

Neural Basis of Word Production

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Abstract

Producing a word from meaning requires activating the semantic features corresponding to a concept, retrieving the word, selecting its segments, ordering those segments into the right sequence, and finally articulating them with the correct timing. While excellent models of word production exist that each capture the details of parts of this process, to date, no single model has been proposed that captures the entire process in enough details for the purpose of neural mapping. In this chapter, I draw on both psycholinguistic and motor control traditions to construct a more complete picture of the neural basis of word production with regard to the components and processes proposed by production models in these two bodies of literature.

Keywords : word production, neural correlates, temporal cortex, parietal cortex, frontal cortex, subcortical structures

29. Neural Basis of Word Production

29.1 General approaches to studying the neural basis of language processing

Two general approaches exist to uncovering the neural basis of language processing. The *empirical approach* entails the manipulation of language processing demands in two (or more) conditions, and the identification of brain regions preferentially involved in the condition(s) with more prominent linguistic demands. While useful for getting a general sense of the network involved in language processing, the absence of a theoretical framework limits the interpretations that can be assigned to regions in this network. The *theoretical approach*, on the other hand, starts with a theoretical model, the components or parameters of which are the target of the neural investigation. This approach thus allows for a more meaningful interpretation of the findings, but the caveat is that such interpretation is dependent on the specific model. Models of language production vary considerably in their scope and assumptions. For example, Hickok (2012) assumes that “speech production is fundamentally a motor control problem.” (p. 137), while psycholinguistic models see the main challenge of production as mapping meaning to sound, which includes a great deal more than motor control of speech (e.g., Dell, 1986; Levelt, Roelofs, & Meyer, 1999). Even when the scope is agreed upon, models still vary substantially in the number and nature of the layers of representations they propose and the dynamics of information flow between these layers (see Chapter 28).

In this chapter, I adopt a theoretical approach inspired by the psycholinguistic tradition. Language production encompasses several tasks including reading, writing, and typing. But given the limited space, I will focus on a hallmark production task; namely, oral production of a word from meaning. Often tested experimentally using picture naming, this task requires activating semantic knowledge, selecting the correct word, mapping it onto a sequence of sounds, and finally articulating it. A neural account of such a process must therefore cover the neural basis of semantic, phonological, and articulatory-motor processing, at a minimum. Instead of adopting a specific psycholinguistic model, however, I will use a schematic model of word production, the components of which have been derived from various models and empirical

findings, and will opt for the minimum number of layers necessary for mapping meaning to sounds.

Figure 1 shows this structure. Because the relationship between semantics and sounds is not systematic (e.g., not all male entities correspond to words that have the sound /m/), it is safe to assume that phonology does not simply spring from semantics, and that the two have distinct representations. But since relevant phonological representations must be activated from semantics, at least one intermediate layer of representation must be assumed between the two to mediate this mapping. Different theories vary in their position regarding the number of these intermediate layers and their nature. The proposed layers of representation include lexical-semantic nodes (representations of unified semantic information), lemmas (representations that link unified semantic information to syntactic information), morphemes (smallest unit that conveys meaning; e.g., “swim” and “er” in “swimmer”), lexemes (domain-specific representations that have access to segments such as phonemes in spoken and graphemes in written production), syllables (structured chunks of phonology), and potentially others proposed by linguistic theory, such as syllable parts (e.g., CV or VC) and consonant clusters.

My decision to compress these into one layer does not imply a theoretical stance against the psychological reality of such representations. Some, like domain-specific lexemes, must exist, since knowing the phonological sequence of a word does not necessarily give you the information about its letter sequence that is necessary for writing the word. I did not include lexemes separately since this chapter’s focus is on a single production modality. Some of the other intermediate representations have been proposed to emerge from other representations. For example, Plaut and Gonnerman (2000) have argued that morphemes are not basic representations; rather, they emerge from learning the relationships between semantics and phonology. Note that the emerging nature of such representations does not mean that they have not formed independent representations. Studies of speech errors have shown that morphemes move independently as units, e.g., “He cleaned the tables” → “He cleans the tabled”. In fact, one could find instances of independent movements for almost all units proposed by linguistic theory, although the rate of movements is much higher for whole words and phonemes (and to a lesser extent, morphemes) than for other units (Dell 1995).

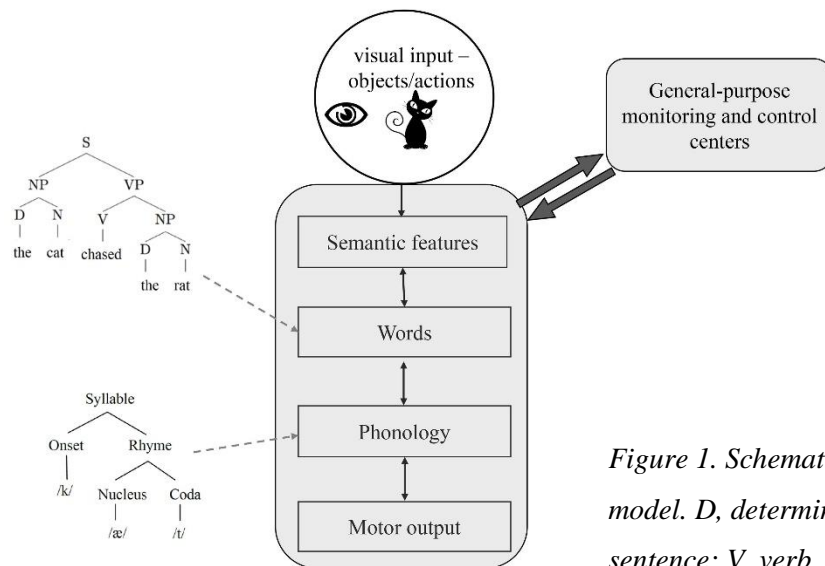


Figure 1. Schematic of a word production model. D, determiner; N, noun; P, phrase; S, sentence; V, verb.

For the purpose of a neural mapping, however, the important question is whether certain representations are distinct enough to have separate neural correlates from others. For example, should one look for lexical semantic nodes in a different region from lemmas? Such distinctions are often difficult to maintain in a neural investigation. When attempts in this vein have been made, they have not led to clearly separate regions, especially for higher levels of language processing like lexical semantic processing. Such distinctions are clearer at the lower levels of production, like representations of learned sequences (chunked into common syllables or consonant clusters) vs. representations of novel sequences (as individuals segments). But even in those cases, as I will discuss in later sections, these two types of sequences are contained in the same neural regions. What is different are the neural pathways that map the abstract representations of these sequences onto motor commands. I will, therefore, commit to one independent layer of representation between semantic features and phonemes, and call it simply “words” (Foygel & Dell, 2000). I will also define a final layer of motor output in the schematic model which I will unpack when discussing the neural correlates of motor production.

Also important for modeling language production is the concept of separation of *content* and *frame* (Chomsky 1975; Garrett 1975; Lashley 1951). The idea is that once a conceptual message has been constructed, two general kinds of frame must be built for the insertion of linguistic content. The *syntactic frame* is built under the guidance of the semantic message and syntactic rules, and identifies the phrasal structure—with syntactically labeled slots—for the insertion of

lexical items. The *segmental frame* is built under the guidance of language-specific phonotactic rules, and contains information about the order, syllabic structure, and perhaps other aspects of segmental encoding, such as the stress pattern. This view has been embraced by both connectionist (e.g., Dell 1988; MacKay 1987; Stemberger 1985) and symbolic models of segmental encoding (e.g., Meyer 1990; Shattuck-Hufnagel 1979), although alternatives such as parallel distributed processing approaches to content-frame separations have also been proposed (Dell, Juliano, & Govindjee 1993). Since the focus of this chapter is on single word production, I will refrain from discussing the syntactic frames, which are primarily relevant to phrase- and sentence-level production, although I adopt the view that such frames exist and interact with representations at a level higher than phonology (Figure 1). However, as will be seen in the section on “articulatory-phonetic encoding and motor production”, the content-frame separation is immediately relevant to the discussion of the neural correlates of motor speech processing.

To summarize, my schematic model (Figure 1) consists of semantic features (i.e., all pieces of information, including sensory-motor representations, that make up a concept), words (conjunctions of semantic features, also linked to syntactic information), phonology (abstract representations of sounds), and motor output, which itself comprises multiple parts. These representations interact closely with different types of frames at different levels (e.g., syntactic frames at the word level, syllabic frames at the phonological layer, etc.). This entire system is constantly monitored and regulated by monitoring and control mechanisms. The next four sections discuss the neural correlates of this schematic model.

Studies of neural correlates of language processing have employed various methodologies, including neuroimaging methods (e.g., PET, fMRI, tractography methods, etc.), lesion studies, brain stimulation (e.g., transcranial magnetic stimulation, or TMS, and transcranial indirect current stimulation, or tDCS), and electrophysiological recordings. We have recently written a comprehensive review of the electrophysiological studies of word production (Nozari & Pinet, under review). In light of the inferior spatial resolution of the most common method in this group (EEG), and the general problems we have laid out in that review regarding the interpretations assigned to the findings from this literature, I will not include the EEG data in the current chapter. Instead, I will use a combination of neuroimaging, lesion-based, and brain stimulation studies to discuss converging findings on the neural basis of word production.

29.2 Neural correlates of lexical semantic processing

Many attempts at word production start with conceptualization, i.e., activation of semantics. Several chapters in the book are dedicated to the nature of semantic representations, so I will refrain from a long discussion here, but will point out two opposing views that have been taken in computational models of word production. Some models assume distributed semantic representations, or “semantic features” (e.g., Caramazza 1997; Foygel and Dell 2000). Others have insisted on non-decompositional semantics (Levelt et al., 1999; Roelofs, 1992), based on two arguments: a) that speakers do not name superordinates of the target (e.g., “animal” instead of “horse”; *the hyperonym problem*; Levelt 1989), and b) that words with more complex feature sets are not harder to access than those with simple feature sets (*the complexity problem*; Levelt, Schreuder, and Hoenkamp 1978). The evidence against the first argument comes from individuals with aphasia, who, not uncommonly, produce superordinates instead of target names. The second argument also need not be true, since under a distributed view activation of a subset of features is sufficient to activate the concept. In fact, activation of concepts through the activation of various subsets of their features is critical in light of the evidence supporting the flexible context-dependent view of concepts (see Yee & Thompson-Schill, 2016 for a review). This position also naturally accommodates embodied views on concept processing (e.g., Barsalou, 1999). I will, therefore, adopt the distributed view.

According to the distributed view of semantics (e.g., classic models such as Meynert and Wernicke’s, Eggert 1977; embodied theories, e.g., Martin 2016; and newer theories such as the hub-and-spokes model of semantic representation, e.g., Lambon Ralph et al. 2017; Patterson, Nestor, and Rogers 2007), concepts are constructed of various pieces of information learned by experience and encoded in modality-specific cortices (Fischer & Zwaan, 2008; Kiefer & Pulvermüller, 2012; Meteyard, Cuadrado, Bahrami, & Vigliocco, 2012). Some theories posit that such features converge onto unifying hubs (called amodal, cross-modal, heteromodal, transmodal, or supramodal representations by various research groups) that are assumed to be housed bilaterally in the anterior temporal lobes (ATLs; see Lambon Ralph et al. 2017 for a review). The claim that ATL is the main semantic hub has been argued primarily on the basis of semantic dementia, a neurodegenerative condition causing atrophy of bilateral anterior ventral and polar temporal regions, which causes consistent and pervasive semantic impairment in all

modalities and almost all types of concepts, except the knowledge of simple numbers (e.g., Bozeat et al. 2000; see also semantic variant of primary progressive aphasia, e.g., Gorno-Tempini et al. 2004; but see Simmons & Martin, 2009 for a different perspective). More recently, additional hubs have been proposed in temporal and parietal regions that are characteristically distant from primary sensory and motor cortices, but have rich connections to the modal association cortices (e.g., Binder 2016; Binder et al. 2009).

There are good arguments for why hubs, i.e., high-level conjunctive representations that summarize a number of semantic features into a concept, would be useful for abstract, yet flexible and context-sensitive, representation of pure semantic knowledge (Binder, 2016). But since the focus of this chapter is mapping semantic features onto sounds, such conjunctive representations are naturally necessary as the mediating layer, for the reasons discussed in the previous section. Some attempts have been made to separate these representations into lexical semantic nodes and lemmas. For example, Kemmerer (2018) identifies the locus of the interference in cyclic blocked naming paradigms (where participants are progressively slowed down by naming a small set of semantically related pictures) as “lexical concepts”, but views pure anomia as a condition targeting “lemmas”. I do not know of any empirical evidence that clearly suggests that, as far as the “word” layer goes, these two cases involve different representations. Similarly, simulations of semantic errors using the lesioned version of the Foygel and Dell (2000) model have been ascribed to lemmas (in contrast to lexical concepts; Kemmerer, 2018), but in this, and most other versions of the 2-step interactive model by Dell and his colleagues, a single “word” layer serves both to combine semantic features and link them to syntactic information, without differentiating between lexical concepts and lemmas.

