

LANGUAGE PRODUCTION AND COMPREHENSION

INTRODUCTION

Language is a system that associates sounds (or gestures) with meanings in a way that uses words and sentences. The complex process of linguistic communication involves a number of interconnected, yet functionally and anatomically separable cognitive processes.

Linguistics is the scientific study of human language. It has several sub-fields:

1. **Phonetics & Phonology:** **Phonetics** - the production and perception of speech sounds as physical entities. **Phonology** - the sound system of a particular language and sounds as abstract entities. Phonemes are the smallest units of sound. A phoneme roughly corresponds to a letter of the alphabet, and different languages have different numbers of phonemes (English has approximately 30 phonemes, whereas some languages such as Mandarin have more than 50).
2. **Morphology:** The word structure and the systematic relations between words. **Morpheme** - The building-blocks of words, the smallest linguistic unit which has a meaning or grammatical function. For example, the word “talked” has two morphemes – “talk” and “-ed”. The first morpheme describes a conversation event, and the second morpheme places this event in the past.
3. **Syntax:** Phrase and sentence structure. The set of rules of a particular language that determine the ways words are combined to make sentences. Syntax refers to word order, for example the exact place of negation in a sentence. It also refers to type of sentences (question, conditional) and grammatical forms (passive, active).
4. **Semantics:** The meaning of morphemes, words, phrases, and sentences. This term overlaps with **semantic memory**.
5. **Pragmatics:** The way language is used, how context influences the interpretation of utterances, and how sentences fit into a conversation (Gill and Damann, 2015). The same phrase (e.g., he is really smart) could be said seriously or ironically, and the interpretation is related to **pragmatics**.

In the process of **language production**, we move **from semantics to phonology**, and in the process of **language comprehension** we move **from phonology to semantics**.

THE FUNCTIONAL ORGANIZATION OF LANGUAGE PRODUCTION AND COMPREHENSION

The enterprise of relating the functional components of word production, such as lexical selection, phonological code retrieval, syllabification, and perception, to regions in a cerebral network requires a detailed, explicit theory of the underlying processes. One classic example is the theory presented by Levelt, Roelofs, and Meyer (1999) (Levelt et al., 1999), henceforth to be called LRM, which explicates the successive computational stages of spoken word production, the representations involved in these computations, and their time course (Figure 1).

The core processes include: **Conceptual preparation** - the production of a content word normally starts by activating some lexical concept and by selecting it for expression. **Conceptual semantics** refers to the knowledge one has about the various attributes of a concept, independent of the linguistic realization. When you are asked to name a picture, you must first recognize the depicted object and select an appropriate concept. For example <DOGS> are typically four-legged and bark. **Lexical semantics**, on the other hand, refers to formal linguistic properties of single words that have precise processing consequences — for example, ‘BITE’ is an ‘eventive verb’ (describes an action) and differs from ‘ADMIRE’, a ‘stative verb’ (describes a state of being), and verb types differ in their processing requirements.

