

COGNITIVE NEUROSCIENCE OF LANGUAGE

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Abbreviations

IFG-Inferior frontal gyrus, SFG-Superior frontal gyrus, MFG-Middle frontal gyrus, PMC-Premotor cortex, STG-Superior temporal gyrus, prCG-Precentral gyrus, poCG-Postcentral gyrus, MTG-Middle temporal gyrus, ITG-Inferior temporal gyrus, AG-Angular gyrus, FG-Fusiform gyrus, MOG-Middle occipital gyrus, PHG-Parahippocampal gyrus, SMG-Supramarginal gyrus, CiG-Cingulate gyrus, RSC-Retrosplenial cortex, STS-Superior temporal sulcus, SFS-Superior frontal sulcus, ATL-Anterior temporal lobe, IPS-Intraparietal sulcus, IPL-Inferior parietal lobule, PFC-Prefrontal cortex, DM-Dorsomedial, VM-Ventromedial, LIFC-Left inferior frontal cortex, OTS-Occipitotemporal sulcus, OTC-Occipitotemporal cortex, ILF-Inferior longitudinal fasciculus, IFOF-Inferior fronto-occipital fasciculus, AF-Arcuate fasciculus, p (prefix)-Posterior, a (prefix)-Anterior, v (prefix)-Ventral, BA-Brodmann's area.

1. Introduction

The study of the neural basis of language is deeply intertwined with, and is indeed the driving force behind, the development of the fields of neuropsychology and cognitive neuroscience. The work of late 19th- and early 20th-century neurologists provided some of the first insights into language processing in the brain. They provided evidence that there is likely to be some level of specialization of function in brain regions. Studies of patients with language-related deficits, most famously by Paul Broca, Carl Wernicke, and Ludwig Lichtheim (Levelt 2013), and later extended by Norman Geschwind and others in the 1960s and 1970s, laid the foundations of the classic model of language processing.

In the 1860s, Broca reported two patients with severe speech production deficits. One patient was able to produce only a single syllable, *tan*, while the other produced five. Broca estimated that they had good language comprehension nonetheless. He examined the brains of these patients after their death and found lesions centered around the left pIFG (approximately pars opercularis and triangularis, or BA 44 and 45, but also extending into the white matter and surrounding areas), which came to be known as 'Broca's area'. In 1874, Wernicke reported a new type of language deficit.

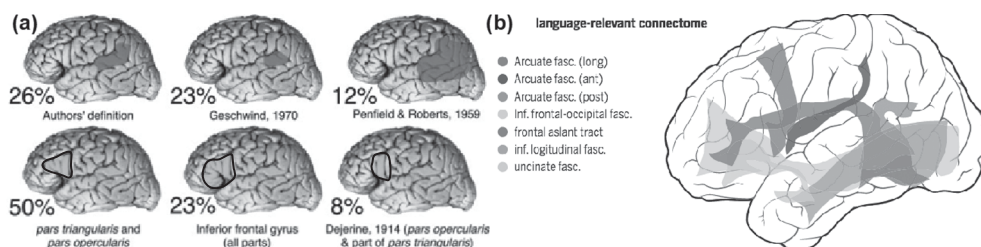


Figure 37.1 (a) Percentage of responders endorsing definitions of ‘Wernicke’s area’ (top row) and ‘Broca’s area’ (bottom row). The three most popular definitions are shown. (b) Major language-relevant white matter pathways. An important pathway not shown is the middle longitudinal fasciculus, which connects ATL and AG.

Source: (a) Adapted from Tremblay & Dick 2016. (b) Adapted from Hagoort 2019.

It was characterized by impaired speech comprehension, fluent but incoherent speech production, frequent phonological distortions, and defective repetition. Wernicke’s original descriptions of the lesions described an extensive territory, including most of STG and MTG, and parts of SMG and AG. In spite of this, over time, the term ‘Wernicke’s area’ became associated mainly with pSTG and surrounding cortex (Binder 2017). The extents of both of these areas have always been unclear, especially for Wernicke’s area (Tremblay & Dick 2016). Figure 37.1a shows some of the more popular opinions regarding their locations.

Based on these findings, the classic model restricted language to these two main areas: Broca’s area supported ‘speech production’, and Wernicke’s area was thought to be responsible for ‘speech comprehension’. The arcuate fasciculus connected these two frontal and temporal areas, which had a strict division of labor for speech production and comprehension. Research over the last three decades, using neuroimaging, lesion, and brain stimulation methods, has shown a more complex picture, rendering this model largely obsolete. Some of the limitations of this model are as follows. Studies have shown that language-related cortex is much more extensive, and includes the inferior parietal lobe, parts of the superior parietal lobe, large parts of the temporal lobe, and frontal lobe structures that extend beyond the pars opercularis and pars triangularis. Subcortical areas and cerebellum also play an important role in many language functions. The connectivity affecting language is much more extensive than the arcuate fasciculus, and includes multiple white matter pathways (Figure 37.1b). Language processing is also more bilateral than suggested by the classic model, which places language exclusively in the left hemisphere. Finally, the traditional Broca’s and Wernicke’s areas are ill-defined both anatomically and functionally. It is not simply that the boundaries of these areas are not agreed upon and therefore the terms are ambiguous (Tremblay & Dick 2016). These areas do not constitute coherent functional units. The concepts of Wernicke’s and Broca’s areas themselves, as speech comprehension and production ‘centers’, are not useful and confound multiple separate functions, as we will see in the sections below. Hence, many investigators now consider these concepts, and the use of these terms, to be outdated. It is more fruitful to use specific anatomical labels (e.g., LIFC, BA 44, pSTG) and discuss them with respect to functions such as phonological storage, lexical selection, and so on.

Here, we present a brief overview of some of the major facets of the neural basis of language, with a point of view informed primarily by neuroimaging and lesion studies. Among major omissions from this bird’s-eye view are valuable insights from EEG studies related to time course of processing, as well as discussions of morphology, sign language, discourse processing, multilingualism, and language development, among other topics.

2. Aphasias

Aphasia is an acquired language deficit resulting from damage to the brain. Approximately 20–40% of all stroke survivors develop aphasia. Other brain injuries such as head trauma and tumors can also lead to this syndrome. The other major cause of aphasia is progressive neurodegenerative disease.

2.1 Classic Aphasias

Language deficits can be manifested in many different and complex ways. Several classifications or groups of symptoms (syndromes) have been proposed that attempt to reduce this complexity. The most popular classification of aphasias uses three key abilities: fluently producing speech, comprehending speech, and repeating words or phrases. Figure 37.2 shows the eight classic aphasias resulting from this method: nonfluent (also known as Broca's or expressive aphasia), fluent (also known as Wernicke's or receptive aphasia), conduction, anomic, transcortical motor, transcortical sensory, mixed transcortical, and global aphasia. While producing speech, common ways in which deficits manifest in patients are paraphasia and anomia. Paraphasia is substitution of a correct word with an incorrect word. The word can be incorrect in a number of ways, which can indicate the types of deficit a patient has. In phonemic paraphasia, an incorrect sound is substituted (e.g., saying 'tephelone' instead of 'telephone'). Semantic paraphasia is saying a word that is semantically but not phonologically related ('orange' instead of 'apple'). In neologistic paraphasia, an unrelated non-word is substituted ('japker' instead of 'shirt'). Anomia is the most common symptom of aphasia and is characterized by persistent word-finding difficulties. Patients often have an understanding of the concept they wish to express (e.g., they can demonstrate how a toothbrush is used with gestures

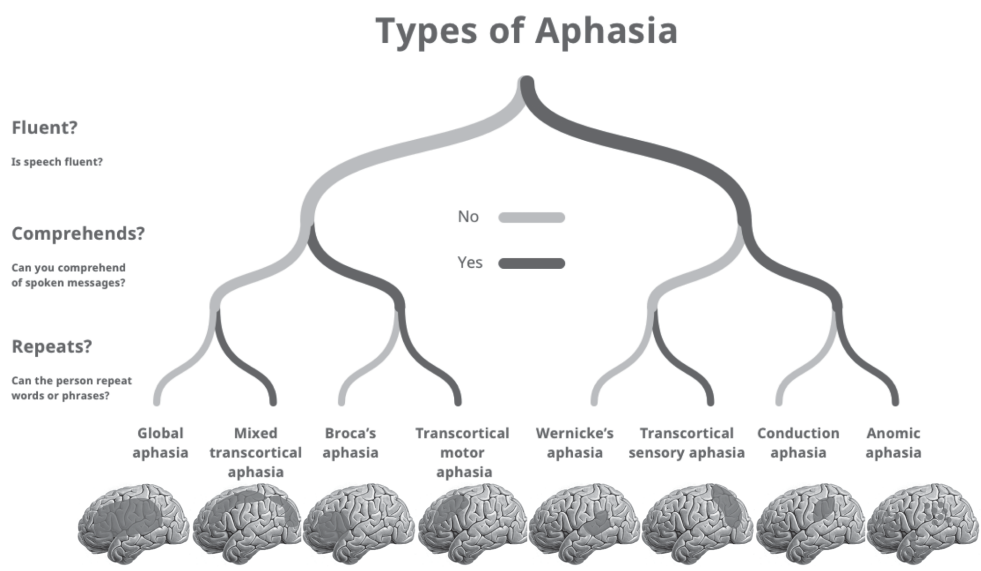


Figure 37.2 A classification of aphasias and associated lesion sites. The classification is based on three criteria: the ability to fluently produce speech, to comprehend speech, and to repeat words and phrases. 'Yes' indicates little or no impairment, 'No' indicates impairment. The lesion sites are 'typical' or commonly observed in group averages, but are neither necessary nor sufficient for producing the corresponding aphasia type.

Source: Image credit: www.aphasia.org.

or with verbal description) but are unable to retrieve the word itself ('toothbrush'). Reading impairment (alexia) and writing impairment (agraphia) also often (but not always) accompany these speech-related deficits in aphasia.