In short, the conjunctive representation of semantic knowledge and the representations that must mediate the mapping of meaning to sound are similar enough, and, as suggested by the evidence below, spatially close enough, to be discussed in one place, although a hierarchy of such representations is not impossible. I will thus discuss them in one place. A similar approach was adopted by Binder et al. (2009). In one of the largest and most meticulously controlled meta-analyses of neuroimaging data in semantic processing, the authors analyzed data from 120 studies targeting semantic access from (spoken or written) words, and identified 1145 foci of activation representing a distributed lexical semantic network. The thresholded activation

likelihood estimate (ALE) map lateralized the effect largely to the left hemisphere (with some extensions to the right in angular gyrus and posterior cingulate cortex), and identified seven key regions in temporal, parietal, frontal, and paralimbic areas (Figure 2). I will briefly review the hypothesized roles of these main areas in light of the empirical evidence.

29.2.1 Temporal regions. A main region implicated in the study of Binder et al. (2009) was the lateral part of temporal lobe, including the entire length of the middle temporal gyrus (MTG) and posterior parts of the inferior temporal gyrus (ITG; Figure 1, region 1). MTG (and less frequently posterior ITG) activation has been reliably reported during picture naming (de Zubicaray, Miozzo, Johnson, Schiller, & McMahon, 2012; Maess, Friederici, Damian, Meyer, & Levelt, 2002; Moore & Price, 1999; Murtha, Chertkow, Beauregard, & Evans, 1999). Moreover, activation of this region is sensitive to the co-activation of words that are semantically similar during picture naming (e.g., de Zubicaray, Wilson, McMahon, & Muthiah, 2001; see Nozari & Pinet, under review for a review). Left mid-MTG is also implicated in the meta-analysis of Indefrey and Levelt (2004), in which the authors contrasted regions activated during picture naming and associative word generation (both of which require lexical retrieval) against regions that they argued do not necessarily require lexical retrieval, i.e., reading words and pseudowords (although the assumption of non-lexical reading of actual words is questionable). In the same vein, along with ATL, damage to MTG has been shown to correlate with semantic errors (e.g., saying “dog” instead of “cat”) in picture naming tasks (Henseler, Regenbrecht, & Obrig, 2014; Mirman et al., 2015; Schwartz et al., 2011, 2009; Walker et al., 2011). Importantly, MTG is also consistently implicated in tasks requiring word comprehension, and although selective damage to MTG is rare, it is often associated with language comprehension and semantic deficits (Dronkers, Wilkins, Van Valin, Redfern, & Jaeger, 2004; Hillis & Caramazza, 1991; Kertesz, Lau, & Polk, 1993). Large lesions to MTG and ITG (sometimes along with the fusiform and angular gyri) lead to transcortical sensory aphasia, a syndrome with impaired speech comprehension despite intact phonological production abilities, such as auditory repetition of words and sentences (Alexander, Hiltbrunner, & Fischer, 1989; Andrew Kertesz, Sheppard, & MacKenzie, 1982; Rapcsak and Rubens 1994). The convergence of lexical semantic deficits in both comprehension and production after damage to anterior and lateral aspects of the temporal

lobe implies that these regions most likely store conjunctive representations that are shared between production and comprehension (Ben Shalom & Poeppel, 2008; Friederici, 2002).

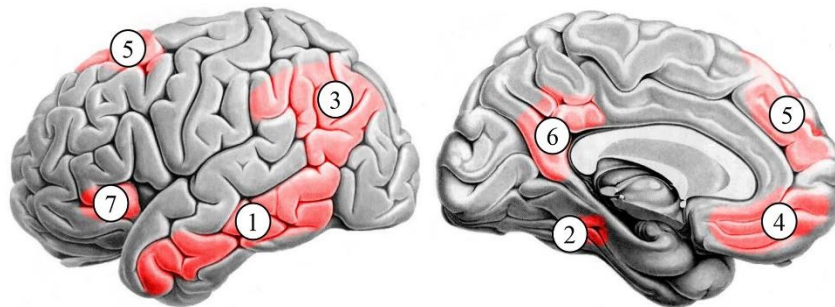


Figure 2. Regions involved in semantic-lexical processing. 1) Lateral temporal lobe, including the entire length of the middle temporal gyrus (MTG) and posterior portions of the inferior temporal gyrus (ITG); 2) a ventromedial region of the temporal lobe centered on mid-fusiform gyrus and adjacent parahippocampus; 3) angular gyrus (AG) and adjacent supramarginal gyrus (SMG); 4) ventromedial and orbital prefrontal cortex; 5) dorsomedial prefrontal cortex in the superior frontal gyrus and adjacent middle frontal gyrus; 6) posterior cingulate gyrus and adjacent ventral precuneus; 7) inferior frontal gyrus (IFG), especially the pars orbitalis.

Reproduced with Permission from Binder et al. (2009).

The role of the more posterior parts of MTG (pMTG) is less clear. Some have linked this region to anomia (Antonucci, Beeson, & Rapcsak, 2004; Baldo, Arévalo, Patterson, & Dronkers, 2013; Raymer et al., 1997), although failure to find a word even in the presence of good semantic comprehension may have different etiologies, including a failure to activate the right word from the concept, failure of inhibiting competing words (e.g., Cloutman et al., 2009; Nozari, 2019), or failure of activating representations further downstream. Thus without a finer-grained analysis of error types and other accompanying deficits, association with anomia is not particularly telling about the function of a neural region. Others have proposed that the most posterior parts of the left middle and inferior lateral temporal cortex, i.e., the temporal-occipital junction, show the greatest concentration of activation foci for processing the meaning of artifacts (as opposed to living things) in neuroimaging studies (see Binder et al. 2009, for a review of these studies). Together with the vicinity of this region to the visual motion processing and parietal praxis-coding regions, this finding has been taken to imply the region's specialization for processing the visual attributes of actions and tools (A. Martin, Ungerleider, & Haxby, 2000). In line with this

claim, Hanna Damasio and her colleagues found lesions to this region to cause a particular difficulty in naming common manipulable objects such as a fork (as opposed to proper nouns and nouns of common animals; H. Damasio, Grabowski, Tranel, Hichwa, & A. Damasio, 1996). This position follows the view that semantic knowledge is systematically organized in the temporal lobe, which is agreed upon by most researchers, although substantial disagreement exists about the nature of this organization (Binder et al., 2009; H. Damasio et al., 1996; Lambon Ralph et al., 2017; A. Martin, 2016). A third account has been proposed for the role of pMTG as a region involved in implementing cognitive control over semantic retrieval (e.g., Lambon Ralph et al., 2017). For example, several studies from the same research group have shown that applying inhibitory TMS to this region disrupts semantic processing most strongly in conditions with high cognitive control demand, such as matching words with low vs. high semantic association (salt-grain vs. salt-pepper; Lambon Ralph et al., 2017; Whitney, Kirk, O’Sullivan, Lambon Ralph, & Jefferies, 2011a, 2011b). Not far from this interpretation, Binder (2017) interprets the more prominent involvement of this region in processing complex sentences vs. simple words as evidence of a work space for integrating the meaning of multiple words while their phonological forms are held active in phonological working memory, a task for which the pMTG is well suited based on its rich connectivity to the angular gyrus, anterior and inferior temporal lobe, and inferior and superior frontal gyri.

In contrast, the superior temporal gyrus (STG) does not seem to be reliably implicated in studies involving semantic processing (Binder et al. 2009; see also e.g., Price 2000). It has sometimes been implicated during overt word production (de Zubicaray et al., 2001; Hocking, McMahon, & de Zubicaray, 2008), but this probably reflects a role in the auditory processing of self-produced speech, in line with the region’s confirmed role in auditory processing (see Chapter 3). I will return to this when discussing speech monitoring. Binder et al.’s (2009) meta-analysis also identified a focal region in the ventral part of the temporal cortex in fusiform and parahippocampal gyri (Figure 1, region 2). These regions are not often reported in studies of language processing, with the exception of reading and writing (e.g., Devlin, Jamison, Gonnerman, & Matthews, 2006). The close proximity of the mid fusiform gyrus to the object perception areas has led to proposals that this region is involved in retrieving knowledge of the visual attributes of objects (Chao & Martin, 1999; Kan, Barsalou, Solomon, Minor, & Thompson-Schill, 2003; Thompson-Schill, Aguirre, Desposito, & Farah, 1999; Vandenberg, &

Peeters, Fannes, & Vandenberghe, 2006). The parahippocampal component has been suggested to link episodic memory to long-term memory by linking hippocampus to lateral cortex (Levy, Bayley, & Squire, 2004).

29.2.2 Parietal regions. The angular gyrus (AG) and a part of the supramarginal gyrus (SMG) just anterior to it were parts of the inferior parietal lobule implicated in the meta-analysis of Binder et al. (2009; Figure 2, region 3). Although receiving little input from primary sensory areas, AG is richly connected to other association regions (Cavada & Goldman-Rakic, 1989a, 1989b; Hyvärinen, 1982; Seltzer & Pandya, 1994). Due to this connectivity, it has been implicated as one of the best candidates for high-level integration and potentially another semantic hub in addition to the ATL (Binder & Desai, 2011; Patterson et al., 2007). In keeping with this notion, damage to AG leads to a host of deficits that reflect problems in integration of complex knowledge such as alexia and agraphia (Dejerine, 1892), anomia (Benson 1979), and acalculia (Cipolotti, Butterworth, & Denes, 1991), among others.

In neuroimaging studies of sentence comprehension, AG's activation has been shown in late stages when all the bits of information are to be integrated into a coherent sentence (Humphries, Binder, Medler, & Liebenthal, 2007), in connected discourse vs. unrelated sentences (Fletcher et al., 1995; Homae, Hashimoto, Nakajima, Miyashita, & Sakai, 2002; Xu, Kemeny, Park, Frattali, & Braun, 2005), in response to semantically anomalous words (Friederici, Rüschemeyer, Hahne, & Fiebach, 2003; Ni et al., 2000), and in the processing of thematic relationships, such as the comparison of “lake house” to its reversed construct “house lake” (right-lateralized effect; (Graves, Binder, Desai, Conant, & Seidenberg, 2010). Further attempts to pinpoint the exact function of AG in linguistic operations have shown AG's sensitivity to event-denoting verbs (Boylan, Trueswell, & Thompson-Schill, 2015), and relational compounds, e.g., “wood stove” (Boylan, Trueswell, & Thompson-Schill, 2017). Moreover, AG has been implicated in metaphor processing (Bambini, Gentili, Ricciardi, Bertinetto, & Pietrini, 2011), and in the production of creative metaphoric language (e.g., “The lamp is a supernova”) vs. literal expressions (“The lamp is bright”) (Benedek et al., 2014). In studies by Lambon Ralph, Jefferies, and their colleagues, dorsal AG, along with pMTG, has been implicated in semantic tasks demanding executive control, with patterns very similar to the left ventral prefrontal cortex discussed below (see Lambon Ralph et al. 2017 for a review).

SMG is often implicated in tasks that tap into the knowledge for actions, and lesions to this region and pMTG lead to ideomotor apraxia (Buxbaum, Kyle, & Menon, 2005; Haaland, Harrington, & Knight, 2000; Jax, Buxbaum, & Moll, 2006; Tranel, Kemmerer, Adolphs, H. Damasio, & A. Damasio, 2003). Consistent with this region's role in the praxis features of object knowledge (e.g., Buxbaum, Kyle, Tang, & Detre, 2006), repetitive TMS to left SMG in a picture naming task selectively impairs the naming of manipulable artifacts (Pobric, Jefferies, & Lambon Ralph, 2010). SMG has a more extensive role in phonological encoding which will be discussed in a later section.

29.2.3 Frontal regions: The meta-analysis of Binder et al. (2009) identified three regions in the medial prefrontal cortex. The first is ventromedial prefrontal cortex (Figure 1, region 4), which has ties to emotion and reward processing, and is likely to be involved in processing the emotional aspects of concepts and words (A. Damasio 1994; Kuchinke et al., 2005; Phillips, Drevets, Rauch, & Lane, 2003). The second is the dorsomedial prefrontal cortex (Figure 1, region 5) anterior to the supplementary motor area (SMA). Because these two regions share a common blood supply isolated damage to them is rare, making functional separation difficult. Damage to this general region leads to transcortical motor aphasia, which is characterized by reduced speech output unless speech is constrained enough (e.g., counting 1-10). This profile has led to the proposal that this region is involved in self-guided retrieval of semantic information, especially to serve a communicative goal. The third region is posterior cingulate cortex (Figure 1, region 6), for which many functions have been proposed, the most likely of which is acting as the interface between semantic retrieval and formation of episodic memories in hippocampal areas (Binder et al., 2009).