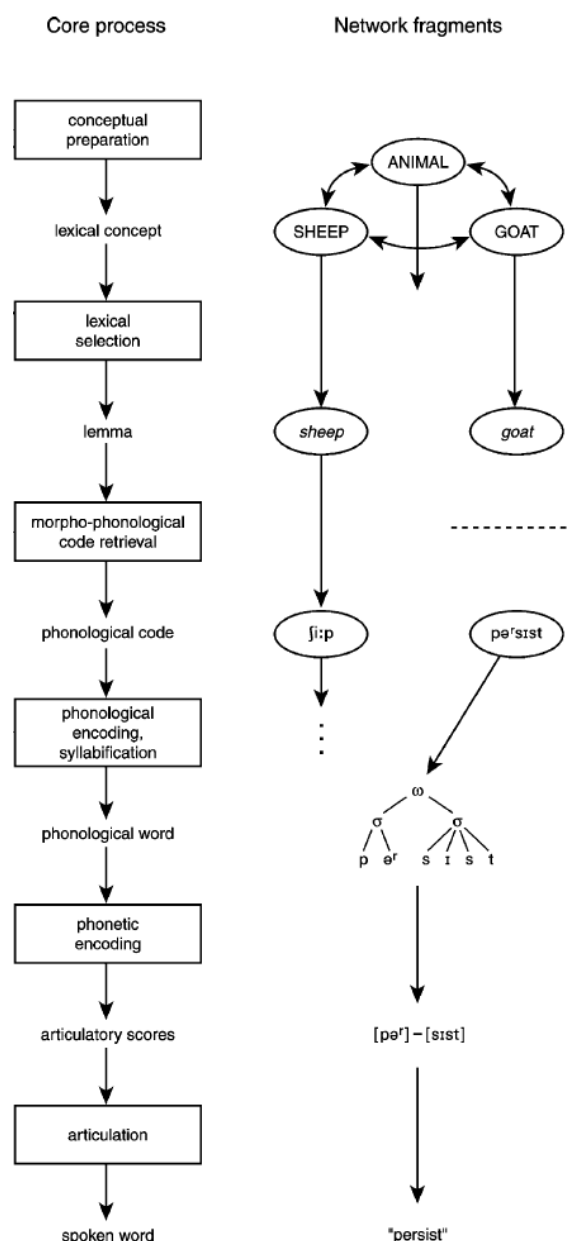


Figure 1: Components and time course of word production. Left column: core processes of word production and their characteristic output. Right column: example fragments of the WEAVER spreading activation network and its output (Indefrey & Levelt (2004). Cognition 92:101-144).

There is normally multiple activation of **lexical concepts** in response to visual input. The picture of a sheep not only activates the concept SHEEP, but probably also concepts such as ANIMAL or GOAT. The communicative situation (or the experimental task) determines which concept is going to be selected for expression. In a categorization task, for instance, selection will often involve the superordinate concept (ANIMAL), whereas a normal naming task usually involves the basic level concept (SHEEP).

Impaired Semantics (conceptual semantics and lexical semantics) - Patients with impaired conceptual knowledge, often use objects, particularly less familiar objects, inappropriately. **Impaired Lexical Semantics** and **impaired access to lexical semantics from vision** – impairment in accessing the subset of semantic features that allow a person to know what makes a horse a horse and what distinguishes it from related items such as a deer or a cow. Patients with impaired lexical semantics could incorrectly label items or incorrectly match pictures to their names. A person with an impaired ability to access lexical semantics from vision (a problem known as **associative visual agnosia** or **optic aphasia**), might point to a cow when asked to point to a horse. In addition, the person might make semantic paraphasias – select incorrect words that are semantically related to the target.

Impaired access to modality-independent lexical representations (Lemmas) - The meaning of the item, or lexical semantic representation, is used to select a lexical representation or lemma that is independent of output modality (oral versus written). Impairments at this level of processing are manifest as **anomia** or impaired word retrieval. This deficit is well-known to all of us (increasingly with age). When we have a word on the tip of the tongue, we can neither write the word nor say it, although we may retrieve some partial information, such as the first letter or sound, or the word's approximate length. This partial information often activates phonologically similar words for output, such that the person makes a **phonemic paraphasia** (e.g., calling a horse a horn) or activates semantically related words for output, such that the patient makes a **semantic paraphasia** (e.g., calling a horse a cow). Sometimes the partial phonological information and partial semantic information combine to result in mixed errors, such as calling a shirt a skirt (Hillis, 2010).

Lemma retrieval (lexical selection) - The next stage involves accessing the target word's syntax. In normal utterance production the most urgent operation after conceptual preparation is the incremental construction of a syntactic frame, i.e. grammatical encoding. Word order, constituent formation, and inflection all depend on the syntactic properties of the lexical items that are accessed. Lemma nodes in the syntactic stratum of the lexical network represent these syntactic properties (such as the part of speech, the gender of nouns, the argument structure of verbs). How is a lemma node selected? Each node at the conceptual stratum is linked to its unique lemma node at the syntactic stratum. **Compositional semantics**, closely connected to syntactic structure,



concerns how meaning is constructed in sentential contexts, for example, allowing one to distinguish ‘dog bites man’ from ‘man bites dog’.

