

David Kemmerer  
Purdue University  
Department of Speech, Language, and Hearing Sciences  
500 Oval Drive  
West Lafayette, IN 47907-2038  
(765) 494-3826  
[kemmerer@purdue.edu](mailto:kemmerer@purdue.edu)

## NEUROBIOLOGY OF LEXICAL PROCESSING

### *REVISED DRAFT*

The lexicon is the store of words in the “mental dictionary.” A typical English-speaking high-school graduate knows about 60,000 words; a literate adult, perhaps twice that number (Miller 1991, 138). A word can be regarded as a long-term memory association of semantic, syntactic, phonological, and orthographic structures. For example, the lexical entry for *rose* includes the following components, with the semantic component symbolized by a picture for convenience:

<i>rose</i>		
meaning:		$\alpha$
part of speech:		noun
phonology:		/roz/
orthography:		ROSE

During the past two decades, there has been remarkable progress in understanding the neural substrates of lexical processing, mainly because of advances in two complementary approaches to investigating the functions of specific brain structures: (1) the lesion method, which, when used with ample numbers of patients who are carefully studied both neuropsychologically and neuroanatomically, can yield indispensable insights about the neural systems that are necessary for particular abilities; and (2) functional imaging techniques, such as *fMRI*, which allow researchers to identify with more fine-grained spatial resolution the brain structures that are engaged during the normal performance of certain tasks (see *NEUROIMAGING*). Much more has been learned about the neural substrates of lexical processing than can be summarized here, so this review concentrates on cortical regions that have been linked with the recognition and production of spoken and written word forms.

### Neural Substrates of Spoken Word Recognition and Production

It is well-established that the sensorimotor aspects of spoken word processing depend on the left *PERISYLVIAN CORTEX*, and there is growing evidence that both the posterior superior temporal (auditory-related) and the posterior inferior frontal (motor-related) sectors of this large anatomical territory contribute to both speech perception and speech production (Imada et al. 2006, Okada and Hickok 2006, Pulvermüller et al. 2006, Skipper et al., 2007). These two regions interact not only via direct connections, but also via an indirect pathway mediated by the inferior parietal lobule (Catani et al. 2005).

To understand spoken words, listeners must first use the auditory input to activate stored representations of lexical-phonological form. It is only after this process of lexical access has been achieved that the semantic and syntactic properties of words can be activated and used to construct higher-level representations of the utterance. Numerous behavioral studies suggest that speech information is continuously projected to the lexicon, so that an initial sequence like *bla...* will activate all the words in the listener's lexicon that begin with those sounds (*black, bland, blanket*, etc.); as the input accumulates, the set of activated words diminishes until only a single one matches the input, at which point recognition can be said to occur (McQueen et al. 2003). Pseudowords (e.g., *blash*) also activate partially matching candidate words, but ultimately no winner is selected.

A broad perspective on the neural correlates of spoken word recognition is provided by Indefrey and Cutler (2004), who report a meta-analysis of 55 experiments in which subjects passively listened to either tones, pseudowords, words, or sentences. It was found that all of the different types of auditory stimuli reliably activate overlapping as well as partially differentiated central and posterior regions of the superior temporal gyri in both hemispheres. In addition, the following hierarchical organization was observed: as the linguistic complexity of the stimuli increases, there is recruitment of progressively more anterior regions of the left superior temporal sulcus. Thus, moving anteriorly, there is first an area responsive to pseudowords but not tones, then an area responsive to words but not pseudowords, and finally an area responsive to sentences but not words. The anterior area that is selectively activated by words may contribute to the resolution of the lexical competition process described above; however, it is also conceivable that this operation is subserved by one of the more posterior word-specific areas (Orfanidou et al. 2006). After the phonological form of a word has been recognized, its semantic and syntactic components are retrieved. As summarized by Indefrey and Cutler (2004), these processes may be executed by a wide distribution of predominantly left-hemisphere brain regions, including most notably the middle and inferior temporal gyri and the posterior inferior frontal gyrus.