On the lateral surface of the frontal cortex, Binder et al.'s (2009) meta-analysis revealed left inferior frontal gyrus (LIFG) as an important locus of lexical semantic processing (Figure 2, region 7). The functions attributed to this region (sometimes referred to as the ventrolateral prefrontal cortex) are numerous and encompass a variety of semantic, phonological, and syntactic operations (see Novick, Trueswell, & Thompson-Schill, 2005, and Nozari & Thompson-Schill, 2016 for reviews). Importantly, LIFG is one of the regions most associated with task difficulty. Along with other regions such as the anterior cingulate cortex (ACC), it is often activated when selection demands are high. This could be because the correct response is

weaker than a prepotent but incorrect response (e.g., naming the ink color “blue” while ignoring the written word “red” in incongruent Stroop trials), because several responses are all equally probable (e.g., generating a verb for a noun that is not strongly associated with a verb, e.g., “cat”: Play? Purr? Meow?; Thompson-Schill, D’Esposito, Aguirre, & Farah, 1997; Thompson-Schill et al., 1998). In keeping with this, picture naming under circumstances of increased competition between lexical semantic alternatives consistently activate this region (Kan & Thompson-Schill, 2004; Schnur et al., 2009). TMS studies suggest that this region’s function, which has often been called “conflict resolution”, is more prominent for lexical-semantic decisions in the anterior part of LIFG. Some have argued for additional regions with a similar function in temporoparietal regions (pMTG and dorsal angular gyrus; Davey et al., 2015; Hoffman, Jefferies, & Ralph, 2010; Whitney et al., 2011a, 2011b; see Noonan, Jefferies, Visser, & Lambon Ralph, 2013, for areview). Posterior LIFG, on the other hand, has often been implicated in tasks that require manipulation of phonological information, such as syllabification and sequencing (Devlin, Matthews, & Rushworth, 2003; Gough, Nobre, & Devlin, 2005; see also Clos, Amunts, Laird, Fox, & Eickhoff, 2013, for a meta-analytic connectivity-based parcellation of LIFG). More fine-grained functional organizations on multiple axes have also been proposed for the lateral frontal cortex (e.g., Bahlmann, Blumenfeld, & D’Esposito, 2015).

Another account of the role of LIFG is that of strengthening associations (R. Martin & Cheng, 2006; Wagner, Paré-Blagoev, Clark, & Poldrack, 2001). In keeping with this view, a TMS study over this region resulted in the disruption of performance when participants had to match items with weak associations (e.g., salt/grain), but performance was unaffected for items with strong associations (e.g., salt/pepper; Whitney et al., 2011a). In a recent eye-tracking study, we showed that a group of individuals with anterior lesions including LIFG were more impaired in using both semantic and phonological cues in locating a referent during sentence comprehension, compared to individuals with posterior lesions (Nozari, Mirman, & Thompson-Schill, 2016). We have discussed the results within the framework of a drift diffusion model, in which LIFG’s role has been proposed as boosting the rate of evidence accumulation for establishing an association. In the context of selection among activated alternatives, this function is equivalent to conflict resolution.

Connectivity measures also support the idea of LIFG implementing control over semantic selection. For example, damage to the uncinated fasciculus, which connects the pars orbitalis of LIFG to ATL, has been shown to be correlated with semantic control deficits (Harvey, Wei, Ellmore, Hamilton, & Schnur, 2013). Harvey and Schnur (2015) also found that damage to the inferior fronto-occipital fasciculus, which connects LIFG with the posterior temporal lobe was related to semantic interference during picture naming.

To summarize, the lexical semantic network can be roughly divided into two parts: regions that store long-term knowledge, and those that are involved in initiating and controlling the retrieval of that knowledge. By most accounts, temporal regions have the former function, with potential subregions for different types of knowledge and varying degrees of integration (Binder, 2017). In contrast, superior and medial frontal structures appear to have a role in motivation and task initiation, and LIFG seems to be involved in strengthening of associations and helping with selection among competing alternatives. The role of inferior parietal regions is less agreed upon, but the evidence point to an integrative function.

29.3 Phonological encoding

The term “phonological code” has sometimes been used to refer exclusively to long-term phonological representations of known words, specifically excluding pronounceable nonword strings like BILF (e.g., Indefrey & Levelt, 2004). Others, however, have included such strings when discussing neural correlates of phonological encoding (e.g., Acheson, Hamidi, Binder, & Postle, 2010; Yue, Martin, Hamilton, & Rose, 2019). Since similar neural regions have been implicated in processing of both words and pronounceable nonwords, I will not emphasize this distinction, and instead define a phonological code as a representation containing an ordered sequence of phonemes to be translated into articulatory gestures, without the representation itself being rich in phonetic details (Oppenheim & Dell, 2008). In the case of real words, such representations naturally link the word representations to sounds.

Binder (2015) summarizes the findings of 14 neuroimaging studies that tap into phonological processing with controls for semantic, articulatory, and auditory processing. Manipulations include comparison of pseudoword vs. word reading, naming pictures with high- vs. low-frequency names, lexical decision with phonologically related and unrelated primes, a variety of rhyme matching tasks with words and pseudowords, and silent rehearsal of words, pseudowords,

or pseudosentences (Binder, 2015; Appendix e-1). Figure 3A shows the activation loci from these studies. Figure 3B shows the result of a lesion-symptom mapping study in 40 individuals with left hemisphere stroke. The map indicates the correlation between lesioned voxels and scores in a silent visual rhyme judgment task (snow/blow/plow; Pillay, Stengel, Humphries, Book, & Binder, 2014). Finally, Figure 3C shows sites where direct cortical stimulation in patients undergoing brain surgery elicited phonological errors during reading without impairing comprehension (Anderson et al., 1999; Roux et al., 2012). Examination of these three figures shows a striking convergence of the results of neuroimaging, lesion, and stimulation studies of phonological processing in pSTG and SMG, with pMTG also implicated in the neuroimaging and stimulation studies but not in the lesion study, suggesting that it may support phonological encoding but not be necessary for it.

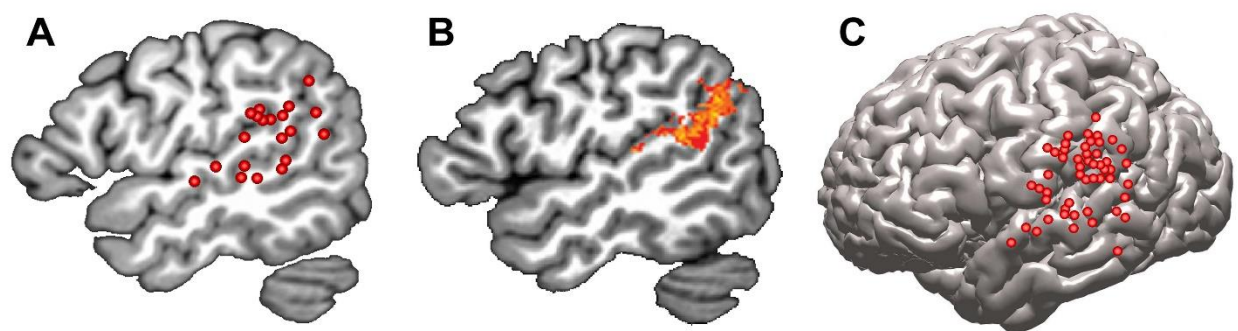


Figure 3. Neural correlates of phonological encoding. A) A summary of 14 functional neuroimaging studies examining phonological encoding. B) Lesion sites in 40 left-hemisphere stroke survivors with selective phonological impairment. C) Locations where cortical stimulation in 14 patients led to phonological errors during reading. See text for descriptions and references. Reproduced with permission From Binder (2015).

The reader may have noticed that the general region implicated by these studies is often referred to as Wernicke's area. It is important to note that damage to this region does not cause Wernicke's aphasia, but a different syndrome, called conduction aphasia, which unlike Wernicke's aphasia does not impact comprehension. Instead, phonological production abilities are visibly impaired (Axer, A. Keyserlingk, Berks, & D. Keyserlingk, 2001; H. Damasio & A. Damasio, 1980; Fridriksson et al., 2010; see Buchsbaum et al., 2011, for a review). Similar symptoms can be evoked in neurotypical speakers by cortical stimulation of the same region

(Anderson et al., 1999; Corina et al., 2010; Hamberger et al., 2016; Quigg & Fountain, 1999). Moreover, cortical degeneration of this region leads to the logopenic variant of primary progressive aphasia, the hallmark of which is phonological paraphasias and impaired verbal short-term memory, anomia, and various degrees of impaired comprehension of sentences (but not single words; Croot Karen, Ballard Kirrie, Leyton Cristian E., & Hodges John R., 2012; Leyton, Ballard, Piguet, & Hodges, 2014; Rohrer et al., 2010; see Henry & Gorno-Tempini, 2010, for a review).

There is now wide agreement that pSTG stores phonological representations. However, researchers disagree on whether the same representations are activated during phonological working memory tasks (Acheson et al., 2010), or whether a different part of cortex acts as a “phonological buffer” (Baddeley & Hitch, 1974), i.e., a region that temporarily keeps phonological representations activated while a task is being performed. In support of the latter view, lesion overlap studies have localized phonological short-term memory to the left SMG (e.g., Paulesu et al., 2017). Also, a recent fMRI study using multivariate pattern analysis showed that stimuli could be decoded from SMG, but not STG, during the delay period in a memory task. Furthermore, a functional connectivity analysis in the same study demonstrated that the connection between the left temporal and parietal regions became stronger as memory load increased, suggesting a greater collaboration between the storage and buffer regions in temporal and parietal cortices, respectively (Yue et al., 2019). I must note that the inferior frontal cortex has also been named as a potential region involved in phonological working memory. I will return to the role of this region and its relevance to speech production in the next section.

One neural region deserves a special mention in this section. Known as area Spt (Sylvian parietal temporal) in the dual-stream models of Hickok and Poeppel (2007), this region has been identified as carrying out the sensory-motor translation of speech. Others, however, disagree with this claim, and propose that the auditory-motor interface involves a much larger portion of the pSTG (Niziolek & Guenther, 2013; Tourville, Reilly, & Guenther, 2008). This debate is difficult to settle, because area Spt is often defined functionally, as a region that exhibits both auditory and motor response properties, albeit within an anatomically constrained area. It is known to have considerable variability across individuals (despite its relative stability within individuals), making it very difficult to localize it in standardized space. Nevertheless, the

findings of Guenther and colleagues, especially the bilateral nature of translational regions, may be important in expanding the anatomical constraints for the functional search for this region.

To summarize, the regions most reliably implicated in the storage and active maintenance of phonological codes are pSTG and SMG, with the former's role as a store for phonological representations, and the latter's role as phonological buffer. Lesions to these areas often lead to phonological paraphasias and sometimes difficulty in understanding long sentences (which hinges on keeping phonological codes active until they could be mapped onto semantic representations). In contrast, impaired comprehension of words and short phrases often observed after damage to MTG and the angular gyrus, which were strongly implicated in lexical semantic processing, is prominently absent (H. Damasio, Tranel, Grabowski, Adolphs, & A. Damasio, 2004; Dronkers et al., 2004; Kertesz et al., 1993; Kertesz et al., 1982; Thothathiri, Kimberg, & Schwartz, 2011). This double dissociation between semantic and phonological impairment is showcased in transcortical sensory vs. conduction aphasia.

29.4 Articulatory-phonetic encoding and motor production

Neural correlates of vocalization are better understood than the more abstract parts of language production, due to more extensive opportunities for single-unit recording and focal lesioning in nonhuman primates. These comprise both cortical and subcortical structures. Psycholinguistic models of word production are often sparse in details regarding motor speech processes. Therefore, for this part of the review, I adopt the framework of a computationally sophisticated and neurally explicit model of motor speech control, DIVA (directions into velocities of articulators; Guenther, 1994, 1995; Tourville & Guenther, 2011), and its more recent version GODIVA (gradient order DIVA; Bohland, Bullock, & Guenther, 2010).

Cerebral cortex. Figure 4 shows the cortical activity on the inflated cortical surface for 116 participants reading mono- and bi-syllabic utterances aloud, along with results of two meta-analyses of similar data (Brown, Ingham, Ingham, Laird, & Fox, 2005; Turkeltaub, Eden, Jones, & Zeffiro, 2002) superimposed as dark dots. The first striking finding is that, unlike the higher cortical functions related to language production reviewed in previous sections, which are largely left-lateralized, articulatory processes (many of them shared between linguistic and non-linguistic vocalization) are largely bilateral. The relevant cortical areas include both medial and lateral surfaces of the frontal and prefrontal cortex, a large portion of the superior temporal

gyrus, and parts of the parietal cortex including the postcentral gyrus, and to a lesser extent the superior parietal lobule. I will present a brief overview of the function of these regions in this and the next section. For a more extensive review of these regions and the neural pathways involved in speech motor control, I refer the reader to Guenther (2016).