Form encoding - The range of operations involved in form encoding begins with accessing the target word’s phonological code and ends while the word is being articulated. Form encoding, however, is itself a staged process. According to LRM, the first operation upon lemma selection is morpho-phonological encoding (morpho-phonological code retrieval). The speaker accesses the phonological codes for all of the target word’s morphemes. The second operation is phonological encoding proper. For spoken word production, this reduces to syllabification and metrical encoding. Syllabification is an incremental process. The ‘spelled-out’ segments of the phonological code are incrementally clustered in syllabic patterns. The third operation is phonetic encoding. As syllables are incrementally created, they are rapidly turned into motor action instructions. These instructions (‘syllable scores’) are stored for the few hundred high-frequency syllables that do most of the work in normal speech production. The repository of articulatory syllable scores is called the ‘mental syllabary’.

Impaired access to modality-specific lexical representations - The lemma is used to select a modality specific lexical representation—the phonological representation (spoken word form or learned pronunciation) or the orthographic representation (written word form or learned spelling). Some patients can write words even when they cannot retrieve their pronunciation (despite intact motor speech). Other patients show the opposite pattern—an ability to say a word but inability to retrieve the spelling of the same word (Hillis, 2010).

Once a spoken word form or phonological representation has been accessed, it still needs to be spoken aloud. There are two aspects to this process. One requires maintaining the phonological representation (the correct sequence of speech sounds that comprise the pronunciation) while the sounds are produced, and the second is motor output—articulation. Failure to activate or maintain activation of the complete phonological representation will result in phonemic paraphasias, such as substitution, insertion, and transpositions of phonemes (speech sounds) resulting in a different word (e.g., horn for horse) or non-words (e.g., porse for horse). Articulation of a word requires motor planning or programming of the complex movements of the lips, tongue, palate, vocal folds, and respiratory muscles, followed by implementation of these movements.

Apraxia of speech - impairment of motor planning or programming of speech articulation. This problem can lead to errors of insertion, deletion, transposition, substitution of speech sounds, or distortions of speech sounds in the absence of impaired strength, range, or rate of any of the speech muscles. Patients with apraxia of speech are very aware of their errors and try to correct them, while those who make phonemic paraphasias are generally unaware of their errors. Apraxia of speech is often characterized by various off-target productions of the word when attempting to say the same word multiple times, and is more apparent in production of polysyllabic words, which require more complex motor planning.

Even when motor planning is intact, the word might be articulated incorrectly because of **dysarthria**, a motor speech impairment caused by impaired strength, range, rate, or timing of movements of the lips, tongue, palate, or vocal folds. Dysarthria can be distinguished from apraxia of speech by its consistency across words (e.g., the same speech sound will typically be distorted in both short and long words consistently across trials in dysarthria, but is much more likely to be inconsistently misarticulated in long words compared to short words in apraxia of speech). Dysarthria is also associated with weakness or reduced range/rate of movement of the muscles involved in speech.

Although a number of sophisticated cognitive models of language production that specify the different stages and the relationships among them have been proposed (Dell, 1986, Levelt et al., 1999, Indefrey, 2011), understanding the precise neural mechanisms by which humans encode and time-causally enact different aspects of a linguistic message, including the division of labor spatially (within and across brain regions) and temporally (across time) has proven to be a major challenge. Functional brain-imaging methods generally do not possess the temporal resolution needed to evaluate the individual components involved in word generation. They also do not afford causal inferences and, although lesions from natural trauma or strokes have critically informed models of language production (Goldrick and Rapp, 2007), they commonly affect extensive cortical areas as well as their underlying white matter tracts, complicating interpretation. Further, to the extent that the same brain region supports different stages of language production, a permanent lesion to a region would not allow for temporal differentiation of those stages.