Common areas where lesions often lead to these syndromes are also shown in Figure 37.2. Note that these regions should be thought of as 'first approximations', and not as necessary and sufficient regions for producing the corresponding aphasia. There is often a great variability in lesion sites associated with each of the aphasias. For example, while pIFG is a region where lesions often lead to nonfluent aphasia, it is neither necessary nor sufficient. That is, there are patients with no damage to pIFG who are classified as nonfluent aphasics based on their symptoms. There are also examples of patients with damage in that region who do not have nonfluent aphasia. An additional caveat is that patients do not necessarily fall neatly into one of these syndromes. They often exhibit a mix of symptoms with varying levels of deficits in the three abilities, as opposed to the binary yes/no decision required for the classification. The levels of impairment can also change with time. Nonetheless, with these limitations in mind, this classification has been useful both clinically and for studying functional organization of language in the brain.

2.2 Primary Progressive Aphasia

When aphasia gradually arises as a result of neurodegenerative disease, it is termed primary progressive aphasia (PPA). Three main variants of PPA are commonly recognized: nonfluent or agrammatic (PPA-G), semantic (PPA-S), and logopenic (PPA-L) (Mesulam et al., 2014). PPA-G is characterized by nonfluent production with impairments in morphology, syntax, and phonology. Comprehension of words and simple phrases is relatively preserved, while repetition is impaired. In PPA-S (also known as semantic dementia), comprehension is impaired, production is fluent but has semantic errors, and repetition is intact. PPA-L is characterized by profound word-finding difficulties in production. Comprehension is mostly unaffected for words and simple sentences, but can be impaired for complex sentences. Repetition performance of these patients is inconsistent, but is often intact for words and short sentences while being impaired for long sentences and improbable word combinations.

Somewhat different regions of cortical atrophy are associated with each of the three variants. A word of caution is in order when associating specific brain regions with PPAs, similar to the caveat in the previous section. While damage due to stroke typically involves several regions and is not commonly circumscribed to a small region, atrophy due to neurodegenerative conditions tends to be even more widely distributed. Hence it is difficult, if not impossible, to associate relatively circumscribed regions (such as pIFG) with symptoms. Investigators often refer to areas of peak atrophy when discussing results. The actual areas of atrophy, however, tend to be widely distributed and are not limited to the peak regions. With this in mind, studies have suggested that atrophy in posterior IFG, MFG, SFG, PMC, and SMG is associated with PPA-G. Atrophy in the bilateral temporal lobe, especially in the anterior and middle sections, often extending into posterior sections both laterally and medially, is seen in PPA-S. In PPA-L, atrophy in occipitotemporal and temporoparietal regions, extending to middle and even anterior lateral temporal regions, as well as superior frontal regions, is seen (Mesulam et al. 2009; Wilson et al. 2010).

3. Semantic Memory

The goal of communication is to convey meaning. Different facets of language, such as syntax, phonology, and orthography, are useful only to the extent that they help convey meaning. Semantic memory (or interchangeably, 'conceptual knowledge') is one of the most defining human characteristics, and is essential to everyday life. It refers to our acquired knowledge about the world, including knowledge about objects, people, actions, relations, beliefs, facts, culture, society,

and meanings of words and phrases. This knowledge is thought to be abstracted over specific experiences or episodes. For example, your knowledge of what typically happens during a birthday party, what is a *cake*, *candle*, or the act of *blowing* a candle, is part of semantic memory. On the other hand, your recollection of what happened during a specific birthday party you attended is part of episodic memory. Episodic memory necessarily relies on semantic memory. When you recall how your friend failed to blow out the candles in that particular party you attended last month, you have to rely on your understanding of candles, blowing, friend, and so on. This brief review focuses on the neural basis of verbal concepts, or the representation of meanings of words and sentences. In the last 25 years, brain imaging, combined with lesion and stimulation methods, has provided a wealth of data on brain regions and networks involved in semantic memory.

3.1 General Semantics

3.1.1 Neuroimaging

Binder, Desai, Graves, and Conant (2009) meta-analyzed 120 neuroimaging studies that used linguistic input (words, sentences, or narratives) and used functional magnetic resonance imaging (fMRI) or positron emission tomography (PET) methods. They included areas activated by two broad types of contrasts: (1) high semantic vs. low semantic conditions, and (2) one semantic category vs. another semantic category. One example of the first type of contrast is a comparison of *cake* (real word) to *feip* (pseudoword). Another example is a task where subjects decide if *horse* and *sparrow* are both living things (living-nonliving judgment), vs. deciding whether *horse* and *force* rhyme (rhyme judgment). The former task emphasizes the semantic properties of the concepts (high semantic condition), while the latter task focuses attention on the phonological properties of the words, expected to result in lower levels of semantic activation. The second type of contrast, on the other hand, examines modulation of brain regions by the type or category of semantic content, such as tools or animals, relative to another category. An example is a contrast of a set of animal words (*horse*, *zebra*) to a set of tool words (*hammer*, *wrench*). The results are shown in Figure 37.3 (ignore the coding for now). Aggregated across concrete and abstract semantic

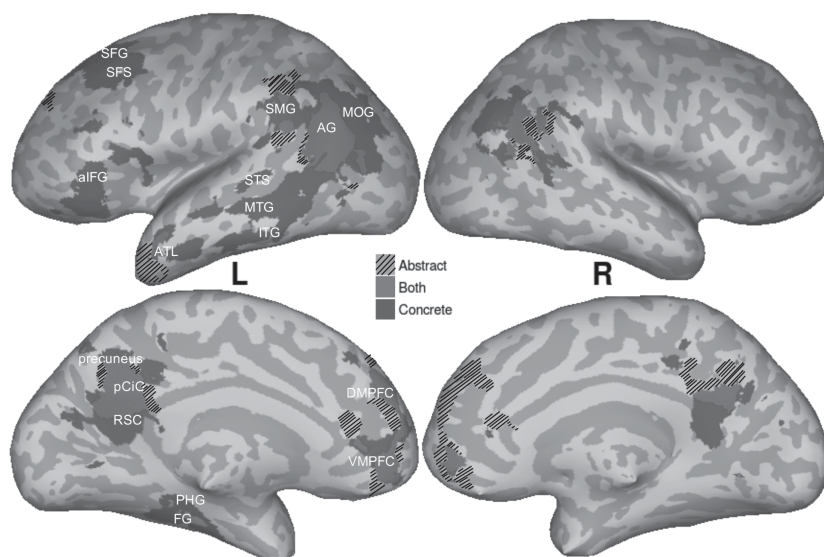


Figure 37.3 Areas involved in general semantics

Source: Based on the meta-analysis from Binder et al. 2009. Adapted from Desai et al. 2018.

categories, grammatical categories, and units (words, sentences, narratives), a distributed set of regions, implicated in semantic processing and storage, was activated. The main regions showing a consistent activation across studies were AG, SMG, MOG, STS, MTG, ITG, ATL, mid-FG, PHG, DMPFC and VMPFC, left SFG, SFS, anterior IFG, pCiG, RSC, and precuneus. Inferior parietal regions as well as medial regions were bilateral, while frontal and temporal regions were mainly left lateralized. This indicates highly distributed, bilateral system for general semantic content, with left-sided dominance. Because these regions are activated across conceptual content related to different sensory modalities, they are considered transmodal or multimodal regions, possibly with integrative functions.

3.1.2 Lesion Studies

Due to the highly distributed nature of semantics, identification of semantic regions from lesion studies is less clear. Transcortical sensory aphasia is a syndrome relevant to semantics because it is characterized by impaired speech comprehension, but intact repetition. It is associated with occipitotemporal and inferior parietal cortex, involving pMTG, pITG, and AG. This can be contrasted with conduction aphasia, with relatively preserved comprehension but disrupted repetition, caused by damage to SMG and pSTG. This dissociation between conduction and transcortical sensory aphasias suggests a phonological role of SMG/pSTG, and a semantic role of pMTG/pITG/AG. In contrast, some PPA studies implicate a different region, ATL, in semantics. The role of ATL is discussed below (see ‘Putative Semantic Hubs’). In sum, lesion literature implicates both anterior and posterior temporal lobes, occipitotemporal cortex, and inferior parietal lobe in semantics. The precise role of these regions—whether they have a role in representation of semantic features, integration of features, or providing access to features—is less understood and remains an area of active investigation.

3.2 Embodiment of Concepts

The regions discussed above represent consistent activation over many different types of verbal concepts, and hence are important parts of the semantic system. It is important to note, however, that representation of concepts is not limited to these regions. An extensive body of research has demonstrated that modality-specific areas also represent concept features. ‘Modality’ here refers to the five senses (vision, hearing, touch, taste, and smell), as well as action. Additional sub-modalities can be added to this list, such as color perception and visual motion under the modality of vision. Brain regions that are primarily involved in processing input in one of these modalities are considered modality-specific, and are collectively referred to as ‘sensory-motor’, or more broadly, ‘action-perception’ systems of the brain. The core components of these systems are well known. For example, the calcarine sulcus and surrounding occipital lobe are crucial for vision. The middle part of the superior temporal lobe, including the mid-STG and STS, forms the auditory cortex. The central sulcus and surrounding regions contain the motor and sensory cortex.

The traditional view of concepts held that conceptual representations are abstract. That is, concept representations in the brain do not contain any modality-specific information. For example, the concept *banana* does not contain sensory-motor information such as shape, color, or taste represented in a modality-specific format. Instead, all our knowledge about bananas is coded in a symbolic way. Symbols are abstract in that the form of the symbol is completely arbitrary and has no relationship to what it represents. The symbol j34ps8 could represent the concept *banana* and c1q5v could represent *apple*. This view predicts a clear separation between the conceptual system and the action-perception system. However, there is now a large body of work, utilizing imaging, neuropsychological/lesion, and brain stimulation methods, that has provided evidence that action and perception systems are involved in representation and processing of concepts. This view falls

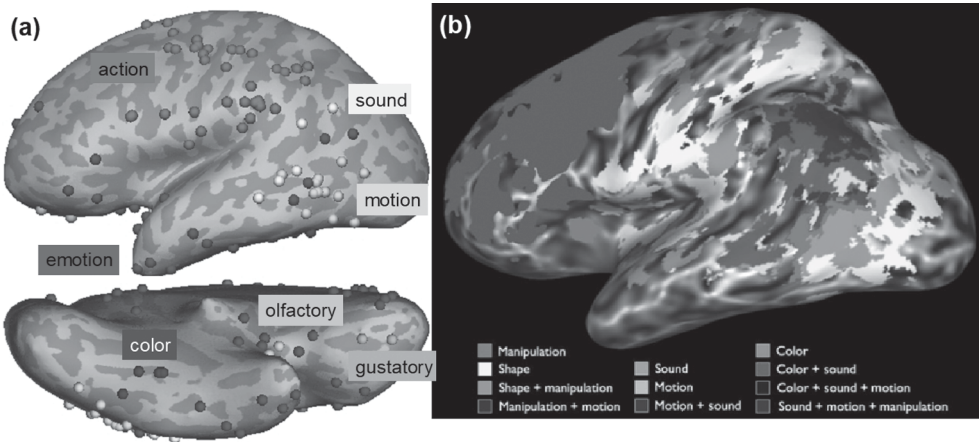


Figure 37.4 (a) Activation peaks from neuroimaging studies that use concepts that load heavily on a particular sensory-motor modality. All studies use linguistic stimuli (words or sentences) and are contrasted with other types of linguistic stimuli (e.g., abstract words). (b) Regions where BOLD activation was positively correlated with sensory-motor attributes of words while performing a semantic decision.