Not surprisingly, some of the most important cortical regions for speech articulation are motor areas, including the primary motor and premotor cortices in the precentral gyrus, supplementary and pre-supplementary motor areas (SMA and preSMA), and motor cingulate cortex. Meta-analyses of somatotopic studies of speech articulators suggests the following dorsoventral ordering in the precentral gyrus: larynx, lips, jaws, tongue, and throat, although this ordering is rough, with multiple representations for each articulator and substantial overlap between the regions for different articulators (Takai, Brown, & Liotti, 2010; see also ECoG studies for additional evidence; Bouchard, Mesgarani, Johnson, & Chang, 2013; Farrell, Burbank, Lettich, & Ojemann, 2007). Unilateral damage to the precentral gyrus usually causes only minor disruptions in face and mouth movements, likely due to the largely bilateral connections in this region (Penfield & Roberts 1959). Bilateral damage to the precentral gyrus in humans is rare, and if found is often accompanied by extensive lesions beyond this area, which makes a neuropsychological interpretation of this region's function difficult. Supplementary motor areas are also often activated during the production of even simple syllables. Unilateral damage to these areas is followed by near-total recovery of speech within months (Laplane, Talairach, Meininger, Bancaud, & Orgogozo, 1977). The hallmark of damage to these areas is transient mutism which is often specific to self-initiated speech, while constrained or automatic speech (e.g., repeating words, reciting a learned sequence such as counting 1-10) could remain intact. This is part of a syndrome called transcortical motor aphasia (alluded to earlier when discussing the simultaneous damage of SMA and the adjacent dorsomedial prefrontal cortex), which may also entail problems such as involuntary vocalization, and anomalies in the rate, prosody, and fluency of speech may also be present (Freedman, Alexander, & Naeser, 1984).

To best understand the difference between the functions of lateral and medial motor areas, recall the content-frame separation discussed at the beginning of this chapter. Generally speaking, the evidence points to a role of the lateral frontal cortex (specifically ventral premotor cortex, vPMC, and ventral primary motor cortex, vMC, both in the precentral gyrus, and left posterior inferior

frontal sulcus, pIFS) in representing the content of speech, while the medial surface of the frontal cortex (SMA and preSMA) represent frames. GODIVA proposes the content-frame separation in the context of two related loops: a planning loop, the main job of which is to temporarily store (i.e., buffer) the utterance to be produced, and a motor loop, which generates the actual motor commands for production (Fig. 5). The planning loop consists of the preSMA, which contains the abstract sequential frame, and its corresponding counterpart on the lateral surface, i.e., left pIFS, which buffers the phonological content. The motor loop comprises the SMA, which generates the abstract initiation map, and its counterpart on the lateral surface, left vPMC, which contains the speech sound map (i.e., nodes whose activation leads to the read out of the motor programs). A combination of signals from SMA and vPMC is sent to the vMC, which contains the actual motor gestures.

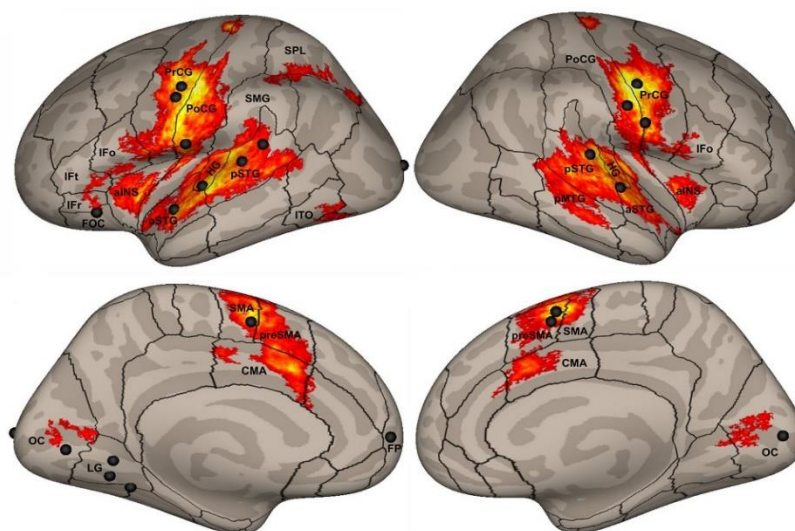


Figure 4. Hot colormap of cortical regions activated during reading aloud of mono- and bi-syllabic utterances compared to passive viewing of letters, plotted on inflated surfaces. $N = 116$. Black dots represent foci from the meta-analyses of Brown (2005) and Turkeltaub et al. (2002). Upper and lower panels show lateral and medial surfaces, respectively. Images on the left and right show left and right hemispheres, respectively. aINS, anterior insula; aSTG, anterior superior temporal gyrus; CMA, cingulate motor area; HG, Heschl's gyrus; IFO, inferior frontal gyrus pars opercularis; IFr, inferior frontal gyrus pars orbitalis; IFt, inferior frontal gyrus pars triangularis; ITO, inferior temporo-occipital junction; OC, occipital cortex; pMTG, posterior middle temporal gyrus; PoCG, postcentral gyrus; PrCG, precentral gyrus; preSMA, pre-supplementary motor area; pSTG, posterior superior temporal gyrus; SMA,

The representations shown in Figure 5 are for the word “blue” when it has already been learned and practiced, hence the “chunked” representations such as the consonant cluster /bl/ at the syllable level in the pIFS, and the holistic /blu/ at the level of speech sound map in the vPMC. These chunked representations do not exist earlier in development when “blue” is a novel sequence. Instead, the individual segments /b/, /l/, and /u/ must be assembled at multiple levels of the system, which puts novel sequences at a disadvantage compared to well-practiced ones. In addition, representations of well-practiced sequences take advantage of subcortical projections via the basal ganglia and cerebellum, which further facilitates quick mapping of chunked representations.

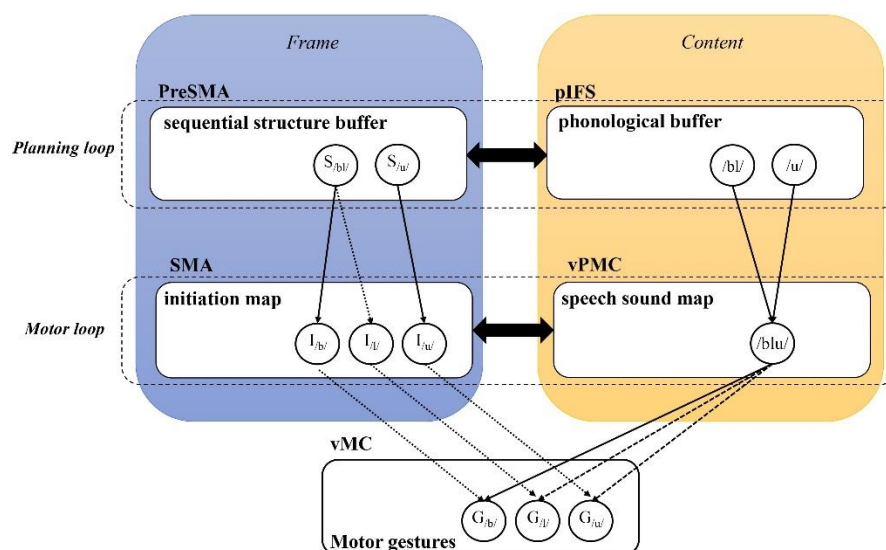


Figure 5. Schematic of the planning and motor loops in speech production. The blue and yellow panels show regions involved in frame and content processing, respectively. Chunked representations in each region are shown for a learned word (“blue”). For a novel syllable (not shown), representations in all boxes would consist of individual segments (e.g., three separate segments for /b/, /l/ and /u/). Solid arrows show cortico-cortical projections. Dotted arrows show connections via basal ganglia. Dashed arrows show connections via cerebellum. G, gestural node; I, initiation map; pIFS, posterior inferior frontal sulcus; preSMA, pre-supplementary motor area; S, syllabic structure node; SMA, supplementary motor area; vMC, ventral primary motor cortex; vPMC, ventral premotor cortex. Adopted with changes from Guenther (2016).

The reader may have noticed that the function attributed to the pIFS by GODIVA, i.e., phonological buffering, is similar to what I discussed in the previous section as having been attributed by some to the SMG (e.g., Yue et al., 2019). When comparing the production of complex syllable sequences (three unique syllables) with simple syllable sequences (same syllable repeated three times), Bohland and Guenther (2006) found that, in addition to vPMC and SMA, greater activation was observed in both IFS and SMG (as well as preSMA and anterior insula), regions that have also been implicated in a large meta-analysis of over 100 neuroimaging studies of working memory (Rottschy et al., 2012). Interestingly, in that meta-analysis the only locus that had been preferentially activated in verbal over non-verbal working memory tasks was IFS, leading Guenther (2016) to conclude that this region may be involved in articulatory rehearsal (see Curtis & D’Esposito, 2003, for a different perspective). Thus while both SMG and IFS could both be parts of Baddeley and Hitch’s (1974) phonological loop, SMG may act as the “phonological store”, whereas IFS could implement the “articulatory process”. Together, they help maintain verbal information in working memory. While such a division of labor is speculative, it aligns well with the greater proximity of SGM to the auditory representations and IFS to motor representations.

IFG is also implicated in speech production, and unlike some of the other cortical regions, its activation is left-lateralized (Ghosh, Tourville, & Guenther, 2008). As discussed in the earlier sections, anterior LIFG has been implicated in controlled semantic retrieval, while posterior LIFG has been tied to lower-level processes. The pSTG (which, as discussed in the previous section, is presumed to contain phonological representations) is connected to LIFG via the long segment of the arcuate fasciculus, and damage to this tract, or intracranial stimulation of it, results in phonemic paraphasias during word production; (Berthier, Lambon Ralph, Pujol, & Green, 2012; Duffau, Moritz-Gasser, & Mandonnet, 2014; Schwartz, Faseyitan, Kim, & Coslett, 2012). Damage to LIFG itself causes apraxia of speech, a condition that impairs motor programming of speech sequences without affecting the articulators themselves (Graff-Radford et al., 2014; Hillis et al., 2004; Richardson, Fillmore, Rorden, LaPointe, & Fridriksson, 2012). Speech apraxia was previously attributed to damage in the insula (Baldo, Wilkins, Ogar, Willock, & Dronkers, 2011; Dronkers, 1996), but as a part of the paralimbic system (a system that integrates the functions of the neocortex with the motivational/emotional functions of the

limbic system), some have suggested that the role of the insula in speech production is better aligned with motivational factors. In keeping with this interpretation, the insula seems to be involved in a large variety of non-linguistic functions with little in common in terms of cognitive processes. A motivational role has also been proposed for motor cingulate cortex, part of the ACC which also belongs to the paralimbic system. Bilateral damage to the ACC leads to akinetic mutism, a condition characterized by an absence of motivation to produce speech, although when speech is occasionally produced, it is intact in both meaning and form (Rosenbeck, 2004).

In summary, various areas in the medial and lateral frontal and prefrontal regions contribute to converting abstract phonology into the sequences of motor gestures that make up speech. In addition to these, some temporoparietal regions have been implicated during production (Figure 4), but these are less likely to be directly involved in the act of production. The activity in the STG, including primary auditory cortex located in Heschel's gyrus, as well as higher-order auditory cortical areas of anterior and posterior STG (aSTG and pSTG), is mostly due to hearing one's own voice. However, magnetoencephalography and fMRI studies have also found activation of these regions during covert speech (Okada & Hickok, 2006), which is compatible with their involvement in the prediction of the sensory consequences of actions. This function, along with the role of the postcentral gyrus in the parietal lobe, will be discussed in the section on monitoring.

Subcortical structures. Several subcortical structures have also been implicated in the motor production of speech (see Guenther 2016 for a review). Most prominent is the combination of the basal ganglia and the thalamic nuclei that are involved in linking the content-frame representations discussed above. Empirical evidence suggests a greater involvement of the caudate nucleus in the planning loop. Electrical stimulation of this nucleus or the anterior thalamic nuclei causes speech that cannot be inhibited (see Crosson 1992 for a review).

According to GODIVA, the basal ganglia in the cortico-basal motor loop, including putamen, in collaboration with the cortico-cerebellar loop, develop chunked representations of practiced sequences in pIFS, preSMA, and vPMC, as explained earlier in this section. In line with this proposal, overt production of novel compared to practiced syllables leads to greater activation in the pIFS, preSMA, and vPMC, as well as the anterior insula and SMG (Segawa, Tourville, Beal, & Guenther, 2015). As such, subcortical structures play a critical role in making production more

efficient as a function of learning. In addition to its role in facilitating the mapping of chunked speech into gestures, the cerebellum is also involved in online monitoring of speech production using sensory information. I will discuss this briefly in the next section.

29.5 Monitoring of word production

The problem of monitoring in language production closely mirrors the problem of model scope, alluded to at the beginning of this chapter. As a model of motor speech production, GODIVA also contains detailed mechanisms for the monitoring and control of speech motor operations. But naturally such mechanisms are restricted to the scope of the model, which addresses lower-level production processes. As noted earlier, this is only one part of the puzzle of language production. Attempts have been made to extend the general framework of GODIVA to higher processes involved in language production, but such attempts either do not extend beyond the level of phonological representations (e.g., Hickok, 2012), or when they claim to extend to higher levels, fail to meet the basic requirements of such a framework at higher levels (e.g., Pickering & Garrod, 2013; see Nozari, under review, for arguments). I will start by discussing GODIVA, as it provides the most detailed predictions regarding the neural correlates of monitoring at the motor level. I will then briefly touch upon what is still missing from the monitoring literature.