Turning to spoken word production, one of the most influential theories is that proposed by Levelt, Roelofs, and Meyer (1999). According to their model, the production of spoken content words depends on multiple processing stages, each of which generates its own characteristic output representation (Figure 1). First, conceptual preparation involves identifying the meaning of the word to be produced. Second, lexical selection involves activating the lemma for the word—i.e., a unit that intervenes between semantics and phonology and that serves as the gateway to syntactic features (e.g., grammatical category, number, tense, etc.; these features are not shown in Figure 1). Third, form retrieval involves calling up the phonological code for the word. Fourth, syllabification involves determining segmental clusters and metrical assignments. Fifth, phonetic encoding involves transforming syllabic units into motor instructions. And sixth, articulation involves the final programming of overt speech.

The neural correlates of the first stage, conceptual preparation, remain mysterious, largely because this stage constitutes the complex interface between language and thought and is also heavily influenced by social-cognitive perspective-taking abilities—e.g., the same piece of real estate can be called *the coast, the shore, or the beach*, depending on one's communicative goals (Tomasello 1999, 119). Future research may show that conceptual preparation is subserved by widespread cortical structures that underlie semantic processing (Kemmerer 2007; see *NEUROBIOLOGY OF SEMANTICS*). The next two stages, lemma selection and phonological form retrieval, both involve core lexical processes, and their neural correlates are beginning to be

understood. In a meta-analysis of 58 functional imaging studies—including several studies employing magnetoencephalography, which has excellent temporal resolution—Indefrey and Levelt (2004) found that lemma selection is linked with the mid section of the left middle temporal gyrus and typically occurs during a time window of 150-225 milliseconds (ms) post-stimulus in oral picture naming tasks (Figure 2). They also found that phonological form retrieval is linked with the posterior portions of the left middle and superior temporal gyri and occurs during a time window of either 200-400 or 275-400 ms, depending on which studies are considered. The three post-lexical stages of spoken word production are known to rely on a variety of motor-related brain structures; however, the exact neural correlates of each stage are not yet clear (Bohland and Guenther 2006).

Independently of Levelt et al.'s model, a great deal of neuroscientific research has focused on the process of mapping the meanings of words onto their corresponding phonological forms during speech production. One important line of work, conducted by Hanna Damasio, Daniel Tranel, and their colleagues, suggests that this process is subserved by intermediary units that are analogous to lemmas insofar as they function as relays, taking lexical-semantic structures as input and then pointing to the appropriate lexical-phonological structures. Interestingly, these intermediary units may be neurally organized according to both semantic and grammatical principles. For example, lesion data suggest that the retrieval of nouns for different categories of concrete entities may hinge on intermediary units that do not reside in the left middle temporal gyrus, contrary to Indefrey and Levelt's (2004) proposal, but rather in the left temporal pole (TP) and inferotemporal (IT) cortices. Specifically, studies in which oral picture naming tasks have been administered to large cohorts of brain-damaged patients have shown that (1) impaired access to proper nouns for unique persons (e.g., *Jennifer Aniston*) is associated with left TP lesions, (2) impaired access to common nouns for animals (e.g., *horse*) is associated with damage to the anterior sector of left IT, and (3) impaired access to common nouns for tools (e.g., *hammer*) is associated with damage to the posterior sector of left IT, a region called IT+ (Damasio et al. 1996, 2004). Crucially, the patients have intact object recognition and conceptual knowledge, since they can accurately describe the entities they cannot name; in other words, the disorders are purely anomic. Furthermore, functional imaging data indicate that the same cortical regions are activated in normal subjects in the same category-specific ways when concrete entities are orally named from either pictures (Damasio et al. 1996, 2004) or characteristic sounds (Tranel et al. 2003, 2005). There is also increasing evidence from several methodologies that the process of retrieving action verbs engages a quite different neural pathway that includes the left ventrolateral premotor/prefrontal cortex (Damasio et al. 2001, Shapiro and Caramazza 2004, Tranel et al. 2001, Tranel et al. submitted). This region is reliably activated when action verbs are accessed, and damage to it frequently impairs the production of verbs but not nouns.