Source: (a) Adapted from Binder & Desai 2011. (b) Adapted from Fernandino et al. 2016.

under the framework of grounded or embodied cognition (Barsalou 2008; Kiefer & Pulvermüller 2012). Figure 37.4a shows activation peaks from imaging studies that examined concepts where features in a particular modality are important. All studies used words or sentences as stimuli. A pattern was observed across studies, where action concepts (e.g., action verbs such as *throw* or manipulable objects such as *hammer*) activated primary and higher-order motor cortex. Concepts with salient auditory features (e.g., *alarm* or *ambulance*) activated sound processing regions in the temporo-parietal cortex. Similarly, motion concepts activated areas in and near motion-processing complex MT+ at the occipitotemporal junction, and color concepts (e.g., verifying that bananas are typically yellow) activated color processing regions in the ventral temporal lobe. It appears that this pattern also generalizes to gustatory and olfactory concepts, although note that very few studies have examined these modalities so far. Another example is a study by Fernandino et al. (2016), who examined 900 nouns that varied in their sensory-motor features in five modalities: sound, color, motion, manipulation, and shape. Their results, shown in Figure 37.4b, again demonstrate modality-specific involvement of sensory-motor systems in lexical concept processing. These neuroimaging findings have been supplemented by numerous studies of patients with brain damage (e.g., stroke, Parkinson's) and brain stimulation (e.g., Transcranial Magnetic Stimulation). These studies show that when sensory-motor systems are damaged or stimulated, processing of corresponding concepts is selectively affected. This body of work suggests that rather than the conceptual system being abstract and separate from action-perception systems, it actually is at least partly based in them. In other words, representation of concepts is embodied by being reliant on bodily (perceptual and motor) systems of the brain. This view has not gone unchallenged (Mahon 2015), and there are examples of negative findings where patients with specific sensory-motor deficits do not show specific impairment for the corresponding type of concepts. While the mounting evidence from lesion, stimulation, and imaging methods has been increasingly difficult to deny, a debate continues regarding the precise nature of the involvement of action-perception systems in concept representation (Kemmerer 2015).

On the other side of the coin, the abstract symbolic theory has trouble explaining how a circular system containing only symbols connected to other symbols can represent conceptual content, without any 'grounding' of symbols in action or perception. In addition to the evidence for

embodiment, the lack of positive evidence for the existence of abstract symbols also puts the viability of the symbolic theory into question.

3.3 Categories of Concepts

3.3.1 Concrete vs. Abstract Concepts

Within the general semantic system, specific categories of concepts have also been found to show affinity for particular brain regions. Two broad categories can be distinguished in the form of concrete and abstract concepts. Concrete concepts can be defined as ones experienced through the five senses (*hammer, lake*), while abstract concepts are not related to these senses in any straightforward manner (*democracy, freedom*). Concrete concepts especially activate bilateral AG, PHG, precuneus, RSC, and pCiG as well as the left pITG and pFG relative to abstract concepts. Abstract concepts show sensitivity in the left dorsal ATL and IFG when directly contrasted with concrete concepts (Wang, Conder, Blitzer, & Shinkareva 2010). (Note that in Figure 37.3, IFG is activated from concrete concepts, but this is relative to control conditions such as nonwords and false fonts. IFG consistently shows an abstract > concrete pattern in direct comparisons.) This can be interpreted as consistent with the ‘Dual Coding’ theory (Paivio 2010). This view suggests that abstract concepts are represented through verbal associations (and hence are more left lateralized), while concrete concepts are represented through direct associations with percepts or image-based representations as well as through verbal associations. The alternative ‘Context Availability’ view (Schwanenflugel & Stowe 1989) suggests that abstract concepts depend significantly more on the contexts in which they occur, which are more diverse. Activation of left IFG for abstract concepts is also consistent with this view, given IFG’s role in concept selection and integration. Involvement of dorsal ATL for abstract concepts is somewhat of a mystery. One explanation is that abstract concepts are typically more emotionally valenced (Kousta et al. 2011), and ATL is thought to have a special role in affective/emotional and social processing. However, this is not likely to be the full story, as parts of the ATL are activated by abstract concepts more than concrete ones even when controlling for emotional valence and arousal. ATL is strongly connected to pSTG/SMG implicated in phonology, which suggests another explanation in keeping with the Dual Coding theory, that abstract concepts have phonologically-based representations.

3.3.2 Living and Nonliving Things

Specific categories within the domain of concrete concepts, such as living things, nonliving things, tools, artifacts, and animals, have been examined extensively through neuroimaging and lesion studies. Behavioral dissociations in brain-damaged patients between living and non-living things have been reported, but anatomical localization of these categories has not been conclusive (Gerlach 2007; Giussani et al. 2011). Some level of localization for more specific categories has been found. Tool concepts, in line with the evidence discussed above, activate higher-order action areas in the left inferior and superior parietal lobe. In the temporal lobe, tools activate bilateral medial pFG, the left pMTG, and vPMC. Animals, on the other hand, activate bilateral LOC and lateral pFG (Chen, Lambon Ralph, & Rogers 2017). ATL is activated by both types of concepts. Lesion studies paint a roughly similar picture, where category-specific deficits for animal concepts are seen due to damage in the ventral temporal cortex, and tool-specific deficits are seen due to damage in pMTG, IPL, or vPMC.

It is worth emphasizing that the representation of categories such as living things, animals, or tools is not localized to a single area, but is distributed among multiple areas. Conversely, areas that contribute significantly towards their representation, such as the ones mentioned above, are not dedicated to just these categories, but also play other roles. The difference between animals

and tools is partly due to their differing reliance on sensory-motor features such as action, motion, shape, or color, but additional factors likely also come into play. It has been suggested that the number of shared vs. distinctive features is an important organizing principle at least in the ventral temporal lobe (Wright, Randall, Clarke, & Tyler 2015). The lateral pFG is found to respond more to animals possibly because they tend to have many shared features (such as having four legs, a tail, eyes, teeth, etc.) and thus form a more tightly intercorrelated network. Tools activate medial pFG more because they tend to have more distinctive and fewer shared features.

3.3.3 Categories of Abstract Concepts

Traditionally, abstract concepts have been treated as a single monolithic category, and were primarily defined negatively, as concepts that are *not* concrete. Abstract concepts present a special challenge for the embodiment view, given that they have no straightforward relationship to action and perception. Some theorists suggest that abstract words (and even concrete words to some extent) can be represented through statistically learned verbal associations (Andrews, Vigliocco, & Vinson 2009; Dove, 2014), minimizing the importance of variation in content within this category. This idea is similar in spirit to the Dual Coding view mentioned above. In recent years, interest in subcategories of abstract concepts and their differing content has increased. Some theories suggest that abstract concepts are grounded just like concrete concepts, but not through action-perception systems. Their grounding is in other systems of the brain, such as affective systems, magnitude processing, interoception (sensory perception of internal body states), metacognition (reflection on one's own mental processes), and event and situation schemas, depending on their content (Desai, Reilly, & Van Dam 2018; Borghi et al. 2019). In a meta-analysis of four types of abstract concepts (emotion, numbers, morality, and theory of mind), Desai et al. (2018) found significant differences as well as common regions across these subcategories, highlighting the heterogeneity within abstract concepts. Moreover, emotion words activated affective systems of the brain. Number concepts activated areas in the IPS associated with magnitude processing and finger representations. Regions salient for episodic memory and event schemas were activated for morality and theory of mind processing. Such results provide hints as to how different types of abstract concepts may be represented and grounded.

Finally, an influential view on how abstract concepts are understood is the Conceptual Metaphor Theory and its neural instantiation (Lakoff 2009). In this view, metaphors are not just linguistic devices, but provide a structure to the conceptual system. Abstract concepts are understood in an embodied manner through metaphorical mappings to sensory-motor systems. A conceptual metaphor is a projection of the basic experiential structure from concrete domains of experience (e.g., action, spatial orientation, movement) to abstract domains (e.g., mental processes, morality, mathematics). For example, the abstract concept of *understanding* something can be based on the action of *grasping* an object (e.g., grasping an idea). A number of neuroimaging and brain stimulation studies have provided evidence that action metaphors such as 'grasp an idea' activate higher-order action planning and execution areas such as aIPL, and are indeed grounded in action-perception systems (e.g., Desai et al. 2013). These findings have been extended to other domains such as texture, body parts, time, space, and motion-related metaphors. To what extent the conceptual system uses metaphors when they are not explicitly used, and how abstract concepts can be understood in those instances, remains controversial. Understanding and refining the neural basis of varieties of abstract concepts is likely to be one of the active fields of investigation in the near future.

3.4 Putative Semantic Hubs

Some regions of the brain show consistent activation for semantic processing of a wide variety of concepts, leading to proposals of semantic hubs. These proposals are motivated by the fact that

conceptual features are distributed and not always experienced simultaneously. The raw sensory features of different members of a category can also be very different (e.g., a tricycle and a train are both vehicles but have many differences). There is a sense that features need to be integrated, reshaped, and perhaps abstracted above, in a single anatomical location to form a coherent concept. Note that while the notion of a single anatomical location where ‘everything comes together’ is intuitively appealing, it is not a logical necessity. Integration and recombination of features can occur in a distributed fashion through synchrony between different areas. Nonetheless, several regions have emerged as potential semantic hubs. In the Fernandino et al. (2016) study mentioned above, five areas showed increasing activation to reliance on any of the five features, and thus are good candidates for integrative hubs: AG, pCiG, PHG, RSC, and medial PFC. Note the similarity of these regions to Figure 37.3, which is based on a meta-analysis of many studies covering a variety of lexical concepts.