According to GODIVA, production starts by activating a speech sound map in the left vPMC, which activates a stored motor program in vMC. At the same time two more representations are activated through a forward model (i.e., a model that anticipates the perceptual consequences of an action): an auditory target and a somatosensory target. The auditory target is part of the auditory state map, which contains a talker-normalized representation related to the formant frequencies of the speech signal, and is localized to pSTG including the planum temporale. The projections from vPMC to pSTG serve the purpose of canceling out the auditory information, thus, if the incoming auditory signal falls within the auditory target region, its excitatory effects will be suppressed. Such auditory suppression of self-produced speech is well documented and contingent on intact cerebellar function (Christoffels, Formisano, & Schiller, 2007; Franken, Hagoort, & Acheson, 2015; Knolle, Schröger, Baess, & Kotz, 2011). If, on the other hand, the incoming auditory information is outside of the target region, a reduced degree of speech-

induced suppression is observed (Heinks-Maldonado, Nagarajan, & Houde, 2006), which generates an error signal.

Note that the error signal in the above model is in the auditory space. In order for it to be used to adjust motor movements it must be transformed into motor coordinates. As discussed earlier, Hickok and colleagues propose that this transformation is carried out by the area Spt, an area at the border between the parietal operculum and planum temporale in the left hemisphere (Buchsbaum, Hickok, & Humphries, 2001; Hickok, Buchsbaum, Humphries, & Muftuler, 2003), whereas Guenther and colleagues propose that the auditory-motor interface involves a much larger portion of the pSTG bilaterally. These areas accomplish the transformation by sending projections to right vPMC and then to vMC through both cortico-cortical projections and cortico-cerebellar loops. Predictions of the model have been confirmed by studies in which the syllables produced by speakers undergo real-time perturbation of formant frequencies (e.g., Tourville et al. 2008; Niziolek & Guenther 2013). In addition to bilateral pSTG, these studies have implicated right IFG as part of the auditory feedback loop. Importantly, adjustments to speech have been subconscious, with participants often unaware of the artificial speech modification or any attempts at correcting it. This independence from conscious awareness is critical for a monitoring mechanism that must continuously assess and regulate production without interfering with its primary processes (Nozari, under review; Nozari, Martin, & McCloskey, 2019).

Activation of the speech sound map also activates a somatosensory target as part of the somatosensory state map in the ventral postcentral gyrus and SMG. The workings of this feedback loop are generally similar to the auditory feedback loop. Similar to the suppression of auditory feedback during the self-produced speech, tactile sensation is reduced by one's own movement, a function that is again attributed to the cerebellum (Blakemore, Frith, & Wolpert, 2001; Blakemore, Wolpert, & Frith, 1998). Thus, by the logic explained for the auditory feedback loop, a mismatch between the predicted and actual somatosensory representations leads to an error signal, which is transmitted to right vPMC for transformation to corrective movements that are then sent to bilateral vMC.

GODIVA thus elegantly explains both the developmental trajectory of learning to imitate the phonology of one's language and the subtle adjustments made to learned speech after auditory or somatosensory perturbation. Note that this mechanism requires that perceptual feedback is

available, i.e., the action has been produced. This requirement is reasonable for the first stages of language learning, where production is rarely on target and must be heavily modified by overt feedback. Later in life, when motor production is mastered, speakers do not rely nearly as much on overt feedback to detect problems in their speech. Evidence for this claim comes from many instances of covert error detection (i.e., detecting errors before they become overt), or intercepting errors early in production and applying fast repairs (Hartsuiker & Kolk, 2001; Levelt, 1983). In this vein, Hickok (2012) proposed a mechanism similar to GODIVA, in which persistent activation of perceptual representations during self-produced speech generates an error signal. But unlike GODIVA, the anticipated activation of perceptual representations does not need to be compared against the actual perceptual input. Instead, it is directly suppressed through the motor program, thus eliminating the need for overt feedback. Even if such direct suppression is possible, the model's basic mechanism still hinges on having two sets of representations (motor and perceptual) corresponding to the same utterance. While this is a reasonable assumption for representations at or below the level of phonemes, I do not know of any evidence supporting such a dichotomy at the higher levels of language production, for example at the level of lexical semantic representations. In fact, as reviewed in earlier sections, neural evidence suggests that such a duplication is unlikely to exist at those levels. This problem, which I have called *the problem of duplicate representations* (Nozari, under review), makes the extension of monitoring mechanisms that rely on sensory-motor comparisons to higher levels of language production infeasible.

Two solutions remain: either language production is only monitored at a late stage, i.e., after phonological encoding, or it is monitored at an earlier stage but with a different mechanism. The differences observed in the detection and repairs of semantic vs. phonological errors (e.g., (Nozari, Dell, & Schwartz, 2011; Schuchard, Middleton, & Schwartz, 2017); see Nozari, under review, for details) make the first possibility unlikely. This has led to proposals for alternative monitoring mechanisms at the higher levels of language production. One such mechanism is conflict-based monitoring (Botvinick, Braver, Barch, Carter, & Cohen, 2001), in which the close activation of multiple representations (i.e., high conflict) signals the higher likelihood of an error (regardless of whether an error is actually committed or not), and leads to the greater recruitment of control resources to resolve this conflict. This mechanism is “layer-specific”, meaning that conflict is computed between different representations (e.g., lexical representations of “cat” and

“dog”; Hanley, Cortis, Budd, & Nozari, 2016; Nozari et al., 2011) within the same layer. This is fundamentally different from the models discussed above, in which computations depend critically on activation at different levels for the same item (e.g., motor vs. perceptual representations of “cat”). The conflict-based account thus eliminates the problem of duplicate representations at the higher levels of the system. To this is added a domain-general component, which reads out the conflict from specific parts of the system and uses this information to regulate top-down control over the parts from which conflict has arisen.

The layer-specificity of the conflict-based account predicts the engagement of the same regions that are involved in the primary production processes in monitoring processes. Neural correlates of the domain-general part of the conflict-based monitor are under debate, but medial prefrontal cortex (especially ACC and preSMA) and lateral prefrontal cortex (especially the LIFG) have been the main candidates. Due to the methodological difficulties involved in eliciting errors from neurotypical adult speakers, very few neuroimaging studies have to date investigated the neural correlates of error detection in natural production tasks. A tongue-twister study by (Gauvin, De Baene, Brass, & Hartsuiker, 2016) implicated pre-SMA, dorsal ACC, anterior insula, and inferior frontal gyrus. Interestingly, that study failed to find a reliable contribution of the auditory or perceptual areas to error detection. But neural correlates of the conflict-based model can be assessed in another way: note that the scope of conflict-based monitoring extends beyond error detection to the online regulation of production, potentially on every production attempt (Nozari & Hepner, 2018, 2019). The need for regulation increases with increased conflict. According to conflict-based monitoring, most errors are simply a subset of this situation. Thus one could test the predictions of the conflict-based monitor by looking at the neural correlates of word production in situations of high conflict, e.g., in the presence of a semantically related competitor. In keeping with the predictions of the conflict-based monitor, middle and posterior MTG, ACC, and LIFG are among the regions most frequently implicated in such studies (e.g., de Zubizaray, McMahon, Eastburn, & Pringle, 2006; de Zubizaray, McMahon, & Howard, 2015; de Zubizaray et al., 2001; Kan & Thompson-Schill, 2004; Schnur, Schwartz, Brecher, & Hodgson, 2006; Schnur et al., 2009).

To summarize, just like the primary production processes themselves, the monitoring processes for motor production are much better understood than those for higher-level production

processes, but given the very different nature of representations in the higher and lower levels of the production system, the most likely possibility is that more than one monitoring mechanism exists for the regulation of the production system (Nozari, under review).

29.6 Summary and conclusion

Given that no model of language production to date covers the entire process of mapping concepts to articulatory gestures, I used theoretical insights from models with different scopes, in the hope of painting as complete of a picture of the neural basis of word production as possible. Despite this heterogeneity, a neural model emerged within which the flow of information roughly tracks the information flow in cognitive models. Conceptualization begins by connecting distributed semantic features in conjunctive zones in the temporal lobe. The mapping of concepts to words and phonology is represented by the flow of information from anterior to middle and finally posterior parts of the MTG and STG. The adjacent SMG helps with the buffering of phonological information until it is time for production. Phonological codes are then mapped onto corresponding representations in the frontal cortex. This region has a complex hierarchy of planning and execution loops, and contains both abstract frames (in SMA and preSMA) and content (in the vPMC and IFS), with the final-stage articulatory gestures stored in the vMC. This architecture is very similar to that proposed by Hickok and Poeppel (2007).

This process is supplemented by several other systems whose roles are less well understood. Medial frontal structures most likely serve motivational and evaluative functions. Closely related to these is the LIFG, which seems to play a role in resolving the conflict between competing alternatives and strengthening associations. Medial temporal regions may be important for connecting episodic memory in the hippocampus to long-term memory in cortical regions, and thus play a critical role in learning. The angular gyrus plays some kind of integrative function for events with relational or complex representations, although the exact nature of this function is not well understood. And last, but not least, subcortical regions such as the basal ganglia and cerebellum seem to play a critical role in learning, both by creating more efficient representations and faster mapping, and, in the case of the cerebellum, by being involved in generating predictions about the consequences of a motor plan.

I end by highlighting the fact that we have come to understand a great deal about the neural basis of word production, but there is a long way to go. Many of the functions attributed to the regions

described in this chapter are speculative, or are too imprecise for us to claim that we have really understood the role of that region. This is particularly true for subcortical structures, which are hard to evaluate by many routine techniques. Moreover, certain problems such as monitoring and control are far from solved in language production, and relevant data are currently sparse. These areas provide great avenues for future research on the neural basis of word production.

References

- Acheson, D. J., Hamidi, M., Binder, J. R., & Postle, B. R. (2010). A Common Neural Substrate for Language Production and Verbal Working Memory. *Journal of Cognitive Neuroscience*, 23(6), 1358–1367.
- Alexander, M. P., Hiltbrunner, B., & Fischer, R. S. (1989). Distributed Anatomy of Transcortical Sensory Aphasia. *Archives of Neurology*, 46(8), 885–892.
- Anderson, J. M., Gilmore, R., Roper, S., Crosson, B., Bauer, R. M., Nadeau, S., ... Heilman, K. M. (1999). Conduction Aphasia and the Arcuate Fasciculus: A Reexamination of the Wernicke–Geschwind Model. *Brain and Language*, 70(1), 1–12.
- Antonucci, S., Beeson, P., & Rapcsak, S. (2004). Anomia in patients with left inferior temporal lobe lesions. *Aphasiology*, 18(5–7), 543–554.
- Axer, H., Keyserlingk, A. G., Berks, G., & Keyserlingk, D. G. (2001). Supra- and Infrasyllabic Conduction Aphasia. *Brain and Language*, 76(3), 317–331.
- Baddeley, A. D., & Hitch, G. (1974). Working Memory. In G. H. Bower (Ed.), *Psychology of Learning and Motivation* (Vol. 8, pp. 47–89).
- Bahlmann, J., Blumenfeld, R. S., & D’Esposito, M. (2015). The Rostro-Caudal Axis of Frontal Cortex Is Sensitive to the Domain of Stimulus Information. *Cerebral Cortex*, 25(7), 1815–1826.
- Baldo, J. V., Arévalo, A., Patterson, J. P., & Dronkers, N. F. (2013). Grey and white matter correlates of picture naming: Evidence from a voxel-based lesion analysis of the Boston Naming Test. *Cortex*, 49(3), 658–667.
- Baldo, J. V., Wilkins, D. P., Ogar, J., Willock, S., & Dronkers, N. F. (2011). Role of the precentral gyrus of the insula in complex articulation. *Cortex*, 47(7), 800–807.

- Bambini, V., Gentili, C., Ricciardi, E., Bertinetto, P. M., & Pietrini, P. (2011). Decomposing metaphor processing at the cognitive and neural level through functional magnetic resonance imaging. *Brain Research Bulletin*, 86(3), 203–216.
- Barsalou, L. W. (1999). Perceptual symbol systems. *Behavioral and Brain Sciences*, 22(4), 577–660.
- Ben Shalom, D., & Poeppel, D. (2008). Functional Anatomic Models of Language: Assembling the Pieces. *The Neuroscientist*, 14(1), 119–127.
- Benson, D. F. (1979). *Aphasia, alexia and agraphia*. New York: Churchill Livingstone.
- Benedek, M., Beaty, R., Jauk, E., Koschutnig, K., Fink, A., Silvia, P. J., ... Neubauer, A. C. (2014). Creating metaphors: The neural basis of figurative language production. *NeuroImage*, 90, 99–106.
- Berthier, M. L., Lambon Ralph, M. A., Pujol, J., & Green, C. (2012). Arcuate fasciculus variability and repetition: The left sometimes can be right. *Cortex*, 48(2), 133–143.
- Binder, J. R. (2015). The Wernicke area: Modern evidence and a reinterpretation. *Neurology*, 85(24), 2170–2175.
- Binder, J. R. (2016). In defense of abstract conceptual representations. *Psychonomic Bulletin & Review*, 23(4), 1096–1108.
- Binder, J. R. (2017). Current Controversies on Wernicke's Area and its Role in Language. *Current Neurology and Neuroscience Reports*, 17(8), 58.
- Binder, J. R., & Desai, R. H. (2011). The neurobiology of semantic memory. *Trends in Cognitive Sciences*, 15(11), 527–536.
- Binder, J. R., Desai, R. H., Graves, W. W., & Conant, L. L. (2009). Where Is the Semantic System? A Critical Review and Meta-Analysis of 120 Functional Neuroimaging Studies. *Cerebral Cortex*, 19(12), 2767–2796.
- Blakemore, S. J., Frith, C. D., & Wolpert, D. M. (2001). The cerebellum is involved in predicting the sensory consequences of action. *Neuroreport*, 12(9), 1879–1884.
- Blakemore, S. J., Wolpert, D. M., & Frith, C. D. (1998). Central cancellation of self-produced tickle sensation. *Nature Neuroscience*, 1(7), 635–640.
- Bohland, J. W., Bullock, D., & Guenther, F. H. (2010). Neural Representations and Mechanisms for the Performance of Simple Speech Sequences. *Journal of Cognitive Neuroscience*, 22(7), 1504–1529.