### Neural Substrates of Written Word Recognition and Production

Reading and writing are recent inventions in human history and must be explicitly taught. For literate individuals, however, word representations include not just a phonological component but also an orthographic component that is efficiently processed by neural circuits that are gradually being elucidated.

The activity of reading recruits numerous brain regions in the temporal, parietal, and frontal lobes (Hillis and Rapp 2004, Hillis and Tuffiash 2002). Perhaps the most controversial region, however, has been the "visual word form area" (VWFA), located in the left

occipitotemporal sulcus bordering the fusiform gyrus (McCandliss et al. 2003; Dehaene 2005). This area responds more strongly to printed words than to other types of visually presented objects such as faces, animals, and tools. Also, disruption of the input projections to this area can induce “pure alexia without agraphia,” a disorder in which reading can only be accomplished in a laborious letter-by-letter manner, while writing and all other linguistic skills are unaffected. Despite these findings, the question of whether the VWFA plays a genuine causal role in reading has been hotly debated (e.g., Price and Devlin 2003). Recently, however, a compelling case study supporting the VWFA was reported by Gaillard et al. (2006; see also Martin 2006). In brief: Prior to surgery for intractable epilepsy, the patient exhibited normal single-word reading, including a lack of increase in reading time for common words varying in length from three to eight letters; moreover, fMRI revealed his VWFA to have normal functional-anatomical characteristics, and local field potentials recorded from implanted electrodes showed that this area was sensitive to word frequency but not word length, again within normal parameters. After excision of tissue just posterior to the VWFA, the patient’s epileptic seizures were successfully eliminated, but his reading was markedly slow and inaccurate, with reading times increasing linearly with word length (i.e., letter-by-letter reading). In addition, the VWFA no longer responded to printed words, even when they were contrasted with a simple fixation point. This study therefore provides powerful new evidence that the VWFA is in fact necessary for access to the stored orthographic forms of words during reading.

Writing also depends on a large network of widely distributed brain regions (Hillis and Rapp 2004, Rapcsak and Beeson 2002). Information about the neural basis of lexical access during written word production comes primarily from patients with “lexical agraphia,” a disorder in which words with regular mappings between phonology and orthography are spelled correctly, but words with irregular mappings (e.g., *choir*) are misspelled. The errors are usually phonologically plausible (e.g., *circuit* → *serkit*) and affect low-frequency words more than high-frequency ones. Lexical agraphia is typically caused by damage to the left temporo-parieto-occipital junction (Brodmann areas 37 and/or 39), although in some cases there is involvement of the left ventral occipitotemporal region, close to if not encompassing the VWFA. Several functional imaging studies with normal subjects provide further support for a role of these cortical regions in written word production (e.g., Petrides et al. 1995, Nakamura et al. 2000).

## Conclusion

When people recognize and produce the spoken and written forms of words, they usually concentrate on the meanings being expressed and remain blithely unaware of the complex computations being executed by their brains in order to rapidly and effectively process the lexical structures themselves. Cognitive neuroscience is beginning to reveal the intricacies of these neural systems, and dramatic advances are likely to happen in the coming years. Exciting new discoveries are appearing in the literature almost daily, and this explosion of research will undoubtedly provide fresh insights into the neurobiology of lexical processing, with significant implications for understanding and treating disorders that result from brain injury.