3.4.1 Angular Gyrus

AG is activated for a wide variety of concepts. Bonner, Peelle, Cook, and Grossman (2013), similarly to the Fernandino et al. (2016) study, found that activation in the AG increased in a lexical decision task regardless of the sensory-motor feature associations of four types (sight, sound, manipulation, abstract). AG is activated more for concrete than abstract concepts, by abstract concepts relative to nonwords, and more by higher compared to lower frequency words. It is also more activated by combinatorial semantic stimuli such as sentences (Humphries, Binder, Medler, & Liebenthal 2006; Lyu et al., 2019) and by event concepts (Matchin et al. 2019). A number of studies have found AG to be important for thematic associations between concepts (e.g., *dog* and *leash*, *justice* and *law*) (Mirman, Landrigan, & Britt 2017). Its location between action and attention areas dorsally, auditory areas anteriorly, and visual areas posteriorly is ideal for a multimodal integrative region (Binder & Desai 2011). It has a likely role in two kinds of integration: one across time, such as the one needed for sentences, phrases, and events, and the second across features from multiple modalities, such as shape, color, sound, and motion. It also has multiple subdivisions that differ in their sensitivity to various factors, as well as in their connectivity to other regions (Seghier 2013).

3.4.2 Anterior Temporal Lobe

An area not present in the studies above, but associated with the role of a semantic hub, is the ATL. It is part of the ‘hub-and-spokes’ model, in which features are distributed in modality-specific cortices (‘spokes’) and are integrated into an abstracted representation in the ATL hub (Ralph, Jefferies, Patterson, & Rogers 2017). This hub is thought to be bilateral, with a mild leftward bias. Recent views suggest only the ventral ATL as a ‘true’ or maximally transmodal hub, with other ATL regions having graded hub-like characteristics (Hoffman & Lambon Ralph 2018). Patients with PPA-S (semantic dementia) with damage to ATLs show deficits in a variety of semantic tasks. Many imaging studies show activation in ATLs for processing words and sentences compared to non-linguistic control conditions. ATL is also implicated in processing of unique entities, such as names and faces of famous people and landmarks (Tranel 2009).

ATL’s status as a semantic hub is, however, controversial for the following reasons. Some patients show mild or no semantic deficits after unilateral ATL resections. This lack of deficits after unilateral damage can potentially be explained, though, by proposing a bilateral rather than a unilateral hub. Many fMRI studies show no activation for semantic tasks, and especially nonverbal semantic tasks not involving unique entities. This lack of activation is usually explained by the fact that ventral and medial aspects of the ATL suffer from signal loss in fMRI. However, note that the majority of the ATL does not suffer from signal loss. Further, activation in ATL is seen commonly in specific cases (such as for abstract concept processing), but not for all types of concepts, and not for semantic tasks lacking a lexical component (such as picture association). Advanced PPA-S

patients, whose damage originates in ATL, do show both verbal and nonverbal semantic deficits. However, damage in these patients is quite extensive, and not restricted to ATL. Atrophy in moderate and severe patients extends to middle and posterior temporal lobes, and affects lateral, ventral, and medial temporal lobe, in addition to inferior frontal and subcortical regions. Hence, which of the deficits are specifically due to ATL atrophy is far from clear. When patients with atrophy restricted to the left ATL are selected, they tend to show only verbal, but not nonverbal, semantic deficits (Hurley, Paller, Rogalski, & Mesulam 2012; Mesulam et al. 2013). One proposal is the ‘dual route’ view, where the left ATL mediates verbal semantics, while the right ATL is critical for nonverbal semantics. However, this view is also controversial because such a clear left/right separation corresponding to a verbal/nonverbal separation is not found in many neuroimaging and lesion studies. In general, the use of methods with low spatial resolution, such as patients with progressive conditions or those with large lesions, to infer functions of relatively small areas of interest, is problematic and the cause of many controversies and inconsistencies in the literature.

Nonetheless, currently the more prevalent view is that ATL is a semantic hub, perhaps with multiple subdivisions, that stores integrated semantic knowledge. Our view is somewhat different. We suggest that the left lateral and polar ATL may have a lexical, rather than a general semantic role bilaterally. This area provides access to semantic features stored elsewhere, by connecting word forms to semantics bilaterally, rather than storing or integrating concepts themselves. Deficits interpreted as semantic are actually lexical in nature (i.e., involve impairments in *access* to concepts, but not to conceptual content itself), under our view. Similarly, it provides access to the names and knowledge about specific or unique entities, by performing the mapping between perceptual features (e.g., a face) and knowledge about the entity, but does not store that knowledge. The medial temporal lobe, including PHG and entorhinal cortex, could have a more salient role in nonverbal semantic processing. Under this view, the verbal/nonverbal distinction does not correspond to left vs. right ATL as suggested by the dual route view, but to a lateral/medial difference. Medial and posterior temporal areas are involved in nonverbal semantics bilaterally. The anterior one-third of the temporal lobe bilaterally only enables access to verbally mediated knowledge. When the atrophy spreads to middle and posterior temporal regions, especially to mid-FG and PHG known to be involving higher-order visual processing, visual semantic deficits are also seen.

Emotional valence and social cognition are also associated with ATL, but specific subdivisions sensitive to these domains are not well understood. ATL is connected to the orbitofrontal cortex and VMPFC through uncinate fasciculus, which has a central role in evaluation of emotional valence and reward processing. It is less clear whether valence processing takes place in ATL itself, or ATL only receives this information from orbitofrontal cortex. In summary, ATL occupies a prominent role in semantic cognition as a potential hub, but its exact role and potential subdivisions remain controversial and a subject of active research.

3.4.3 Posterior MTG/ITG

In addition to these two areas, the left pMTG/pITS/pITG complex is frequently activated by concrete concepts, verbs, and sentences, and damage or stimulation of this region impairs comprehension tasks (Dronkers, Wilkins, Van Valin Jr., Redfern, & Jaeger 2004). Damage to this general region, often including AG, causes transcortical sensory aphasia. Here, lexical comprehension abilities are impaired, but phonological and speech production abilities (e.g., repeating words or sentences) are intact. Based on these findings, combined with activation from a number of imaging studies, this region has been proposed as a hub or a ‘lexical interface’. However, this interpretation is applicable mainly to concrete concepts, as standard clinical tasks such as picture naming, word-picture matching, and sentence-picture matching involve only concrete items. Imaging studies show that abstract concepts do not strongly engage this complex. In an MEG study of sentence processing, Lyu et al. (2019) found activity in left pMTG to be reflective of verb meaning, and a directional

connectivity from pMTG to AG/SMG. They suggested that information about verb semantic content is continuously generated in the pMTG as the speech input accumulates, and is continuously delivered to AG/SMG for further integration.

While pMTG is often lumped together with pITG in lesion literature, it is worth distinguishing these areas. Selective damage to pMTG or to pITG is rare, and hence imaging is more useful in parcellating their functions. PMTG is at the intersection of a number of different white matter pathways (Figure 37.1b), and is especially important for sentence-level processes (see Sentence Comprehension section below). Some investigators have suggested that it is important for ‘semantic control’, giving it a more executive role in retrieval and comparison or selection of concepts rather than storage and integration of features (Lambon Ralph et al., 2017). PITG, extending into FG, on the other hand is important for motion- and action-related processing, and also other visual features such as shape and color. This is consistent with its role in representation of concrete concepts.

3.4.4 Posterior Cingulate Complex

This region consists of pCiG, RSC, and precuneus, and is consistently activated in semantic processing (Figure 37.3). The precise role of this region for language and semantics is not well understood. A possible function can be linked to episodic and spatial memory evoked by concepts. Two functional subdivisions of this complex have been suggested: an anterior section involved in mental imagery, and a posterior section important for episodic memory retrieval. RSC also has a prominent role in spatial memory, and in egocentric vs. allocentric spatial processing. Greater activation of RSC and anterior pCiG is seen for concrete concepts. This can be related to mental imagery and spatial nature of episodes associated with concrete concepts. Abstract concepts activate a more posterior/dorsal section, associated with episodic memory retrieval that may be less spatial and more social/emotional in nature. This explanation supports the notion of ‘situated conceptualization’, according to which concepts are understood and processed in terms of situations or contexts in which they occur. Categories are formed by a large collection of situated simulations, and not by abstracting over all contexts that objects or actions occur in (Barsalou 2016), explaining the role of the posterior cingulate complex.

3.4.5 Content of Representations

One unanswered question relates to the nature of representations in these putatively integrative regions. It is clear that in many cases, raw sensory information has to be abstracted over in order to form coherent categories (e.g., a vehicle category that abstracts over features of trains and tricycles). When sensory-motor features are integrated into a whole (assuming that they are), is this modality-specific information retained or completely discarded? Opinions fall into two broad groups. One view is that modality-specific information is retained in some fashion (e.g., an image-like representation of an object that represents its shape and color features). Perceptual information may be recombined, weighted, and transformed, but the concept still carries a ‘stamp’ or format of the original modalities. Thus, integrated concepts are *multimodal* or *heteromodal* because the modality-specific information is still ‘there’ in some respect. An alternative view is that information in sensory-motor format is discarded in the service of abstraction. Concepts sit above any sensory-motor or action-perception traces, and hence are described as *amodal* or *supramodal*. Some authors have argued that both forms of representations exist simultaneously, and are used in a task-dependent manner.