- Bohland, J. W., & Guenther, F. H. (2006). An fMRI investigation of syllable sequence production. *NeuroImage*, 32(2), 821–841.
- Botvinick, M. M., Braver, T. S., Barch, D. M., Carter, C. S., & Cohen, J. D. (2001). Conflict monitoring and cognitive control. *Psychological Review*, 108(3), 624–652.
- Bouchard, K. E., Mesgarani, N., Johnson, K., & Chang, E. F. (2013). Functional organization of human sensorimotor cortex for speech articulation. *Nature*, 495(7441), 327–332.
- Boylan, C., Trueswell, J. C., & Thompson-Schill, S. L. (2015). Compositionality and the angular gyrus: A multi-voxel similarity analysis of the semantic composition of nouns and verbs. *Neuropsychologia*, 78, 130–141.
- Boylan, C., Trueswell, J. C., & Thompson-Schill, S. L. (2017). Relational vs. Attributive interpretation of nominal compounds differentially engages angular gyrus and anterior temporal lobe. *Brain and Language*, 169, 8–21.
- Bozeat, S., Lambon Ralph, M. A., Patterson, K., Garrard, P., & Hodges, J. R. (2000). Non-verbal semantic impairment in semantic dementia. *Neuropsychologia*, 38(9), 1207–1215.
- Brown, S., Ingham, R. J., Ingham, J. C., Laird, A. R., & Fox, P. T. (2005). Stuttered and fluent speech production: An ALE meta-analysis of functional neuroimaging studies. *Human Brain Mapping*, 25(1), 105–117.
- Buchsbaum, B. R., Baldo, J., Okada, K., Berman, K. F., Dronkers, N., D’Esposito, M., & Hickok, G. (2011). Conduction aphasia, sensory-motor integration, and phonological short-term memory – An aggregate analysis of lesion and fMRI data. *Brain and Language*, 119(3), 119–128.
- Buchsbaum, B. R., Hickok, G., & Humphries, C. (2001). Role of left posterior superior temporal gyrus in phonological processing for speech perception and production. *Cognitive Science*, 25(5), 663–678.
- Buxbaum, L. J., Kyle, K. M., & Menon, R. (2005). On beyond mirror neurons: Internal representations subserving imitation and recognition of skilled object-related actions in humans. *Cognitive Brain Research*, 25(1), 226–239.
- Buxbaum, L. J., Kyle, K. M., Tang, K., & Detre, J. A. (2006). Neural substrates of knowledge of hand postures for object grasping and functional object use: Evidence from fMRI. *Brain Research*, 1117(1), 175–185.

- Caramazza, A. (1997). How Many Levels of Processing Are There in Lexical Access? *Cognitive Neuropsychology*, 14(1), 177–208.
- Cavada, C., & Goldman-Rakic, P. S. (1989a). Posterior parietal cortex in rhesus monkey: I. Parcellation of areas based on distinctive limbic and sensory corticocortical connections. *Journal of Comparative Neurology*, 287(4), 393–421.
- Cavada, C., & Goldman-Rakic, P. S. (1989b). Posterior parietal cortex in rhesus monkey: II. Evidence for segregated corticocortical networks linking sensory and limbic areas with the frontal lobe. *Journal of Comparative Neurology*, 287(4), 422–445.
- Chao, L. L., & Martin, A. (1999). Cortical Regions Associated with Perceiving, Naming, and Knowing about Colors. *Journal of Cognitive Neuroscience*, 11(1), 25–35.
- Chomsky, N. (1957). *Syntactic structures*. The Hague: Mouton.
- Christoffels, I. K., Formisano, E., & Schiller, N. O. (2007). Neural correlates of verbal feedback processing: An fMRI study employing overt speech. *Human Brain Mapping*, 28(9), 868–879.
- Cipolotti, L., Butterworth, B., & Denes, G. (1991). A SPECIFIC DEFICIT FOR NUMBERS IN A CASE OF DENSE ACALCULIA. *Brain*, 114(6), 2619–2637.
- Clos, M., Amunts, K., Laird, A. R., Fox, P. T., & Eickhoff, S. B. (2013). Tackling the multifunctional nature of Broca’s region meta-analytically: Co-activation-based parcellation of area 44. *NeuroImage*, 83, 174–188.
- Cloutman, L., Gottesman, R., Chaudhry, P., Davis, C., Kleinman, J. T., Pawlak, M., ... Hillis, A. E. (2009). Where (in the brain) do semantic errors come from? *Cortex*, 45(5), 641–649.
- Corina, D. P., Loudermilk, B. C., Detwiler, L., Martin, R. F., Brinkley, J. F., & Ojemann, G. (2010). Analysis of naming errors during cortical stimulation mapping: Implications for models of language representation. *Brain and Language*, 115(2), 101–112.
- Croot Karen, Ballard Kirrie, Leyton Cristian E., & Hodges John R. (2012). Apraxia of Speech and Phonological Errors in the Diagnosis of Nonfluent/Agrammatic and Logopenic Variants of Primary Progressive Aphasia. *Journal of Speech, Language, and Hearing Research*, 55(5), 1562–1572.
- Crosson, B. A. (1992). *Subcortical functions in language and memory*. New York: Guilford Press.

- Curtis, C. E., & D'Esposito, M. (2003). Persistent activity in the prefrontal cortex during working memory. *Trends in Cognitive Sciences*, 7(9), 415–423.
- Damasio, H. (1981). Cerebral localization of the aphasias. In M. T. Sarno (Ed.), *Acquired aphasia* (pp. 27-50). Orlando: Academic Press.
- Damasio, A. R. (1994). *Descarte's error: emotion, reason, and the human brain*. New York: Putnam.
- Damasio, H., Damasio, A. R. (1980). The anatomical basis of conduction aphasia. *Brain*, 103, 337–50.
- Damasio, H, Tranel, D., Grabowski, T., Adolphs, R., & Damasio, A. (2004). Neural systems behind word and concept retrieval. *Cognition*, 92(1), 179–229.
- Damasio, Hanna, & Damasio, A. R. (1980). THE ANATOMICAL BASIS OF CONDUCTION APHASIA. *Brain*, 103(2), 337–350. <https://doi.org/10.1093/brain/103.2.337>
- Damasio, Hanna, Grabowski, T. J., Tranel, D., Hichwa, R. D., & Damasio, A. R. (1996). A neural basis for lexical retrieval. *Nature*, 380, 499-505.
- Davey, J., Cornelissen, P. L., Thompson, H. E., Sonkusare, S., Hallam, G., Smallwood, J., & Jefferies, E. (2015). Automatic and Controlled Semantic Retrieval: TMS Reveals Distinct Contributions of Posterior Middle Temporal Gyrus and Angular Gyrus. *Journal of Neuroscience*, 35(46), 15230–15239.
- de Zubicaray, G. I., McMahon, K., Eastburn, M., & Pringle, A. (2006). Top-down influences on lexical selection during spoken word production: A 4T fMRI investigation of refractory effects in picture naming. *Human Brain Mapping*, 27(11), 864–873.
- de Zubicaray, G. I., McMahon, K., & Howard, D. (2015). Perfusion fMRI evidence for priming of shared feature-to-lexical connections during cumulative semantic interference in spoken word production. *Language, Cognition and Neuroscience*, 30(3), 261–272.
- de Zubicaray, G. I., Miozzo, M., Johnson, K., Schiller, N. O., & McMahon, K. L. (2012). Independent Distractor Frequency and Age-of-Acquisition Effects in Picture–Word Interference: FMRI Evidence for Post-lexical and Lexical Accounts according to Distractor Type. *Journal of Cognitive Neuroscience*, 24(2), 482–495.

- de Zubicaray, G. I., Wilson, S. J., McMahon, K. L., & Muthiah, S. (2001). The semantic interference effect in the picture-word paradigm: An event-related fMRI study employing overt responses. *Human Brain Mapping, 14*(4), 218–227.
- Dejerine, J. (1892). Contribution à l'étude anatomopathologique et clinique des différents variétés de cécité verbale. *Mémoires de La Société de Biologie, 4*, 61–90.
- Dell, G. S. (1986). A spreading-activation theory of retrieval in sentence production. *Psychological Review, 93*(3), 283–321.
- Dell, G. S. (1988). The retrieval of phonological forms in production: Tests of predictions from a connectionist model. *Journal of Memory and Language, 27*, 124–142.
- Dell, G. S. (1995). Speaking and misspeaking. In L. R. Gleitman, D. N. Osherson, & M. Liberman (Eds.), *An invitation to cognitive science: language* (pp. 183–208). Cambridge, MA: MIT press.
- Dell, G. S., Juliano, C., & Govindjee, A. (1993). Structure and content in language production: A theory of frame constraints in phonological speech errors. *Cognitive Science, 17*(2), 149–195.
- Devlin, J. T., Jamison, H. L., Gonnerman, L. M., & Matthews, P. M. (2006). The Role of the Posterior Fusiform Gyrus in Reading. *Journal of Cognitive Neuroscience, 18*(6), 911–922.
- Devlin, J. T., Matthews, P. M., & Rushworth, M. F. S. (2003). Semantic Processing in the Left Inferior Prefrontal Cortex: A Combined Functional Magnetic Resonance Imaging and Transcranial Magnetic Stimulation Study. *Journal of Cognitive Neuroscience, 15*(1), 71–84.
- Dronkers, N. F. (1996). A new brain region for coordinating speech articulation. *Nature, 384*, 159–161.
- Dronkers, N. F., Wilkins, D. P., Van Valin, R. D., Redfern, B. B., & Jaeger, J. J. (2004). Lesion analysis of the brain areas involved in language comprehension. *Cognition, 92*(1), 145–177.
- Duffau, H., Moritz-Gasser, S., & Mandonnet, E. (2014). A re-examination of neural basis of language processing: Proposal of a dynamic hodotopical model from data provided by brain stimulation mapping during picture naming. *Brain and Language, 131*, 1–10.

- Eggert, G. H. (1977). Wernicke's works on aphasia: a source book and review. The Hague: Mouton.
- Farrell, D. F., Burbank, N., Lettich, E., & Ojemann, G. A. (2007). Individual variation in human motor-sensory (rolandic) cortex. *Journal of Clinical Neurophysiology*, 24(3), 286–293.
- Fischer, M. H., & Zwaan, R. A. (2008). Embodied language: A review of the role of the motor system in language comprehension. *The Quarterly Journal of Experimental Psychology*, 61(6), 825–850.
- Fletcher, P. C., Happé, F., Frith, U., Baker, S. C., Dolan, R. J., Frackowiak, R. S. J., & Frith, C. D. (1995). Other minds in the brain: A functional imaging study of “theory of mind” in story comprehension. *Cognition*, 57(2), 109–128.
- Foygel, D., & Dell, G. S. (2000). Models of Impaired Lexical Access in Speech Production. *Journal of Memory and Language*, 43(2), 182–216.
- Franken, M. K., Hagoort, P., & Acheson, D. J. (2015). Modulations of the auditory M100 in an imitation task. *Brain and Language*, 142, 18–23.
- Freedman, M., Alexander, M. P., & Naeser, M. A. (1984). Anatomic basis of transcortical motor aphasia. *Neurology*, 34(4), 409–409.
- Fridriksson, J., Kjartansson, O., Morgan, P. S., Hjaltason, H., Magnúsdóttir, S., Bonilha, L., & Rorden, C. (2010). Impaired Speech Repetition and Left Parietal Lobe Damage. *Journal of Neuroscience*, 30(33), 11057–11061.
- Friederici, A. D. (2002). Towards a neural basis of auditory sentence processing. *Trends in Cognitive Sciences*, 6(2), 78–84.
- Friederici, A. D., Rüschemeyer, S.-A., Hahne, A., & Fiebach, C. J. (2003). The Role of Left Inferior Frontal and Superior Temporal Cortex in Sentence Comprehension: Localizing Syntactic and Semantic Processes. *Cerebral Cortex*, 13(2), 170–177.
- Garrett, M. F. (1975). The analysis of sentence production. In G. H. Bower (Ed.), *The psychology of learning and motivation* (pp. 133–177). New York: Academic press.
- Gauvin, H. S., De Baene, W., Brass, M., & Hartsuiker, R. J. (2016). Conflict monitoring in speech processing: An fMRI study of error detection in speech production and perception. *NeuroImage*, 126, 96–105.