--David Kemmerer

## Works Cited and Suggestions for Further Reading

- Bohland, J.W., and Guenther, F.H. 2006. "An fMRI investigation of syllable sequence production." *NeuroImage* 32: 821-841.
- Catani, M., Jones, D.K., and Ffytche, D.H. 2005. "Perisylvian language networks of the human brain." *Annals of Neurology* 57: 8-16.
- Damasio, H., Grabowski, T.J., Tranel, D., Hichwa, R.D., and Damasio, A.R. 1996. "A neural basis for lexical retrieval." *Nature* 380: 499-505.
- Damasio, H., Grabowski, T.J., Tranel, D., Ponto, L.L.B., Hichwa, R.D., and Damasio, A.N. 2001. "Neural correlates of naming actions and of naming spatial relations." *Neuroimage* 13: 1053-1064.
- Damasio, H., Tranel, D., Grabowski, T., Adolphs, R., and Damasio, A. 2004. "Neural systems behind word and concept retrieval." *Cognition* 92: 179-229.
- Dehaene, S. 2005. "Evolution of human cortical circuits for reading and arithmetic: The 'neuronal recycling' hypothesis." In *From Monkey Brain to Human Brain*, ed. Dehaene, Duhamel, Hauser, & Rizzolatti, 133-158. Cambridge: MIT Press.
- Gaillard, R., Naccache, L., Pinel, P., Clemenceau, S., Volle, E., Hasboun, D., Dupont, S., Maulac, M., Dehaene, S., Adam, C., and Cohen L. 2006. "Direct intracranial, fMRI, and lesion evidence for the causal role of left inferotemporal cortex in reading." *Neuron* 50: 191-204.
- Hillis, A.E., and Rapp, B.C. 2004. Cognitive and neural substrates of written language: Comprehension and production. In *The Cognitive Neurosciences III*, ed. Gazzaniga, 775-787. Cambridge: MIT Press.
- Hillis, A.E., and Tuffiash, E. 2002. Neuroanatomical aspects of reading. In *The Handbook of Adult Language Disorders: Integrating Cognitive Neuropsychology, Neurology, and Rehabilitation*, ed. Hillis, 15-26. Philadelphia: Psychology Press.
- Indefrey, P. and Cutler, A. 2004. "Prelexical and lexical processing." In *The Cognitive Neurosciences III*, ed. Gazzaniga, 759-774. Cambridge: MIT Press.
- Indefrey, P., and Levelt, W.J.M. 2004. "The spatial and temporal signatures of word production components." *Cognition* 92: 101-144.
- Kemmerer, D. 2007. "How words capture visual experience: The perspective from cognitive neuroscience." In *Words and the World: How Words Capture Human Experience*, ed. Malt and Wolff, XXX-XXX. Oxford: Oxford University Press.
- Imada, T., Zhang, Y., Cheour, M., Taulu, S., Ahonen, A., and Kuhl, P.K. 2006. "Infant speech perception activates Broca's area: A developmental magnetoencephalographic study." *NeuroReport* 17: 957-962.
- Levelt, W.J.M., Roelofs, A., and Meyer, A.S. 1999. "A theory of lexical access in speech production." *Behavioral and Brain Sciences* 22: 1-38.
- Martin, A. 2006. "Shades of Dejerine—Forging a causal link between the visual word form area and reading." *Neuron* 50: 173-175.
- McCandliss, B.D., Cohen, L., and Dehaene, S. 2003. "The visual word form area: Expertise for reading in the fusiform gyrus." *Trends in Cognitive Sciences* 7: 293-299.
- McQueen, J.M., Dahan, D., and Cutler, A. 2003. "Continuity and gradedness in speech processing." In *Phonetics and Phonology in Language Comprehension and Production: Differences and Similarities*, ed. Schiller and Meyer, 37-76). New York: Mouton de Gruyter.