RELATIONS BETWEEN WORD PRODUCTION AND WORD COMPREHENSION

An important asymmetry exists between production and comprehension. In production, the goal is to express a particular meaning, about which we generally have little or no uncertainty. To do so, we have to utter a precise sequence of words where each word takes a particular form, and the words appear in a particular order. In contrast, the goal of comprehension is to infer the intended meaning from the linguistic signal. Abundant evidence suggests that comprehension is affected by both bottom-up, stimulus-related information and top-down expectations, and the representations we extract and maintain during comprehension are probabilistic and noisy (Kuperberg and Jaeger, 2016, Karimi and Ferreira, 2016, Levy, 2008, Nelken et al., 1999, Kidd et al., 2011, Coady and Aslin, 2004). In production, these pressures for precision and for linearization of sounds, morphemes, and words might lead to a clearer temporal and/or spatial segregation among the different stages of the production process, and, correspondingly, to functional dissociations among the many brain regions that have been implicated in production (Indefrey and Levelt, 2004, Indefrey, 2011), compared to comprehension, where the very same brain regions appear to support different aspects of the interpretation (like understanding individual word meanings and inferring the syntactic/semantic dependency structure) (Fedorenko et al., 2012, Blank et al., 2016, Bautista and Wilson, 2016).

NEUROANATOMY OF LANGUAGE

Since the late 19th century, it has generally been accepted that core language processes underlying spoken word production, comprehension, and repetition are enabled by left perisylvian regions of the human brain, including Broca's area and Wernicke's area (Broca, 1861; Wernicke, 1874). Production concerns saying words to express meaning, comprehension concerns understanding the meaning of heard words, and repetition concerns saying heard words or pseudo-words. According to the seminal Wernicke-Lichtheim model (Lichtheim, 1885; Wernicke, 1874), the perisylvian language areas contain memory representations of the input “auditory images” (in Wernicke's area) and output “motor images” (in Broca's area) of words. The presumed deficit and common lesion locations of the aphasia have led to the connectionist models developed by Broca, Wernicke, Lichtheim, and Heilman (Gill and Damann, 2015) (Figure 3). In this model, the frontal lobe may play a role in activating the semantic-conceptual areas, which then activate the phonological lexicon, allowing the person to produce spontaneous speech. When the phonological lexicon activates the semantic-conceptual field, the person is able to comprehend speech. The phonological lexicon is thought to contain memories of word sounds. Therefore, to understand speech, speech information enters the system through the auditory cortex, and is then sent to Wernicke area as well as to more widely distributed semantic-conceptual areas to allow comprehension of the speech in the semantic-conceptual areas.

To produce spontaneous speech, the frontal lobe (intentional/motivational systems) would activate the semantic-conceptual areas in order to activate the corresponding areas in Wernicke area, which would then project to Broca area and then to the motor cortex to activate the appropriate motor programs to produce the desired speech (Heilman, 2015).

Figure 4 shows the areas involved in language function in the classic connectionist model (Kirshner HS, Saunders, 2004). The conceptual framework behind this model is that Wernicke area (Brodmann area 22) and the surrounding area mediate comprehension. Auditory stimuli are projected to Wernicke area from the nearby Heschl gyrus (Brodmann areas 41 and 42), whereas visual forms of communication (e.g., reading and sign language) are processed by the primary and secondary visual cortices that then project to Wernicke area through the ventral visual stream. The arcuate fasciculus then projects from Wernicke area to Broca area