One terminological clarification is warranted here. Labels such as ‘amodal’ or ‘multimodal’ used above refer to the *content* of concepts. The same labels are frequently used in literature to refer to the modality of the *input* through which the concept is accessed. For example, a word can be presented in a written or spoken form. An area that is activated by both of these forms

is called an amodal area, in that it is insensitive to the visual or auditory modality of the input channel. Similarly, areas activated both by printed words and pictures are often referred to as amodal, this time treating verbal and nonverbal inputs as modalities. However, common activation by different input channels does not imply that content of the concept—the nature of information that is activated by these inputs—is amodal or abstract. For example, if modality-specific shape and color information is activated by auditory presentation of the word *banana* (as suggested by embodiment theories), it would also be activated by a picture of a banana. The activation that is common between these two presentation methods is modal (higher visual cortex sensitive to shape and color) with respect to conceptual content, but is amodal with respect to input channel (activated for both auditory and visual input, and for both verbal and nonverbal input). When reading literature or evaluating arguments about modality, it is essential to distinguish between these two uses of terms such as ‘amodal’: modality of input channel and modality of conceptual content.

4. Speech Perception and Production

Speech is a critical modality through which we access language. Children typically acquire language through speech well before they learn to read or write. Our auditory system is exquisitely tuned to rapidly process speech, so that we can comprehend several words per second, each containing many phonemes that have a great variety in their physical signatures. Heschl’s gyrus in the superior temporal lobe houses the primary auditory cortex bilaterally, where all speech and nonspeech sounds are processed. Heschl’s gyrus and planum temporale, an area located just posterior to it, perform a spectrotemporal analysis of sounds (i.e., the analysis of sound waves over time with respect to amplitude and frequency content). The lateral STG represents subphonemic features and feature combinations (Chang et al. 2010). Moving ventrally, the mid- and posterior STS process phonemic sounds (Desai, Liebenthal, Waldron, & Binder 2008; Yi, Leonard, & Chang 2019). Investigators have looked for a ‘map of phonemes’ in STG, where neurons might be laid out according to their preference for a particular phoneme. However, there is no clear evidence for such a map. Rather, neurons that respond to onset of speech (in pSTG), and neurons that are responsive to the sustained part of speech (in mid-STG), were found (Hamilton et al. 2018). Parts of pSTG, pSTS, and SMG are especially associated with representing phonological structure of whole words (Okada & Hickok 2006; Stefanatos 2008). These regions process speech sounds bilaterally, but there may be a difference in the sensitivity to temporal features in the two hemispheres. The ‘Asymmetric Sampling in Time’ hypothesis suggests that the LH is more dominant for processing rapid auditory variations (20–80 ms range), while the RH is more tuned to auditory patterns in the longer 150–300 ms range (Arnal, Poeppel, & Giraud 2016).

4.1 The Dual Stream Model

After initial spectrotemporal analysis of speech, according to the Dual Stream Model (Hickok & Poeppel 2007), further processing of speech proceeds along two pathways: the ventral and dorsal streams (Figure 37.5). The ventral stream interfaces with semantics and is used for comprehension (the ‘what’ pathway). It is proposed to have a lexical interface in pMTG/pITS that maps sound structure of words to semantics. This lexical interface connects to the conceptual network to retrieve meanings of words, which is proposed to be widely distributed. A combinatorial network in the lateral ATL is also part of this pathway, and combines lexical units to create larger units such as phrases and sentences. The dorsal stream, on the other hand, is used for speech production, and converts auditory representation of words into articulatory codes (the ‘how’ pathway). It is proposed to have a sensorimotor interface that maps sound structures of words onto motoric representations. This interface is localized to area ‘Spt’ at the posterior end of the Sylvian fissure

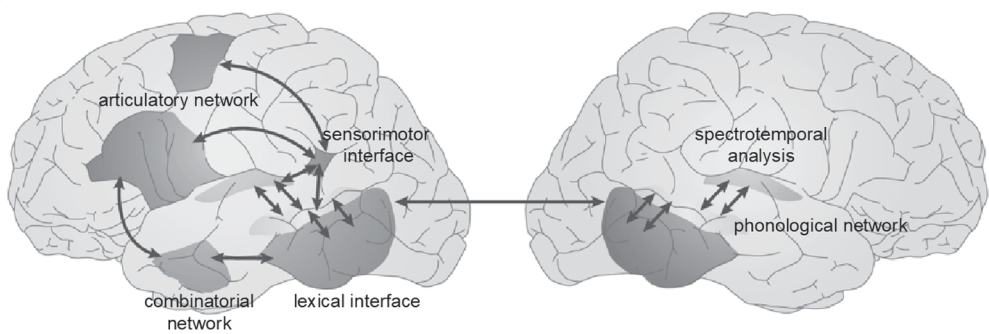


Figure 37.5 The Dual Stream Model. The lexical interface (pMTG/pITS), phonological network (light shading; mid-post STS), and spectrotemporal analysis (dark shading; dorsal STG) are bilateral. Other components are left lateralized.

Source: Adapted from Hickok & Poeppel 2007.

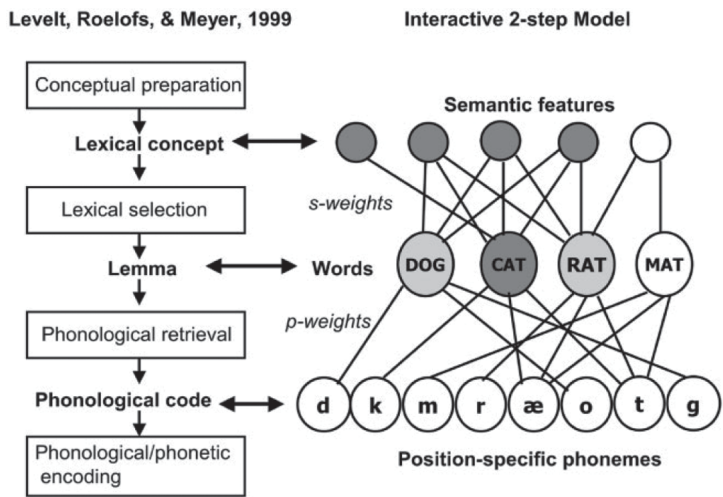


Figure 37.6 The Lemma Model (left) and the interactive two-step model (right)

Source: Adapted from Schwartz et al. 2009.

at the junction of parietal and temporal lobes. The dorsal stream ends in an articulatory network in the frontal lobe, involving the left pIFG, premotor cortex, and anterior insula, and is responsible for the production of an utterance. Thus, a broad distinction between form-to-articulation mapping (including the feedback necessary for prediction, error detection, and correction) carried out by the dorsal route, and form-to-meaning mapping in the ventral route, is proposed.

4.2 The Lemma Model

A prominent model of speech production is Levelt’s Lemma Model (Levelt 2001) (Figure 37.6, left). It consists of two major subsystems that operate in a sequence: lexical selection and form encoding. Each subsystem is composed of discrete stages that also operate sequentially. Lexical selection starts with lexical concept retrieval, which consists of selecting a semantic structure that corresponds to the meaning one wishes to express. The next stage is lemma retrieval and

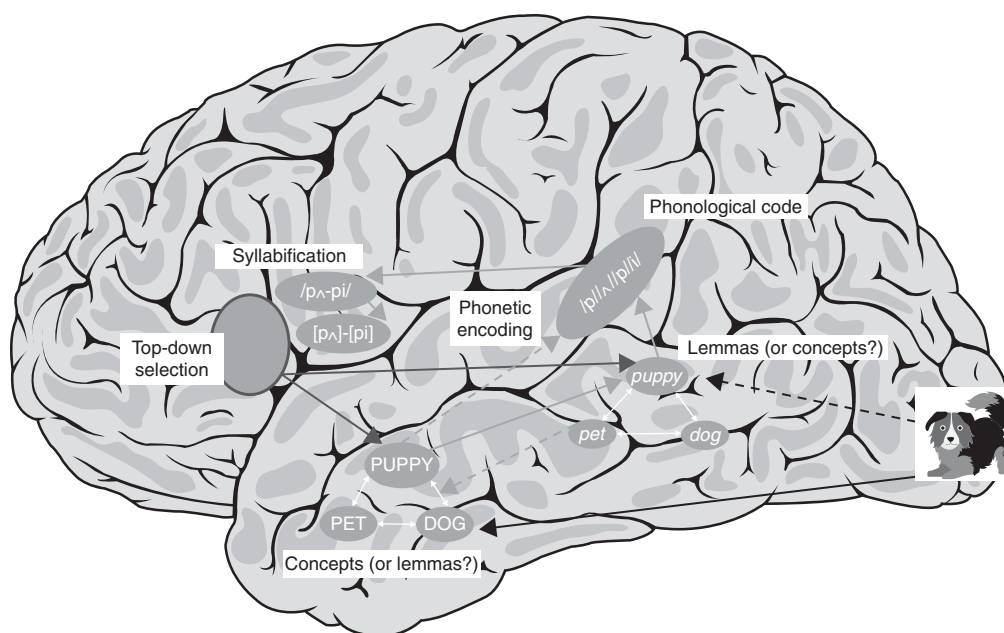


Figure 37.7 Potential neural correlates of components of the Lemma Model. Activation flow in a picture naming task starting from a picture of a ‘puppy’ is shown, which ends at the phonetic encoding stage, leading to the eventual motor output (not shown). The notion of, and distinction between, lemmas and lexical concepts is controversial. Solid lines indicate a more commonly accepted pathway. The dashed lines indicate an alternative pathway we suggest. (Some components of this figure are modified versions of a figure kindly provided by David Kemmerer.)

selection. Lemmas are abstract word nodes in the model that connect semantics and phonology, and point to morphosyntactic features such as grammatical class of a concept. In this stage, the lemma corresponding to the lexical concept is selected and its relevant morphosyntactic features are activated. The neural correlates of these two stages are not clear, but some suggestions have been made. Lexical concept retrieval is suggested to be underpinned by the ATLs, and lemma retrieval is associated with pMTG/pITG, at least when concepts are concrete nouns. However, some evidence is also consistent with the reverse scenario, with concepts and lemmas being associated with pITG/pMTG and ATLs respectively. The difficulty arises because in neuroimaging and in common neuropsychological tasks, it is difficult to distinguish between lemma and concept activation. In lesion studies, the spatial resolution is low (multiple areas are lesioned simultaneously), and damage to one area can have effects of processing in distal areas (diaschisis). Less controversial is the role of left IFG in both of these stages. The selection, or resolution of conflicts, between co-activated lemmas and concepts likely depends on the left IFG.