- Ghosh Satrajit S., Tourville Jason A., & Guenther Frank H. (2008). A Neuroimaging Study of Premotor Lateralization and Cerebellar Involvement in the Production of Phonemes and Syllables. *Journal of Speech, Language, and Hearing Research*, 51(5), 1183–1202.
- Gorno-Tempini, M. L., Dronkers, N. F., Rankin, K. P., Ogar, J. M., Phengrasamy, L., Rosen, H. J., ... Miller, B. L. (2004). Cognition and anatomy in three variants of primary progressive aphasia. *Annals of Neurology*, 55(3), 335–346.
- Gough, P. M., Nobre, A. C., & Devlin, J. T. (2005). Dissociating Linguistic Processes in the Left Inferior Frontal Cortex with Transcranial Magnetic Stimulation. *Journal of Neuroscience*, 25(35), 8010–8016.
- Graff-Radford, J., Jones, D. T., Strand, E. A., Rabinstein, A. A., Duffy, J. R., & Josephs, K. A. (2014). The neuroanatomy of pure apraxia of speech in stroke. *Brain and Language*, 129, 43–46.
- Graves, W. W., Binder, J. R., Desai, R. H., Conant, L. L., & Seidenberg, M. S. (2010). Neural correlates of implicit and explicit combinatorial semantic processing. *NeuroImage*, 53(2), 638–646.
- Guenther, F. H. (1994). A neural network model of speech acquisition and motor equivalent speech production. *Biological Cybernetics*, 72(1), 43–53.
- Guenther, F. H. (1995). Speech sound acquisition, coarticulation, and rate effects in a neural network model of speech production. *Psychological Review*, 102(3), 594–621.
- Guenther, F.H. (2016). *Neural Control of Speech*. Cambridge, MA: MIT Press.
- Haaland, K. Y., Harrington, D. L., & Knight, R. T. (2000). Neural representations of skilled movement. *Brain*, 123(11), 2306–2313.
- Hamberger, M. J., Miozzo, M., Schevon, C. A., Morrison, C., Carlson, C., Mehta, A. D., ... Williams, A. C. (2016). Functional differences among stimulation-identified cortical naming sites in the temporal region. *Epilepsy & Behavior*, 60, 124–129.
- Hanley, J. R., Cortis, C., Budd, M.-J., & Nozari, N. (2016). Did I say dog or cat? A study of semantic error detection and correction in children. *Journal of Experimental Child Psychology*, 142, 36–47.
- Hartsuiker, R. J., & Kolk, H. H. J. (2001). Error Monitoring in Speech Production: A Computational Test of the Perceptual Loop Theory. *Cognitive Psychology*, 42(2), 113–157.

- Harvey, D. Y., & Schnur, T. T. (2015). Distinct loci of lexical and semantic access deficits in aphasia: Evidence from voxel-based lesion-symptom mapping and diffusion tensor imaging. *Cortex*, 67, 37–58.
- Harvey, D. Y., Wei, T., Ellmore, T. M., Hamilton, A. C., & Schnur, T. T. (2013). Neuropsychological evidence for the functional role of the uncinate fasciculus in semantic control. *Neuropsychologia*, 51(5), 789–801.
- Heinks-Maldonado, T. H., Nagarajan, S. S., & Houde, J. F. (2006). Magnetoencephalographic evidence for a precise forward model in speech production. *Neuroreport*, 17(13), 1375–1379.
- Henry, M. L., & Gorno-Tempini, M. L. (2010). The logopenic variant of primary progressive aphasia. *Current Opinion in Neurology*, 23(6), 633–637.
- Henseler, I., Regenbrecht, F., & Obrig, H. (2014). Lesion correlates of patholinguistic profiles in chronic aphasia: Comparisons of syndrome-, modality- and symptom-level assessment. *Brain*, 137(3), 918–930.
- Hickok, G. (2012). Computational neuroanatomy of speech production. *Nature Reviews Neuroscience*, 13(2), 135–145.
- Hickok, G., Buchsbaum, B., Humphries, C., & Muftuler, T. (2003). Auditory–Motor Interaction Revealed by fMRI: Speech, Music, and Working Memory in Area Spt. *Journal of Cognitive Neuroscience*, 15(5), 673–682.
- Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Reviews Neuroscience*, 8(5), 393–402.
- Hillis, A. E., & Caramazza, A. (1991). Category-specific naming and comprehension impairment: a double dissociation. *Brain*, 114(5), 2081–2094.
- Hillis, A. E., Work, M., Barker, P. B., Jacobs, M. A., Breese, E. L., & Maurer, K. (2004). Re-examining the brain regions crucial for orchestrating speech articulation. *Brain*, 127(7), 1479–1487.
- Hocking, J., McMahon, K. L., & de Zubicaray, G. I. (2008). Semantic Context and Visual Feature Effects in Object Naming: An fMRI Study using Arterial Spin Labeling. *Journal of Cognitive Neuroscience*, 21(8), 1571–1583.
- Hoffman, P., Jefferies, E., & Ralph, M. A. L. (2010). Ventrolateral Prefrontal Cortex Plays an Executive Regulation Role in Comprehension of Abstract Words: Convergent

- Neuropsychological and Repetitive TMS Evidence. *Journal of Neuroscience*, 30(46), 15450–15456.
- Homae, F., Hashimoto, R., Nakajima, K., Miyashita, Y., & Sakai, K. L. (2002). From Perception to Sentence Comprehension: The Convergence of Auditory and Visual Information of Language in the Left Inferior Frontal Cortex. *NeuroImage*, 16(4), 883–900.
- Humphries, C., Binder, J. R., Medler, D. A., & Liebenthal, E. (2007). Time course of semantic processes during sentence comprehension: An fMRI study. *NeuroImage*, 36(3), 924–932.
- Hyvärinen, J. (1982). Posterior parietal lobe of the primate brain. *Physiological Reviews*, 62(3), 1060–1129.
- Indefrey, P., & Levelt, W. J. M. (2000). The neural correlates of language production. In M. Gazzaniga (Ed.), *The new cognitive neurosciences* (pp. 845–865). Cambridge, MA: MIT Press.
- Indefrey, P., & Levelt, W. J. M. (2004). The spatial and temporal signatures of word production components. *Cognition*, 92(1), 101–144.
- Jax, S. A., Buxbaum, L. J., & Moll, A. D. (2006). Deficits in Movement Planning and Intrinsic Coordinate Control in Ideomotor Apraxia. *Journal of Cognitive Neuroscience*, 18(12), 2063–2076.
- Kan, I. P., Barsalou, L. W., Solomon, K. O., Minor, J. K., & Thompson-Schill, S. L. (2003). Role of Mental Imagery in a Property Verification Task: Fmri Evidence for Perceptual Representations of Conceptual Knowledge. *Cognitive Neuropsychology*, 20(3–6), 525–540.
- Kan, I. P., & Thompson-Schill, S. L. (2004). Selection from perceptual and conceptual representations. *Cognitive, Affective, & Behavioral Neuroscience*, 4(4), 466–482.
- Kemmerer, D. (2018). From blueprints to brain maps: The status of the Lemma Model in cognitive neuroscience. *Language, Cognition and Neuroscience*. Retrieved from <https://doi.org/10.1080/23273798.2018.1537498>
- Kertesz, A., Lau, W. K., & Polk, M. (1993). The Structural Determinants of Recovery in Wernicke's Aphasia. *Brain and Language*, 44(2), 153–164.
- Kertesz, Andrew, Sheppard, A., & MacKenzie, R. (1982). Localization in Transcortical Sensory Aphasia. *Archives of Neurology*, 39(8), 475–478.

- Kiefer, M., & Pulvermüller, F. (2012). Conceptual representations in mind and brain: Theoretical developments, current evidence and future directions. *Cortex*, 48(7), 805–825.
- Knolle, F., Schröger, E., Baess, P., & Kotz, S. A. (2011). The Cerebellum Generates Motor-to-Auditory Predictions: ERP Lesion Evidence. *Journal of Cognitive Neuroscience*, 24(3), 698–706.
- Kuchinke, L., Jacobs, A. M., Grubich, C., Võ, M. L.-H., Conrad, M., & Herrmann, M. (2005). Incidental effects of emotional valence in single word processing: An fMRI study. *NeuroImage*, 28(4), 1022–1032.
- Lambon Ralph, M. A., Jefferies, E., Patterson, K., & Rogers, T. T. (2017). The neural and computational bases of semantic cognition. *Nature Reviews Neuroscience*, 18(1), 42–55.
- Laplane, D., Talairach, J., Meininger, V., Bancaud, J., & Orgogozo, J. M. (1977). Clinical consequences of corticectomies involving the supplementary motor area in man. *Journal of the Neurological Sciences*, 34(3), 301–314.
- Lashley, K. S. (1951). The problem of serial order in behavior. In L.A. Jeffress (Ed.), *Cerebral mechanisms in behavior*. New York: Wiley.
- Levelt, W. J. M. (1983). Monitoring and self-repair in speech. *Cognition*, 14(1), 41–104.
- Levelt, W. J. M. (1989). *Speaking: From Intention to Articulation*. Cambridge, MA: MIT Press.
- Levelt, W. J. M., Roelofs, A., & Meyer, A. S. (1999). A theory of lexical access in speech production. *Behavioral and Brain Sciences*, 22(1), 1–38.
- Levelt, W. J. M., Schreuder, R. & Hoenkamp, E. (1978). Structure and use of verbs of motion. In R. N. Campbell & P. T. Smith (Eds.), *Recent advances in the psychology of language* (pp. 137-162). Boston, MA: Springer.
- Levy, D. A., Bayley, P. J., & Squire, L. R. (2004). The anatomy of semantic knowledge: Medial vs. lateral temporal lobe. *Proceedings of the National Academy of Sciences*, 101(17), 6710–6715.
- Leyton, C. E., Ballard, K. J., Piguet, O., & Hodges, J. R. (2014). Phonologic errors as a clinical marker of the logopenic variant of PPA. *Neurology*, 82(18), 1620–1627.
- MacKay, D. G. (1987). *The organization of perception and action: A theory of language and other cognitive skills*. New York: Springer.

- Maess, B., Friederici, A. D., Damian, M., Meyer, A. S., & Levelt, W. J. M. (2002). Semantic Category Interference in Overt Picture Naming: Sharpening Current Density Localization by PCA. *Journal of Cognitive Neuroscience*, 14(3), 455–462.
- Martin, A. (2016). GRAPES—Grounding representations in action, perception, and emotion systems: How object properties and categories are represented in the human brain. *Psychonomic Bulletin & Review*, 23(4), 979–990.
- Martin, A., Ungerleider, L. G., Haxby, J. V. (2000). Category-specificity and the brain: the sensory-motor model of semantic representations of objects. In M. S. Gazzaniga (Ed.), *The new cognitive neurosciences* (pp.1023-1036). Cambridge, MA: MIT Press.
- Martin, R. C., & Cheng, Y. (2006). Selection demands versus association strength in the verb generation task. *Psychonomic Bulletin & Review*, 13(3), 396–401.
- Meteyard, L., Cuadrado, S. R., Bahrami, B., & Vigliocco, G. (2012). Coming of age: A review of embodiment and the neuroscience of semantics. *Cortex*, 48(7), 788–804.
- Meyer, A. S. (1990). The phonological encoding of successive syllables. *Journal of Memory and Language*, 29, 524-545.
- Mirman, D., Chen, Q., Zhang, Y., Wang, Z., Faseyitan, O. K., Coslett, H. B., & Schwartz, M. F. (2015). Neural organization of spoken language revealed by lesion–symptom mapping. *Nature Communications*, 6(6762), 1–9.
- Moore, C. J., & Price, C. J. (1999). Three Distinct Ventral Occipitotemporal Regions for Reading and Object Naming. *NeuroImage*, 10(2), 181–192.
- Murtha, S., Chertkow, H., Beauregard, M., & Evans, A. (1999). The Neural Substrate of Picture Naming. *Journal of Cognitive Neuroscience*, 11(4), 399–423.
- Ni, W., Constable, R. T., Mencl, W. E., Pugh, K. R., Fulbright, R. K., Shaywitz, S. E., ... Shankweiler, D. (2000). An Event-related Neuroimaging Study Distinguishing Form and Content in Sentence Processing. *Journal of Cognitive Neuroscience*, 12(1), 120–133.
- Niziolek, C. A., & Guenther, F. H. (2013). Vowel Category Boundaries Enhance Cortical and Behavioral Responses to Speech Feedback Alterations. *Journal of Neuroscience*, 33(29), 12090–12098.