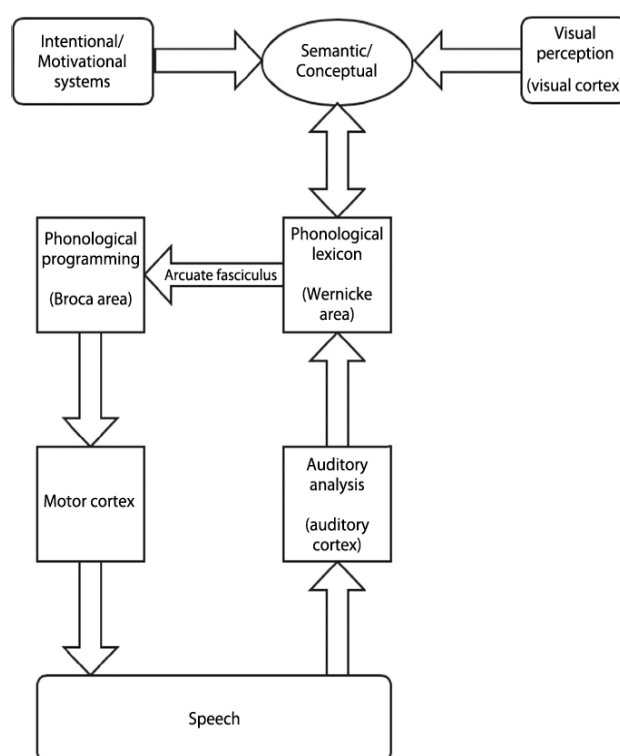


Figure 3: Classic connectionist model of language function

(Brodmann areas 44 and 45) and the surrounding area to permit repetition. Broca area is the center for expressive language planning.

Lateralization of language is associated with handedness, with approximately 90% of right-handed individuals and 70% of left-handed individuals being left-hemisphere dominant for language, although some debate exists about exact percentages. In left-handed individuals, about a third are either right-hemisphere dominant or have bilateral language dominance. The right hemisphere is thought to play a role in the prosody of language. The right hemisphere, in an analogous organization to the language

representation in the left hemisphere, mediates both prosody and the interpretation of gesture. The connectionist model of language function, however, does not fully explain how words are organized into sentences. Functional brain imaging (Poeppel et al., 2012) suggests that language function is mediated by larger scale, distributed global networks in the brain, explaining why many patients with aphasia do not fit well into any of the classic connectionist aphasia syndromes. The new models of the neuroanatomic basis of language are still under development. Some of the emerging concepts include sub-regions of Broca area that serve different language functions (Amunts et al., 2010), a dual-stream, cortical organization of speech processing similar to that found for visual processing (Hickok and Poeppel, 2007), and a role for the cerebellum and subcortical structures in the temporal processing of speech (Kotz and Schwartze, 2010). The fact that there are different types of meaning makes unsurprising the observation that the ‘neural basis of meaning’ has been associated with many different activation profiles (Poeppel, 2006). For instance, imaging data suggest that left inferior frontal gyrus anterior to Broca’s area plays a critical role in verbal meaning (Thompson-Schill et al., 1997); and the potential role of parietal cortex has been highlighted as well (Price, 2000). To complicate things further, electrophysiological studies show that right superior and middle temporal lobe structures are robustly implicated (Federmeier and Kutas, 1999). The data across methods and studies have not yet converged on a single model of the calculation of meaning in the brain.

THE APHASIAS

Normal language function requires proper neural function over a wide geography of brain regions. A person with dysfunction in this neural network has aphasia.

Table 1 summarizes the classic types of aphasias and their characteristics (Gill and Damann, 2015).

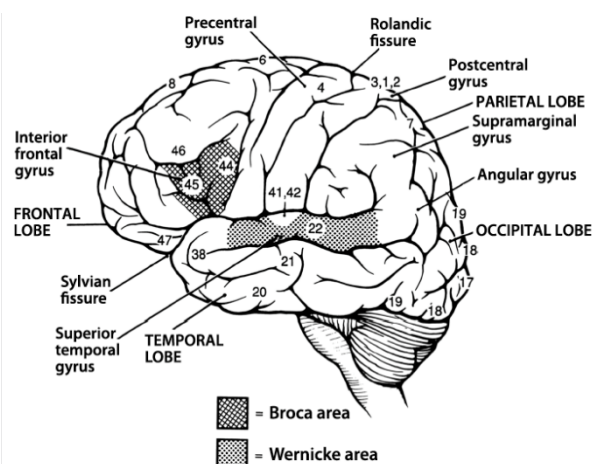


Figure 4: The areas involved in language function in the classic connectionist model (Kirshner & Saunders, 2004)

ASSESSMENT OF LANGUAGE FUNCTION - BEDSIDE TESTING

The bedside assessment of language function is often more qualitative than quantitative; many examiners use one of their own creation. The following is a suggested approach to the bedside language examination (Gill and Damann, 2015):