The lemma is then passed on to the form encoding subsystem, which has three discrete stages. Incremental construction of the phonological representation of the word to be produced is carried out in the phonological code retrieval stage. The left pSTG and SMG are likely where this process takes place. The next is syllabification, which is determination of the syllabic structure of the target word in a context-specific manner. The area most associated with syllabification is BA 44. The final stage is phonetic encoding, which involves specifying speech motor tasks to be accomplished (e.g., lip closure). It is associated with left frontal regions, including the anterior insula, BA 44, and the ventral prCG. The potential neural correlates of these components are shown in Figure 37.7.

4.3 The Interactive Two-Step Model

A key characteristic of the Lemma Model is its unidirectional and discrete stages, where activity is modular and flows only in one direction. Later stages of processing, such as phonological code retrieval, do not influence prior stages, such as lemma retrieval. Under this model, it is difficult to explain some empirical findings, such as the fact that ‘mixed errors’ are much more common in speech production than expected. An example of a mixed error is saying *rat* instead of *cat*, where the error is both semantically and phonologically related to the intended word. High proportion of these errors is explained more easily by a model where phonology and semantics influence each other. The interactive two-step model by Dell and colleagues (Dell, Schwartz, Martin, Saffran, & Gagnon 1997; Dell, Martin, & Schwartz 2007) is such a model (Figure 37.6, right).

The core of this model consists of three layers. A distributed ‘semantic’ layer contains units representing features of concepts, such as having four legs or making a ‘meow’ sound. This layer is connected to a ‘word’ layer that contains units representing whole words (*dog*, *cat*). The word units are in turn connected to the output ‘phonology’ layer that contains units corresponding to phonemes (/k/, /æ/, /t/). Activation flows in both directions between layers. Semantic units are activated by a picture of a cat, which activate the word node *cat*, and also activate semantically overlapping concepts such as *dog* and *rat*. Word units send activation to the phonology layer. The phonology layer feeds activation back to the word layer, activating the target word (*cat*) but also phonologically overlapping words such as *rat* and *mat*. When there is noise in the system, a word that is both semantically and phonologically similar to the target word is more likely to be produced, explaining the higher frequency of mixed errors.

In the Lemma Model, there are two separate representational levels called ‘lexical concepts’ and ‘lemmas’. It is not clear to what extent these distinct levels exist. They are difficult to distinguish experimentally, as lexical tasks end up requiring or activating both, assuming that they exist. In Dell’s model, there is instead a single ‘words’ layer. It is activated by the conjunction of semantic features (like ‘lexical concepts’) and connects to syntactic information (like ‘lemmas’). Semantic knowledge is assumed to be distributed among many feature units, hence there is no notion of a separate lexical concept unit. The equivalence shown in Figure 37.6 between the lexical concept layer and semantic features is somewhat misleading in this sense, because there is no equivalent of semantic features in the Lemma Model, and lexical concepts and lemmas are combined into the ‘words’ layer in Dell’s model.

Anatomical localization of the components of the model has also been attempted (Dell, Schwartz, Nozari, Faseyitan, & Branch Coslett 2013). The two main components of the model are *s-weights* that connect semantic units to word units, and *p-weights*, that connect word units to phoneme units. The p-weights were localized mainly to SMG, prCG, poCG, and insula, which are part of the dorsal stream in the Dual Stream Model. This is consistent with the role of these regions in creating representations related to output phonology, and then planning and producing the speech output. The s-weights were associated with ATL, IFG, MFG, and AG. These regions can be interpreted as involved in representation and retrieval of semantic information, and access of lemmas.

The extent to which speech production relies on modular and sequential processes, as opposed to interactive and cascaded activation, continues to be debated. A broad distinction between fronto-parietal areas responsible for phonological processing and speech output, and temporo-parietal cortex involved mainly in lexical access and semantics, with selection and control processes in frontal regions, is supported. The problem of speech motor control, required to produce an actual utterance, is not discussed here (for an advanced neuro-computational model, see Kearney & Guenther 2019).

5. Sentence Comprehension and Production

The expressive power of language relies crucially on the ability to combine words in novel ways. Comprehending sentences involves a number of processes beyond accessing lexical properties of words. This includes grouping words into phrases and clauses, and assigning participant roles to noun phrases. More so than in single word processing, these processes rely on short-term memory (STM), which keeps the linguistic material active while new words are integrated. Cognitive control also plays a more salient role in sentence processing, and is essential for extracting relationships between different units in a sentence, and monitoring and adjusting the interpretation of an utterance when needed.

A variety of neuroimaging and lesion-symptom mapping studies have identified important neuroanatomical components of the sentence processing network. Neuroimaging meta-analyses have implicated a large swath of lateral temporal, posterior frontal, and inferior parietal cortex of the left hemisphere in sentence comprehension, with temporal and parts of frontal cortex implicated bilaterally (Figure 37.8a; Vigneau et al. 2006; Hagoort & Indefrey 2014; Walenski, Europa, Caplan, & Thompson 2019). Lesion-symptom mapping studies have also implicated a mostly overlapping, but somewhat more restricted, set of regions important for sentence comprehension. For example, in a study of stroke patients, Dronkers et al. (2004) identified the following regions in relation to sentence comprehension deficits: pMTG/pITG, ATL, pSTS/pSMG extending into AG, aIFG (BA 47), aMFG, and LIFC (Figure 37.8c). Den Ouden et al. (2019) examined the impact of lesions to

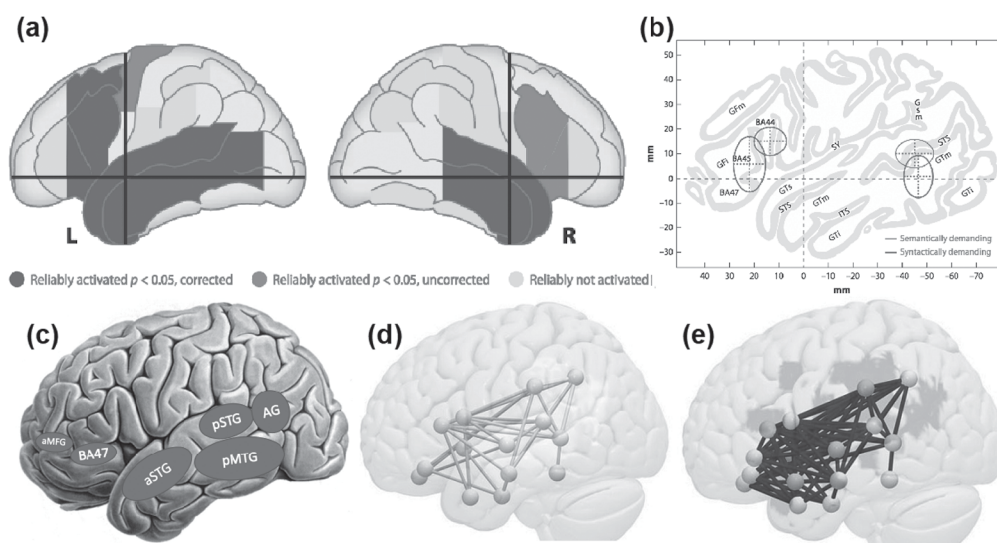


Figure 37.8 (a) Areas involved in sentence comprehension identified by a meta-analysis of neuroimaging studies. (b) Mean and standard deviations of peak locations from studies that manipulated semantic demands or syntactic demands, compared with corresponding less demanding sentences. (c) The main areas for sentence comprehension identified by Dronkers et al. (2004) in a lesion-symptom mapping study, with one modification. They identified a single area in pSTG that extended into AG. Here, pSTG and AG are shown as different areas because their likely functions are different (pSTG in phonology and AG in semantics). (d) Areas (with light shading) and white matter connections identified by Den Ouden et al. (2019) for an auditory sentence comprehension test in a lesion-symptom and connectome-symptom mapping study. (e) Areas and connections important for sentence production identified by the same study using a sentence production priming test.

Source: Both (a) and (b) adapted from Hagoort & Indefrey 2014; (d) and (e) adapted from Den Ouden et al. 2019.

areas and to connections between areas on sentence comprehension and found a network of mostly peri-sylvian regions (Figure 37.8d). These regions play different roles in sentence processing, though the specific roles of all of these regions remain controversial. Below, some of the prominent theories regarding their role are summarized.

PMTG is activated more for nouns and verbs that have ambiguous (compared to unambiguous) grammatical class in sentences (Snijders et al. 2009), dispreferred interpretations of ambiguous phrases (Tyler et al. 2011), verb meaning (Lyu et al. 2019), and lexical syntactic processing (Matchin et al. 2019a). Damage to pMTG is associated with decline in performance of many sentence types, including simple declarative sentences (Dronkers et al. 2004). Pillay, Binder, Humphries, Gross, and Book (2017) found that damage to pMTG/pSTS impairs auditory sentence comprehension even after regressing out picture naming (which controls for speech production and lexical semantics), pointing to its special importance for sentence-level processing. Thus, it could be important for keeping syntactic properties of words and phrases active while an auditorily presented sentence is processed. PMTG and more inferior regions (pITS/pITG) are also important for processing semantic information, especially related to action and motion, as mentioned above. PMTG has extensive structural and functional connectivity with other areas in the sentence processing network (Turken & Dronkers 2011), and hence can be thought of as a ‘hub’ that is centrally important for sentence processing. This is partly consistent with earlier views such as the Dual Stream Model, which designates pMTG as a ‘lexical interface’, taking phonological forms of words as input and producing syntactic and semantic codes. However, these results suggest extending its role to incorporate sentence-level operations (in conjunction with LIFC) as well as semantic contributions, especially action-related concepts. These data perhaps also weaken the traditional strict linguistic distinction between lexicon and syntax (or words and rules) and point to their intertwined nature. Keeping with this expanded view, in the framework of Matchin and Hickok (2020), pMTG creates hierarchical structures from sequential phonological structures in pSTG, and links them with semantics, in both comprehension and production.