- Miller, G.A. 1991. *The Science of Words*. New York: Freeman.
- Miozzo, M., and Caramazza, A. (eds.) 2007. Special issue of *Cognitive Neuropsychology* on lexical processing.
- Nakamura, K., Honda, M., Okada, T., Hanakawa, T., Toma, K., Fukuyama, H., Konishi, J., and Shibasaki, H. 2000. "Participation of the left posterior inferior temporal cortex in writing and mental recall of kanji orthography: A functional MRI study." *Brain* 123: 954-967.
- Okada, K., and Hickok, G. 2006. "Left posterior auditory-related cortices participate both in speech perception and speech production: Neural overlap revealed by fMRI." *Brain and Language* (in press).
- Orfanidou, E., Marslen-Wilson, W.D., and Davis, M.H. 2006. "Neural response suppression predicts repetition priming of spoken words and pseudowords." *Journal of Cognitive Neuroscience* 18: 1237-1252.
- Petrides, M., Alivisatos, B., and Evans, A.C. 1995. "Functional activation of the human ventrolateral frontal cortex during mnemonic retrieval of verbal information." *Proceedings of the National Academy of Sciences* 92: 5803-5807.
- Price, C.J., and Devlin, J.T. 2003. "The myth of the visual word form area." *NeuroImage* 19: 473-481.
- Pulvermüller, F., Huss, M., Kherif, F., del Prado Martin, F.M., Hauk, O., and Shtyrov, Y. 2006. "Motor cortex maps articulatory features of speech sounds." *Proceedings of the National Academy of Sciences* 103: 7865-7850.
- Rapp, B., and Goldrick, M. 2006. "Speaking words: Contributions of cognitive neuropsychological research." *Cognitive Neuropsychology* 23: 39-73.
- Rapcsak, S.Z., and Beeson, P.M. 2002. "Neuroanatomical correlates of spelling and writing." In *The Handbook of Adult Language Disorders: Integrating Cognitive Neuropsychology, Neurology, and Rehabilitation*, ed. Hillis, 71-100. Philadelphia: Psychology Press.
- Shapiro, K., and Caramazza, A. 2004. "The organization of lexical knowledge in the brain: The grammatical dimension." In *The Cognitive Neurosciences III*, ed. Gazzaniga, 803-814. Cambridge: MIT Press.
- Skipper, J.I., van Wassenhove, V., Nusbaum, H.C., & Small, S.L. 2007. "Hearing lips and seeing voices: How cortical areas supporting speech production mediate audiovisual speech perception." *Cerebral Cortex*.
- Tomasello, M. 1999. *The Cultural Origins of Human Cognition*. Cambridge: Harvard University Press.
- Tranel, D., Adolphs, R., Damasio, H., and Damasio, A.R. 2001. "A neural basis for the retrieval of words for actions." *Cognitive Neuropsychology* 18: 655-70.
- Tranel, D., Damasio, H., Eichhorn, G.R., Grabowski, T.J., Ponto, L.L.B., and Hichwa, R.D. 2003. "Neural correlates of naming animals from their characteristic sounds." *Neuropsychologia* 41: 847-854.
- Tranel, D., Grabowski, T.J., Lyon, J., and Damasio, H. 2005. "Naming the same entities from visual or from auditory stimulation engages similar regions of left inferotemporal cortices." *Journal of Cognitive Neuroscience* 17: 1293-1305.
- Tranel, D., Manzel, K., Asp, E., and Kemmerer, D. Submitted. "Naming dynamic actions: Neuropsychological evidence." *Journal of Physiology (Paris)*.

## Figure Captions

Figure 1. The LRM (i.e., Levelt, Roelofs, and Meyer) model of spoken word production. Left column: Word production tasks involving “lead-in” processes that enter the central word production architecture at different stages. Middle column: Core processes of word production and their characteristic output. Right column: Example fragments of outputs generated at each stage. (Adapted from Indefrey and Levelt 2004.)

Figure 2. Schematic representation of results of meta-analysis of functional imaging studies of spoken word production. Left panel: Identical colors indicate relations between brain regions and processing components (right panel). The numbers indicate the time windows (in milliseconds) during which the regions are activated in picture naming. Right panel: Time course of picture naming as estimated from chronometric data obtained in separate behavioral studies. (Adapted from Indefrey and Levelt 2004.)