1. Observation: Listen to the patient's spontaneous speech to assess articulation of words, fluency, and prosody. If the patient produces little spontaneous verbal output, ask him or her to describe a picture such as the Cookie Theft picture from the Boston Diagnostic Aphasia Examination, although any picture showing action may be used. Paraphasic errors are often identified during observation of speech and are the production of unintended phonemes, morphemes, words, or phrases. These are generally placed into the two categories of phonemic and semantic paraphasic errors, although other classification schemes exist. A phonemic paraphasic error occurs when a person mispronounces a word's sounds or says a non-word that retains a significant proportion (often over one-half) of the intended word (the non-word sounds similar to the intended word).
2. Comprehension (verbal and written): Start with one-step midline commands ("close your eyes"); progress to distal one-step commands ("hold up your left hand"); then progress to complex commands ("point to the door after you point to the window").
3. Repetition: Start with short complete sentences and progress to an open-ended phrase of at least five words in length, such as the one used in the Boston Diagnostic Aphasia Examination ("near the table in the dining room").
4. Naming: Start with whole items. Ask, "What is this?" and point to the object (e.g., pen, watch), then progress to parts (e.g., watchband, cuff of shirt). In patients who either cannot perform these tasks or are non-fluent, test receptive naming by stating, "Point to the pen," and hold out a pen and a watch.
5. Writing: Have the patient write a sentence spontaneously. If the patient cannot produce a sentence spontaneously, have him or her try to write by dictation. Because written expression can be affected separately from verbal expression, writing should be tested in addition to testing verbal output.
6. Testing for apraxia of speech should be part of the evaluation process for patients with a progressive aphasia. An apraxia of speech is a motor speech disorder characterized by a slow rate of speech and distorted speech sounds. To test for apraxia of speech, have the patient attempt to alternate between labial (produced by the lips), lingual (produced by the tongue), and guttural (produced by the soft palate and other throat structures) sounds by saying words such as "patty-cake" or "irresponsibility."

Aphasia	Disorder of Language	Classical Localization	Spoken fluency	Auditory Comprehension	Writing	Reading	Repetition	Naming
Broca	Disruption of speech planning and production	Left posterior inferior frontal lobe involving Broca area	Impaired: Speech is sparse and effortful; function words and bound morphemes are often missing	Mostly normal	Impaired: Writing is effortful; function words and bound morphemes are often missing	Mostly normal	Impaired	Expressive naming affected
Transcortical motor	Disruption of speech planning and production	Left frontal cortex and white matter sparing Broca area	Impaired: Speech is sparse and effortful; function words and bound morphemes are often missing	Mostly normal	Impaired: Writing is effortful; function words and bound morphemes are often missing	Mostly normal	Normal	Expressive naming affected
Wernicke	Disruption of representations of word sounds	Posterior half of left superior temporal gyrus involving Wernicke area	Normal, but speech has abnormal word sound and structure (paraphasic errors)	Impaired	Mostly normal, but contains paraphasic errors	Impaired	Impaired	Both expressive and receptive naming affected
Transcortical sensory	Disruption of representations of word sounds	Left posterior temporal/parietal cortex and white matter sparing Wernicke area	Normal, but speech has abnormal word sound and structure (paraphasic errors)	Impaired	Mostly normal, but contains paraphasic errors	Impaired	Normal	Both expressive and receptive naming affected
Global	Disruption of all language processing	Left hemisphere involving the majority of the perisylvian area	Impaired	Impaired	Impaired	Impaired	Impaired	Impaired
Conduction	Disconnection of representation of words and the motoric process of speech	Lesion of arcuate fasciculus	Mildly impaired with frequent paraphasic errors	Intact	Intact	Mildly impaired with paraphasic errors	Impaired	Mostly normal
Anomic	Disruption of the network allowing proper sound structure of words	Does not localize well; can involve the inferior parietal lobe	Intact with word finding pauses	Intact	Intact	Intact	Intact	Impaired