ATL is especially sensitive to complex sentences, and could play a role in syntactic analysis and structure building. The dorsal ATL (aSTG/aMTG) is responsive to complex sentence structure even when sentences are not semantically sensible (Humphries et al. 2006). It shows greater activation with increasing syntactic complexity (Obleser, Meyer, & Friederici 2011). Two studies suggest that rather than a general role in processing syntax, its role is related to STM load. An fMRI study showed increasing activation with increasing ‘syntactic depth’ of words in a sentence tree structure (Brennan et al. 2012). An intracranial recording study by Nelson et al. (2017) found that activity in anterior and middle temporal lobe neurons was correlated with the number of open ‘nodes’ during sentence processing (e.g., in the sentence ‘Ten sad students should often sleep’, there are three open nodes when ‘should’ is processed, which are then thought to be merged into a single node—a closed constituent—that indicates an entity that should often sleep). Activity in ATL was also correlated with the number of closed constituents. These findings are consistent with a role of aSTG/aMTG in STM, used to temporarily hold elements while a complex sentence is parsed.

PSTS/pSMG is associated with auditory-verbal STM. It stores the sound-based representations of verbal material in an activated state for short durations, a vital aspect of the effective comprehension of spoken sentences (Binder 2017; Leff et al. 2009).

The neighboring AG is sometimes grouped together with pSTS relating to its role in STM. However, its likely function is different. As discussed above, it is activated for processing sentences compared to word lists in general, but is especially important for semantically reversible and noncanonical sentences (e.g., passives such as ‘The bride was carried by the groom’ and object clefts such as ‘It was the bride who the groom carried’) (Thothathiri, Kimberg, & Schwartz 2012). Thus, it could have a role in integrating semantic and syntactic structures over time, allowing determination of ‘who is doing what to whom’.

The most controversial is perhaps the role of LIFC (or more specifically, Broca's area roughly corresponding to BA 44/45), which was thought to be central to syntactic processing and should be involved in processing all types of sentences. Perhaps surprisingly, several fMRI studies have found no activation in LIFC for sentence comprehension relative to word lists (e.g., Humphries et al. 2006). This is consistent with multiple lesion-symptom mapping studies (Dronkers et al. 2004; Pillay et al. 2017; Rogalsky et al. 2018), which found no relationship between damage to LIFC and sentence comprehension. On the other hand, some imaging and patient studies have found an association between LIFC and comprehension of certain types of complex sentences (e.g., Den Ouden et al. 2019), such as reversible passives and syntactically ambiguous sentences, as well as for syntactic violations. This has led to a number of different hypotheses regarding the role of LIFC. These hypotheses include: (1) extracting hierarchical structure from linear sequences, (2) implementing syntactic movement, (3) cognitive control and general cognitive task demands (Rogalsky et al. 2018), (4) rehearsal component of auditory-verbal STM (Rogalsky & Hickok 2011), and (5) implementing the process of 'unification'. Unification refers to deriving higher-level meaning from phonological, morphological, semantic, and syntactic building blocks (Hagoort 2016). A partial reconciliation between these proposals may be the idea that LIFC is recruited only when hierarchical phrase structure analysis is especially demanding, but not for relatively simpler bottom-up processing, and for generating morpheme sequences, which is always necessary during production.

Specific regions of LIFC have also been proposed to have different functions. For example, in Friederici's (2012) proposal, the frontal operculum (situated in ventromedial LIFC) works in tandem with aSTG to build local phrase structures. BA 44 links with aSTG, pSTG, and AG to build complex, hierarchically structured sequences. BA 45 and 47 work in tandem with temporal lobe structures to process semantic aspects of sentence comprehension. In Rogalsky and Hickok's proposal (2011), BA 44 primarily subserves the articulatory rehearsal component of auditory-verbal STM, while BA 45 implements a domain-general sequence processing mechanism. Matchin and Hickok (2020) suggest that BA 45 is critical only for production, because its role is to take the hierarchical structure developed in pMTG as input, and convert it to a sequence of morphemes. This view endorses the intertwined nature of syntax and semantics by arguing for a lexicalized view of syntax, where lexico-syntactic functions are jointly carried out by pMTG and BA 45. A lack of clear separation between lexical and syntactic processing, even in areas such as LIFC, pMTG, and pSTG, argues against the lexicon/syntax or words/rules dichotomy at the core of traditional linguistic theories.

Note that meta-analyses of neuroimaging studies (Hagoort & Indefrey 2014, shown in Figure 37.8a; and also Walenski et al. 2019; and Vignau et al. 2006) show reliable activation of LIFC and other frontal areas. One might say that this activation is 'for sentence comprehension', but it is important to ask 'compared to what'? These analyses included studies that compared sentence conditions with low-level baselines, such as unintelligible sentences or false fonts, and some included lexical conditions such as word lists. In comparisons with low-level baselines, it is not clear whether activations reflect processes specific to sentence-level processing, or those related to general processing of linguistic materials such as phonemes, morphemes, and words, or general task-related demands not specific to sentences. Sentences compared to non-linguistic baselines almost always activate the LIFC, but comparisons with linguistic baselines such as word lists frequently do not. To eliminate activations due to low-level or nonspecific processes, Hagoort and Indefrey (2014) also compared sentences with high vs. low syntactic demands and high vs. low semantic demands (Figure 37.8b). High syntactic demands activate posterior LIFC (BA 44/46), while high semantic demands tend towards anterior LIFC (BA 45/47). In the posterior temporal lobe, peaks due to higher syntactic demands were centered around pSTS and dorsal pMTG, while those due to semantic demands were distributed around ventral pMTG, pITS, and pITG. Activations

in posterior LIFC and pSTS can be explained as specifically related to syntactic operations, or due to greater general cognitive demands required for syntactically complex sentences. The results also highlight the fact that just like LIFC, pMTG is also a heterogeneous area. While damage or activation in the vicinity of this general area is subsumed under a single label ‘pMTG’, giving rise to the notion that it is a ‘hub’, there are likely different functions subserved by pSTS, dorsal and ventral pMTG, pITS, and pITG.

In summary, sentence comprehension is a complex process subserved by a network of brain regions with dominance in the left hemisphere. A variety of roles have been proposed for these areas, that vary from more specific to language, such as building phrase structure, to less specific, such as extracting hierarchy and cognitive control.

5.1 Sentence Production

Sentence production deals with the important question of how we can put together a series of words to produce full sentences. Concepts are thought to go through the process of syntactic encoding that creates the surface structure of a sentence. The surface structure is then passed to phonological and articulatory processes. Relatively few neuroimaging studies have examined the process of syntactic encoding in the context of sentence production, mainly due to the methodological issue of head movement that is likely to be caused by producing sentences in a scanner.

Some of the first imaging studies of sentence production (Indefrey et al. 2001; Indefrey 2011) showed activation in the left pIFG (BA 44) for saying sentences such as ‘The red square launches the blue ellipse’ compared to saying ‘square red, ellipse blue, launch’. Haller, Radue, Erb, Grodd, and Kircher (2005) found activation in the left BA 44 and 45 for sentence generation compared to sentence reading and word generation, and also in the left SMA and SPL.

A number of neuropsychological investigations of syntactic encoding that test patients with stroke as well as PPA also exist. Faruqi-Shah et al. (2014) tested stroke patients on picture description, picture naming, sentence, and nonword repetition tasks. They found that impaired sentence production was uniquely linked with pIFG, SMG, aSTG, insula, and putamen. Den Ouden et al. (2019) used three sentence production tasks on stroke patients, and found a similar network of regions. Examining the white matter damage, they found that sentence production deficits were related to connectivity between IFG and inferior parietal as well as anterior and middle temporal areas (Figure 37.8e).

Several studies have also examined patients with PPA-G where patients have sentence production deficits. For example, Sapolsky et al. (2010) found that atrophy in the IFG, MFG, SFG, prCG, and SMA was especially associated with sentence production deficits. Wilson et al. (2010) similarly found atrophy in IFG, prCG, and MFG to be associated with nonfluent sentence production, predicting effects on syntactic complexity, elicited from a picture description task.

Thus, the LIFC and other frontal lobe structures (SFG, MFG, prCG) are associated specifically with sentence production relative to word production. Additionally, connectivity of IFG to aSTG, pMTG, and SMG is also likely to be critical to sentence production. As noted above, the specific role of LIFC in sentence processing is controversial. It can be related to building hierarchical sequences and phrase structure, and selection of lemmas and words during sentence production. Relative to comprehension, sentence production also places greater demands on some executive and cognitive control processes, such as decision making, selection, and response inhibition. The role of other frontal structures may be tied to these processes.

6. Reading and Writing

While the vocal mode of communication is the most common, use of visually represented symbols—orthography—is another major form of communication that is important, especially in

modern life. Reading and writing are among the most important inventions in human history, as they enable preservation and accurate transmission of knowledge and culture across generations, without reliance on memorization.

6.1 Reading

What we know about words can be represented as a triangle, where the three vertices represent orthography, phonology, and semantics. In reading, the input comes through the orthography node, and leads to activation of the corresponding semantics and phonology. Because reading and writing are relatively recent inventions, developed only about 5,000–5,500 years ago, there are no evolutionary pathways specifically for processing orthography and connecting it to semantics and phonology. The goal of reading is to exact meaning. Two possible routes to meaning are the ‘direct’ route, orthography → semantics, and an ‘indirect’ route, orthography → phonology → semantics. Both routes contribute to reading to different extents, depending on the characteristics of the word. The major neural components of the reading system are shown in Figure 37.9a.

The vOTC plays a prominent role in reading. The reading pathway in vOTC starts with the analysis of low-level visual features of print in the occipital lobe (shaded regions in Figure 37.9a). A prominent model, the Local Combination Detector (LCD) (Dehaene, Cohen, Sigman, & Vinckier 2005), suggests that the pathway contains multiple levels of feature detectors, organized hierarchically. As one moves anteriorly along the vOTC surface, increasingly complex features are processed; starting from parts of letters, then whole letters, and then combinations of letters such as bigrams and trigrams are handled. The pathway culminates in the mid-FG, in what has been called the ‘visual word form area’ (VWFA) (McCandliss 2003), centered on the pOTS. According to the LCD model, the processing is also increasingly abstract, such that sensitivity to lower-level features such as location, font, and case is reduced as one moves anteriorly along this pathway (Vinckier et al. 2007).