Figure 1

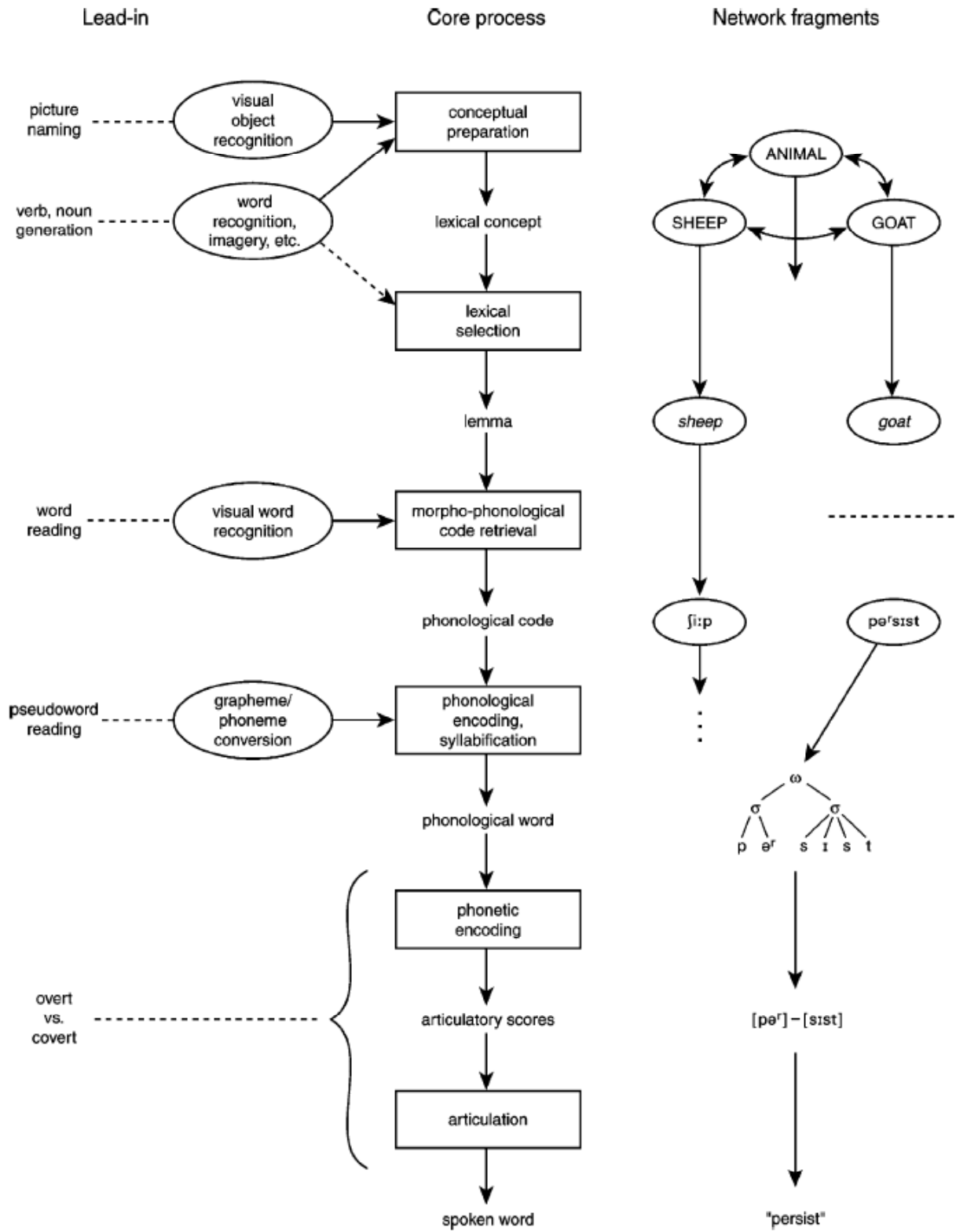


Figure 2