Table 1: Adapted from Gill and Damann, 2015

REFERENCES

- AMUNTS, K., LENZEN, M., FRIEDERICI, A. D., SCHLEICHER, A., MOROSAN, P., PALOMERO-GALLAGHER, N. & ZILLES, K. 2010. Broca's region: novel organizational principles and multiple receptor mapping. *PLoS Biol*, 8.
- BAUTISTA, A. & WILSON, S. M. 2016. Neural responses to grammatically and lexically degraded speech. *Lang Cogn Neurosci*, 31, 567-574.
- BLANK, I., BALEWSKI, Z., MAHOWALD, K. & FEDORENKO, E. 2016. Syntactic processing is distributed across the language system. *Neuroimage*, 127, 307-323.
- COADY, J. A. & ASLIN, R. N. 2004. Young children's sensitivity to probabilistic phonotactics in the developing lexicon. *J Exp Child Psychol*, 89, 183-213.
- DELL, G. S. 1986. A spreading-activation theory of retrieval in sentence production. *Psychol Rev*, 93, 283-321.
- FEDERMEIER, K. D. & KUTAS, M. 1999. Right words and left words: electrophysiological evidence for hemispheric differences in meaning processing. *Brain Res Cogn Brain Res*, 8, 373-92.
- FEDORENKO, E., NIETO-CASTANON, A. & KANWISHER, N. 2012. Lexical and syntactic representations in the brain: an fMRI investigation with multi-voxel pattern analyses. *Neuropsychologia*, 50, 499-513.
- GILL, D. J. & DAMANN, K. M. 2015. Language dysfunction. *Continuum (Minneap Minn)*, 21, 627-45.
- GOLDRICK, M. & RAPP, B. 2007. Lexical and post-lexical phonological representations in spoken production. *Cognition*, 102, 219-60.
- HICKOK, G. & POEPPPEL, D. 2007. The cortical organization of speech processing. *Nat Rev Neurosci*, 8, 393-402.
- HILLIS, A. E. 2010. Naming and language production. *Continuum (Minneap Minn)*, 16, 29-44.
- INDEFREY, P. 2011. The spatial and temporal signatures of word production components: a critical update. *Front Psychol*, 2, 255.
- INDEFREY, P. & LEVELT, W. J. 2004. The spatial and temporal signatures of word production components. *Cognition*, 92, 101-44.
- KARIMI, H. & FERREIRA, F. 2016. Good-enough linguistic representations and online cognitive equilibrium in language processing. *Q J Exp Psychol (Hove)*, 69, 1013-40.
- KIDD, C., WHITE, K. S. & ASLIN, R. N. 2011. Toddlers use speech disfluencies to predict speakers' referential intentions. *Dev Sci*, 14, 925-34.
- KOTZ, S. A. & SCHWARTZE, M. 2010. Cortical speech processing unplugged: a timely subcortico-cortical framework. *Trends Cogn Sci*, 14, 392-9.
- KUPERBERG, G. R. & JAEGER, T. F. 2016. What do we mean by prediction in language comprehension? *Lang Cogn Neurosci*, 31, 32-59.
- LEVELT, W. J., ROELOFS, A. & MEYER, A. S. 1999. A theory of lexical access in speech production. *Behav Brain Sci*, 22, 1-38; discussion 38-75.
- LEVY, R. 2008. Expectation-based syntactic comprehension. *Cognition*, 106, 1126-77.
- NELKEN, I., ROTMAN, Y. & BAR YOSEF, O. 1999. Responses of auditory-cortex neurons to structural features of natural sounds. *Nature*, 397, 154-7.
- POEPPPEL, D. 2006. Language: specifying the site of modality-independent meaning. *Curr Biol*, 16, R930-2.
- POEPPPEL, D., EMMOREY, K., HICKOK, G. & PYLKKANEN, L. 2012. Towards a new neurobiology of language. *J Neurosci*, 32, 14125-31.
- PRICE, C. J. 2000. The anatomy of language: contributions from functional neuroimaging. *J Anat*, 197 Pt 3, 335-59.

THOMPSON-SCHILL, S. L., D'ESPOSITO, M., AGUIRRE, G. K. & FARAH, M. J. 1997.
Role of left inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation.
Proc Natl Acad Sci U S A, 94, 14792-7.