Much research has been dedicated to characterizing the putative VWFA (Dehaene & Cohen 2011). It is generally accepted that it is more sensitive to printed words than to spoken words, and is not sensitive to location, font, and case of the text. It responds to words regardless of task demands

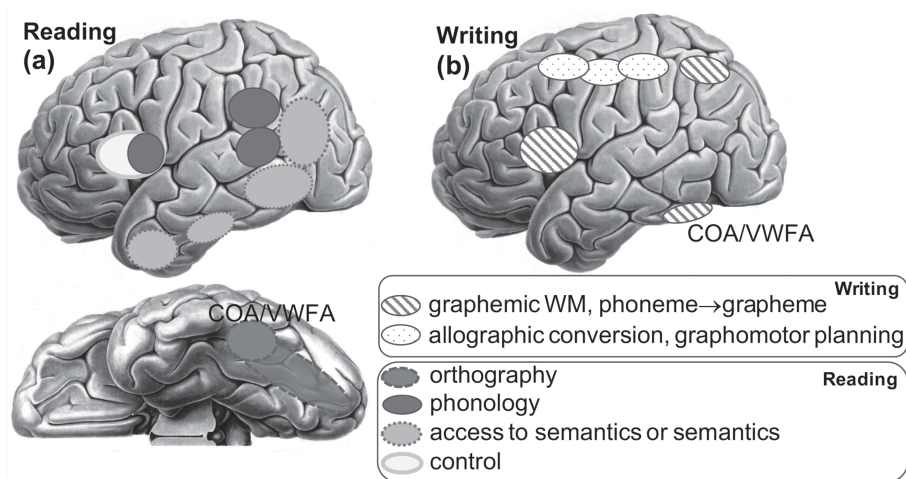


Figure 37.9 (a) Some of the main brain regions involved in reading. The semantic regions are especially more distributed; only some are shown. (b) Some of the main brain regions involved in writing.

Source: Based on a meta-analysis by Purcell et al. 2011.

and awareness, is sensitive to sublexical properties such as bigram frequency, and to pseudowords. Whether VWFA is dedicated solely to processing printed word forms, or it is also sensitive to other types of objects, has been controversial. Examining individual subjects to exploit high spatial resolution fMRI, and to avoid smoothing across neighboring areas, Mano et al. (2013) found patches in the pOTS in each individual subject that were more sensitive to orthographic stimuli (words + pseudowords) than to object pictures, controlled for low-level visual properties. They also found neighboring patches in and around pOTS that showed the reverse pattern. This suggests that the pOTS does contain sub-regions that are relatively tuned or specialized for orthographic material, and is not simply a general visual object processor. VWFA has been suggested to contain an ‘orthographic lexicon’ (i.e., an inventory of the orthographic forms of all known words). Using repetition priming with words and nonwords that are either identical or differ by one letter, Glezer, Jiang, and Riesenhuber (2009) found the left pOTS contains whole-word representations, supporting such a proposal. This idea runs into difficulty when you consider that VWFA is also sensitive to sublexical properties such as bigram and trigram frequencies within nonwords (Binder, Medler, Westbury, Liebenthal, & Buchanan 2006), and pseudowords often produce *more* activation in VWFA than words. Hence, it is not likely to contain only whole-word representations. Rather, it contains units or sub-networks that are finely tuned to familiar letter combinations of varying lengths, including whole words. In that sense, the name ‘visual word form area’ is a partial misnomer. A better term might be ‘combinatorial orthographic area’ (COA). This area is, nonetheless, a critical part of the system of orthographic expertise, and links spellings of words to their meanings and sounds.

Damage to vOTC can cause alexia, but this is not always the case. Severely impaired patients are not able to recognize even single letters. Less impacted patients are unable to read whole words with a quick glance, but instead read in a laborious manner one letter at a time and put them together. A different type of reading disorder is acquired dyslexia, in which reading is also impaired. The three main types of acquired dyslexia are phonological, surface, and deep dyslexia. (Note that these are different from dyslexia affecting children due to congenital abnormalities.) In phonological dyslexia, patients are especially poor at reading pseudowords, but can read most words. Damage to the shaded regions in Figure 37.9a is associated with phonological dyslexia, namely pIFG/BA 44, pSTG, and SMG (Rapcsak et al. 2009). Surface dyslexia is characterized by difficulty reading words with irregular spelling-sound correspondence (such as *yacht* or *pint*), especially if they are low frequency. These patients tend to make overregularization errors (*pint* pronounced to rhyme with *mint*). They perform relatively well at reading pseudowords and regular words. Surface dyslexia is often, but not always, seen in PPA-S (semantic dementia) patients (Patterson et al. 2006; Wilson et al. 2009), and is associated with damage to the shaded lateral temporal regions in Figure 37.9a. The co-occurrence of semantic deficits in PPA-S with surface dyslexia has led to the suggestion that for reading low frequency words with irregular spelling-sound correspondence, semantic retrieval is necessary. Because the direct orthography → phonology route is not sufficient (the orthography does not transparently tell you what the word is supposed to sound like), the indirect orthography → semantics → phonology route is used (word meaning is used to retrieve the sound of the word). This idea is somewhat controversial, due to a few reports of patients who have semantic deficits but are not surface dyslexic. Lastly, deep dyslexic patients are impaired at reading both regular and irregular words, as well as pseudowords. Errors tend to be semantic in nature and worse for abstract words. Damage in these patients is often more extensive, and involves temporal and inferior parietal areas.

Now we are in a position to delineate the likely locations of the nodes in the orthography/phonology/semantics triangle. VWFA/COA is the main combinatorial orthographic processor node. For combinatorial phonological processing, SMG/pSTG is most likely centrally important. As discussed earlier in the chapter, there is no one location in the brain that can be said to house semantics. However, middle and anterior temporal regions potentially provide access to distributed semantic knowledge. Thus, pathways connecting both phonology and orthography to distributed

semantics likely go through the anterior half of the temporal lobe. White matter tracts likely playing an important role in the orthography ↔ semantics and phonology ↔ semantics pathways are ILF and IFOF. There is no direct white matter pathway connecting pOTS with pSTG/SMG. Hence, the orthography ↔ phonology connection likely proceeds through multiple tracts, possibly including ILF and posterior segment of the AF.

6.2 Writing

Writing involves activating semantic and phonological structures of words first. These forms are then converted to letter strings on a medium such as paper, using tools such as a pen or a keyboard. In writing to dictation, phonemic analysis leads to activation of a phonological lexicon under some models. Activation of orthographic forms can proceed through phonology → semantics → orthography, or phonology → orthography routes. Once the target forms in the orthographic lexicon are available, they are thought to be stored temporarily in a *graphemic working memory* (WM) that keeps these forms active during the spelling process, and monitors and updates them (Figure 37.9b). The process of *allographic conversion* takes abstract representations in the graphemic WM, and translates them to specific letter shapes. *Graphomotor planning* refers to the specific movements required to draw these letter shapes that are the result of allographic conversion, which are then executed by the motor system. Activation of the phoneme system can also directly lead to orthographic activation, without intervening contributions from phonological or orthographic lexicons, or semantics. This is the direct phoneme → grapheme conversion route, which can be used for writing nonwords.

Orthographic units in the VWFA/COA, both at whole word and sublexical levels, are used for writing, just as they are used for reading. One of the candidate areas associated with graphemic WM is the left pIFG (Purcell, Turkeltaub, Eden, & Rapp 2011). The left pIPS and VWFA itself may also play a role, and these regions may jointly implement processes associated with graphemic WM. The phoneme → grapheme conversion pathway is also likely implemented jointly by these three regions, VWFA, pIFG, and pIPS. Allographic conversion and graphomotor planning are likely subserved by three fronto-parietal regions, pSFS/MFG, M1/S1, and aIPS/SPL. The aIPS/SPL region is important for selection and representation of letter shapes, and serves as an interface between motoric and linguistic processes. It is likely related to graphomotor planning. The pSFS/MFG has been linked to allographic conversion, but it is not clear if it has a role in planning as well.

Three types of acquired dysgraphia, or impairments in writing, have been distinguished that parallel the three acquired types of dyslexia: phonological, surface, and deep dysgraphia. Dysgraphia usually co-occurs with the corresponding type of dyslexia (Patterson et al. 2006), and hence the neural substrates of the two are similar at a broad scale. It is important to note, however, that rare instances of double dissociations have been reported (e.g., a patient with phonological dyslexia but no phonological dysgraphia, and vice versa for another patient). Existence of such cases suggests potential differences in pathways connecting phonology, orthography, and semantics for reading and writing.

7. Concluding Remarks

Building on the foundations laid by the 19th- and 20th-century neurologists, research on the neural basis of language has come a long way. As the review above demonstrates, major parts of the brain, including most of the temporal lobe and inferior parietal lobes, and parts of the frontal lobe, are among ‘language areas’. While historically the lion’s share of research was focused on understanding the two classic areas, other parts of the language network have now come to the fore. In particular, pMTG, ATL, and AG are the new ‘rising stars of language’, so to speak. Research is continually refining our understanding of their function as critical components of language processing.

The importance of networks and connectomics in providing a more holistic picture has also been appreciated, and our understanding of functional and structural pathways is also being refined.

Some methodological obstacles remain. The lesion method is a powerful tool due to its ability to causally identify important or critical areas for a function. At the same time, contradictions and confusion caused by the low spatial resolution (multiple functional areas damaged simultaneously), long-distance effects, reorganization of function in the lesioned brain, and biased distribution of lesions (some regions are damaged much more frequently than others; damage in multiple regions is correlated) are problematic and caution us against taking results of all studies at face value. These limitations can be partly overcome by rigorously testing very large samples of patients, but this is usually very difficult in practice. The correlational nature of neuroimaging methods is a limitation too. Both methods will continue to be the pillars of progress in the coming years nonetheless, importantly supplemented by brain stimulation studies. Examining individual subjects at the spatial scale of millimeters, and delineating information flow between regions (e.g., using high temporal resolution methods such as MEG and TMS), are likely to be two important avenues for future progress. Computational modeling for a more mechanistic understanding of language function, and studies of naturalistic discourse-level stimuli, have much to offer and are also likely to be fruitful areas of research in the near future.

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Related Topics

embodiment; categorization; concepts and conceptualization; cognitive linguistics and language pedagogy; cognitive linguistics and second language acquisition

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