- Noonan, K. A., Jefferies, E., Visser, M., & Lambon Ralph, M. A. (2013). Going beyond inferior prefrontal involvement in semantic control: Evidence for the additional contribution of dorsal angular gyrus and posterior middle temporal cortex. *Journal of Cognitive Neuroscience*, 25(11), 1824–1850.
- Novick, J. M., Trueswell, J. C., & Thompson-Schill, S. L. (2005). Cognitive control and parsing: Reexamining the role of Broca's area in sentence comprehension. *Cognitive, Affective, & Behavioral Neuroscience*, 5(3), 263–281.
- Nozari, N. (2019). The dual origin of semantic errors in access deficit: Activation vs. inhibition deficit. *Cognitive Neuropsychology*, 36, 31–53.
- Nozari, N. (under review). A comprehension- or a production-based monitor? Response to Roelofs (2019).
- Nozari, N., Dell, G. S., & Schwartz, M. F. (2011). Is comprehension necessary for error detection? A conflict-based account of monitoring in speech production. *Cognitive Psychology*, 63(1), 1–33.
- Nozari, N., & Hepner, C. R. (2018). To select or to wait? The importance of criterion setting in debates of competitive lexical selection. *Cognitive Neuropsychology*. Retrieved from <https://doi.org/10.1080/02643294.2018.1476335>
- Nozari, N., & Hepner, C. R. (2019). To select or to wait? Response to the commentaries. *Cognitive Neuropsychology*. <https://doi.org/10.1080/02643294.2019.1632280>
- Nozari, N., Martin, C. D., & McCloskey, N. (2019). Is repairing speech errors an automatic or a controlled process? Insights from the relationship between error and repair probabilities in English and Spanish. *Language, Cognition and Neuroscience*. Retrieved from <https://doi.org/10.1080/23273798.2019.1637007>
- Nozari, N., Mirman, D., & Thompson-Schill, S. L. (2016). The ventrolateral prefrontal cortex facilitates processing of sentential context to locate referents. *Brain and Language*, 157–158, 1–13.
- Nozari, N. & Pinet, S. (under review). A critical review of the behavioral, neuroimaging, and electrophysiological studies of co-activation of representations during word production.

- Nozari, N., & Thompson-Schill, S. L. (2016). Left Ventrolateral Prefrontal Cortex in Processing of Words and Sentences. In G. Hickok & S. L. Small (Eds.), *Neurobiology of Language* (pp. 569–584). San Diego, CA: Academic press.
- Okada, K., & Hickok, G. (2006). Left posterior auditory-related cortices participate both in speech perception and speech production: Neural overlap revealed by fMRI. *Brain and Language*, 98(1), 112–117.
- Oppenheim, G. M., & Dell, G. S. (2008). Inner speech slips exhibit lexical bias, but not the phonemic similarity effect. *Cognition*, 106(1), 528–537.
- Patterson, K., Nestor, P. J., & Rogers, T. T. (2007). Where do you know what you know? The representation of semantic knowledge in the human brain. *Nature Reviews Neuroscience*, 8(12), 976–987.
- Paulesu, E., Shallice, T., Danelli, L., Sberna, M., Frackowiak, R. S. J., & Frith, C. D. (2017). Anatomical Modularity of Verbal Working Memory? Functional Anatomical Evidence from a Famous Patient with Short-Term Memory Deficits. *Frontiers in Human Neuroscience*. Retrieved from <https://doi.org/10.3389/fnhum.2017.00231>
- Penfield, W. & Roberts, L. (1959). *Speech and brain mechanisms*. Princeton: Princeton University Press.
- Phillips, M. L., Drevets, W. C., Rauch, S. L., & Lane, R. (2003). Neurobiology of emotion perception II: Implications for major psychiatric disorders. *Biological Psychiatry*, 54(5), 515–528.
- Pickering, M. J., & Garrod, S. (2013). An integrated theory of language production and comprehension. *Behavioral and Brain Sciences*, 36(4), 329–347.
- Pillay, S. B., Stengel, B. C., Humphries, C., Book, D. S., & Binder, J. R. (2014). Cerebral localization of impaired phonological retrieval during rhyme judgment. *Annals of Neurology*, 76(5), 738–746.
- Plaut, D. C., & Gonnerman, L. M. (2000). Are non-semantic morphological effects incompatible with a distributed connectionist approach to lexical processing? *Language and Cognitive Processes*, 15(4–5), 445–485.
- Pobric, G., Jefferies, E., & Lambon Ralph, M. A. (2010). Amodal semantic representations depend on both anterior temporal lobes: Evidence from repetitive transcranial magnetic stimulation. *Neuropsychologia*, 48(5), 1336–1342.

- Price, C. J. (2000). Functional imaging studies of aphasia. In J. C. Mazziotta, A. W. Toga, & R. S. J. Frackowiak (Eds.), *Brain mapping: the disorders* (pp. 181-200). San Diego: Academic Press.
- Quigg, M., & Fountain, N. (1999). Conduction aphasia elicited by stimulation of the left posterior superior temporal gyrus. *Journal of Neurology, Neurosurgery, and Psychiatry*, 66(3), 393–396.
- Rapcsak, S. Z. & Rubens, A. B. (1994). Localization of lesions in transcortical aphasia. In A. Kertesz (Ed.), *Localization and neuroimaging in neuropsychology* (pp. 297-329). San Diego: Academic Press.
- Raymer, A. M., Foundas, A. L., Maher, L. M., Greenwald, M. L., Morris, M., Rothi, L. J. G., & Heilman, K. M. (1997). Cognitive Neuropsychological Analysis and Neuroanatomic Correlates in a Case of Acute Anomia. *Brain and Language*, 58(1), 137–156.
- Richardson, J. D., Fillmore, P., Rorden, C., LaPointe, L. L., & Fridriksson, J. (2012). Re-establishing Broca's initial findings. *Brain and Language*, 123(2), 125–130.
- Roelofs, A. (1992). A spreading-activation theory of lemma retrieval in speaking. *Cognition*, 42(1), 107–142.
- Rohrer, J. D., Ridgway, G. R., Crutch, S. J., Hailstone, J., Goll, J. C., Clarkson, M. J., ... Warren, J. D. (2010). Progressive logopenic/phonological aphasia: Erosion of the language network. *NeuroImage*, 49(1), 984–993.
- Rosenbeck, J. C. (2004). Neurogenic mutism. In R.D. Kent (Ed.), *The MIT encyclopedia of communication disorders* (pp. 145-147). Cambridge, MA: MIT press.
- Rottschy, C., Langner, R., Dogan, I., Reetz, K., Laird, A. R., Schulz, J. B., ... Eickhoff, S. B. (2012). Modelling neural correlates of working memory: A coordinate-based meta-analysis. *NeuroImage*, 60(1), 830–846.
- Roux, F.-E., Durand, J.-B., Jucla, M., Réhault, E., Reddy, M., & Démonet, J.-F. (2012). Segregation of Lexical and Sub-Lexical Reading Processes in the Left Perisylvian Cortex. *PLOS ONE*, 7(11). Retrieved from <https://doi.org/10.1371/journal.pone.0050665>
- Schnur, T. T., Schwartz, M. F., Brecher, A., & Hodgson, C. (2006). Semantic interference during blocked-cyclic naming: Evidence from aphasia. *Journal of Memory and Language*, 54(2), 199–227.

- Schnur, T. T., Schwartz, M. F., Kimberg, D. Y., Hirshorn, E., Coslett, H. B., & Thompson-Schill, S. L. (2009). Localizing interference during naming: Convergent neuroimaging and neuropsychological evidence for the function of Broca's area. *Proceedings of the National Academy of Sciences*, 106(1), 322–327.
- Schuchard, J., Middleton, E. L., & Schwartz, M. F. (2017). The timing of spontaneous detection and repair of naming errors in aphasia. *Cortex*, 93, 79–91.
- Schwartz, M. F., Faseyitan, O., Kim, J., & Coslett, H. B. (2012). The dorsal stream contribution to phonological retrieval in object naming. *Brain*, 135(12), 3799–3814.
- Schwartz, M. F., Kimberg, D. Y., Walker, G. M., Brecher, A., Faseyitan, O. K., Dell, G. S., ... Coslett, H. B. (2011). Neuroanatomical dissociation for taxonomic and thematic knowledge in the human brain. *Proceedings of the National Academy of Sciences*, 108(20), 8520–8524.
- Schwartz, M. F., Kimberg, D. Y., Walker, G. M., Faseyitan, O., Brecher, A., Dell, G. S., & Coslett, H. B. (2009). Anterior temporal involvement in semantic word retrieval: Voxel-based lesion-symptom mapping evidence from aphasia. *Brain*, 132(12), 3411–3427.
- Segawa, J. A., Tourville, J. A., Beal, D. S., & Guenther, F. H. (2015). The Neural Correlates of Speech Motor Sequence Learning. *Journal of Cognitive Neuroscience*, 27(4), 819–831.
- Seltzer, B., & Pandya, D. N. (1994). Parietal, temporal, and occipital projections to cortex of the superior temporal sulcus in the rhesus monkey: A retrograde tracer study. *Journal of Comparative Neurology*, 343(3), 445–463.
- Shattuck-Hufnagel, S. (1979). Speech errors as evidence for a serial-order mechanism in sentence production. In W. E. Cooper & E. C. T. Walker (Eds.), *Sentence processing: Psycholinguistic studies presented to Merrill Garrett* (pp. 295–342). Hillsdale, NJ: Erlbaum.
- Simmons, W. K., & Martin, A. (2009). The anterior temporal lobes and the functional architecture of semantic memory. *Journal of the International Neuropsychological Society*, 15(5), 645–649.
- Stemberger, J. P. (1985). An interactive activation model of language production. In A. Ellis, (Ed.), *Progress in the psychology of language* (Vol. 1, pp. 143–186). London: Erlbaum.
- Takai, O., Brown, S., & Liotti, M. (2010). Representation of the speech effectors in the human motor cortex: Somatotopy or overlap? *Brain and Language*, 113(1), 39–44.

- Thompson-Schill, S. L., Aguirre, G. K., Desposito, M., & Farah, M. J. (1999). A neural basis for category and modality specificity of semantic knowledge. *Neuropsychologia*, 37(6), 671–676.
- Thompson-Schill, Sharon L., D’Esposito, M., Aguirre, G. K., & Farah, M. J. (1997). Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation. *Proceedings of the National Academy of Sciences*, 94(26), 14792–14797.
- Thompson-Schill, Sharon L., Swick, D., Farah, M. J., D’Esposito, M., Kan, I. P., & Knight, R. T. (1998). Verb generation in patients with focal frontal lesions: A neuropsychological test of neuroimaging findings. *Proceedings of the National Academy of Sciences*, 95(26), 15855–15860.
- Thothathiri, M., Kimberg, D. Y., & Schwartz, M. F. (2011). The Neural Basis of Reversible Sentence Comprehension: Evidence from Voxel-based Lesion Symptom Mapping in Aphasia. *Journal of Cognitive Neuroscience*, 24(1), 212–222.
- Tourville, J. A., & Guenther, F. H. (2011). The DIVA model: A neural theory of speech acquisition and production. *Language and Cognitive Processes*, 26(7), 952–981.
- Tourville, J. A., Reilly, K. J., & Guenther, F. H. (2008). Neural mechanisms underlying auditory feedback control of speech. *NeuroImage*, 39(3), 1429–1443.
- Tranel, D., Kemmerer, D., Adolphs, R., Damasio, H., & Damasio, A. R. (2003). Neural Correlates of Conceptual Knowledge for Actions. *Cognitive Neuropsychology*, 20(3–6), 409–432.
- Turkeltaub, P. E., Eden, G. F., Jones, K. M., & Zeffiro, T. A. (2002). Meta-Analysis of the Functional Neuroanatomy of Single-Word Reading: Method and Validation. *NeuroImage*, 16(3, Part A), 765–780.
- Vallar, G. & Shallice, T. (Eds.). (1990). *Neuropsychological impairments of short-term memory*. Cambridge: Cambridge University Press.
- Vandenbulcke, M., Peeters, R., Fannes, K., & Vandenberghe, R. (2006). Knowledge of visual attributes in the right hemisphere. *Nature Neuroscience*, 9(7), 964–970.
- Wagner, A. D., Paré-Blagoev, E. J., Clark, J., & Poldrack, R. A. (2001). Recovering Meaning: Left Prefrontal Cortex Guides Controlled Semantic Retrieval. *Neuron*, 31(2), 329–338.
- Walker, G. M., Schwartz, M. F., Kimberg, D. Y., Faseyitan, O., Brecher, A., Dell, G. S., & Coslett, H. B. (2011). Support for anterior temporal involvement in semantic error

- production in aphasia: New evidence from VLSM. *Brain and Language*, 117(3), 110–122.
- Whitney, C., Kirk, M., O’Sullivan, J., Lambon Ralph, M. A., & Jefferies, E. (2011a). Executive 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(1), 133–147.
- Whitney, C., Kirk, M., O’Sullivan, J., Lambon Ralph, M. A., & Jefferies, E. (2011b). The Neural Organization of Semantic Control: TMS Evidence for a Distributed Network in Left Inferior Frontal and Posterior Middle Temporal Gyrus. *Cerebral Cortex*, 21(5), 1066–1075.
- Xu, J., Kemeny, S., Park, G., Frattali, C., & Braun, A. (2005). Language in context: Emergent features of word, sentence, and narrative comprehension. *NeuroImage*, 25(3), 1002–1015.
- Yee, E., & Thompson-Schill, S. L. (2016). Putting concepts into context. *Psychonomic Bulletin & Review*, 23(4), 1015–1027.
- Yue, Q., Martin, R. C., Hamilton, A. C., & Rose, N. S. (2019). Non-perceptual Regions in the Left Inferior Parietal Lobe Support Phonological Short-term Memory: Evidence for a Buffer Account? *Cerebral Cortex*, 29(4), 1398–1413.