]). Consistent with the past findings, SA patients showed selective impairment when the correct response required biasing towards the weak association. In Experiment 4, participants were asked to select which of four words was related in meaning to a probe word presented at the top of the page. In half of the trials, the target referred to the dominant meaning of the probe word (FIRE → HOT). In the remaining trials, the target word was related to the subordinate meaning of the probe word (FIRE → RIFLE) while distractors remained the same. Three cue conditions preceded these trials: no cues, correct cues (e.g., "I lit a fire" → HOT), or miscues (e.g., "Fire at will" → HOT). SA patients showed great difficulty activating the less frequent meaning, and this was the condition that specifically benefitted from cueing.

On the production side, the cue/miscue paradigm has been used to probe the sensitivity of SA patients to constraining and distracting information. Jefferies, Patterson, and Ralph (2008) showed that phonological onset cues (e.g., /k/) when naming pictures (e.g., a cup) were very useful in helping SA patients overcome their difficulty in suppressing competing

names (e.g., tea). Noonan et al. (2010; Experiment 3) showed that the opposite manipulation in the cuing paradigm of Jeffries et al. (2008) does yield the opposite effect. Miscuing the picture name (e.g., /t/ for the picture of a cup) impaired the SA patients' ability to name the pictures correctly and elicited additional semantic errors.

It is noteworthy that semantic control deficits in SA patients are not restricted to the verbal domain. Corbett, Jefferies, Ehsan, and Ralph (2009) compared object use in SD and SA patients and found that SD, but not SA, patients' performance was sensitive to item frequency and was consistent irrespective of task demands. Straightforward object use demonstration, for example, was relatively intact in SA patients in comparison with much poorer performance on an executively demanding, mechanical-puzzles task (see also Corbett, Jefferies, & Ralph, 2009).

## 46.5 CONCLUDING REMARKS AND FUTURE AVENUES

Although left temporal cortex is consistently implicated in storing long-term representations of knowledge (Binder, Desai, Graves, & Conant, 2009; Indefrey & Levelt, 2004; Vigneau et al., 2006), VLPFC seems to mediate processes necessary for controlling the use of this knowledge. We reviewed evidence from multiple sources in single-word and sentence production and comprehension consistent with a crucial role of this region in implementing top-down biasing at the semantic/lexical level. It is important to point out that this is not restricted to the language domain. VLPFC's involvement has been shown in selecting the target among nontarget items in target detection tasks, even when items are complex symbols without known lexical labels (Hampshire, Duncan, & Owen, 2007). More generally, VLPFC has been proposed as a critical part of a system involved in processing hierarchical structure of goal-directed behavior (Koechlin & Jubault, 2006).

Although we have made considerable progress in understanding the role of VLPFC in processing language, much remains to be explored. We close by posing four main questions that we consider to be excellent avenues for promoting our understanding of the role of VLPFC in language:

1. How many stages are there in (controlled) lexicosemantic retrieval, and which stage/stages requires VLPFC? Badre and Wagner (2007) proposed that VLPFC implements semantic control in two steps. Step 1 constitutes controlled access to stored representations when bottom-up input is not enough. Step 2 operates postretrieval and is thought to bias competition among representations that have been activated during Step 1. A similar idea has been expressed by Thompson-Schill and Botvinick (2006) using a Bayesian framework. According to Badre and Wagner (2007), both steps recruit VLPFC, albeit different parts of it (BA 47 and BA 45, respectively; Whitney et al., 2012). The exact computations by which this is achieved are not clear.

2. Are subdivisions of VLPFC specialized based on different materials or different processes? An example of a material-based parcellation in the context of language is the semantic-phonological distinction, born out of the differential sensitivity of the posterior parts of VLPFC to phonological, and the anterior parts to semantic processing (Devlin et al., 2003; Gold, Balota, Kirchhoff, & Buckner, 2005; Gough et al., 2005; Poldrack & Wagner, 2004). Studies of statistical mapping between speech errors and lesion sites using Voxel-based Lesion-Symptom Mapping also link damage to the posterior aspects of VLPFC to phonological errors (Schwartz, Faseyitan, Kim, & Coslett, 2012) and its anterior aspects to semantic errors (Schwartz, Kimberg, Walker, Faseyitan, & Brecher, 2009). Similarly, using a version of the technique that maps lesions to parameters in a computational model of language production, Dell, Schwartz, Nozari, Faseyitan, and Branch Coslett (2013) showed that lesions in the more posterior parts of VLPFC correspond to the phonological parameter of the model, whereas lesions in the more anterior parts of VLPFC are associated with semantic errors.

   The semantic-phonological distinction, however, does not negate a process-based organization. Semantic and phonological processing may differ not only in the materials they use but also in the operations performed on those materials. One dominant process-based view is that of a rostrocaudal functional gradient of abstraction, with more anterior regions processing more abstract information (Badre, 2008; Badre & D'Esposito, 2009). This view has found support in the dorsolateral prefrontal cortex (Badre & D'Esposito, 2007; Koechlin & Jubault, 2006; Koechlin, Ody, & Kouneiher, 2003) and, more recently, also in the VLPFC (Race, Shanker, & Wagner, 2009). It remains to be seen if such a view is sufficient for explaining the separation of semantic and phonological processing in VLPFC.

3. Do the same regions in the prefrontal cortex that support domain-general mechanisms also support language processing? Although some have argued for domain-generality (January et al., 2009), some have contested this view (Fedorenko, Behr, &

Kanwisher, 2011) and some have proposed a middle ground, identifying both language-specific and domain-general regions in the PFC (Sakai & Passingham, 2002). A recent study tested whether the rostrocaudal gradient of abstraction is sensitive to the nature of the representations (spatial versus verbal). Bahlmann, Blumenfeld, and D'Esposito (2014) found an indistinguishable pattern of activity for the two stimulus types along this rostrocaudal axis. However, a task-sensitive topographic segregation was also found in the dorsolateral axis, such that processing of spatial information was localized to more dorsal areas, whereas processing of verbal information activated more ventral regions.

4. What other regions are in the control network that VLPFC is part of, and what role do they play? As pointed out, semantic control deficits of the SA type can also arise from lesions to posterior temporal or inferior parietal lobes. These two areas are heavily connected to the prefrontal cortex via arcuate and longitudinal fasciculi (Parker et al., 2005) and have both been previously implicated in tasks requiring controlled semantic access (Badre, Poldrack, Paré-Blagoev, Insler, & Wagner, 2005; Gennari, MacDonald, Postle, & Seidenberg, 2007; Lee & Dapretto, 2006; Rodd, Davis, & Johnsrude, 2005; Thompson-Schill et al., 1997; Wagner et al., 2001; Whitney et al., 2012; Zempleni, Renken, Hoeks, Hoogduin, & Stowe, 2007). It remains to be demonstrated how labor is divided in this frontotemporoparietal network that supports semantic and lexical retrieval.

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